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# Introducción

## INTRODUCCIÓN

En la última década del siglo XX, coincidiendo con los foros internacionales, como la Cumbre de la Tierra en Río de Janeiro (1992) o la de Tokio (2002) sobre Diversidad Biológica, se puso de manifiesto la necesidad urgente de aumentar el conocimiento de la Biodiversidad del planeta a escala global. La biodiversidad puede definirse como la riqueza biológica de este planeta (Wilson, 1988) y, utilizándose indicadores capaces de representarla, su estudio sería útil tanto para la descripción de las comunidades ecológicas como estimar su variación geográfica (Halffter & Ezcurra, 1992). La biodiversidad es, además, de gran utilidad para medir el efecto directo o indirecto de las actividades humanas en los ecosistemas. La más llamativa transformación provocada por el hombre sobre los sistemas naturales es la simplificación de la estructura biótica y la mejor manera de medirla es a través del análisis de la biodiversidad (Halffter & Ezcurra, 1992; Beattie, 1995). Así pues, el estudio de la Biodiversidad, considerada como rama científica, abordaría asuntos generalmente tratados por materias o disciplinas científicas diversas, que irían desde cuestiones genéticas a ecológicas o biogeográficas, pretendiendo estudiar el resultado más innegable del proceso evolutivo, manifestado como diversidad o variabilidad biológica en todos los niveles jerárquicos de la vida: desde moléculas a ecosistemas, pasando por genes, células, individuos, poblaciones y comunidades (Norse et.al., 1986; Solbrig, 1991a, 1991b; Martín-Piera, 1997).

Los estudios sobre Biodiversidad han experimentado un aumento en los últimos años. Aún así, todavía se sigue teniendo un gran desconocimiento acerca de la mayoría de los grupos biológicos, sobre todo en el caso de los insectos (Gaston, 1991), a pesar de ser el conjunto de organismos con un mayor número de especies (Gaston, 1994; Groombridge & Jenkins, 2002). Se estima que el número de insectos conocidos se sitúa en torno a las 750.000 especies (Wilson, 1994). Algunas estimaciones más recientes elevan esta cifra incluso a 1.112.000 (Samways, 1994). No obstante, otros investigadores opinan que la diversidad de insectos podría ser aún mayor (Williams, 1964) y que número de especies descritas en la actualidad sería menos del diez por cierto de los insectos que habitan el planeta (Samways, 1993; Groombridge & Jenkins, 2002; Mackay, 2002). Así pues, si el ser humano está dañando la estructura y funcionamiento de la diversidad en la biosfera y los insectos son el componente mayoritario de esta biodiversidad, estaremos dañando, primordialmente, la diversidad de insectos, antes incluso de que lleguemos a conocer su papel ecológico en los ecosistemas.

Los insectos, en general, son un grupo poco atractivo, debido a su pequeño tamaño, esqueleto quitinoso y la gran variabilidad de sus poblaciones, lo que hace que la mayoría de los estudios de conservación excluyan frecuentemente a este grupo (Rosas *et al.*, 1992; Galante & Verdú, 2000). Sin embargo, es importante considerarlos por su papel en la mayor parte de los ecosistemas terrestres como depredadores, parasitoides, recicladores de nutrientes y de materia orgánica, polinizadores, etc. (Samways, 1993); además, los hábitats y paisajes en los que ellos viven deberían ser también preservados y, en todo caso, utilizados de manera sustentable y duradera.

El conocimiento de la distribución geográfica de los insectos es esencial para tomar decisiones sobre su conservación y preservación. La escala espacial tiene un importante impacto en la percepción de la rareza, amenaza y estabilidad de las poblaciones. En términos de urgencia, el cartografiado de especies, paisajes, ecosistemas y tipos de biótopos (Clark & Samways, 1993) y la predicción de las áreas potenciales de distribución (Bartlein *et al.*, 1986; Buckland & Elston, 1993; Scott *et al.*, 1993; Huntley *et al.*, 1995) mediante metodologías predictivas (por ejemplo, como los modelos de regresión que permitan estimar la presencia/ ausencia de especies en parcelas de territorio con respecto a las variables ambientales; Smith, 1994) y/o la utilización de *Sistemas de Información Geográfica* (SIG; Jones *et al.*, 1997; Skov & Borchsenius, 1997), son algunos de las tareas más inmediatos y realistas que deben perseguirse para incluir a estas especies en las estrategias de conservación, máxime si se considera que los distintos estados ontogenéticos (especialmente en insectos holometábolos) se comportan como individuos muy diferentes desde el punto de vista ecológico, fisiológico,

etológico y demográfico. Conservar una especie de insecto holometábolo puede implicar la preservación de hábitats muy diferentes, dado que el adulto y las fases larvarias pueden vivir en medios diferentes, alimentarse de recursos igualmente diferentes y sufrir presiones competitivas distintas. Es por ello que el conocimiento y la conservación de la biodiversidad en estos animales, debe presentarse actualmente como una tarea prioritaria para poder completar estudios globales sobre la Biodiversidad en el planeta (Pimm *et al.*, 1995).

#### Los Geotrupinae mexicanos

La subfamilia Geotrupinae (*sensu* Howden, 2003) pertenece a la gran superfamilia Scarabaeoidea (Balthasar, 1963). Comprende alrededor de 50 géneros y más de 650 especies repartidas por todo el mundo (Martín-Piera & López-Colón, 2000). En esta subfamilia, Howden (2003) ha incluido cuatro tribus: Geotrupini, Bolboceratini, Athyreini y Lethrini. Los Geotrupini presentan una distribución Holártica, los Bolboceratini mundial, los Athyreini una distribución constreñida a las zonas tropicales de America, Asia y Africa, mientras que los Lethrini están restringidos al Viejo Mundo (Howden, 2003).

Los geotrúpidos forman parte del grupo de escarabajos coprófagos o del estiércol, puesto que explotan este recurso como fuente de alimentación y para su reproducción (Halffter & Edmonds, 1982). Como consecuencia, juegan un papel indispensable en la eliminación de los excrementos de los vertebrados, en el aumento de la capacidad de retención y de permeabilidad de los suelos, y en el reciclaje y la reincorporación de la materia orgánica y de los nutrientes al medio (Bornemissza, 1976; Halffter & Edmonds, 1982; Martín-Piera & Lobo, 1995). De esta manera, favorecen la productividad y la calidad de los pastos (Bornemissza & Williams, 1970; Fincher, 1981; Rougon *et al.*, 1988). Además, los escarabajos del estiércol son los principales controladores biológicos de las poblaciones de insectos hematófagos, principalmente dípteros, vectores de enfermedades del ganado (Waterhouse, 1974; McQueen, 1975; McQueen & Beirne, 1975; Bornemissza, 1976). Por tanto, los Geotrupinae representan un grupo de insectos con interés económico, sanitario, agrícola y ecológico.

Introducción

México cuenta con representantes de las tribus Geotrupini, Bolboceratini y Athyreini teniendo un total de 45 especies repartidas en ocho géneros (*Geotrupes*, Latreille, 1796; *Ceratotrupes* Jekel, 1865; *Neoathyreus* Howden & Martínez, 1963; *Bolbocerosoma* Schaeffer, 1906; *Bolborhombus* Cartwright, 1953; *Bolbocerastes* Cartwright, 1953; *Bolboleasmus* Boucomont, 1911; y, *Eucanthus* Westwood, 1848). En México existe una amplia zona de solapamiento e intercomunicación entre las dos grandes regiones biogeográficas del continente americano, la Neártica y la Neotropical (Halffter, 1964). Esta región de solapamiento es conocida como Zona de Transición Mexicana, la cual está constituida por conjuntos faunísticos de origen diferente que han evolucionado a partir de grupos ancestrales distintos (Halffter, 1976). Además, México está situado en la franja intertropical y posee una pronunciada orografía (Williams-Linera *et al.*, 1992). Todo ello determina una gran diversidad de condiciones ambientales y, por tanto, una composición faunística de las comunidades de insectos caracterizada por poseer una mezcla de especies con diferentes relaciones biogeográficas (Halffter, 1964, 1972, 1976, 1978, 1987; Kohlmann, 1991).

A pesar de la singularidad de la fauna mexicana, de la importancia económica que tienen los Geotrupinae y de que México cuenta con representantes de tres tribus que forman parte de esta subfamilia, los estudios realizados sobre este grupo de insectos en este país son bastante escasos y, la mayoría de ellos, se han centrado en cuestiones de tipo taxonómico. Los primeros trabajos efectuados fueron los realizados por Halffter (1962) sobre *Ceratotrupes* y los de Howden (1964) sobre geotrúpidos del Norte y Centro-América. Estos trabajos sentaron las bases taxonómicas empleadas hoy en día para separar e identificar las distintas especies de geotrúpidos mexicanos. Posteriormente, Zunino (1984) hizo un estudio taxonómico a nivel mundial basado en el estudio de la genitalia de algunas especies, propuso una nueva clasificación y las primeras hipótesis biogeográficas del grupo. El último trabajo realizado ha sido el de Howden (2003), en el cual se recopilan las nuevas especies descritas y se renuevan los criterios de clasificación, insistiendo en que aún es importante llevar a cabo más estudios que aclaren la situación taxonómica interna del grupo.

Apenas existen otros trabajos para México que no sean de tipo taxonómico. La especie más estudiada hasta ahora ha sido *Geotrupes (Megatrupes) cavicollis*, Bates, 1887, de la cual se conocen tres trabajos: López Guerrero & Benítez (1982) analizan la estructura del testículo y neurosecreción durante la etapa reproductora; Halffter *et al.* (1985) estudian su comportamiento reproductor, en especial la nidificación, asociándolo con el estado y función del ovario; y, Pluot-Sigwalt & Martínez (1998) describen el aparato reproductor masculino completo y lo comparan con el del género *Ceratotrupes*. Otros trabajos similares son los de López-Guerrero (1987) y Martínez & Cruz (1999), que analizan la estructura del testículo de varias especies de geotrúpidos.

Por tanto, en la actualidad, apenas se conocen datos sobre la biología de las especies de geotrupinos de México, no se han estudiado las probables causas de actual diversidad de este grupo, su singularidad con respecto a otras faunas próximas y sus patrones de distribución en la región de transición mexicana. Por todo ello, la presente tesis de investigación pretende contribuir a aumentar el conocimiento sobre la biodiversidad en insectos y en particular de las especies de Geotrupinae en México. Se pretende así mejorar el conocimiento de la historia evolutiva, la biogeografía, la biología y la ecología de los geotrupinos en este país. Humildemente, esperamos que los estudios que aquí se presentan sirvan para incentivar el estudio de este grupo en México, tanto en sus aspectos básicos como aplicados, así como promover los estudios relacionados con la elaboración de planes de manejo y de conservación de estas especies y de los distintos ambientes y biotopos que ocupan.

#### El estudio de los Geotrupinae en México

A la hora de estudiar un grupo como los Geotrupinae en México, el primer problema que se plantea, como se ha mencionado anteriormente, es que el conocimiento que se tiene sobre este grupo en este territorio es muy escaso. Así pues, las primeras tareas básicas que deben abordarse para llevar a cabo un estudio sobre los geotrupidos mexicanos deben buscar y recopilar la información disponible a fin de estimar cuál es el estado actual de su conocimiento y conocer cuál ha sido la trayectoria histórica que ha seguido este conocimiento. El primer trabajo que se presenta en esta tesis trata de abordar diferentes cuestiones preliminares básicas, como, por ejemplo, ¿cuántas especies se han descrito hasta ahora en México? ¿Cuántas especies quedarían por describir? ¿Cómo ha sido este proceso descriptivo a lo largo de los años? ¿Es similar este proceso a lo que ha ocurrido en otras regiones biogeográficas, por ejemplo, en el Paleártico Occidental? ¿Qué factores han influido y en qué grado de importancia a la hora de describir las especies?

Una vez abordadas estas cuestiones y conociendo como a sido el proceso descriptivo a lo largo de estos años, los trabajos siguientes se centran en conocer las distribuciones reales y potenciales de este grupo. El conocimiento de estas distribuciones es esencial para localizar áreas de distribución actualmente desconocidas en las que aún no se han colectado ejemplares, pero también pueden permitir realizar un reconocimiento preliminar de los patrones generales de distribución de la riqueza específica de Geotrupinae. Así, en un segundo trabajo, hemos elaborando mapas individuales de distribución para cada especie. Estos mapas no sólo proporcionan una imagen razonable de la distribución observada y potencial de las especies, sino que constituyen una herramienta útil para el diseño y planificación de nuevas colectas, sobre todo en el caso de regiones poco muestreadas. Las distribuciones potenciales que se presentan en este trabajo podrían considerarse imágenes que nos muestran, en general, cuáles serían las tendencias de distribución de estas especies si a lo largo de la historia evolutiva no hubiera habido ninguna otra influencia más que la climática. Sin embargo, la fauna de Geotrupinae mexicana está compuesta por grupos taxonómicos con diferentes orígenes e historias biogeográficas que han marcado la distribución actual de sus especies. El conocimiento de esta información biogeográfica complementa y da sentido a las distribuciones ofrecidas en el trabajo.

Una consecuencia importante de esta última aproximación es que los modelos predictivos de distribución sobreestiman, en general, la riqueza de especies, puesto que la suma de los modelos individuales no se ajusta a la riqueza total de especies que hemos calculado para los distintos estados mexicanos mediante la utilización de otros estimadores

basados en subrogados del esfuerzo de colecta. Como los modelos de distribución producen una variable continua, hemos elegido un umbral para convertir los valores de favorabilidad de estas especies en una variable binaria (presencia/ausencia) y así comparar los valores de riqueza resultantes de sumar todos los modelos individuales con los datos de riqueza de los estados cuyos inventarios pueden considerarse fiables.

Como unos de los patrones más notables del anterior trabajo indicaba que la mayor riqueza de geotrúpidos se distribuía, principalmente, a lo largo de las cadenas montañosas, se procedió a hacer un estudio más localizado destinado a analizar la distribución espacial a escala regional de las diferentes especies presentes a lo largo de un gradiente altitudinal. Con este fin, se escogió una la región del volcán Cofre de Perote (Veracruz) en la que se realizaron con anterioridad otros estudios (ver Arellano, 1992, 2002) y cuyo conocimiento faunístico es relativamente fiable. El muestreo altitudinal en la vertiente menos estudiada de este volcán tuvo como objetivo conocer y completar la distribución de los Geotrupini en dicha zona y también estudiar la ecología y fenología de este grupo a escala local. Estas colectas permitieron, también por primera vez, la descripción completa del sistema reproductor masculino y femenino de la especie *Geotrupes (Halfterius) ruffoclavatus*, Jekel, 1965 que fue la especie predominante en dicho muestreo.

En el último trabajo que se presenta en esta tesis, se estudia el sistema reproductor de las especies de Geotrupini mexicanos de una forma comparativa. El sistema reproductor masculino y femenino apenas ha sido estudiado para las especies mexicanas, pese a que los estudios elaborados para Geotrupinae han demostrado la importancia del conocimiento del sistema reproductivo de machos y hembras para la revisión sistemática y filogenética de este grupo (Nikolaev, 1977; Krikken, 1981; Zunino, 1984). Este trabajo pretende aportar datos que pudieran servir de base para posibles estudios futuros que tengan en cuenta la evolución y las relaciones próximas entre las especies de esta subfamilia.

A modo de resumen, en la presente tesis se abordan diferentes cuestiones relacionadas con la biogeografía y la historia natural de los Geotrupinae de México, aportando nuevos datos sobre la distribución, ecología y anatomía del grupo, con la finalidad de aportar nuevos conocimientos sobre un grupo poco estudiado en México. Esperamos que los resultados que se presentan puedan ayudar a incrementar el interés futuro por este interesante grupo.





### **OBJETIVOS**

El objetivo principal de la presente tesis es el de es **aumentar el conocimiento biológico sobre un grupo de insectos poco conocido en México a nivel biogeográfico, ecológico y anatómico**. Para llevar a cabo este objetivo general se procederá al desarrollo de los siguientes objetivos específicos relacionados con la biogeografía, la ecología y la biología de estas especies:

- Estimar el grado de conocimiento existente sobre los Geotrupinae de Norte y Centro-América y compararlo con el existente para los Geotrupinae del Paleártico Occidental (tradicionalmente más estudiados y conocidos).
- Examinar el proceso de descripción de estas especies en Norte y Centro-América y tratar de predecir la posible ubicación de las especies aún sin describir, comparando este proceso de descripción con el ocurrido en el Paleártico Occidental.
- Presentar mapas de distribución reales y potenciales para todas las especies de Geotrupinae mexicanas, recopilando para ello la información taxonómica y biogeográfica existente en la bibliografía y en diversas colecciones entomológicas.
- Examinar los patrones de variación de la riqueza de especies de Geotrupinae en México a partir de los datos generados por modelos individuales de distribución.
- Estudiar la variación altitudinal, estacional y de hábitat de las especies de Geotrupinae a lo largo de un transecto altitudinal en el estado de Veracruz (volcán Cofre de Perote).
- Analizar la fenología, preferencia de hábitat e influencia de la altitud sobre las poblaciones de (*Geotrupes (Halffterius) ruffoclavatus* Jekel, 1865).
- Recopilar la información existente acerca de los sistemas reproductivos de Geotrupinae.
- Describir los sistemas reproductivos masculinos y femeninos de los diferentes grupos de Geotrupinae mexicanos, a partir de ejemplares frescos.
- Comparar los sistemas reproductivos estudiados con los de otros Geotrupinae y Scarabaeoidea, en general.





# Species description process of North and Central American Geotrupinae (Coleoptera: Scarabaeoidea: Geotrupidae

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# 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)

Nuria TROTTA-MOREU & Francisco José CABRERO-SAÑUDO

#### 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 three 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 around 10-20 species remain yet to be described. Body size has not shown any influence on the Geotrupinae description species 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 range, could become progressively more important, as for the Geotrupinae species in the Western Palaearctic region. **Key words:** body size, distribution range, dung beetles, factors influencing description, 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 tres 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 alrededor de 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, factores que influyen en la descripción, geotrúpidos, localización geográfica, rango de distribución, región Neártica, tamaño corporal.

#### INTRODUCCIÓN

The subfamily Geotrupinae groups approximately 1000 species around the world, included in four 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). From them, 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 are some recent taxonomic publications describing and revising Geotrupinae from this region. In the last years, 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 been developed recently, whose aim has been to define the geographical ranges and their causes for these species, such as those of Trotta-Moreu et al. (2007, 2008).

The percentage of species yet to be described in relation to the complete inventory is at present unknown, as well as how many species remain yet to be described or the magnitude of the total number of species. To answer this question it would be useful to analyze how the species descriptive process in this region has been developed until now, as well as what factors have influenced such process (Cabrero-Sañudo and Lobo, 2003). Besides, estimating the geographic and morphologic species characteristics related to their description probability could be very valuable to establish effective strategies to look for and locate new species (Arnett, 1967; Medellín and Soberón, 1999).

The possible influence of several factors on the species description process, such as the species size, geographic range and geographic location, has been previously analyzed in some studies (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 the geographic location influences the description process: generally, more studies of the fauna have been developed 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, being the pure effect of the geographic location the factor which justified a higher explained percentage (Figure 2a; Cabrero-Sañudo and Lobo 2003).

Our objective is to analyze how the Geotrupinae description process has been developed 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 in order to emphasize their similarities and their differences.

#### **MATERIAL AND METHODS**

In order to develop the analyses on the estimation of the number of species known at present and the factors which influenced the description process, several taxonomic studies related to this Coleopteran group from North and Central America were considered (Howden, 1955, 1964, 1974, 1985, 1995, 1999, 2003, 2005; Woodruff, 1973; Howden and Gill, 1984). So, a total of 102 species were included: 38 of them Geotrupini, 15 Athyreini, and 49 Bolboceratini (6 of them *Eucanthus* Westwood 1848).

In the last ten years, many changes of the nomenclature of this group have been proposed. Some authors have considered the Geotrupidae family as the Geotrupinae subfamily (Howden, 2003). Scholtz and Browne (1996), supported by phylogenetic hypotheses, have proposed that the Bolboceratini, including the Athyreini, must be raised to a 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, the *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, nine information variables were also gathered for each species: year of description, species body size (in mm.), geographic size (according to the criteria observed at Lumaret and Lobo (1996)), and the mean, maximum, and minimum latitude (in °N) and longitude (in °W) of the species distribution range. Geographic location variables were estimated with an approximate maximum error of 2.5°.

The species description process was represented on a curve, considering the accumulated species number per year. An attempt was made to adjust the curve to different types of functions that are present in the literature employing both classic formula and others

recurrently 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-lineal estimation method.

Statistical analyses based on Generalized Linear Models (GLM; McCullagh and Nelder, 1989; Crawley, 1993) were developed 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 lineal, quadratic or cubic functions was examined for each of the independent variables, choosing that which presented all the significant terms at the same time. 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 explicative 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 three interdependent variables was considered (Cabrero-Sañudo and Lobo, 2003).

All the statistical analyses were carried out by means of the Statistica 7.1 package (StatSoft, 2006). To compare the obtained 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).

Capítulo 1

#### RESULTS

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

|  | <b>Description process</b> |                 | 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)          | $0.29 \pm 0.76$            | 0.41 ± 1.36     | $0.40 \pm 0.96$   | $0.24 \pm 0.85$ | $0.18 \pm 0.46$   | 0.58 ± 1.72 |
| Percentage of years without descriptions                 | 80                         | 81              | 74                | 85              | 85                | 77          |
| Percentage of years with more than two 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                | $3.24 \pm 5.92$ | 1.86 ± 1.69       | 2.00 ± 1.89     | $2.75 \pm 2.66$   | 4.21 ± 7.69 |
| Percentage of authors with only one description          | 60                         | 47              | 61                | 60              | 63                | 37          |
| Percentage of authors with at least five descriptions    | 11                         | 15              | 7                 | 7               | 25                | 21          |
| Maximum number of descriptions per author                | 9                          | 35              | 9                 | 8               | 8                 | 35          |
| Author with maximum number of descrip-<br>tions          | Jekel                      | Howden          | Jekel             | Jekel           | Reitter           | Howden      |
| Number of coincident authors between regions             | 4                          |                 | 4                 |                 | 0                 |             |

 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).

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 four years. There were no species descriptions for 85% of years, and only 2% of years with two or more described species. There were a total of 15 different authors, three-fifths of them describing only one species and most of them less than five species. The mean number of descriptions per author was around two species, but Jekel was the author with the highest number of descriptions, with a total of eight described species (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 three species every five years. There were no species descriptions for 77% of years, and 6% of years with two or more descriptions. A total of 19 authors described new NCA Geotrupinae species, for a mean of more than four described species per author. However, around two-fifths of authors described only one species, whereas only one fifth of authors five 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 function was that which 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 retained more than 98% of the variation. According to this curve, the description process tends towards an asymptote, reaching a total of 122 described species (Figure 1). This implies that the estimated percentage of described species at present is around 84% and that 20 species would remain yet to be described. Moreover, it predicts that 90% of total species would be described by year 2012, 95% by year 2021 and 100% by year 2024 (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.

However, the description process has been quite homogeneous since the most recent revision for NCA Geotrupinae species was published (Howden, 1964). So, taking into account the last 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 (Figure 1). This result gives a result of 91% of described species in year 2005 and predicts that 95% of species would have been described by year
2028, 99% of species by year 2094, and all the NCA Geotrupinae species by year 2134 (Table 2).

|   | WP    | NCA*  | NCA** |
|---|-------|-------|-------|
| Explained variance (R <sup>2</sup> 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 2. Compared estimations of the Geotrupinae species description process for WesternPalaearctic (WP) and North and Central America (NCA) regions. The relationships of the accumulatednumber of described species with respect to the year of description have been fitted to Beta-p functions. Datafor 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 tothe last forty years of the curve (from 1965 to 2005), respectively.

The results of GLM for Geotrupinae showed that six from eight considered variables seemed significantly related to the species description process. Minimum and mean longitudes became 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 distribution 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 maximum latitude, explaining almost a quarter of the total variation (24.31%; Table 3).

| Geotrupinae | Selected<br>terms              | Abbreviation  | Deviance | d.f. | Change in deviance | F    | Sign | % Explained deviance |
|-------------|--------------------------------|---------------|----------|------|--------------------|------|------|----------------------|
| BS          |                                | •             |          |      |                    |      |      |                      |
|             | Minimum longi-<br>tude         | Lonmin        | 294590.0 | 100  | 58870.49           | 0.20 | +    | 16.67                |
|             | Mean longitude                 | Lonmed        | 332808.3 | 100  | 20652.23           | 0.06 | +    | 5.84                 |
| GL          | 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 explana-<br>tory model | Lonmin+Latmax | 267529.2 | 100  | 85931.30           | 0.32 | +/-  | 24.31                |

 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.

Regarding exclusively the tribe Geotrupini, the results of GLM showed that six from eight considered variables seemed 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 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 regards to the tribe Bolboceratini, four variables resulted 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 a wider and northern distribution have been described earlier. A general explanatory model coincides with the maximum latitude and explains 13.42% of the total variation (Table 4).

|               | Selected terms            | Abbreviation | Devian-<br>ce | d.f. | Change in deviance | F     | Sign | % Explained deviance |
|---------------|---------------------------|--------------|---------------|------|--------------------|-------|------|----------------------|
| Geotrupini    |                           |              |               |      |                    |       |      |                      |
| BS            |                           |              |               |      |                    |       |      |                      |
|               | 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                |
| GL            | 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                |
|               | Geographic range          | Range        | 118379.2      | 36   | 36042.62           | 10.96 | -    | 23.34                |
| GR            | General explanatory model | Latmax       | 108329.3      | 36   | 46092.53           | 15.32 | -    | 29.85                |
| Bolboceratini |                           |              |               |      |                    |       |      |                      |
| BS            | •                         | •            | •             | •    | •                  | •     | •    | •                    |
|               | Minimum longitude         | Lonmin       | 101797.0      | 41   | 11613.43           | 4.68  | +    | 10.24                |
|               | Maximum latitude          | Latmax       | 98194.58      | 41   | 15215.88           | 6.35  | -    | 13.42                |
| GL            | 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 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.

None of the considered variables resulted 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 seven species present in the NCA region.

Subsequently, as interactions among variables could frequently have a higher explicative 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.

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

 Table 5. Percentages of variance of the North and Central American Geotrupinae description process

 explained by size (BS), geographic location (GL) and distribution range size (GR), according to the variance

 hierarchical decomposition analysis.

The variance hierarchical decomposition analysis for Geotrupinae showed that the most important variables explaining the description process were those related to geographic location and range, 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 (Figure 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 (Figure 2c).



**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 three considered explanatory groups of variables: BS, GR, and GL. BS: Body size; GR: geographic range; GL: geographic location.

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 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.** 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.

Figure 3 resumes the combined effects between GL and GR for Geotrupini and Bolboceratini. Within Geotrupinae two 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 (Figure 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 two methods point that ten to twenty 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; Figure 1a). Comparing the two 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 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 eight 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 nine 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.

Besides, 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 one 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 composition of the species inventories 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 two groups are more difficult to collect and are typically found in low numbers (Howden, 1955); thus, 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 GL and GR, especially the combined effect of both variables, which explains the higher percentage —compared to the whole group— of considered variables. For Geotrupini, those species with smaller geographic ranges and 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, whereas the geographic range hardly had any effect. Nevertheless, the last described species were 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 two groups. Athyreini is a specious group in South America, but only 15 species 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 the location and the 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; Figure 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 the geographic 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 exposed (the NCA region is bigger than the WP region, less populated, less accessible, and presents historically a lower concentration of taxonomists per area than the WP region).

The geographic range size has been usually considered an important factor for the 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 the 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, 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. It is due, likely, to the fact that Geotrupinae from the WP and NCA regions usually live in well delimited habitats, which have been determinant on the species description. 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 us to 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 30° 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 40°, 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 resulted significant for the species of both regions. However, a lot of different factors, especially those related to their history, could well be acting and the relative importance of these factors 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 some simple analyses like these are important to increase the knowledge about a peculiar group and to help in its conservation (May, 1988; Sutton and Collins, 1991). Determining the completion degree of the faunistic inventories from a region and estimating the geographic and morphologic 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. & 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. & 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. & 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 & 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 & A. Crock. 1995b. Patterns in species description: a case study using the Geometridae (Lepidoptera). *Biological Journal of the Linnean Society* 55:225-237.
- Guisan, A. & 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. & 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, España. 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. & 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 & G. Holloway. 2007. Digging down under: Australian Bolboceratini, their habits and a list of species (Coleoptera: Scabarabaoidea: Geotrupidae). Zootaxa 1499:47-59.
- Legendre, P. & L. Legendre. 1998. Numerical ecology. 2nd Edition. Elsevier, Amsterdam. 853p.
- Lumaret, J. P. & 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* 9:655-671Macnally, 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 & 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. & J. A. Nelder. 1989. Generalized linear models. *Chapman & Hall, London*. 532 p.
- Medellín, R. A. & 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 & 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. & 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. & 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. & 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 & 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 & 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.





# Distribución conocida y potencial de Geotrupinae (Coleoptera: Scarabaeoidea) en México

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# DISTRIBUCIÓN CONOCIDA Y POTENCIAL DE GEOTRUPINAE (COLEOPTERA: SCARABAEOIDEA) EN MÉXICO

Nuria Trotta-Moreu, Jorge M. Lobo y Francisco J. Cabrero-Sañudo

#### RESUMEN

Se recopiló la información disponible acerca de los geotrúpidos presentes en la República Mexicana, teniendo en cuenta las citas de recolección presentes en la literatura y en diversas colecciones entomológicas. A partir de estos datos se elaboró una base de datos (GEOMEX), la cual se utilizó, en primer lugar, para presentar un listado actualizado de todas las especies presentes en el territorio mexicano. También se elaboraron mapas de la distribución conocida de dichas especies, así como mapas que muestran la distribución potencial utilizando una metodología basada en modelos de máxima entropía (Maxent). Se presentan, así mismo, algunos datos biogeográficos así como los valores climáticos óptimos para cada especie.

**Palabras clave:** Geotrupini, Bolboceratini, Athyreini, mapas de distribución, modelos predictivos, escarabajos del estiércol, México.

#### ABSTRACT

The available data on the geotrupids species present in the Mexican Republic was compiled, taking into account the literature citations as well as the available data in several entomologic collections. A database (GEOMEX) was developed based on these data, which was useful to extract an actualized list of all the species present in the Mexican territory. Distribution maps, both observed and potential, were produced, those latter by means of a methodology based on maximum entropy models (Maxent). Some other biogeographic data are also supplied, as well as climatic optimum values for each species.

Key words: Geotrupini, Bolboceratini, Athyreini, distribution maps, predictive models, dung beetles, Mexico.

# **INTRODUCCIÓN**

El grado de conocimiento actual de los Geotrupinae a nivel taxonómico y faunístico en México está soportado, principalmente, por diversos trabajos realizados desde mediados del siglo pasado, en especial por Howden (1955, 1964, 2003, 2005), Halffter y Martínez (1962) y Zunino (1984). A partir de estos trabajos, actualmente es posible establecer un listado de las especies de Geotrupinae en México y de sus posibles distribuciones geográficas. Sin embargo, tal y como ocurre incluso en países en los que se ha realizado un esfuerzo de colecta mayor y más prolongado en el tiempo y, además, poseen una menor riqueza taxonómica

(Dennis *et al.*, 1999; Dennis & Thomas, 2000; Zaniewski *et al.*, 2002; Reutter *et al.*, 2003; Graham *et al.*, 2004; Martínez-Meyer, 2005; Romo *et al.*, 2006; Hortal *et al.*, 2007; Lobo et al., 2007), la información corológica suele estar plagada de sesgos y únicamente permite esbozar una distribución general muy incompleta para la gran mayoría de las especies.

En la actualidad existen diversas herramientas estadísticas, las cuales, con el concurso de Sistemas de Información Geográfica, permiten elaborar hipótesis de distribución a partir de los datos biológicos disponibles y de información sobre distintas variables ambientales que actúan como predictores (ver Guisan and Zimmermann, 2000). Evidentemente, la distribución real de los organismos esta influida por variables geográficas, históricas o por limitantes de dispersión (ver por ejemplo Pulliam, 2000), de modo que no todos los enclaves con condiciones climáticas o ambientales favorables son colonizados por las especies. Debido a ello y a la carencia de información fiable sobre la ausencia verdadera de las especies, las hipótesis de distribución generadas mediante estas técnicas de modelización representan simulaciones de la distribución potencial de las especies (Soberón & Peterson, 2005; Peterson, 2006). Es decir, mapas de idoneidad o probabilidad que indican la presencia de lugares favorables desde el punto de vista climático para la aparición de la especie.

Tras elaborar un listado actualizado de las especies de Geotrupinae presentes actualmente en México, poniendo al día la última revisión hecha por Howden (2003), el presente trabajo proporciona mapas individualizados para cada una de las especies de Geotrupinae presentes en México, en los cuales se incluye tanto la distribución conocida como la distribución potencial, generada mediante una de las técnicas de modelización actualmente considerada muy fiable.

# **MATERIAL Y MÉTODOS**

**Procedencia de los datos biológicos:** Se elaboró una base de datos recopilando toda la información disponible en la bibliografía, así como diversos estudios no

publicados a los que se ha tenido acceso (tesis de licenciatura, maestría y doctorado), destacando los trabajos de Howden (1955, 1964, 1974, 2003, 2005); Halffter & Martínez (1962); y, Gómez & López-Rojas (2004). También se consultaron diversas colecciones entomológicas, como las colecciones particulares de G. & V. Halffter, E. Montes de Oca, F. Vaz de Mello, M. A. Morón, H. F. & A. Howden, I. Martínez, L. Arellano, así como la colección del Instituto de Ecología A. C. (Xalapa, Veracruz, México)

La base de datos, que hemos nombrado GEOMEX, contiene hasta la fecha 1193 registros, correspondientes a 45 especies mexicanas de Geotrupinae (clasificación sensu Howden 2003; Cuadro 1). Aunque la taxonomía de alto rango para este grupo y sus relaciones filogenéticas internas no se encuentran aún bien establecidas (ver Howden 1982, Zunino 1984, Browne & Scholtz 1995, 1999), el listado de especies puede considerarse fiable. En nuestro caso hemos incluido las nuevas especies descritas en los últimos años, completando así el catálogo proporcionado por la última revisión de Howden (2003) de las especies de Geotrupinae mexicanas. GEOMEX consta de 24 campos de información, pertenecientes a las siguientes categorías: a) campos taxonómicos (género y especie); b) campos geográficos (localidad, estado, altitud, latitud y longitud); c) campos relativos a la captura (día, mes y año, número de ejemplares capturados, método de captura, colector); d) campos ecobiológicos (sexo de los individuos, alimentación y hábitat); y, e) otros campos relacionados con el manejo ulterior de los ejemplares o de la información sobre estos (colección donde está depositado el ejemplar, persona que realizó la identificación, cita bibliográfica, otras observaciones). Tras georreferenciar las localidades en las que ha sido citada cada una de las especies (ver <u>http://geonames.usgs.gov/gnishome.html</u>) a una resolución de 0.08° (25,080 celdas para el territorio mexicano), se construyeron mapas de la distribución observada de cada una de las especies utilizando el programa Idrisi Kilimanjaro (Clark Labs. 2003).

**Datos climáticos utilizados :** Como predictores se utilizaron las diecinueve variables climáticas tomadas de la base de datos WorldClim (Hijmans et al. 2007): temperatura media anual, rango medio de temperaturas diurnas, isotermalidad,

estacionalidad de temperaturas, temperatura máxima del mes más cálido, temperatura mínima del mes más frío, rango de temperaturas anuales, temperatura media del cuatrimestre más húmedo, temperatura media del cuatrimestre más seco, temperatura media del cuatrimestre más cálido, temperatura media del cuatrimestre más frío, precipitación anual, precipitación del mes más húmedo, precipitación del mes más seco, estacionalidad de las precipitaciones, precipitación del cuatrimestre más húmedo, precipitación del cuatrimestre más seco, precipitación del cuatrimestre más calido y precipitación del cuatrimestre más frío.

| <u>Subf.Geotrupinae</u>  | Fam. Geotrupidae   |
|--|--|
| Tribu Geotrupini   | <u>Subj. Geotrupinae</u><br>Tribu Geotrupini   |
| Gen. Geotrupes   | Gen Megatrupes   |
| Subg. Megarupes<br>cavicollis Bates, 1887<br>fisheri Howden, 1967<br>Subg. Onthotrupes   | <i>cavicollis</i> (Bates, 1887)<br><i>fisheri</i> (Howden, 1967)<br><u>Tribu Ceratotrupini</u>   |
| lobatus Howden, 1974<br>sobrinus Jekel, 1865<br>herbeus Jekel, 1865<br>viridiobscurus Jekel, 1865<br>truncaticornis Howden, 1864<br>sallei Jekel, 1865<br>nebularum Howden, 1964<br>guerreroensis Howden, 1964<br>pecki Howden, 1964<br>onitidipes Bates, 1887 | Gen Onthotrupes         *lobatus (Howden, 1974)         sobrinus (Jekel, 1865)         herbeus (Jekel, 1865)         viridiobscurus (Jekel, 1865)         *truncaticornis (Howden, 1864)         *sallei (Jekel, 1865)         nebularum (Howden, 1864)         guerreroensis (Howden, 1864)         pecki (Howden, 1864)         onitidipes (Bates, 1887) |
| chephosus Howden, 1964   | Gen. Geohowdenius<br>*cnephosus (Howden, 1864)   |
| <i>rufoclavatus</i> Jekel, 1865<br><i>Subg. Haplogeotrupes</i><br><i>guatemalensis</i> Howden, 1974<br><i>reddelli</i> Howden, 1980  | Gen. Halffterius<br>rufoclavatus (Jekel, 1865)<br>Gen. Haplogeotrupes<br>guatemalensis (Howden, 1974)  |
| Gen. Ceratotrupes  | reddelli (Howden, 1967)  |
| fronticornis (Ericsson, 1847)<br>sturmi Jekel, 1865<br>bolivari Halffter & Martínez, 1962  | <i>Gen. Ceratotrupes</i><br>fronticornis (Ericsson, 1847)<br><i>Sturmi</i> Jekel, 1865<br><i>bolivari</i> Halffter & Martínez, 1962  |

**Cuadro 1.** Listado de las especies de Geotrupidae mexicanas según las dos clasificaciones taxonómicas principales comúnmente aceptadas: Howden (2003) a la izquierda y Zunino (1984) a la derecha. Las especies marcadas con un asterisco no fueron asignadas a ningún género por Zunino (1984).

| <u>Tribu Bolboceratini</u>             | <u>Subf. Bolbocerinae</u><br><u>Tribu Bolboceratini</u> |
|--|---|
| Gen. Bolbocerosoma                     | Gen. Bolbocerosoma                                      |
| ritchert Howden, 1955                  | ritcheri Howden, 1955                                   |
| confusum Brown 1928                    | pusillum Howden, 1955                                   |
| mexicanum Howden 2005                  | confusum Brown, 1928                                    |
| Gan Balbarhambus                       | mexicanus Howden, 2005                                  |
| sallei (Bates 1887)                    | Gen. Bolborhombus                                       |
| magnus (Howden, 1964)                  | sallei (Bates, 1887)                                    |
| parvulus Cartwright, 1953              | magnus (Howden, 1964)                                   |
| nitidus Howden, 1964                   | <i>parvulus</i> Cartwright, 1953                        |
|  | nitidus Howden, 1964                                    |
| Gen. Bolbocerastes                     | Gen. Bolbocerastes                                      |
| regalis Cartwright, 1953               | regalis Cartwright, 1953                                |
| serratus (LeConte, 1854)               | serratus (LeConte, 1854)                                |
| imperials Cartwright, 1953             | imperiales Cartwright, 1953                             |
| peninsularis (Schaeffer, 1906)         | peninsularis (Schaeffer, 1906)                          |
| Gen. Bolbelasmus                       | Gen. Bolbelasmus  |
| arcuantus (Bates, 1887)                | arcuantus (Bates, 1887)                                 |
| hornii (Rivers, 1886)                  | hornii (Rivers, 1886)                                   |
| <i>bajaensis</i> Howden, 1964          | <i>bajaensis</i> Howden, 1864                           |
| rotundipennis Howden, 1964             | rotundipennis Howden, 1864                              |
| variabilis Howden, 1964                | variabilis Howden, 1864                                 |
| Gen. Eucanthus                         | Gen. Eucanthus  |
| mexicanus Howden, 1964                 | mexicanus Howden, 1864                                  |
| impressus Howden, 1964                 | impressus Howden, 1864                                  |
| <u>Tribu Athyreini</u>                 | <u>Tribu Athyreini</u>                                  |
| Gen. Neoathyreus                       | Gen. Neoathyreus  |
| excavatus (Laporte de Castelnau, 1840) | <i>excavatus</i> (Laporte de Castelnau, 1840)           |
| fissicornis (Harold, 1880)             | fissicornis (Harold, 1880)                              |
| granulicollis Howden, 1964             | granulicollis Howden, 1864                              |
| hamifer (Boucomont, 1932)              | hamifer (Boucomont, 1932)                               |
| interruptus Howden, 1964               | interruptus Howden, 1964                                |
| mexicanus (Klug, 1845)                 | mexicanus (Klug, 1845)                                  |
| mixtus (LeConte, 1854)                 | mixtus (LeConte, 1854)                                  |

**Cuadro 1.** Listado de las especies de Geotrupidae mexicanas según las dos clasificaciones taxonómicas principales comúnmente aceptadas: Howden (2003) a la izquierda y Zunino (1984) a la derecha. Las especies marcadas con un asterisco no fueron asignadas a ningún género por Zunino (1984).

Elaboración de las distribuciones potenciales: La estimación de la distribución potencial se llevo a cabo mediante MaxEnt 2.2 (Maximum Entropy; Phillips *et. al.* 2006) utilizando los parámetros definidos por defecto en el programa, pero incluyendo únicamente características lineares y cuadráticas. Entre las diversas técnicas disponibles, se ha elegido este método porque requiere únicamente información sobre la presencia de las especies y porque un reciente análisis comparado lo avala y recomienda (Elith *et al.*, 2006). MaxEnt es un método de "aprendizaje automático" (*machine learning*) que busca encontrar la distribución más cercana a la homogeneidad (situación de entropía máxima en la que

todos los valores tienen la misma probabilidad de ocurrir) pero restringiendo ésta según la información biológica disponible y las condiciones ambientales del área de estudio. El resultado es un mapa en el que cada celda posee un valor de favorabilidad que, oscilando entre 0 y 100, es proporcional a la suma del valor de probabilidad de cada celda y de todas aquellas celdas con probabilidades iguales o menores a ella (ver Phillips *et. al.* 2006).

Validación de las distribuciones: Estimar la capacidad de los modelos obtenidos para reflejar con fiabilidad la distribución de los organismos es un requisito esencial para que estas hipótesis sean útiles en conservación y biogeografía (Vaughan & Ormerod, 2005). Debido a la escasez de datos disponibles, la precisión de las hipótesis de distribución generadas fue estimada superponiendo cada uno de los modelos individuales obtenidos y calculando el número total de especies resultantes en distintos estados de México, cuyo inventario completo fue previamente estimado como fiable (Cuadro 2). Para calcular si el número conocido de especies en cada estado representa una estima fiel de la riqueza total existente, se calculó el estimador no paramétrico Chao2 (Colwell & Coddington, 1994), algoritmo que considerando el número de especies que aparecen en una o dos unidades de esfuerzo permite establecer la riqueza teórica total. En nuestro caso, se utilizó como medida de esfuerzo el número de registros existentes en GEOMEX de cada especie para cada estado de México (Hortal *et al.*, 2006). Los cálculos fueron realizados mediante el programa *EstimateS* (Colwell, 2000).

Comolasuperposición de los modelos individuales claramente generas obrepredicciones en la riqueza total de especies (Cuadro 2), los mapas continuos de favorabilidad individuales fueron convertidos a mapas binarios (presencia-ausencia), eligiendo el punto de corte óptimo capaz de producir la mejor correlación entre los valores de riqueza observados y los valores de riqueza generados por la superposición de los modelos individuales. Dicho punto de corte se halló a una favorabilidad de 70 (coeficiente de correlación de Spearman entre la riqueza observada en cada estado bien muestreado y la riqueza predicha por superposición de los modelos individuales = 0.641, p = 0.003). De este modo, los mapas que se presentan a continuación constituyen la hipótesis de distribución potencial consecuencia de la aplicación del mencionado punto de corte. En el caso de aquellas especies en las que la aplicación de dicho punto de corte impedía que todos los puntos de presencia observados estuviesen incluidos en la distribución potencial (n = 17), se ha representado la distribución potencial predicha por MaxEnt aplicando como punto de corte el valor de favorabilidad mínimo encontrado en un punto de presencia. En el caso de aquellas especies con un único dato de distribución conocido (*G. (Onthotrupes) lobatus, Bolbocerosoma mexicanus, Bolborhombus nitidus, Bolbelasmus horni, Bolbelasmus. bajaensis* y *Eucanthus impressus*), el modelo de distribución potencial que se presenta es el resultante de ampliar un 30% los valores ambientales de las celdas en la que se observó la especie.

| Estado              | S <sub>OBS</sub> | S <sub>CHAO2</sub> | S <sub>maxent</sub> | S <sub>optimo</sub> |
|---------------------|------------------|--------------------|---------------------|---------------------|
| Baja California Sur | 3                | 3                  | 23                  | 10                  |
| Chiapas             | 7                | 7                  | 26                  | 12                  |
| Chihuahua           | 7                | 13                 | 18                  | 9                   |
| Coahuila            | 5                | 5                  | 23                  | 8                   |
| Distrito Federal    | 4                | 4                  | 19                  | 8                   |
| Durango             | 10               | 13                 | 22                  | 11                  |
| Estado de México    | 5                | 5                  | 22                  | 16                  |
| Guerrero            | 11               | 12                 | 29                  | 19                  |
| Hidalgo             | 10               | 17                 | 25                  | 9                   |
| Jalisco             | 11               | 11                 | 28                  | 12                  |
| Michoacán de Ocampo | 10               | 11                 | 29                  | 17                  |
| Morelos             | 10               | 11                 | 23                  | 15                  |
| Nayarit             | 5                | 5                  | 23                  | 9                   |
| Nuevo León          | 9                | 11                 | 22                  | 9                   |
| Oaxaca              | 15               | 16                 | 31                  | 25                  |
| Puebla              | 10               | 10                 | 31                  | 23                  |
| Sinaloa             | 8                | 9                  | 19                  | 8                   |
| Sonora              | 7                | 7                  | 14                  | 9                   |
| Veracruz            | 14               | 15                 | 24                  | 16                  |

**Cuadro 2.** Número de especies observadas en cada estado Mexicano (S<sub>OBS</sub>), número de especies estimadas mediante el estimador no paramétrico Chao2 considerando el número de registros como medida de esfuerzo (S<sub>CHAO2</sub>), número de especies estimadas mediante la superposición de los modelos individuales de distribución generados con MaxEnt (S<sub>MAXENT</sub>) y número de especies resultante de aplicar el punto de corte sobre los valores de favorabilidad (entre 0 y 100) que permite obtener una mejor correlación con los valores de riqueza de especies observados (S<sub>OPTIMO;</sub> ver métodos). Sólo se incluyen los 19 estados cuyo número de especies observados es, al menos, el 50% del estimado mediante Chao2.

# RESULTADOS

El sumatorio de los modelos de distribución obtenidos para las distintas especies y su comparación con los valores de riqueza de especies observados o estimados en cada estado demuestra que las áreas de distribución potencial obtenidas constituyen hipótesis de distribución que sobrepredicen la distribución real (Cuadro 2). A pesar de ello, se puede afirmar que los valores de riqueza de especies resultantes de aplicar el punto de corte óptimo siguen una pauta similar a la de los valores observados, no existiendo una sobreprediccion excesivamente acusada ni sesgada espacialmente (Fig. 1a. y Fig. 1b.).



Fig. 1a. Relación entre el numero de especies observadas en diferentes estados mexicanos (S<sub>OBS</sub>) y el número de especies estimadas mediante Chao2 (círculos), considerando el número de registros como medida de esfuerzo, la superposición de los modelos individuales de distribución generados con MaxEnt (cuadrados) y el número de especies resultante de aplicar el punto de corte sobre los valores de favorabilidad (entre 0 y 100) que permite obtener una mejor correlación con los valores de riqueza de especies observados (triángulos).



Fig. 1b. Se presentan los estados mexicanos con sobrepredicciones mayores del 100% (negro), entre el 50% y el 100% (gris oscuro), sobrepredicciones menores del 50% (gris claro) e infrapredicciones menores del 50% (gris más claro). Sólo se incluyen los 19 estados cuyo número de especies observado es, al menos, el 50% del estimado mediante Chao2 (Ver Cuadro 2)

Los datos topográficos y climáticos de los puntos de presencia de cada una de las especies, así como el tamaño del área potencial de distribución aparecen en la Cuadro 3. Las especies de las tres principales tribus de Geotrupinae aparecen en diferentes condiciones ambientales. En lo que respecta a la altitud, la tribu Geotrupini se encuentra distribuida desde los 1500 y los 3200 metros. Sin embargo los Bolboceratini y Athyreini presentan una altitud media menor, casi desde el nivel del mar hasta los 1700 metros en la primera, y desde los 50 a los 1400 metros la segunda. Respecto a los valores climáticos, los Geotrupini se encuentran presentes en territorios con valores de precipitación mínima anual entre los 500 y los 2000 mm, temperaturas mínimas de alrededor de 14°C y máximas de 22° C.

| Especies                     | Área   | Altitud | Т               | Р               |
|------------------------------|--------|---------|-----------------|-----------------|
| Megatrupes cavicollis        | 17101  | 1695    | $17.9 \pm 0.90$ | 820± 629        |
| Megatrupes fisheri           | 7275   | 2088    | $15.9 \pm 0.75$ | $1156 \pm 103$  |
| Onthotrupes lobatus          | 247    | 1800    | 22.1            | 1727            |
| Onthotrupes sobrinus         | 5526   | 1960    | 14.5 ± 7        | $1224 \pm 475$  |
| Onthotrupes herbeus          | 4684   | 1869    | $14.8 \pm 8$    | $1033 \pm 949$  |
| Onthotrupes viridiobscurus   | 3352   | 1973    | 15.4 ± 3        | $1357 \pm 936$  |
| Onthotrupes truncaticornis   | 1388   | 2268    | 16 ± 4          | $1452 \pm 6$    |
| Onthotrupes sallei           | 15116  | 1777    | 18.6 ± 7        | $1275 \pm 1052$ |
| Onthotrupes nebularum        | 4847   | 1755    | $16.4 \pm 6$    | $1948 \pm 1803$ |
| Onthotrupes guerreroensis    | 3843   | 1670    | $19.7 \pm 2$    | $1297 \pm 340$  |
| Onthotrupes pecki            | 5254   | 1862    | 18.5 ± 5        | $1524 \pm 287$  |
| Onthotrupes onitidipes       | 1900   | 1664    | $20.4 \pm 3$    | $2003 \pm 352$  |
| Geohowdenius cnephosus       | 10115  | 1962    | 13.5 ± 3        | 533 ± 352       |
| Halffterius rufoclavatus     | 4778   | 1955    | $15.4 \pm 11$   | $1105 \pm 725$  |
| Haplogeotrupes guatemalensis | 903    | 2127    | $14 \pm 0.49$   | $1151 \pm 16$   |
| Haplogeotrupes reddelli      | -      | -       | -               | -               |
| Ceratotrupes fronticornis    | 18695  | 1615    | 18.5 ± 12       | $949\pm716$     |
| Ceratotrupes sturmi          | 12278  | 1693    | 20 ± 2          | $1033 \pm 598$  |
| Ceratotrupes bolivari        | 34050  | 1379    | $14.7 \pm 14$   | $1490 \pm 1597$ |
| Bolbocerosoma ritcheri       | 3161   | 669     | $21.3 \pm 1$    | $538 \pm 105$   |
| Bolbocerosoma pusillum       | 55916  | 1476    | $18.3 \pm 0.57$ | 324 ± 12        |
| Bolbocerosoma confusum       | 5094   | 379     | $21.8 \pm 1$    | $685\pm103$     |
| Bolbocerosoma mexicanus      | 2871   | 191     | $22.6 \pm 3$    | $758\pm107$     |
| Bolborhombus sallei          | 90678  | 1126    | $20.4 \pm 7$    | $845\pm868$     |
| Bolborhombus magnus          | 300228 | 621     | $21.1 \pm 2$    | $453 \pm 313$   |
| Bolborhombus parvulus        | 12292  | 237     | $21.7 \pm 3$    | 273 ± 187       |
| Bolborhombus nitidus         | 405    | 600     | $27.6 \pm 138$  | $777 \pm 389$   |
| Bolbocerastes regalis        | 5579   | 168     | $21.5 \pm 0.57$ | $136 \pm 88$    |
| Bolbocerastes serratus       | 93137  | 979     | $20.9 \pm 3$    | $998\pm998$     |
| Bolbocerastes imperialis     | 181998 | 531     | $20.8 \pm 4$    | $437\pm449$     |
| Bolbocerastes peninsularis   | 11905  | 210     | 21.6 ± 3        | 255±221         |
| Bolbelasmus arcuantus        | 31473  | 899     | 23.1 ± 6        | $2483 \pm 2495$ |
| Bolbelasmus horni            | 885    | 500     | 18.4            | 188             |
| Bolbelasmus rotundipennis    | 229363 | 1427    | 20 ± 4          | $1410 \pm 1129$ |
| Bolbelasmus variabilis       | 37462  | 1192    | $20.3 \pm 7$    | $1191 \pm 1254$ |
| Bolbelasmus bajaensis        | 1133   | 9       | 21 ± 3          | 92 ± 13         |
| Eucanthus mexicanus          | 61671  | 1732    | $17.4 \pm 7$    | $1288\pm1291$   |
| Eucanthus impressus          | 6007   | 1207    | $17.2 \pm 2$    | $228 \pm 33$    |
| Neoathyreus excavatus        | 68316  | 854     | $20 \pm 11$     | $1620 \pm 1656$ |
| Neoathyreus fissicornis      | 11907  | 1079    | 20.1 ± 8        | $1655 \pm 1364$ |
| Neoathyreus granulicollis    | 38477  | 1442    | 17 ± 9          | $1059 \pm 1067$ |
| Neoathyreus hamifer          | 815    | 54      | $24.4 \pm 0.92$ | 3154 ± 133      |
| Neoathyreus interruptus      | 47164  | 762     | 21.2 ± 9        | $2083 \pm 1698$ |
| Neoathyreus mexicanus        | 79477  | 923     | 22.6 ± 7        | $2373 \pm 2651$ |
| Neoathyreus mixtus           | 164100 | 750     | $21 \pm 6$      | $995 \pm 773$   |

**Cuadro 3.** Tamaño del área de distribución potencial de cada especie (en km<sup>2</sup>), así como altitud media (en metros), precipitación (P) y temperatura medias (T) de las celdas de 0.08° en las que se ha observado cada especie (± SD). Los datos de altitud provienen de un modelo digital del terreno a una resolución de 1 Km<sup>2</sup> (ver United Status Geological Survey, 2006), mientras que los datos climáticos provienen de WorldClim (Hijmans *et al.* 2007). Como *Geotrupes (Haplogeotrupes) reddelli* está **a**sociada a cuevas no hemos incluido datos ambientales para ella.

Por otra parte, los Bolboceratini se encuentran entre valores de precipitación mínima de 90 mm y máxima de 2500 mm, temperaturas mínima de 17º y máxima de 23º C. Los Athyreini se encuentran presentes en enclaves con valores más altos de temperatura y precipitación que los otros dos grupos; precipitación mínima de 990 mm, precipitación máxima de 2400 mm, temperatura mínima de 17º y máxima 24º C (Cuadro 3).

Estos datos muestran que los Geotrupini suelen vivir en localidades montañosas, más frías y con mayores precipitaciones que las especies de las otras tribus. Debido a ello, existiría un recambio altitudinal de especies, de manera que los Bolboceratini y Athyreini se encontrarían en altitudes bajas, bajo climas tropicales y áridos, mientras que los Geotrupini se hallarían en altitudes superiores, bajo climas templados o fríos. Esta ocupación de condiciones ambientales diferentes podría ser consecuencia del distinto origen biogeográfico de ambas subfamilias (Zunino 1984, Browne & Scholtz 1995, 1999).

#### Distribución de los Geotrupini

**Subgénero** *Megatrupes:* Este subgénero, endémico de México, está formado por dos especies con distribuciones disyuntas. *Geotrupes. cavicollis* (Fig. 2a) se encuentra distribuida en el Noroeste de México, en la Sierra Madre Occidental, mientras que *G. fisheri* (Fig. 2b) se distribuye por el Sistema Volcánico Transversal. *Geotrupes. cavicollis* parece ocupar lugares más cálidos y secos con una temperatura media de 17.9 °C y una precipitación media de 820 mm, mientras que *Geotrupes. fisheri* habitaría localidades algo más frías y húmedas con una temperatura media de alrededor de 16°C y una precipitación media alrededor de los 1150 mm (Cuadro 3).

Las distribuciones potenciales obtenidas para las dos especies amplían el rango de distribución conocido en ambas especies. Así, *G. cavicollis* también poseería condiciones ambientales adecuadas en la Sierra Madre Oriental y algunas zonas del Altiplano hacia la costa del Pacífico. *Geotrupes fisheri* podría también extender su distribución hacia algunos puntos de la Sierra Madre del Sur.





Fig. 2. Mapas de distribución del subgénero Megatrupes.

Los puntos en rojo representan la distribución observada, mientras que la distribución potencial estimada mediante el punto de corte óptimo se representa en gris oscuro y la distribución potencial con el valor de favorabilidad mínimo encontrado en los lugares con presencia en gris claro. a) *M. cavicollis;* b) *M.* 

## fisheri.

**Subgénero** *Onthotrupes:* Este subgénero es, básicamente, endémico de la República Mexicana, salvo por la especie *G. onitidipes*, que se extiende también hacia Guatemala y El Salvador (Fig. 3a). Las especies del subgénero *Onthotrupes* presentan en general distribuciones restringidas que apenas se solapan entre sí. En general, su distribución se constriñe a la Sierra Madre del Sur y al Sistema Volcánico Transversal, habitando localidades con temperaturas medias que oscilan entre los 14º y los 22ºC y precipitaciones medias entre los 1000 y los 2000 mm (Cuadro 3).

Se pueden discriminar tres grupos de especies de *Onthotrupes* diferentes, según la localización de su distribución. Un primer grupo, constituido únicamente por G. onitidipes, se distribuiría por la Sierra de Chiapas y Guatemala (Fig. 3a). Un segundo grupo (G. pecki, G. guerreroensis y G. truncaticornis) estaría formado por aquellas especies distribuidas principalmente por la Sierra Madre del Sur, aunque G. pecki también se encontraría presente en la Sierra de Chiapas (Fig.3b, c y d). Geotrupe. lobatus, especie conocida únicamente de una localidad de la Sierra de Oaxaca (Fig. 3e), podría encontrase también en zonas cercanas a ésta, según sugiere la distribución potencial realizada. Por último, un tercer grupo de Onthotrupes estaría formado por aquellas especies que presentan distribuciones en el Sistema Volcánico Transversal (G. viridiobscurus, G. herbeus, G. sobrinus, G. sallei y G. nebularum); éstas son las que, en general, muestran rangos de distribución conocidos y potenciales más amplios. *Geotrupes viridiobscurus* se distribuye por la Sierra Madre del Sur, sugiriendo su distribución potencial una ampliación de su rango a diversos puntos interiores de esta Sierra (Fig. 3f). Geotrupes herbeus y G. sobrinus se distribuyen por el Sistema Volcánico Transversal, siendo su localización observada muy restringida (Fig. 3g, h). Sin embargo, en ambas especies la distribución potencial amplia su área de distribución hacia la Sierra Madre del Sur y la Sierra de Chiapas. Geotrupes sallei y G. nebularum son las especies con una distribución más amplia. La primera se distribuye por la Sierra Madre del Sur y el Sistema Volcánico Transversal; la distribución potencial amplia su rango hacia la Sierra de Chiapas (Fig. 3i). Geotrupes nebularum se distribuye por la Sierra Madre Oriental, el Sistema Volcánico Transversal y la Sierra Madre del Sur. Los mapas de distribución potencial también amplían la presencia de esta especie a diversos puntos del interior de estas sierras (Fig 3j).

Subgénero *Geohowdenius:* Este es un subgénero neártico (Howden, 2003), que presenta una sola especie en México, *G. cnephosus*, con una distribución bastante restringida hacia zonas con precipitaciones bajas (alrededor de 500 mm) y temperaturas templado-frías (13°C; Cuadro 3). Tanto su área de distribución potencial, como su distribución conocida, corresponden a la parte norte de la Sierra Madre Occidental (Fig. 4). Esta especie está muy relacionada con *G. opacus* Haldeman 1853 y *G. egeriei* Germar, 1824, que presentan una amplia distribución en los Estados Unidos.

**Subgénero** *Halffterius:* Este subgénero esta compuesto por una única especie, *G. rufoclavatus* (Fig. 5), endémica de México. Su distribución conocida se limita al Sistema Volcánico Transversal, habitando praderas o claros de bosque de pinos, encinos y oyameles situados a partir de los 1900 m (Howden, 2003), en localidades con una temperatura media de unos 15 °C y una precipitación media de 1100 mm (Cuadro 3). La hipótesis de distribución potencial generada extiende su presencia hasta la Sierra Madre Oriental, la Sierra Madre del Sur y Chiapas.



Fig. 3a. Mapas de distribución del subgénero Onthotrupes (ver Figura 2) G. onitidipes;



Fig. 3b. Mapas de distribución del subgénero Onthotrupes: G. pecki



Fig. 3c. Mapas de distribución del subgénero Onthotrupes: G. guerreroensis



Fig. 3d. Mapas de distribución del subgénero Onthotrupes: G. truncaticornis



Fig. 3e. Mapas de distribución del subgénero Onthotrupes: G. lobatus


Fig. 3f. Mapas de distribución del subgénero Onthotrupes: G. viridiobscurus



Fig. 3g. Mapas de distribución del subgénero Onthotrupes: G. herbeus



Fig. 3h. Mapas de distribución del subgénero Onthotrupes: G. sobrinus



Fig. 3i. Mapas de distribución del subgénero Onthotrupes: G. sallei

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Fig. 3j. Mapas de distribución del subgénero Onthotrupes: G. nebularum



Fig. 4. Mapa de distribución de G. (Geohowdenius) cnephosus.



Fig. 5. Mapa de distribución de G. (Halffterius) rufoclavatus



Fig. 6. Mapas de distribución de G. (Haplogeotrupes) guatemalensis.

**Subgénero** *Haplogeotrupes:* Al igual que el resto de Geotrupini, *Haplogeotrupes* es un subgénero neártico. Los mapas de distribución potencial de las especies de este subgénero coinciden con los de su distribución conocida. En el caso de *G. redelli* no se han elaborado mapas de distribución potencial ya que, al tratarse de una especie troglobia, sería erróneo estimar su distribución en base a variables climáticas del medio exterior. Únicamente ha sido citada de las cuevas de Tasalolpan y Xochitlan en el estado de Puebla. En el caso de *G. guatemalensis* solamente se conocen citas muy puntuales del Estado de Chiapas (Fig. 6), en concreto de la localidad de San Cristóbal de las Casas, aunque su distribución se extiende hacia Guatemala. Los mapas de distribución potencial para esta especie muestran escasas localidades adicionales muy cercanas a la localidad de colecta.

**Género** *Ceratotrupes:* Se trata de un subgénero actualmente endémico de México de origen neártico (ver Halffter & Martínez, 1962 y Halffter 1987), cuyas especies poseen distribuciones extensas y, por tanto, gradientes ambientales amplios (entre los 14 y 20°C de temperatura y los 950 y 1500 mm de precipitación) (Cuadro 3). Las tres especies de *Ceratotrupes* se distribuyen principalmente por el Sistema Volcánico Transversal, la Sierra Madre Occidental y la Sierra Madre del Sur, a altitudes que oscilan entre los 1300 y los 1600 metros de altitud.



Fig. 7a. Mapas de distribución del género Ceratotrupes: C. bolivari



Fig. 7b. Mapas de distribución del género Ceratotrupes: C. fronticornis



Fig. 7c. Mapas de distribución del género Ceratotrupes: C. sturmi

Los mapas potenciales obtenidos indican que las tres especies de este género solaparían sus áreas de distribución en los estados de Oaxaca y Guerrero, extendiéndose también por Chiapas y Guatemala, aunque no se han observado individuos de *Ceratotrupes* al este del estrecho de Tehuantepec. *Ceratotrupes bolivari* (Fig. 7a) es la especie del género que presenta una distribución más amplia llegando hasta el norte de México. *Ceratotrupes fronticornis* (Fig. 7b) también se distribuye por el norte de México, aunque parece ser capaz de habitar en el occidente del país. Por último, *C. sturmi* (Fig. 7c) es la especie que presenta una distribución más restringida, habitando únicamente diversas áreas de los estados de Oaxaca y Guerrero.

### Distribución de los Bolboceratini mexicanos

Género *Bolbocerosoma:* Este género neártico se distribuye en la República Mexicana por el norte de la Sierra Madre Oriental y el Altiplano Mexicano, desde los 200 a los 1500 m de altitud, áreas con temperaturas medias que oscilan entre los 18°C y los 22°C y precipitaciones medias entre los 300mm y los 750 mm. (Cuadro 3). De las cuatro especies mexicanas, *B. pusillum* es la que presenta una distribución más amplia, extendiéndose a lo largo de todo el Altiplano Mexicano hasta la Sierra Madre Occidental (Fig. 8a). Su distribución potencial amplia su presencia en diversos puntos del Altiplano Mexicano. El resto de las especies que forman este género (*B. ritcheri, B. confusum* y *B. mexicanum*) son especies con distribuciones conocidas y potenciales muy restringidas (la última incluso endémica del país), situadas casi exclusivamente en el norte de la Sierra Madre Oriental (Fig. 8b, c y d).



Fig. 8a. Mapas de distribución del género Bolbocerosoma: B. pusillum



Fig. 8b. Mapas de distribución del género Bolbocerosoma: B. ritcheri



Fig. 8c. Mapas de distribución del género Bolbocerosoma: B. confusum



Fig. 8d. Mapas de distribución del género Bolbocerosoma: B. mexicanus

Capítulo 2

Género *Bolborhombus:* Todas las especies de este género de distribución neártica se encuentran presentes en México, habitando localidades desde los 200 a los 1100 m de altitud con temperaturas medias entre los 20°C y los 27°C y precipitaciones que oscilan entre los 270 mm y los 850 mm (Cuadro 3)

*Bolborhombus sallei* y *B. magnus* muestran distribuciones amplias, estando presente la primera en casi todo el territorio mexicano, salvo en algunas zonas del Golfo de México y de la Península de Yucatán. Los datos de distribución potencial para *B. sallei* amplían su presencia en zonas de la costa oeste (Fig. 9a). *Bolborhombus magnus* se distribuye por el Altiplano Mexicano y el Sistema Volcánico Transversal; su mapa potencial amplia su rango hasta Baja California, Sonora y la Depresión del Balsas (Fig. 9b). *Bolborhombus parvulus* y *B. nitidus* presentan distribuciones mucho más restringidas; la primera se distribuye por Baja California, Sinaloa y Sonora, y la segunda en Michoacán (Fig. 9c, d). Las distribuciones potenciales para estas dos especies no amplían apenas su rango de distribución, salvo algunos puntos dispersos en Baja California y en Michoacán para *B. nitidus*.



Fig. 9a. Mapas de distribución del género Bolborhombus: B. sallei

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Fig. 9b. Mapas de distribución del género Bolborhombus: B. magnus



Fig. 9c. Mapas de distribución del género Bolborhombus: B. parvulus



Fig. 9d. Mapas de distribución del género Bolborhombus: B. nitidus

Género Bolbocerastes: Este es otro género neártico presente en la Zona de Transición Mexicana, habitando localidades entre los 160 y los 1000 metros con temperaturas medias en torno a los 20° C y precipitaciones entre 130mm y los 250 mm (Cuadro 3). La mayor parte de las especies de este género se encuentran distribuidas por la mitad occidental de México, mientras que sólo una especie habita en la mitad oriental. Así, *B. serratus* se distribuye principalmente por el noreste de México, aunque potencialmente podría también estar presente por toda la costa oriental, sobre todo hacia el estado de Tamaulipas (Fig. 10a). Por el contrario, B. regalis, B. peninsularis y B. imperialis aparecen principalmente en la zona noroccidental de México (estados de Baja California, Sonora y, para la última, también Chihuahua). Bolbocerastes imperialis presenta la distribución más extensa, ampliando la distribución potencial su presencia hasta el Altiplano y la Depresión del Balsas (Fig. 10b). Bolbocerastes peninsularis ha sido colectada en Baja California y su distribución potencial sólo amplia en diversos puntos su rango conocido (Fig 10c). Por último, B. regalis se distribuye por los estados de Baja California Norte y Sonora. El mapa de distribución potencial sugiere que la distribución de esta especie podría ampliarse a otras localidades de la misma región (Fig. 10d)



Fig. 10a. Mapas de distribución del género Bolbocerastes: B. serratus



Fig. 10b. Mapas de distribución del género Bolbocerastes: B. imperialis

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Fig. 10c. Mapas de distribución del género Bolbocerastes: B. peninsularis



Fig. 10d. Mapas de distribución del género Bolbocerastes: B. regalis.

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**Género** *Bolbelasmus:* El género *Bolbelasmus* presenta una distribución bastante amplia, pues se extiende por las regiones Paleártica, Oriental, Neártica y Neotropical (Howden, 2003). Cinco especies se encuentran presentes en México, de las cuales tres son endémicas. Pueden hallarse desde los 900 a los 1500 metros de altitud media, en lugares con temperaturas medias que oscilan entre los 18°C y los 23°C y precipitaciones medias entre los 90 mm y los 2500 mm. (Cuadro 3).

*Bolbelasmus arcuatus* es una especie de distribución básicamente Neotropical, que se extiende en la República Mexicana por la región central y meridional, mostrando una distribución potencial que amplia notablemente su área conocida (ver Fig. 11a). *B. variabilis* es la especie mexicana que presenta una distribución más amplia, incluyendo la región Neártica y la Neotropical, y siendo más abundante hacia la costa oeste, donde se ampliaría su distribución potencial (Fig. 11b). *Bolbelasmus rotundipennis* se distribuye exclusivamente por la zona central de México, aunque su distribución potencial muestra que su rango podría extenderse hacia las costas occidentales y orientales, la Sierra de Chiapas y Guatemala (Fig. 11c). Por último, *B. bajaensis* y *B. horni* presentan distribuciones muy restringidas en Baja California; de *B. horni* solamente se conoce una cita puntual de la localidad de Ensenada (Fig. 11d) y de *B. bajaensis* de la localidad de Mulege (Fig. 11e). Los mapas potenciales apenas amplían su distribución conocida como consecuencia de la escasez de datos.



Fig. 11a. Mapas de distribución del género Bolbelasmus: B. arcuantus



Fig. 11b. Mapas de distribución del género Bolbelasmus: B. variabilis



Fig. 11c. Mapas de distribución del género Bolbelasmus: B. rotundipenis

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Fig. 11d. Mapas de distribución del género Bolbelasmus: B. horni



Fig. 11e. Mapas de distribución del género Bolbelasmus: B. bajaensis.

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**Género** *Eucanthus:* Este género posee una amplia distribución, incluyendo las regiones Neártica, Neotropical y Australiana (Howden, 2003), aunque en México solo pueden encontrarse dos especies, una de ellas endémica (*E. mexicanus*) distribuida por el Sistema Volcánico Transversal y la Sierra Madre Occidental. La distribución potencial de *E. mexicanus* sugiere una extensión de área conocida en el Sistema Volcánico Transversal y también en la Sierra de Chiapas (Fig. 12a). *Eucanthus impressus* se extiende principalmente por el norte de México mostrando una distribución observada y potencial restringida al norte del estado de Chihuahua (Fig. 12b). Ambas especies se localizan en enclaves con temperaturas medias en torno a los 17°C, aunque *E. mexicanus* habita localidades con mayores precipitaciones medias (1280 mm) que *E. impressus* (230 mm; Cuadro 3).



Fig. 12a. Mapas de distribución del género Eucanthus: E. mexicanus



Fig. 12b. Mapas de distribución del género *Eucanthus: E. impresus*.

### Distribución de los Athyreini mexicanos

Esta tribu esta distribuida por las regiones Neotropical, Afrotropical y Oriental (Howden, 2003), existiendo un único género en México, *Neoathyreus*, el cual posee una distribución típicamente Neotropical.

**Género** *Neoathyreus:* El género *Neoathyreus* presenta un gran número de especies en Sudamérica (Howden, 1985); en México, la mayoría de las especies se distribuyen por las regiones centrales y meridionales en altitudes que oscilan entre los 50 y los 1400 metros de altitud, temperaturas medias que varían entre los 17°C y los 24°C, y precipitaciones medias que fluctúan entre los 990 mm y los 3200 mm (Cuadro 3). *Neoathyreus fissicornis, N. granulicollis* y *N. mixtus* son especies que alcanzan latitudes superiores a las de las demás especies y presentan una distribución más extensa en el territorio mexicano. *Neoathyreus granulicollis* y *N. mixtus* son las únicas especies endémicas del género; mientras *N. mixtus* parece distribuirse por costa oriental (Fig. 13a).



Fig. 13a. Mapas de distribución del género Neoathyreus: N. mixtus



Fig. 13b. Mapas de distribución del género Neoathyreus: N. granulicollis



Fig. 13c. Mapas de distribución del género Neoathyreus: N. fissicornis



Fig. 13d. Mapas de distribución del género Neoathyreus: N. excavatus

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Fig. 13e. Mapas de distribución del género Neoathyreus: N. mexicanus



Fig. 13f. Mapas de distribución del género Neoathyreus: N. interruptus

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*N. granulicollis* se extiende hacia la mitad occidental (Fig. 13b). Las áreas de distribución potencial para *N. mixtus* amplían su rango conocido hacia la costa oriental y los estados de Yucatán, Campeche y Quintana Roo. El área de distribución potencial de *N. granulicollis* amplia notablemente su rango hacia el este y el noroeste del país. Algo similar ocurre con *N. fissicornis*, especie colectada en diversas localidades alejadas del centro y sur de México que, potencialmente, podría habitar extensas áreas del país, excepto la región más septentrional (Fig. 13c).

El resto de las especies de este género presentes en México (*N. excavatus, N. mexicanus, N. interruptus* y *N. hamifer*) poseen una distribución más meridional, apenas sobrepasando las distribuciones potenciales el Sistema Volcánico Transversal (Fig. 13d, e, f, g). Sólo *N. hamifer*, únicamente citada del estado de Veracruz, muestra una distribución potencial restringida.

## DISCUSIÓN

Cuando los datos conocidos de distribución de las especies son escasos y sesgados, la aplicación de modelos predictivos permite realizar distribuciones hipotéticas de utilidad en conservación y biogeografía. Ello es así, porque sus resultados son reproducibles y coherentes, al estar basados en las condiciones climáticas del territorio de interés. Estos mapas, no sólo nos proporcionan una imagen razonable de la distribución de las especies, sino que constituyen una herramienta útil para el diseño y planificación de nuevas colectas, sobre todo en el caso de regiones poco muestreadas.

Los mapas así generados deben considerarse una aproximación al conocimiento de la distribución potencial de los organismos, en el hipotético caso de que los factores capaces de restringir el rango de distribución no operasen (factores históricos, interacciones bióticas o limitantes de dispersión). Las distribuciones potenciales que hemos presentado podrían considerarse imágenes que nos muestran, en general, cuáles serían las tendencias de distribución de estas especies si a lo largo de la historia evolutiva de estos taxones no hubiera habido ninguna otra influencia que la climática. Sin embargo, la fauna de Geotrupinae mexicana está compuesta por grupos taxonómicos con diferentes orígenes e historias biogeográficas, los cuales han marcado la distribución actual de sus especies. El conocimiento de esta información biogeográfica complementa y da sentido a las distribuciones presentes en los mapas.

Así, según se ha sugerido, la tribu Geotrupini habría penetrado en América siguiendo un patrón de dispersión neártico (Halffter 1976). Los antecesores de esta tribu habrían colonizado este continente a través del estrecho de Bering a partir del Plioceno, utilizando probablemente como corredores para su dispersión los sistemas orográficos occidentales de la región Neártica, ya que estas especies poseen una mayor afinidad por las zonas de montaña y los climas templado-fríos; estas zonas podrían haber favorecido también su aislamiento tras el último periodo de glaciación Pleistocénica.

Para los Bolboceratini, existen actualmente dos teorías acerca de su origen. Howden (1982) propone que los Bolboceratini puedan ser, junto con Lethrini y Athyreini, el grupo hermano de los demás Geotrupinae; Zunino (1984) también admite esta hipótesis y sugiere una cladogénesis mesozoica que habría dado lugar a la vicarianza geográfica de un grupo Laurásico, anterior a los actuales Geotrupini, y otro Gondwánico, del que procederían los Bolboceratini. Por su parte, Browne & Scholtz (1995 y 1999) no aceptan una relación próxima entre estas dos tribus, puesto que sitúan a los Bolboceratini como el grupo hermano de la familia Pleocomidae. En cualquiera de los casos, según muestran nuestros mapas, la mayor parte de los Bolboceratini mexicanos poseen una afinidad hacia enclaves con temperaturas cálidas y precipitaciones moderadas, lo cual correspondería a un linaje típico con un patrón Paleoamericano, cuya entrada en Norteamérica se habría producido a partir del Cretácico (Halffter 1976). Esto coincide con Howden (2003), que opina que las especies mexicanas de Bolboceratini tendrían un origen totalmente Laurásico.

Dentro de Bolboceratini, los *Eucanthus* merecen una mención especial, puesto que, aunque actualmente se encuentran incluidos dentro de esta tribu, serían en realidad el grupo hermano natural del resto de Bolboceratini y Athyreini (Browne 1991; Verdú et al. 2004). Para *Eucanthus* se han observado en las Américas dos linajes con distribuciones diferentes, Neártica y Neotropical/Australasiática, respectivamente (Browne 1991), desconociéndose si el origen de ambos linajes es idéntico (ambos Gondwánicos) o diferente (uno Gondwánico y otro Laurásico). Los mapas conocidos y predichos nos ofrecen distribuciones muy diferentes para las dos especies de este género. De este modo, hasta no confirmarse filogenéticamente las relaciones de las especies incluidas dentro de *Eucanthus*, no puede aventurarse nada sobre la región de origen de las especies presentes en México.

En cuanto a los Athyreini, la mayor parte de los autores los consideran el grupo hermano de los Bolboceratini (Howden 1982; Browne 1991; Browne & Scholtz 1995 y 1999). Según Halffter (1987), la colonización mexicana de este linaje se habría producido durante el Plio-Pleistoceno desde la región Neotropical. Este posible origen coincide con el hecho de que presenten una afinidad hacia climas tropicales, de que, en efecto, existan muchas más especies en Sudamérica y de que se distribuya también por la región Afrotropical y Oriental (Howden 2003). Muy probablemente, esto esté indicando que el origen de los Athyreini sea Gondwánico.

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# LITERATURA CITADA

- 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(2):221-230.
- Browne, D. J. & C. H., Scholtz. 1995. Phylogeny of the families of the Scarabaeoidea (Coleoptera) based on characters of the hindwing articulation, hindwing base and wing venation. *Systematic Entomology* 20:145-173.
- Browne, D. J. & C. H., Scholtz. 1999. A phylogeny of the families of Scarabaeoidea (Coleoptera). Systematic Entomology 24:51-84.
- Clark Labs. 2003. Idrisi Kilimanjaro. Gis software package. Clark Labs, Worcester, M.A.
- Colwell, R. K. & J. A., Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series Biological Sciences* 345:101-118.
- Colwell, R. K. 2000. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples (Shoftware and User's Guide), version 6.0. Disponible en http://viceroy.eeb.uconn.edu/estimates.
- Dennis, R.L.H., T.H. Sparks, & P.B., Hardy. 1999. Bias in butterfly distribution maps: the effects of sampling effort. *Journal of Insect Conservation* 3:33-42.
- **Dennis, R.L.H. & C.D., Thomas. 2000.** Bias in butterfly distribution maps: the influence of hot spots and recorder's home range. *Journal of Insect Conservation* 4:73-77.
- Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129-151.
- Gómez, B. & López-Rojas. 2004. Primer registro de *Geotrupes (Onthotrupes) onitidipes*Bates, 1887 para México (Coleoptera: Scarabaeidae: Geotrupidae). Entomotropica. *Boletín de Entomología Venezolana* 19:47-48.

- Graham, C.H., S. Ferrier, F. Huettman, C. Moritz, & A.T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution* 19:497-503.
- Guisan, A. & N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological. Modelling* 135:147-1
- 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. 1987. Biogeography of the Montane Entomofauna of México and Central America. Annual Reviews of Entomology 32: 97-114
- Halffter, G. & A. Martínez. 1962. Monografía del Género Ceratotrupes Jekel (Coleopt. Scarab. Geotrup.). *Ciencia* 11(4):145-159.
- Halffter, V., Y. López-Guerrero & G. Halffter. 1985. Nesting and ovarian development in *Geotrupes cavicollis* Bates (Coleoptera: Scarabaeidae). *Acta Zoológica Mexicana* 7:1-28.
- Hijmans, R. J., S. Cameron, J. Parra, P. Jones, A. Jarvis & K. Richardson. 2006. WorldClim version 1.4. *Museum of Vertebrate Zoology of the University of California*, CIAT, and Rainforest CRC. <u>http://www.worldclim.org/</u>.
- Hortal, J., P. A. V. Borges, & C. Gaspar. 2006. Evaluating the performance of species richness estimators: sensitivity to sample grain size. *Journal of Animal Ecology* 75: 274–287.
- Hortal, J., J.M. Lobo & A. Jiménez-Valverde. 2007. Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife (Canary Islands). *Conservation Biology* 21(3): 853-863.
- Howden, H. F. 1955. Biology and taxonomy of North American beetles of the Subfamily Geotrupinae with revisions of the Genera *Bolbocerosoma, Eucanyhus, 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. 1982. Larval and adult characters of *Frickius* Germain, its relationship to the *Geotrupini*, and a phylogeny of some mayor taxa in the Scarabaeoidea (Insecta:Coleoptera). *Canadian Journal of Zoology* 60:2713-2724.
- Howden, H. F. 1985. A revision of the Southamerican species in the genus Neoathyreus Howden and Martínez (Coleoptera: Scarabaeidae, Geotrupinae). Contributions of the American Entomological Institute 21:1-95.
- Howden, H. F. 2003. Geotrupinae [95-106]. In: Morón M. A. (Editor), Atlas de los escarabajos de México (Coleoptera: Lamellicornia: Scarabaeidae, Trogidae, Passalidae y Lucanidae)Vol. II (4). 227 pp.
- Howden, H. F. 2005. Notes on Bolboceratini from Northeastern México with description of a new *Bolbocerosoma* Schaeffer (Coleoptera: Scarabaeidae: Geotrupinae). *Folia Entomológica Mexicana* 44 (2):213-218.
- Lobo, J.M., A. Baselga, J. Hortal., A. Jiménez-Valverde, & J.F. Gómez. 2007. How does the knowledge about the spatial distribution of Iberian dung beetle species accumulates over time? *Diversity and Distributions* (in press). doi:10.1111/j.1472-4642.2007.00383.x
- Martín-Piera, F., & J. I. López-Colón. 2000. Coleoptera, Scarabaeoidea I. Fauna Ibérica 14. Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain.
- Martínez-Meyer, E. 2005. Climate change and biodiversity: some considerations in forecasting shifts in species potential distributions. *Biodiversity Informatics* 2:42-55.
- Nix, H. A. 1986. A biogeographic análisis of Australian elapid snakes in R.C. Longmore (ed). Atlas of Australian elapid snakes. *Australian Flora and Fauna Series* No. 7:4-15. Australian Government Publishing Service, Canberra.
- Peterson, A. T. & A. Navarro-Sigüenza, H. Benítez-Díaz. 1998. The need for continued scientific collecting: a geographic análisis of Mexican bird specimens. *Ibis* 140:288-294.

- Peterson, A.T. 2006. Uses and requirements of ecological niche models and related distributional models. *Biodiversity Informatics* 3:59-72.
- Phillips, S. J., R. P. Anderson & R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231-259.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* 3: 349-361.
- Reutter, B.A., V. Helfer, A.H. Hirzel & P. Vogel. 2003 Modelling habitat-suitability using museum collections: an example with three sympatric *Apodemus* species from the Alps. *Journal of Biogeography* 30:581–590.
- Romo, H., E. García-Barros & J.M. Lobo. 2006. Identifying recorder-induced geographic bias in an Iberian butterfly database. *Ecography* 29(6):873-885.
- Soberón, J. & A.T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2:1-10
- Trotta-Moreu, N., E. Montes de Oca & M. Martínez. 2007. Ecological and reproductive characteristics of *Geotrupes (Halffterius) rufoclavatus* Jekel, 1865 (Coleoptera: Scarabaeoidea: Geotrupinae) on the Cofre de Perote Volcano (Veracruz, Mexico). *Coleopterists Bulletin* (in press).
- Vaughan, I.P. & S.J. Ormerod. 2005. The continuing challenges of testing species distribution models. *Journal of Applied Ecology* 42:720-730.
- Verdú, J. R., E. Galante, J. P. Lumaret & F. J. Cabrero-Sañudo. 2004. Phylogenetic análisis of Geotrupidae (Coleoptera, Scarabaeoidea) based on larvae. *Systematic Entomology* 29:509-523.
- Zaniewski, A.E., A. Lehmann & J.M. Overton. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling* 157:261-280.
- Zunino, M. 1984. Sistematica genérica dei Geotrupinae (Coleoptera, Scarabaeoidea: Geotrupinae) filogenesi della sottofamiglia e consideración biogeografiche. *Bolletino del Museo Regionale di Scienze Naturale di Torino* 2:9-162.





# Deriving a species richness distribution from the overlap of individual model predictions: The distribution of Geotrupinae (Coleoptera: Scarabaeoidea) species in Mexico

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# DERIVING THE SPECIES RICHNESS DISTRIBUTION OF GEOTRUPINAE (COLEOPTERA: SCARABAEOIDEA) IN MEXICO FROM THE OVERLAP OF INDIVIDUAL MODEL PREDICTIONS

# Obteniendo la distribución de la riqueza de Geotrupinae (Coleoptera: Scarabaeoidea) en México a partir de la superposición de modelos de predición individuales

Nuria TROTTA-MOREU & Jorge M. LOBO

#### ABSTRACT

Predictions from individual distribution models for Mexican Geotrupinae species were overlaid to obtain a total species richness map for this group. A database (GEOMEX) that compiles available information from the literature and from several entomological collections was used. A Maximum Entropy method (MaxEnt) was applied to estimate the distribution of each species, taking into account nineteen climatic variables as predictors. For each species, suitability values ranging from 0 to 100 were calculated for each grid cell on the map, and 21 different thresholds were used to convert these continuous suitability values into binary ones (presence-absence). By summing all of the individual binary maps, we generated a species richness prediction for each of the considered thresholds. The number of species and faunal composition thus predicted for each Mexican state were subsequently compared with those observed in a pre-selected set of well-surveyed states. Our results indicate that the sum of individual predictions tends to over-estimate species richness but that the selection of an appropriate threshold can reduce this bias. Even under the most optimistic prediction threshold, the mean species richness error is 61% of the observed species richness, with commission errors being significantly more common than omission errors (71%  $\pm$  29% vs. 18%  $\pm$  10%). The estimated distribution of Geotrupinae species richness in Mexico in discussed, although our conclusions should be considered preliminary and contingent upon the scarce and probably biased available data.

Key Words: Geotrupinae, Mexico, species richness distribution, predictive distribution models

#### RESUMEN

Se superpusieron las predicciones de los modelos individuales de distribución de las especies de Geotrupinae mexicanas, obteniéndose un mapa de riqueza total para este grupo. Se utilizó una base de datos (GEOMEX) que recopilaba la información disponible presente en la literatura y de varias colecciones entomológicas. Se aplicó un método de Máxima Entropía (MaxEnt) para estimar la distribución de cada especie, teniendo en cuenta diecinueve variables climáticas como predictores. Para cada especie, se calcularon

los valores de favorabilidad, con valores de entre 0 a 100, de cada celda del mapa y se utilizaron 21 umbrales diferentes para convertir los valores continuos de favorabilidad en valores binarios (presencia-ausencia). Sumando todos los mapas binarios, generamos una predicción de la riqueza de especies para cada umbral considerado. El número de especies y la composición faunística predicha para cada estado mexicano fueron posteriormente comparados con los observados en un conjunto preseleccionado de estados bien muestreados. Nuestros resultados indican que la suma de las predicciones individuales tiende a sobrestimar la riqueza de especies, pero que la selección de un umbral apropiado puede reducir este problema. Incluso bajo los umbrales más optimistas de predicción, el error medio de riqueza de especies es 61% de la riqueza de especies observada, siendo los errores de comisión significativamente más comunes que los de omisión (71%±29% vs. 18%±10%). Se discute la distribución estimada de la riqueza de especies de Geotrupinae en México, aunque nuestras conclusiones deben ser consideradas preliminares y contingentes a consecuencia de los escasos y probablemente parciales datos disponibles.

Palabras clave: Geotrupinae, México, distribución de la riqueza de especies, modelos predictivos de distribución.

### **INTRODUCCIÓN**

Species richness is frequently correlated with other measures of ecological, morphological, phylogenetic and functional diversity (Gaston 1996). It provides a useful measure of biodiversity, and the study of its distribution and causes has been among the principal aims of ecology almost since the foundation of the discipline (Ricklefs 2004). Unfortunately, accurate descriptions of species richness patterns for hyper-diverse groups, such as insects, mainly depend on the sampling effort of collectors. Distributional data for such groups are often incomplete and biased (Whittaker et al. 2005).

Recently, several modeling methods have been proposed to overcome gaps in species distributional information (Guisan and Zimmermann 2000, Elith et al. 2006, Tsoar et al. 2007). However, the individual species predictions provided by such methods are difficult to validate (Lobo et al. 2008), and it is necessary to define *a priori* whether the distribution to be modeled represents the potential or the realized niche. Distribution models that approximate the potential distribution (all of the environmentally suitable locations in which a species could occur according to a set of environmental variables; see Soberón and Peterson 2005,

Peterson 2007) can be obtained without the necessity of using absence data or of extracting pseudo-absence data from environmentally unsuitable locations (Chefaoui and Lobo 2008, Jimenez-Valverde et al. 2008). In contrast, the estimation of realized distributions requires the use of absence data from environmentally favorable locations in order to account for historically or geographically contingent factors (Lobo 2008). Thus, the difficulty of discriminating the causes of species absence hinders the reliability of predictions based on distribution models for obtaining accurate geographical representations of actual species distributions.

When many individual distribution models are overlaid to obtain a species richness pattern, the bias in these predictions can be inflated (Hortal and Lobo 2006). As in other studies (Cumming 2000, Ortega-Huerta and Peterson 2004, Domínguez-Domínguez et al. 2006, García 2006), we here overlay predictions derived from individual distribution models that use only presence data (a "modeling-then-classification" procedure; see Ferrier 2002 and Ferrier et al. 2002).

Because the accuracy of these individual models cannot be evaluated due to the lack of reliable absence data, the resulting species richness values and community compositions are validated by comparison to those obtained for Mexican states previously defined as well surveyed by using a non-parametric estimator (Colwell and Coddington 1995). To perform these comparisons, we use an exhaustive database of the distribution of Geotrupinae species in Mexico, applying a well-known presence-only modeling technique to estimate the distribution of each species. The spatial distributions of the model errors obtained for both species richness and species composition were subsequently explored, and the results were used to partially correct the over-prediction of the models.

# **MATERIAL AND METHODS**

**Study area:** Mexico is bordered by the United States on the north and by Guatemala and Belize on the southeast, and it has a continental area of 1,972,550 km<sup>2</sup>. Mexico has great

climatic diversity. The nation may be roughly divided into tropical and temperate areas, separated by the Tropic of Cancer. However, the uneven topography and the presence of two oceans (Atlantic and Pacific) greatly influence the climatic configuration of the country. Thus, it is possible to find high, cold mountains within a few kilometers of the warmest climates in the coastal plains. Mexico is considered to be a transitional area between the Nearctic and Neotropical regions (Williams-Linera et al. 1992). This fact, together with its high environmental diversity, makes the Mexican flora and fauna exceptionally rich and diverse in origins (Halffter 1987).

**Biological data:** We developed a database compiling information available in the literature and in several unpublished studies (bachelor's, master's, and doctoral theses). The studies of Howden (1955, 1964, 1974, 2003, 2005), Halffter and Martínez (1962), and Gómez and López-Rojas (2004) were especially important. Information from the Instituto de Ecología A.C. (Xalapa, Veracruz, México) and from private entomological collections (G. and V. Halffter, E. Montes de Oca, F. Vaz de Mello, M.A. Morón H.F. and A. Howden, I. Martínez, L. Arellano) was also included.

The database, named GEOMEX (Trotta-Moreu et al. 2008), currently contains 1,191 records, corresponding to the 45 Mexican Geotrupinae species (classification *sensu* Howden, 2003; see Table 1). Although the higher-level taxonomy and internal phylogenetic relationships of this group are not yet well established (see Howden 1982, Zunino 1984, Browne and Scholtz 1995 and 1999), the whole species catalogue can be considered reliable.

GEOMEX incorporates information in 24 data fields, which include information about the taxonomy, geographic location, date, ecological/biological characteristics, and origin of all database records. After georeferencing the localities at which each species was recorded (see <a href="http://geonames.usgs.gov/gnishome.html">http://geonames.usgs.gov/gnishome.html</a>) at a 0.08° resolution (making 25,080 grid cells across Mexico), we built distribution maps for each Geotrupinae species (see Trotta-Moreu et al. 2008) using the Idrisi Kilimanjaro program (Clark Labs 2003).
| State                 | Nº DR | Area    | N°OC | Data origin | Year range |
|-----------------------|-------|---------|------|-------------|------------|
| Veracruz              | 241   | 71,699  | 79   | B, C        | 1955-2006  |
| México                | 126   | 21,355  | 51   | B, C        | 1931-2006  |
| Durango               | 122   | 123,451 | 44   | B, C        | 1905-2006  |
| Oaxaca                | 92    | 93,952  | 44   | B, C        | 1937-2006  |
| Jalisco               | 80    | 78,599  | 43   | B, C        | 1903-2003  |
| Michoacán de Ocampo   | 67    | 59,928  | 31   | B ,C        | 1947-2005  |
| Chiapas               | 61    | 73,289  | 31   | B, C        | 1939-2003  |
| Morelos               | 51    | 4,950   | 19   | B, C        | 1947-1988  |
| Sonora                | 41    | 185,052 | 14   | B, C        | 1939-1998  |
| Guerrero              | 37    | 63,621  | 15   | B, C        | 1937-1994  |
| Sinaloa               | 37    | 58,328  | 13   | B, C        | 1917-1997  |
| Nayarit               | 33    | 27,815  | 17   | B, C        | 1937-1997  |
| Puebla                | 33    | 33,902  | 18   | B, C        | 1901-2006  |
| Distrito Federal      | 30    | 1,479   | 13   | B, C        | 1939-2003  |
| Nuevo León            | 27    | 64,924  | 8    | B, C        | 1942-2006  |
| Baja California Sur   | 21    | 73,922  | 19   | B, C        | 1938-1997  |
| Hidalgo               | 19    | 20,813  | 13   | B, C        | 1960-2002  |
| Chihuahua             | 18    | 247 938 | 16   | B, C        | 1934-2005  |
| Coahuila              | 10    | 150,615 | 3    | В           | 1938-1971  |
| Colima                | 9     | 5 ,191  | 4    | В           | 1918-1993  |
| San Luis Potosí       | 9     | 63, 068 | 4    | B,C         | 1954-1983  |
| Baja California Norte | 7     | 69,921  | 2    | B, C        | 1938-1973  |
| Guanajuato            | 6     | 30, 491 | 4    | B, C        | 1954-1962  |
| Tamaulipas            | 4     | 79,384  | 3    | В           | 1969-1983  |
| Yucatán               | 3     | 38, 402 | 2    | B, C        | 1937-1995  |
| Zacatecas             | 3     | 73, 252 | 2    | B, C        | 1983-1989  |
| Campeche              | 2     | 57, 924 | 2    | В           | 1983       |
| Querétaro             | 1     | 11,499  | 1    | В           | 1957       |
| Tabasco               | 1     | 25,267  | 1    | В           | 1969       |
| Aguascalientes        | 0     | 5, 471  | 0    | -           | -          |
| Quintana Roo          | 0     | 50,844  | 0    | -           | -          |
| Tlaxcala              | 0     | 4,016   | 0    | -           | -          |

**Table 1.** Number of database records (N° DR), area (in km<sup>2</sup>), and number of 0.08° grid cells in which each species was observed (N° OC) for each Mexican state. Data origin indicates whether the data came from the literature (B) or from natural history collections (C). The year ranges of the database records are also shown.

**Environmental variables**: Nineteen climatic variables from the WorldClim database were used as predictors in the modeling process (Hijmans et al. 2006): mean annual temperature, mean daily temperature range, isothermality, temperature seasonality,

maximum temperature of the warmest month, minimum temperature of the coldest month, annual temperature range, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter.

Model building: A maximum entropy approach (MaxEnt) was used to estimate the potential distribution of each species in Mexico (see Phillips et al. 2004 and Phillips et al. 2006). This machine-learning approach is considered to be one of the best techniques requiring presence-only data (Elith et al. 2006). MaxEnt tries to find the closest distribution that agrees (under maximum entropy) with the available biological information and the selected environmental variables. Recommended default parameter values were used in all model runs (Phillips et al. 2006), but only linear and quadratic terms were included to obtain flexible curvilinear responses to the response variable. The MaxEnt output for each grid cell is the sum of the probability value of that cell and of all other cells with equal or lower probability. These values are multiplied by a factor of 100, producing a continuous variable that varies from 0 to 100 and that measures the relative suitability for each species. All models were run using Maximum Entropy Species Distribution Modeling v. 2.3 software (for free download, see http://www.cs.princeton.edu/~schapire/maxent/). For the six species with only one known locality (Geotrupes (Onthotrupes) lobatus, Bolbocerosoma mexicanus, Bolborhombus nitidus, Bolbelasmus horni, Bolbelasmus bajaensis, and *Eucanthus impressus*), the potential distribution was estimated by a 30% enlargement of the environmental values of the cell in which each species was observed. This procedure allowed us to slightly enlarge the known distribution of these rare species, encompassing other localities that are environmentally similar to those in which the species occur.

*Geotrupes (Haplogeotrupes) reddelli* (Howden), a narrowly distributed cave species that specializes in the consumption of bat dung, was not considered (Halffter and Deloya 2007).

**Statistical analysis:** Overlaying the individual suitability values to obtain a species richness map inevitably requires transforming the continuous predicted values into presence-absence data. Therefore, we selected twenty-one decision thresholds, evenly spaced across the range from 0-100. These thresholds were used to derive presence-absence maps for each species, recognizing as a "presence" each cell with a suitability score equal to or greater than 1, 5, ..., 95, or 100. The accuracy of the model predictions generated using each of these thresholds was determined by comparing the observed species richness in previously defined well-surveyed states against the total number of species predicted for those states when individual models were overlapped.

The number of database records was used as a surrogate for the sampling effort carried out in each Mexican state (see Hortal et al. 2007), and the Chao2 nonparametric species richness estimator was calculated (see Colwell 2005) for each Mexican state. Chao2 is an efficient (Walther and Moore 2005) nonparametric estimator based on incidence. In our case, it takes into consideration only the number of species with a unique database record  $(U_{DR})$  and the number of species with two database records  $(T_{DR})$ , applying the following formula:  $S_{CHAO2} = S_{obs} + (U_{DR}^2/2T_{DR})$ , where  $S_{CHAO2}$  is the estimated richness and  $S_{obs}$  is the observed number of species in each state (see Colwell and Coddington 1995).

The species richness values predicted by Chao2 for each state were used to estimate the survey completeness of each state ( $S_{obs}/S_{CHAO2} \ge 100$ ). Those states with completeness values higher than 75% (n = 17; see Table 2) were considered to be well surveyed, and they were selected to compare their observed species richness against the species richness values derived from the overlaying of individual distribution models ( $S_{PDM}$ ). The Pearson Product Moment Correlation coefficient was used in these comparisons. To obtain the predicted species richness for each state, a species was considered to occur in a state if it was present in at least one cell within that state. Since states with similar observed and predicted species richness can differ in their species composition, Mantel tests were also applied (Sokal 1979). These tests measure the correlation (*R*) between two distance or similarity matrices. Significance testing is based on the Monte Carlo permutational method to overcome the problem of lack of independence between site pairs. First, the Jaccard index was calculated among the observed assemblages in each state and the twenty-one predicted assemblages obtained under the various thresholds. PAST v. 1.68 software was used for these computations (Hammer et al. 2001). The threshold that generated the highest correlations in both species richness and composition values was selected as the best representation of Geotrupinae species richness distribution in Mexico. In order to provide an error measure for the map thus generated, we examined the errors in both species richness (differences between predicted and observed species richness values) and species composition (differences in composition between predicted and observed state inventories) for each well-surveyed state. False positives (commission errors) and false negatives (omission errors) were estimated for each state in order to assess the real magnitude of prediction errors according to the observed number of species.

#### RESULTS

**Comparison between observed and predicted values:** The correlations between  $S_{OBS}$  and  $S_{PDM}$  species richness values for the 17 well-surveyed states are statistically significant for all of the thresholds used to convert the continuous suitability values for each species into presence-absence data (Fig. 1). The mean correlation is 0.60 (95% confidence interval between 0.55 and 0.64), with higher correlation values when the selected threshold is above 65 (i.e., when the threshold is more restrictive). On the other hand, the results of the Mantel tests show that all correlation values are statistically significant above a threshold of 40 (mean = 0.39; 95% confidence interval between 0.29 and 0.50). The optimum compositional correlation value was found at a threshold of 75 (R = 0.70; p < 0.0001). Because Pearson correlation values for species richness are also high at this threshold (r = 0.68; p<0.001), it was chosen as the most appropriate to represent the variation in Geotrupinae species richness in Mexico.



Fig. 1. Pearson correlation coefficients (triangles) and Mantel correlations (R) measuring the compositional similarity (circles) between the observed Geotrupinae species richness and composition values in the 17 well-surveyed Mexican states and those predicted by the overlaying of individual model predictions at different suitability thresholds. The dashed lines represent the limits of statistically significant ( $p \le 0.05$ ) values for both tests.

**Examination of model errors:** Once this optimum threshold was selected, the errors produced by this model prediction (Table 2) were analyzed.

The mean species richness error is 61% of the observed species richness in each state (95% confidence interval between 29% and 94%). Except in Durango and Sinaloa, the inventory of each state is frequently overestimated. Commission errors are significantly higher than omission errors (71%  $\pm$  29% vs. 18%  $\pm$  10%; 95% confidence intervals). The states with the greatest percentage of errors are Baja California Sur, México and Puebla, with overestimations of 233%, 160%, and 140% of the observed species, respectively.

Considering each species separately (Table 3), omission errors vary from 0% to 38% of cells in which the species were observed (mean = 5.8%).

| States              | Area    | SOBS | SERROR | %COM  | %OMI |
|---------------------|---------|------|--------|-------|------|
| Baja California Sur | 73,922  | 3    | 7      | 233.3 | 0.0  |
| Chiapas             | 73,289  | 7    | 4      | 57.1  | 0.0  |
| Coahuila            | 150,615 | 5    | 1      | 80.0  | 60.0 |
| Durango             | 123,451 | 10   | -2     | 10.0  | 30.0 |
| Guerrero            | 63,621  | 11   | 8      | 81.8  | 9.1  |
| Jalisco             | 78,599  | 11   | 0      | 27.3  | 27.3 |
| México              | 21,355  | 5    | 8      | 140.0 | 0.0  |
| México D.F.         | 1,479   | 4    | 3      | 75.0  | 0.0  |
| Michoacan           | 59,928  | 10   | 4      | 60.0  | 20.0 |
| Morelos             | 4,950   | 10   | 3      | 20.0  | 10.0 |
| Nayarit             | 27,815  | 5    | 4      | 100.0 | 20.0 |
| Nuevo León          | 64,924  | 9    | 0      | 22.2  | 22.2 |
| Oaxaca              | 93,952  | 15   | 8      | 66.7  | 6.7  |
| Puebla              | 33,902  | 10   | 14     | 140.0 | 0.0  |
| Sinaloa             | 58,328  | 8    | -3     | 25.0  | 62.5 |
| Sonora              | 185,052 | 7    | 1      | 42.9  | 28.6 |
| Veracruz            | 71,699  | 14   | 2      | 21.4  | 7.1  |

**Table 2.** Area (in km<sup>2</sup>), number of Geotrupinae species observed ( $S_{OBS}$ ), species richness errors ( $S_{ERROR}$ ), and percentage of commission and omission errors over the observed number of species ( $\%_{COM}$  and  $\%_{OMI}$ , respectively) in the 17 well-surveyed states (see methods). Errors were estimated by comparing the observed species in each state against the predicted ones generated by the application of individual distribution models in which a threshold suitability value of 75 was used to transform continuous suitability values into binary (presence/absence) predictions.

The lack of reliable absence information prevents us from calculating the rate of commission errors for individual species. However, for the well-surveyed states, we calculated the number of predicted presence cells in those states in which the species has not been recorded. The percentage of such cells against the total number of predicted presence cells was used as a measure of commission errors. This percentage varies from 0% to 80% depending on the species (mean = 12%; Table 3).

| Species                           | Nº DR | N°OC | Area   | OE      | СЕ         |
|-----------------------------------|-------|------|--------|---------|------------|
| Geotrupes (Megatrupes) cavicollis | 90    | 31   | 17101  | 0 (0%)  | 0 (0%)     |
| G. (Megatrupes) fisheri           | 24    | 14   | 7275   | 0 (0%)  | 4 (6%)     |
| G. (Onthotrupes) lobatus          | 1     | 1    | 247    | -       | -          |
| G. (Onthotrupes) sobrinus         | 9     | 4    | 5526   | 1 (25%) | 38 (69%)   |
| G. (Onthotrupes) herbeus          | 40    | 16   | 4684   | 3 (19%) | 0 (0%)     |
| G. (Onthotrupes) viridiobscurus   | 22    | 7    | 3352   | 0 (0%)  | 2 (6%)     |
| G. (Onthotrupes) truncaticornis   | 8     | 2    | 1388   | 0 (0%)  | 2 (14%)    |
| G. (Onthotrupes) sallei           | 25    | 15   | 15116  | 1 (7%)  | 18 (12%)   |
| G. (Onthotrupes) nebularum        | 32    | 18   | 4847   | 2 (11%) | 0 (0%)     |
| G. (Onthotrupes) guerreroensis    | 12    | 4    | 3843   | 0 (0%)  | 4 (10%)    |
| G. (Onthotrupes) pecki            | 5     | 4    | 5254   | 0 (0%)  | 21 (40%)   |
| G. (Onthotrupes) onitidipes       | 6     | 2    | 1900   | 0 (0%)  | 0 (0%)     |
| G. (Geohowdenius) cnephosus       | 8     | 7    | 10115  | 0 (0%)  | 0 (0%)     |
| G. (Halffterius) rufoclavatus     | 162   | 25   | 4778   | 2 (8%)  | 2 (4%)     |
| G. (Haplogeotrupes) guatemalensis | 18    | 3    | 903    | 0 (0%)  | 0 (0%)     |
| Ceratotrupes fronticornis         | 182   | 77   | 18695  | 8 (10%) | 12 (6%)    |
| Ceratotrupes sturmi               | 11    | 5    | 12278  | 0 (0%)  | 13 (11%)   |
| Ceratotrupes bolivari             | 123   | 63   | 34050  | 7 (11%) | 9 (3%)     |
| Bolbocerosoma ritcheri            | 5     | 3    | 3161   | 0 (0%)  | 0 (0%)     |
| Bolbocerosoma pusillum            | 5     | 3    | 55916  | 0 (0%)  | 46 (8%)    |
| Bolbocerosoma confusum            | 2     | 2    | 5094   | 0 (0%)  | 0 (0%)     |
| Bolbocerosoma mexicanus           | 1     | 1    | 2871   | -       | -          |
| Bolborhombus sallei               | 52    | 30   | 90678  | 1 (3%)  | 14 (2%)    |
| Bolborhombus magnus               | 4     | 3    | 300228 | 0 (0%)  | 2406 (80%) |
| Bolborhombus parvulus             | 10    | 9    | 12292  | 1 (11%) | 9 (7%)     |
| Bolborhombus nitidus              | 3     | 1    | 405    | -       | -          |
| Bolbocerastes regalis             | 3     | 3    | 5579   | 0 (0%)  | 0 (0%)     |
| Bolbocerastes serratus            | 15    | 8    | 93137  | 3 (38%) | 0 (0%)     |
| Bolbocerastes imperialis          | 5     | 4    | 181998 | 1 (25%) | 444 (24%)  |
| Bolbocerastes peninsularis        | 14    | 10   | 11905  | 0 (0%)  | 3 (3%)     |
| Bolbelasmus arcuantus             | 45    | 28   | 31473  | 2 (7%)  | 7 (2%)     |
| Bolbelasmus horni                 | 1     | 1    | 885    | -       | -          |
| Bolbelasmus rotundipennis         | 7     | 6    | 229363 | 1 (17%) | 1489 (65%) |
| Bolbelasmus variabilis            | 86    | 55   | 37462  | 3 (5%)  | 4 (1%)     |
| Bolbelasmus bajaensis             | 2     | 1    | 1133   | -       | -          |
| Eucanthus mexicanus               | 17    | 13   | 61671  | 0 (0%)  | 106 (17%)  |
| Eucanthus impressus               | 1     | 1    | 6007   | -       | -          |
| Neoathyreus excavatus             | 17    | 15   | 68316  | 0 (0%)  | 219 (32%)  |
| Neoathyreus fissicornis           | 44    | 20   | 11907  | 3 (15%) | 0 (0%)     |
| Neoathyreus granulicollis         | 32    | 20   | 38477  | 2 (10%) | 50 (13%)   |
| Neoathyreus hamifer               | 5     | 2    | 815    | 0 (0%)  | 0 (0%)     |
| Neoathyreus interruptus           | 18    | 14   | 47164  | 0 (0%)  | 7 (2%)     |
| Neoathyreus mexicanus             | 13    | 11   | 79477  | 0 (0%)  | 5 (1%)     |
| Neoathyreus mixtus                | 6     | 5    | 164100 | 0 (0%)  | 149 (9%)   |

**Table 3.** List of Mexican Geotrupinae species, showing the number of database records for each species (N° DR), the number of 0.08° grid cells in which each species was observed (N° OC), the area of the predicted distribution (in km<sup>2</sup>), and the number of cells in which the species was erroneously predicted to be absent (omission errors; OE) or present (commission errors; CE). The percentage of omission errors (in brackets) was calculated based on the total number of cells in which the species was observed, while the percentage of commission errors was estimated based on the number of erroneously included cells within the 17 well-surveyed states.

# DISCUSSION

In this study, the individual model predictions for each species of an insect group in a large and heterogeneous region (Mexico) were overlaid to generate a geographical representation of the distribution of species richness. This method is able to exploit the scarce and biased information available for most insect groups. The main advantage of the procedure is the ability to provide an error measure based on information from a priori wellsurveyed territories. Of course, as frequently happens with insects, the available geographical data are fragmentary and probably biased (Soberón and Peterson 2004); however, this situation will not change in the near future unless a huge sampling effort is carried out. Geographical representations of species richness obtained using this procedure should be considered provisional, since they depend upon the quality of the observation dataset used to evaluate the model predictions. However, in contrast to other species richness representations generated by overlaying species distribution models (Cumming 2000, Ortega-Huerta and Peterson 2004, Domínguez-Domínguez et al. 2006, García 2006), our method provides an error measure that will decrease in future iterations as more data become available that are better distributed across the spectrum of environmental and spatial conditions present in Mexico.

Despite selecting the most appropriate threshold to convert continuous suitability values into binary presence-absence predictions, our method overestimates observed species richness values in a high percentage of well-surveyed states (61%). This overestimation is generally due to the erroneous inclusion of species that are not currently known to inhabit the state in question. The averaged errors of individual species predictions are lower, but this should be interpreted with caution because it is almost impossible to evaluate a species model without reliable information on the locations in which the species is absent.

In spite of these drawbacks, our method should be considered as the first attempt to provide a species richness distribution map for an insect group over a large territory with many taxonomic and distributional deficiencies. According to the species richness map that we obtained (Fig. 2), almost 53% of the territory of Mexico is inhabited by at least one Geotrupinae species, 44% is inhabited by one or two species, and only 0.4% (around 8,200 km<sup>2</sup>) is predicted to have five or more Geotrupinae species within a 0.08° cell. These species-rich areas are located in the mountain zones of the states of Guerrero, Oaxaca and Veracruz.



Fig. 2. Estimated distribution of Geotrupinae species richness in Mexico at a 0.08° resolution, produced by overlaying all individual species models generated by MaxEnt. The representation shown used a suitability value of 75 as the threshold to convert continuous suitability values into binary ones (presence/ absence). This threshold produced higher correlations of species richness and composition with the data from previously identified well-surveyed states. White areas represent absence of Geotrupinae species.

From a methodological point of view, our study highlights four important conclusions. First, this type of modeling approach generally overestimates species' distributions. Second, the overlaying of individual models does not produce an accurate picture of the distribution of species richness. Third, the selection of an appropriate suitability threshold can reduce the occurrence of species richness and compositional errors. Finally, the combined use of non-parametric estimators and individual models permits estimation of the accuracy of such predictions.

Predictive models of distribution tend to overestimate species' distributions, mainly due to their inability to incorporate absences due to historical factors, dispersal limitation, or other biotic factors (Pulliam 1988, Ricklefs and Schluter 1993, Hanski 1998, Pulliam 2000). Several authors have recognized that overprediction of species' distributions is a common shortcoming of this kind of model, particularly when limited distribution localities are used (Fielding and Haworth 1995; Araújo and Williams 2000, Stockwell and Peterson 2002, Brotons et al. 2004, Segurado and Araújo 2004, Stockman et al. 2006).

The overlaying of many individual predictions to build a representation of species richness across a territory may produce an even more unreliable representation of reality by increasing the error level in regions affected by non-environmental restrictions (Hortal and Lobo 2006). To partially correct these overestimations, a suitability threshold can be selected that provides higher correlations between predicted and observed species richness and compositional values for territories previously recognized as well surveyed. In this study, the most appropriate threshold is high (around 75), due to the high level of overprediction in each species model. The results of similar modeling studies (Pineda and Lobo, 2009) suggest different suitability threshold values depending on the taxonomic group and, probably, on the extent and characteristics of the target region.

Our method combines the use of inventory completeness measures as non-parametric estimators and distribution modeling techniques. The main advantage of this procedure is that it can provide a measure of uncertainty that can be used to show the spatial distribution of the model errors. Any model prediction must incorporate a reasonable measure of its accuracy (Fielding and Bell 1997); this is a scientific requirement to sequentially improve our knowledge of the dynamic distribution patterns of organisms.

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### LITERATURE CITED

- Araújo, M. B., & P. H. Williams. 2000. Selecting areas for species persistence using occurrence data. *Biol. Conserv.* 96:331–345.
- Brotons, L., W. Thuiller, M. B. Araújo, & A. H. Hirzel. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* 27:437-448.
- Browne, D. J., & C. H. Scholtz. 1995. Phylogeny of the families of the Scarabaeoidea (Coleoptera) based on characters of the hindwing articulation, hindwing base and wing venation. Syst. Entomol. 20:145-173.
- Browne, D. J., & C. H. Scholtz. 1999. A phylogeny of the families of Scarabaeoidea (Coleoptera). Syst. Entomol. 24:51-84.
- Chefaoui, R., & J. M. Lobo. 2008. Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecol. Modell*. 210:478-486.
- Clark Labs. 2003. Idrisi Kilimanjaro. GIS software package. Clark Labs, Worcester, MA, USA.
- **Colwell, R. K. 2005.** EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5, http://purl.oclc.org/estimates.
- Colwell, R. K., & J. A.Coddington. 1995. Estimating terrestrial biodiversity through extrapolation. Biodiversity Measurement and Estimation (ed D.L. Hawksworth), pp. 101–118. Chapman & Hall, New York.
- Cumming, G. S. 2000. Using habitat models to map diversity: pan-African species richness of ticks (Acari: Ixodida). J. Biogeogr. 27:425–440.
- Domínguez-Domínguez, O., E. Martínez-Meyer, L. Zambrano, & Pérez-Ponce de León,
   G. 2006. Using ecological-niche modeling as a conservation tool for freshwater species: live-bearing fishes in central Mexico. *Conserv. Biol.* 30:1730–1739.
- Elith J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans,
  F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A.
  Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A.
  T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire,

J. Soberón, S. Williams, M. S. Wisz, N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129-151.

- Ferrier, S. 2002. Mapping spatial pattern biodiversity for regional conservation planning: where to from here? *Syst. Biol.* 51:331-363.
- Ferrier, S., M. Drielsma, G. Manion, & G. Watson. 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. Community-level modelling. *Biodiv. Conserv.* 11:2309-2338.
- Fielding, A. H., & J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24:38-49.
- Fielding, A. H., & P. F. Haworth. 1995. Testing the Generality of Bird-Habitat Models. *Conserv. Biol.* 9:1466-1481.
- García, A. 2006. Using ecological niche modelling to identify diversity hotspots for the herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. *Biol. Conserv.* 130:25–46.
- Gaston, K. J. 1996. Species richness: measure and measurement.. En Gaston, K.J. (ed.), págs. 77-113. Biodiversity. A biology of numbers and difference. *Blackwell Science Ltd.*, Oxford.
- Gómez, B., & López-Rojas. 2004. Primer registro de *Geotrupes (Onthotrupes) onitidipes*Bates, 1887 para México (Coleoptera: Scarabaeidae: Geotrupidae). *Entomotropica*.
  Boletín de Entomol. Venezolana 19:47-48.
- Guisan, A., & N. E.Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135:147-186.
- Halffter, G., & A. Martínez. 1962. Monografía del Género Ceratotrupes Jekel (Coleopt. Scarab. Geotrup.). *Ciencia* 11(4):145-159.
- Halffter, G., & C. Deloya. 2007. Primer caso de nidificación de un geotrupino (Scarabaeoidea: Geotrupinae) en cuevas: un fenómeno excepcional. *Acta Zool. Mex.* 23:139-142.
- Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. *Ann. Revi. Entomol.* 32:95-114.

Hammer, O., D. A. Harper, & P. D. Ryan. 2001. PAST: Palaeontological Statistics software package for education and data analysis. *Palaeont. Electro.* 4 (1):9 pp.

Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41–49.

- Hijmans, R. J., S. Cameron, J. Parra, P. Jones, A. Jarvis, & K. Richardson. 2006. WorldClim version 1.4. Museum of Vertebrate Zoology of the University of California, CIAT, and Rainforest CRC. <u>http://www.worldclim.org/</u>.
- Hortal, J., & J. M. Lobo. 2006. Towards a synecological framework for systematic conservation planning. *Biodiv. Informa*. 3:16-45.
- Hortal, J., J. M. Lobo, & A. Jiménez-Valverde. 2007. Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife (Canary Islands). *Conserv. Biol.* 21:853-863.
- Howden, H. F. 1955. Biology and taxonomy of North American beetles of the Subfamily Geotrupinae with revisions of the Genera *Bolbocerosoma, Eucanyhus, Geotrupes* and *Peltotrupes* (Scarabaeidae). *Proc. of the U.S. Nation. Museum* 104:151-319.
- Howden, H. F. 1964. The Geotrupinae of North and Central America. Memoirs of the Entomol. *Soc. of Canada* 39:1-91.
- Howden, H. F. 1974. Additional records and descriptions of North and Central American Geotrupinae (Coleoptera, Scarabaeidae). *Can. Jour. of Zool.* 52:567-573
- Howden, H. F. 1982. Larval and adult characters of *Frickius* Germain, its relationship to the *Geotrupini*, and a phylogeny of some mayor taxa in the Scarabaeoidea (Insecta:Coleoptera). *Can. Jour. of Zool.* 60:2713-2724.
- Howden, H. F. 2003. Geotrupinae [95-106]. In: Morón M. A. (Editor), Atlas de los escarabajos de México (Coleoptera: Lamellicornia: Scarabaeidae, Trogidae, Passalidae y Lucanidae) Vol. II (4). 227 pp.
- Howden, H. F. 2005. Notes on Bolboceratini from Northeastern México with description of a new *Bolbocerosoma* Schaeffer (Coleoptera: Scarabaeidae: Geotrupinae). *Folia Entomol. Mex.* 44 (2):213-218.
- Jiménez-Valverde, A., J. M. Lobo, & J. Hortal. 2008. Not as good as they seem: the importance of concepts in species distribution modeling. *Diversity and Distributions*

14:885-890.

- Jiménez-Valverde, A., & J. Hortal. 2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Revi. Ibe. Aracnol.* 8: 151-161.
- Lobo, J.M. 2008. More complex distribution models or more representative data? *Biodiv. Informa.* 5: 14-19.
- Lobo, J. M., A. Jiménez-Valverde, & R. Real. 2008. AUC: A misleading measure of the performance of predictive distribution models. *Global Ecol. Biogeogr.* 17:145-151.
- **Ortega-Huerta, M. A., & A. T. Peterson. 2004.** Modelling spatial patterns of biodiversity for conservation priorization in north-eastern Mexico. *Div. Distrib.* 10:39–54.
- Peterson, A. T. 2007. Uses and requirements of ecological niche models and related distributional models. *Biodiv. Informa*. 3:59-72.
- Phillips, S. J., R. P. Anderson, & R. E. Schapire. 2006. Maximum entropy modelling of species geographic distributions. *Ecol. Modell*. 190:231-259.
- Phillips, S. J., M. Dudík, & R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. In: Proceedings of the 21<sup>st</sup> International Conference on Machine Learning, ACM Press, New York, pp. 665-662.
- Pineda, E. & J. M. Lobo. 2009. Assessing the accuracy of species distribution models to predict amphibian species richness patterns. J. Anim. Ecol. 78:182-190.
- Pulliam, H. R. 1988. Sources, sinks and population regulation. Am. Naturalist 132:652-661.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecol.Lett.*, 3:349–361.
- Ricklefs, R. E., & D. Schluter. 1993. Species Diversity in Ecological Communities. *Historical and Geographical Perspectives*. University Chicago Press, Chicago
- Ricklefs, R. E. 2004 A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* 7:1–15.
- Segurado, P., & M. B. Araújo. 2004. An evaluation of methods for modelling species distributions. *J. Biogeogr.* 31:1555-1569.

- Soberón, J., & A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiv. Informa*. 2:1-10.
- **Soberón, J., & A.T. Peterson. 2004.** Biodiversity informatics: managing and applying primary biodiversity data. *Philosophical Transactions of the Royal Society of London series B.* 359:689–698.
- Sokal, R. R. 1979. Testing statistical significance of geographic variation patterns. *Syst. Zool.* 28:627-632.
- Stockman, A. K., D. A. Beamer, & J. E. Bond. 2006. An evaluation of a GARP model as an approach to predicting the spatial distribution of non-vagile invertebrate species. *Div. Distrib.* 12:81–89.
- Stockwell, D. R. B., & A. T. Peterson. 2002. Effects of sample size on accuracy of species distribution models. *Ecol. Modell.* 148:1–13.
- Trotta-Moreu, N., J. M. Lobo, & F. J. Cabrero-Sañudo. 2008. Distribución conocida y potencial de Geotrupinae (Coleoptera: Scarabaeoidea) en México. Acta Zool. Mex. 24: 39-65.
- Tsoar, A., O. Allouche, O. Steinitz, D. Rotem, & R. Kadmon. 2007. A comparative evaluation of presence-only methods for modelling species distribution. *Div. Distrib.* 13:397-405.
- Walther, B. A., & J. Moore, J. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* 28:815-829.
- Whittaker, R. J., M. B. Araúujo, P. Jepson, R. J. Ladle, J. E. M. Watson, & K. J. Willis.
  2005. Conservation biogeography: assessment and prospect. *Div. Distrib.* 11:3–23.
- Williams-Linera, G., G. Halffter, & E. Ezcurra. 1992. El estado de la biodiversidad en México. In: G. Halffter (comp.) La diversidad biológica de Iberoamérica. *Coedición Instituto de Ecología, SEDESOL, and CYTED-D*. Xalapa, Veracruz. pp. 285–312.
- Zunino, M. 1984. Sistematica genérica dei Geotrupinae (Coleoptera, Scarabaeoidea: Geotrupinae) filogenesi della sottofamiglia e consideración biogeografiche. Boll. Mus. Reg. Scien. Natur. di Torino. 2:9-162.





# Ecological and reproductive characteristics of Geotrupes (Halffterius) rufoclavatus Jekel, 1865 (Coleoptera: Scarabaeoidea: Geotrupinae) on the Cofre de Perote Volcano (Veracruz, Mexico)

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# ECOLOGICAL AND REPRODUCTIVE CHARACTERISTICS OF *GEOTRUPES (HALFFTERIUS) RUFOCLAVATUS* JEKEL, 1865 (COLEOPTERA: GEOTRUPIDAE: GEOTRUPINAE) ON THE COFRE DE PEROTE VOLCANO (VERACRUZ, MEXICO)

# Ecología y características reproductivas de *Geotrupes (Halffterius) rufoclavatus* Jekel, 1865 (Coleoptera: Geotrupidae: Geotrupinae) en el Volcán del Cofre de Perote (Veracruz, Mexico)

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#### ABSTRACT

We investigated the dung beetle *Geotrupes (Halffterius) rufoclavatus* Jekel on the eastern slope of the Cofre de Perote Volcano, Veracruz, Mexico, with monthly trapping samples taken during the years 1999 to 2001. Monthly beetle abundances were related to habitat and collection period. The distributions of geotrupinae species on the Cofre de Perote are mapped, providing new data on geographical distribution in the State of Veracruz. The highest quantities of *G. rufoclavatus* were collected in the forest habitat. Above 3000 m, more adults were collected in pastures and cultivated fields, showing a single activity peak per year, whereas at lower altitudes, there were lower numbers in those habitats, but several activity peaks per year. In Tonalaco, Veracruz, monthly samples were taken during 2005-2006 to assess the reproductive state of the population. Male and female reproductive systems are similar to those of other geotrupine species. All adults collected were in a maturing state; one female collected in February was ready to oviposit.

Key words: Dung beetle, Geotrupinae, Cofre de Perote, habitat, fenology, reproductive system.

#### RESUMEN

Se estudió el escarabajo estercolero *Geotrupes (Halffterius) rufoclavatus* Jekel en la vertiente oriental del Cofre de Perote, Veracruz, México haciendo un muestreo altitudinal mensual durante los años 1999-2001. Se relacionaron estadísticamente las abundancias mensuales de los individuos con la altitud, hábitat y periodo de colecta. Así mismo se elaboró un mapa con la distribución de las distintas especies de Geotrúpidos que habitan en el Cofre de Perote y se aportaron nuevos datos de distribución geográfica para el estado de Veracruz.

La mayor cantidad de *G. rufoclavatus* fue capturada en el bosque de pinos. Por encima de los 3000 m de altitud, el número de individuos es mayor en campos de cultivo y potreros, y se presenta un solo pico de abundancia alta al año. Por debajo de los 3000 m. de altitud, la mayor cantidad de individuos está en bosque

de pinos y se presentan varios picos de abundancia altas al año. En la localidad de Tonalaco, Veracruz se obtuvieron mensualmente individuos durante los años 2005-2006, para valorar el estado reproductivo de la población.

El sistema reproductor de machos y hembras es similar al de otras especies de geotrúpidos. Todas las hembras y los machos se encontraban madurando, menos una hembra en febrero que se encontró madura. **Palabras clave:** Escarabajos estercoleros, Geotrupinae, Cofre de Perote, hábitat, fenología, sistema reproductor.

# **INTRODUCCION**

Studies of Scarabaeoidea in Mexico increased greatly beginning in the 1970s, as reflected by the number of scientific reports and the number of researchers who have developed multiple lines of investigation of these organisms (Onore *et al.* 2003). Nevertheless, there have been few studies of members of the Mexican Geotrupinae. Perhaps one reason is that, compared to other Scarabaeoidea, the geotrupines are more difficult to collect and rear in the laboratory, given that most of their life cycle takes place considerably deep under the surface of the soil (Howden 1955).

Most of the work on *Geotrupes rufoclavatus* Jekel has been taxonomic. After Jekel described the species in 1865, Howden redescribed it in 1964, specifying some localities and placing it in the subgenus *Cnemotrupes*, which had been previously established by Jekel. In 1984, Zunino considered the male and female genitalia and suggested that it be included in a new genus, *Halffterius*, created exclusively for this species. Finally, in 2003, Howden returned to consider the Mexican Geotrupinae and relegated *Halffterius* to a subgenus. López-Guerrero (1987) carried out the only morphological study of this species, looking at the histology of the testes and neurosecretory cells.

*Geotrupes rufoclavatus* lives in meadows or clearings in pine-oak-fir forests at altitudes greater than 2500 m in the mountains surrounding Mexico City and the states of Morelos, Puebla, and Michoacán (Howden 2003). The lack of records and information on this

species and other geotrupines can lead to errors of identification, because the only existing key (Howden 1980) in many cases fails to separate this species by morphology, and often individuals must be distinguished by geographic distribution, of which there are few studies.

The objective of the present work is to provide additional information on the distribution, ecology and reproductive morphology and state of *G. rufoclavatus* on the Cofre de Perote Volcano in Veracruz, México.

#### MATERIAL AND METHODS

**Distribution.** A distribution map was developed for *G. rufoclavatus* on the Cofre de Perote volcano based on captures by one of the authors (EMO), and including other localities and other species of Geotrupinae according to bibliographic sources that refer to areas near the study site (Arellano 1992; 2002; Arellano and Halffter 2003).

**Beetle sampling.** To determine habitat preference and altitudinal and temporal distribution of *G. rufoclavatus*, a commonly used pitfall-trapping technique for dung beetles was used (see Lobo *et al.* 1988; Veiga *et al.* 1989 and references therein). Traps consisting of plastic containers (0.5 L) with a mouth (10 cm) covered by wire screen mesh (8 mm) were buried in the ground at rim level. Commercial propylene glycol was added to up to one-fifth of the container as a preservative. Traps were baited with fresh, homogenized cow dung placed over the wire mesh as a small, artificially-deposited dung pat. A roof made of plywood (15 x 15 cm) sustained by two nails 12 cm in length was placed over each trap to reduce disturbance and flooding by rain. Beetles were collected from traps and fresh dung was provided after each of 16 sampling periods that varied from 28 to 62 days from September 1999 to February 2001.

Traps were located in three adjacent and contrasting habitats: 1) pine-oak forest or forest remnants; 2) open area used as pasture for cattle and sheep grazing; 3) within one

of either of two available crops, corn at 2260-2600 m and potato at 3070-3200 m. These habitats represent the typical land-use mosaic in the municipalities of Xico and Ixhuacán de Los Reyes, Veracruz, on the southeastern slope of the Cofre de Perote Volcano. Sampling followed an altitudinal gradient from 2260 to 3200 m and was distributed by six sampling sites as follows: 2260 m (on the road before the intersection to San José de Paso Nuevo), 2539 m (Tonalaco), 2600 m (Los Laureles), and 3070, 3100, and 3200 m (Tembladeras). Three traps were placed at least 7 m apart in each of the habitats. Thus, 57 traps (3 traps per habitat x 3 habitats x 6 sites plus another 3 traps, as two different forests were considered for the first site) were used in each sampling period.

Material gathered in each trapping period was brought to the laboratory for sorting. Specimens were kept in vials with 70% ethanol, labeled by trap number, habitat, altitude, and collecting period. Afterwards, all specimens of Geotrupinae were separated and mounted on pins. Voucher specimens have been placed in a reference collection at the Instituto de Ecología, A. C., Xalapa, Veracruz, Mexico.

Generalized linear models (McCullagh and Nelder 1989; Crawley 1993) were used to explore correlations between the number of trapped individuals (dependent variable) and altitude, collection period, and habitat. We used the pooled number of individuals from the sum of specimens caught in the three traps per habitat, therefore a total of 304 samples were used in the analyses [(57 traps/3) x 16 collecting periods]. Altitude was considered as a variable category with two ranges, the first being all localities up to 3000 m, and the second being all localities at higher altitudes. Collection period was divided into 16 categories corresponding to the sampling periods. Three types of habitat were compared: forest, pasture and cultivated fields. Relationships of number of individuals with collection period and habitat were analyzed according to the two altitude ranges. To determine the role of potentially critical variables, a partitioning of variation analysis was also applied (Legendre and Legendre 1998; Guisan and Zimmermann 2000; MacNally 2000, 2002). All statistical analyses were carried out using the program STATISTICA 6.0 (StatSoft, Inc. 2001).

The phenology of *G. rufoclavatus* was established based on the number of individuals encountered monthly in the municipalities of Xico and Ixhuacán de los Reyes, Veracruz, during the trapping period (1999-2001) and the systematic dung sampling in Tonalaco (2005-2006) described below.

**Reproductive state and anatomy of** *G. rufoclavatus.* Each month during 2005 and 2006 at the Tonalaco site, 10 dung pats were selected at random from all those naturally occurring in the grazing pastures. Samples of approximately 250 g of dung were taken. Individuals found in these samples were manually separated and counted. The reproductive system of each individual was removed by dissection, then fixed in AFATD (ethanol-formaldehyde-trich-loroacetic acid-dimethylsulfoxide) and conserved in 96% alcohol, stained with Feulgen green light and chlorazol black, and drawn to scale with a photomicroscope with a camera lucida using the morphological techniques described by Martínez (2002). The descriptive terminology used was that of Matsuda (1976) and Dupuis (2005). Subsequently, reproductive systems were analyzed to determine the proportions of males and females in different stages of maturation, using the technique described by Martínez (2002).

# RESULTS

**Distribution.** From 702 pitfall traps placed along the east slope of the Cofre de Perote Volcano, 63% (442) captured 412 individuals of *G. rufoclavatus*. This was the only species of Geotrupinae gathered in abundance during all sampling periods. One individual of *Geotrupes* (*Onthotrupes*) sobrinus Jekel, 1865 and another of *Geotrupes* (*Onthotrupes*) *herbeus* Jekel, 1865 were also taken. In addition to these geotrupine species, two other species are known to occur on the Cofre de Perote Volcano based on data from the literature: *Geotrupes* (*Onthotrupes*) *nebularum* Howden, 1964, and *Ceratotrupes bolivari* Halffter and Martínez, 1962. It seems that all these species are distributed in well-differentiated areas on the Cofre de Perote Volcano: *G. rufoclavatus* occupies the eastern slope, *G. herbeus* the western slope, and *G. nebularum* and *C. bolivari* the northern slope. There is one zone of sympatry among these species, in the northeastern area where the distributions of *G. rufoclavatus*, *G. herbeus*, and *C. bolivari* overlap (Fig. 1). **Ecological characteristics.** The number of captured *G. rufoclavatus* was not significantly related to altitude (F = 2.92; df = 302; p>0.05) and no significant difference was found between the numbers of individuals trapped at the two altitude ranges (Student-t = -1.71; df = 302; p>0.05).

Significant differences between numbers of trapped individuals were detected among habitats (F = 23.76; df = 301; p<0.001). More individuals were trapped in forests than in cultivated lands (Student-t = 4.16; df = 206; p<0.001) and in pastures (Student-t = 3.57; df = 206; p<0.001), but there was no significant difference between these last two last habitats (Student-t = -0.42; df = 190; p<0.001) (Fig. 2a, b).



Figure 1. Distribution of geotrupine species at the Cofre de Perote volcano, Veracruz México.
Geotrupes rufoclavatus; Geotrupes nebularum; Geotrupes herbeus; Ceratotrupes bolivari. 1, 2, 3, 4, and 5 are sampling localities during 1991-2000; City/Town.

Numbers of trapped individuals also significantly differed according to collecting periods (F = 57.31; df = 288; p<0.001). Peak captures were seen for the months of January, April, and September. At the same time, abundance peaks diminished somewhat at higher altitudes. At 2260 m, the number of individuals was fairly high during almost all months, with three principal abundance peaks.



Figure 2. Mean number of individuals per trap per habitat. Vertical bars represent standard errors of the mean. a) altitudes lower than 3000 m; b) altitudes higher than 3000 m.

At 2539 m, these three peaks were more notable. At 2600 m and 3070 m, the January and April peaks declined, and at 3100 and 3200 m, just one peak was seen in October (Fig. 3).

During the 1999-2001 sampling period, a total of 32 *G. rufoclavatus* were found at Tonalaco over the course of all months except November, March, and July. Abundance peaks were seen in the months of January, April-May, and September (Fig. 4a), with January registering the highest abundance peak. Also at Tonalaco from January 2005 to February 2006, a total of 11 individuals, 7 females and 4 males, were collected during the months of January, February, and September, with January again showing greatest abundance (Fig. 4b).

Significant correlations were detected between habitat type (F = 42.06; df = 157; p<0.001) and collection period (F= 23.99; df= 144; p<0.001) and number of individuals trapped at locations below 3000 m elevation, with 21.1% of captures potentially explained by the habitat type, and 14.3% explained by the collection period. At locations above 3000 m, habitat type (F = 4.50; df = 141; p<0.05) and collection period (F = 71.49; df = 128; p<0.001) were also significantly correlated with number of trapped individuals, explaining 3.1% and 35.8% of its variation, respectively.

Partitioning of variation analysis of data for both altitudinal ranges showed that the two factors of collection period and habitat type do not interact, but rather exert their own effects individually on capture numbers. Thus, the factors habitat type and collection period together accounted for up to 35.4% (21.1% + 14.3%) of the variation in the number of individuals collected at altitudes below 3000 m and up to 38.9% (3.1% + 35.8%) of the variation in the number of individuals trapped at altitudes above 3000 m.

**Reproductive state and anatomy of** *G.rufoclavatus.* Two female *G. rufoclavatus* collected in September 2005 and four in January 2006 contained maturing ovaries. In these females, the ovaries measured  $1.30 \pm 0.24$  mm in length (n = 8) and the basal oocytes of the two ovaries measured  $0.73 \pm 0.24$  mm in length (n = 15). In this species, all basal oocytes do not mature simultaneously; one in each ovary matures faster than the others. In the only mature female found, in February 2006, the mature ovary measured  $3.29 \pm 0.30$  mm in length (n = 2). In only one of the ovaries was there a mature oocyte with chorion, just prior to oviposition; this oocyte measured 2.87 mm in length, while the other oocytes, in varying states of maturation, measured  $1.01 \pm 0.48$  mm in length (n = 7).

# Capítulo 4



Figure 3. Phenologies of Geotrupes rufoclavatus at different sampling altitudes. J: January, F: February, M: March, A: April, M: May, J: June, J: July, A: August, S: September, O: October, N: November, D: December.



Figure 4. Phenology of Geotrupes rufoclavatus at Tonalaco (2539 m): a) 1999-2001; b) 2005.



**Figure 5.** Geotrupes rufoclavatus female reproductive system. Prepared with Feulgen green light technique: a) dorsal view; b) ventral view. Prepared with Chlorazol black technique: c) dorsal view; d) ventral view; e) coxosubcoxite (dorsal view) Scale bar = 1 mm. cxs: coxosubcoxite; go: gonopore; lo: lateral oviduct; mo: median oviduct; ova: ovariole; pe: pedicellum; sg: spermatheca gland; sp: spermatheca; va:

vagina.

Only four males were collected, two in February and one in September of 2005, and one in January 2006. Maturation stage is more difficult to determine in males, and more so when the sample size is low. However, all the collected males were in a maturing stage. These males did not show appreciable variation in the size of their testes, which measured  $0.94 \pm 0.08$  (n = 10), or in the size of their glandular reservoirs, which measured  $2.63 \pm 0.1.23$  (n = 3).

The reproductive system of female *G. rufoclavatus* (Figs. 5a, b) is formed by two ovaries with six ovarioles each. Each ovary terminates in a lateral oviduct. The two lateral oviducts disgorge into a common oviduct that in turn terminates in the vagina. In the ventral and posterior region of the vagina, near the genital orifice, two cuticular structures are found, called the coxosubcoxites. The anterior and middle regions of these structures are found in the vaginal walls between the muscles, while the posterior region is outside the vaginal wall, covering the genital orifice (Figs. 5 c, d, e).

The spermatheca is formed by a receptacle, which continues with a wide, short duct, which itself terminates in the dorsal, anterior region of the vagina, close to the base of the common oviduct. A spermathecal gland disgorges into the base of the receptacle (Fig. 5 c, d).

The male reproductive system is formed by a pair of testes, each with six spherical follicles. A vas deferens issues from each testes. There are two pairs of accessory glands. One pair is very large and doubles over themselves, and each gland disgorges into its own glandular reservoirs. The other pair is very short without reservoirs. The two vas deferens and two glandular reservoirs terminate in the anterior part of the ejaculatory bulb. The posterior part of the ejaculatory bulb disgorges in the aedeagus (Fig. 6a); the aedeagus of this species (Fig. 6b) was characterized by Zunino (1984).



Figure 6. Geotrupes rufoclavatus male reproductive system. a) prepared with Feulgen green light technique (dorsal view), b) aedeagus prepared with Chlorazol black technique (right lateral view). Scale bar =1mm. dd: deferens duct; eb: ejaculatory bulb; ej: ejaculatory duct; gr: gland reservoir; ag1: accessory gland 1; ag2: accessory gland 2; ml: median lobe; pa: parameres; ph: phallobase; sg: spiculum gastrale ; tf: testes follicles; rl: right lateral view; d: dorsal view; v: ventral view; ll: left lateral view.

# DISCUSSION

**Distribution.** *Geotrupes rufoclavatus* is found in Mexico in the upper elevations of Mexico City and the states of Morelos, Puebla, and Michoacán (Howden 2003). In an ecological study, Arellano (2002) and Arellano and Halffter (2003) cited the species for Veracruz, and the results of our work confirm the species' presence in the state. On the Cofre de Perote Volcano, it occurs above 2000 m elevation, in the localities of Los Laureles, Tonalaco, San José Paso Nuevo, Tembladeras (the sampling locations in this work) and Las Lajas (Arellano 2002).

As shown in Fig. 1, the other species of Geotrupinae also found on the volcano occupy distinct areas. *Geotrupes herbeus* is found on the western slope, while *G. nebularum* and *C. bolivari* are found on the northern slope. These four species overlap in the northeastern area of the volcano, and probably in other zones. More sampling is needed to determine other possible overlapping areas. For example, *G. herbeus* and *G. rufoclavatus* may overlap on the southern slope, and *G. herbeus* and *G. nebularum* on the northern slope.

The fact of having collected mostly *G. rufoclavatus* and just singletons of *G. herbeus* (in Tembladeras) and *G. sobrinus* (in Ixhuacán) despite the trapping effort carried out, perhaps indicates the marginal distribution of these latter species on this side of the mountain and that more sampling is needed to determine their distribution zones. In the case of *G. sobrinus*, only the type collected in Hidalgo has been known (Howden, 2003; Delgado and Márquez 2006). We have also encountered this species in Cuiyachapa on the Pico de Orizaba, in the central part of Veracruz.

The segregated distribution of geotrupinae species on the Cofre de Perote Volcano may be due to various factors, including habitat, given that the different species appear to select a slope with different environmental characteristics. Alternatively, the species may be competing while available area is simultaneously being reduced with elevation and historical factors may also be involved (Huston 1994). The Sierra Madre Oriental might have divided the original area of a common precursor species, thus creating allopatric species with vicariant distributions.

**Ecological characteristics.** *Geotrupes rufoclavatus* was collected in pine-oak forest, pasture, and cultivated fields of corn and potatoes. It is known that the species inhabits pastures and clearings in pine-oak-fir forests (Howden, 2003). Although the species has been found in all these habitats, it appears to prefer pine forest. This habitat is a more stable environment (Rzedowski 1978) with cool temperatures (12 to 18° C, Gómez 1991) and high humidity. It can serve as a refuge from high temperatures, but still provide sufficient food given the passage of livestock (cows and sheep). Before the introduction of cattle, *G. rufoclavatus* and other forest species probably fed on ancient wild mammal dung (Hanski and Cambefort 1991). Pastures and cultivated land are more open, exposed, and unstable, but dung is often more plentiful from the livestock living and using these habitats.

Abundance depends partially on altitude. From 2200 to 2600 m, habitat has a stronger influence on adult population size than time of year. A greater number of *G. rufoclavatus* are found in forests than in pastures or fields at lower elevations, probably because this environment is a refuge from higher temperatures. For this reason, time of year would not be such a critical variable as it is at higher altitudes. At higher altitudes (3000-3200 m), temperature is lower, with a mean range from 5 to 12° C (Gómez, 1991) and a greater abundance of individuals is found in pastures than at lower altitudes. As temperature decreases with altitude the contrast between forest and open land temperatures is also reduced, so individuals may come out of the forest more frequently to enter open areas with more abundant food.

Altitude plays an important role in the phenology of *G. rufoclavatus*. At altitudes below 3000 m, the species shows three abundance peaks (January, April, and September), which progressively diminish with higher altitudes; above 3000 m, there is only one abundance peak in October. In other species, such as *G. herbeus*, examples are found

from March through November, with two abundance peaks in April and August (Arellano 1992). In other regions, two species of Geotrupinae show different patterns. In Durango, *Geotrupes (Megatrupes) cavicollis* Bates, 1887 has one generation per year, emerging in June and remaining active until September (Halffter *et al.* 1980; 1985). In Oaxaca, adults of *Geotrupes (Onthotrupes) viridiobscurus* Jekel, 1865 are active from June to December, with peak abundance in June and September (Martínez and Suárez 2006).

These patterns may have strong implications for conserving *G. rufoclavatus*. Deforestation at altitudes higher than 3000 m may not drastically affect populations of this species, as long as patches of forest and access to sufficient food remain. However, at altitudes of less than 3000 m, populations of *G. rufoclavatus* are more dependent on forest environments, and habitat conservation is essential for the survival of the species. Thus, land use changes affecting forest extensions may have profound effects on the species' distribution.

**Reproductive state and anatomy of** *G. rufoclavatus.* The reproductive cycle of *G. rufoclavatus* could not be determined given the low number of individuals collected. However, it appears that, in the locations studied, females oviposit in February.

This study is the first time that the female reproductive anatomy of *G. rufoclavatus* has been completely described. Vaginal anatomy is very similar to that described by Dupuis (2005) for various non-Mexican species of Geotrupinae. The male reproductive system of *G. rufoclavatus* is very similar to that of *G. cavicollis*, which was described by Pluot-Sigwalt and Martínez (1998). The greatest differences are in the morphology of the aedeagus, which is species-characteristic (Zunino 1984), and at the level of the accessory glands, which are shorter than those of *G. cavicollis*.

Various studies on the Geotrupinae have demonstrated the importance of research on male and female reproductive systems for a systematic and phylogenetic review of this group (Nikolaev 1977; Krikken 1981; Zunino, 1984). For this reason, it would be valuable to continue with this type of study with other geotrupine species to help resolve these systematic, phylogenetic, and taxonomic problems. Moreover, it would also be useful to know the different reproductive systems of those geotrupinae species with allopatric or sympatric distributions to help discern possible peculiarities among them.

The present work has attempted to recognize the possible relationships between the abundance of *G. rufoclavatus* at different altitudes and habitat and seasonality. These variables play reasonably important roles in the abundance of the species at specific localities. Nevertheless, the explanatory role of these factors in general is moderate (around 35%-40% of the deviance), so that other variables may be influential in determining the distribution of this species. Among these variables, some may be ecological, such as temperature, rain, or solar radiation, but some may also be historical, such as the implicit affinity of a species for a particular climate over another given its place of origin, the isolation that it may have experienced in some areas of the Sierra Madre Oriental, or anthropogenic factors, such as land use changes. Knowledge of all these ecological factors, and of the species' reproductive characteristics, can yield better understanding of the distribution of Geotrupinae in Mexico, as well as clarify various taxonomic, systematic, and phylogenetic issues for the group.

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### LITERATURE CITED

- Arellano, L. 1992. Distribución y abundancia de Scarabaeidae y Silphidae (Insecta: Coleoptera) en un transecto altitudinal en el Estado de Veracruz. *Tesis de Licenciatura*. *Universidad Nacional Autónoma de México*. 205 pp.
- Arellano, L. 2002. Evaluación de la diversidad alfa, beta y gamma de Scarabaeoidea y Silphidae (Insecta: Coleoptera) en la región Cofre de Perote, Veracruz, México. *Tesis de Maestria. Universidad Nacional Autónoma de México.* 197 pp.
- Arellano, L. & G. Halffter. 2003. Gamma diversity: derived from and a determinant of alpha diversity and beta diversity. An analysis of three tropical landscapes. Acta Zoológica Mexicana 90:27-76.
- Crawley, M. J. 1993. LIM for ecologists. *Blackwell Scientific Publications*. Oxford, UK. I-ix + 379 pp.
- Delgado, L. & J. Márquez. 2006. Estado del conocimiento y conservación de los Coleóptros Scarabaeoidea (Insecta) del Estado de Hidalgo, México. Acta Zoológica Mexicana 22(2):57-108.
- **Dupuis, F. 2005.** L'abdomen et les genitalia des femelles de coléoptères Scarabaeoidea (Insecta, Coleoptera). *Zoosystema* 27(4):733-822.
- Gómez, M. 1991. Atlas climático del Municipio de Xico (Estado de Veracruz). Serie de Estudios Climáticos Nº7. Ortiz, S.A. ed. *Instituto de Ecología A.C. Xalapa*, Veracruz, México 47 pp.
- Guisan, A. & N. E. Zimmermann. 2000. Predictive habitat distributions models in ecology. *Ecological Modelling* 135:147-186.
- Halffter, V. Y. López-Guerrero, & G. Halffter. 1980. Comportamiento sexual de *Geotrupes* (Coleoptera: Scarabaeidae: Geotrupinae). *Folia Entomológica Mexicana* 45:63-65.
- Halffter, V. Y. López-Guerrero, & G. Halffter. 1985. Nesting and ovarian development in *Geotrupes cavicollis* Bates (Coleoptera: Scarabaeidae). Acta Zoológica Mexicana 7:1-28.
- Hanski, I., & Y. Cambefort. 1991. Biogeography and Evolution [pp. 51-54]. In: Dung

beetle ecology. (I. Hanski and Y. Cambefort, editors). *Princeton University Press*, Princeton, New Jersey. 481 pp.

- 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. 1980. Key to the Geotrupini of Mexico and Central America, with description of a new species (Scarabaeidae, Geotrupinae). *Canadian Journal of Zoology* 58(11): 1959-1963.
- Howden, H. F. 2003. Geotrupinae [95-106]. In: Morón M. A. (Editor), Atlas de los escarabajos de México (Coleoptera: Lamellicornia: Scarabaeidae, Trogidae, Passalidae y Lucanidae) Vol. II (4). 227 pp.
- Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge: *Cambridge University Press*. 681 pp.
- Jekel, H. 1865. Essai sur la classification naturelle des *Geotrupes* Latreille et descriptions d'espéces nouvelle. *Annales de la Société Entomologique de France* 5:513-618.
- Krikken, J. 1981. Geotrupidae from the Nepal Himalayas. New flightless species of Geotrupes Latreille, with a biogeographical discussion. Senkenberg. *Biology* 61(5-6): 369-381.
- Legendre, P. & L. Legendre. 1998. Numerical ecology. 2<sup>nd</sup> Edition. Elsevier, Ámsterdam. 853pp.
- Lobo, J. M., F. Martín-Piera & C. M. Veiga. 1988. Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de *Scarabaeoidea* (Col.).
  I. Características determinantes de su capacidad de captura. *Revue d'Écologie et de Biologie du Sol* 25(1):77-100
- López-Guerrero, Y. 1987. Análisis de la estructura del testículo y de las células neurosecretoras de la *pars intercerebralis* de *Halffterius rufoclavatus* (Jekel)
(Coleoptera: Geotrupinae: Ceratotrupini). *Estratto dal Bolletino del Museo Regionale de Scienze Naturali – Torino*. 5(2):433-445.

- 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.
- Martínez, M. I. 2002. Técnicas básicas de anatomía microscópica y de morfometría para estudiar los insectos. *Boletín de la Sociedad Entomológica Aragonesa* 30:187-195
- Martínez, M. I. & M. T. Suárez. 2006. Phenology, trophic preferences and reproductive activity in some dung-inhabiting beetle (Coleoptera: Scarabaeoidea) in El Llano de las Flores, Oaxaca, México. Proceedings of the Entomological Society of Washington 108(4):774-784
- Matsuda, R. 1976. Morphology and evolution of the insect abdomen. *Pergamon Press*, Oxford, 534 pp.
- McCullagh, P. & J. A. Nelder. 1989. Generalized linear models. Chapman and Hall. London. 532 pp.
- Nikolaev, G.V. 1977. Materialy k izučenju plastinčatousykh žukov podroda Odontotrupes Fairm. Roda Geotrupes Latr. (Coleoptera, Scarabaeidae). *Entomologicheskoye Obozreniye* 61(2):375-382.
- Onore, G., P. Reyes-Castillo & M. Zunino. 2003. Escarabeidos de Latinoamérica: Estado del conocimiento. *Monografias Tercer Milenio*, vol. 3, SEA, Zaragoza. 86pp.
- Pluot-Sigwalt, D. & I. Martínez. 1998. Anatomie morpho-fonctionnelle de L'Appareil génital mâle des Coléoptères Scarabaeoidea coprophages : Données comparatives. Annales de la Société Entomologique de France 34(4):419-444.
- Rzedowski, J. 1978. Vegetación de México. Editorial Limusa. México D.F. 432 pp.
- StatSoft, Inc. 2001. STATISTICA (data analysis software system), version 6. <u>www.statsoft.</u> <u>com</u>. (21<sup>th</sup>-March-2007).

- Veiga, C. M., J. M. Lobo, & F. Martín-Piera. 1989. Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de *Scarabaeoidea* (Col.).
  II : Analisis de efectividad. *Revue d'Écologie et de Biologie du Sol* 26(1):91-109.
- Zunino, M. 1984. Sistematica generica dei Geotrupinae (Coleoptera, Scarabaeoidea: Geotrupidae), filogenesi della sottofamiglia e consideración biogeografiche. *Bolletino del Museo Regionale di Scienze Naturali Torino* 2(1):9-162.





# Male and female reproductive systems in various Geotrupini species (Coleoptera: Geotrupinae) in Mexico: Comparative data

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# REPRODUCTIVE SYSTEMS IN VARIOUS GEOTRUPINI SPECIES (COLEOPTERA: GEOTRUPINAE) IN MEXICO: COMPARATIVE DATA

## Sistemas reproductivos en varias especies de Geotrupini (Coleoptera: Geotrupinae) en México: Datos comparativos

Imelda MARTÍNEZ M. and Nuria TROTTA-MOREU

#### ABSTRACT

We examined the reproductive systems, including genitalia, of ten Geotrupini species collected at different Mexican sites. The females all present six ovarioles in each ovary. Spermathecae and genitalia of all the species are similar, but the palpi vaginalis show marked morphological differences at the species level. Males all have six follicles per testicle, while aedeagus structure varies among species. Morphological features of palpi vaginalis in the female are useful in taxonomic and phylogenetic studies of this group of insects, just as features of the aedeagus are in the male.

Key words: Dung beetles, Geotrupes, Ceratotrupes, females, males, reproductive organs, genitalia.

#### RESUMEN

Se estudiaron los sistemas reproductivos, incluyendo las genitalias, en diez especies de Geotrupini colectados en diferentes sitios de México. Todas las hembras presentan 6 ovariolas en cada ovario. Las espermatecas y las genitalias son semejantes de una especie a otra pero los palpos vaginales presentan diferencias morfológicas marcadas a nivel específico. Los machos tienen 6 folículos testiculares por testículo y la estructura de los edeagos es diferente dependiendo de la especie. Los caracteres morfológicos de los palpos vaginales pueden ser útiles para estudios taxonómicos y filogenéticos de este grupo de insectos, así como se han empleado los caracteres de los edeagos en los machos.

**Palabras clave:** Escarabajos estercoleros, *Geotrupes*, *Ceratotrupes*, hembras, machos, órganos reproductores, genitalia.

#### **INTRODUCCION**

The Geotrupinae subfamily includes about 1,000 species worldwide, classified in four tribes. Lethrini are restricted to the Old World. The other three tribes, comprising roughly

227 species, are represented in America (Howden 2003). Recent findings suggest that 45 Geotrupini species are found in Mexico, together with 19 Bolboceratini and 7 Athyreini species (Trotta-Moreu et al. 2008).

Over the last 10 years, changes have been proposed in Geotrupinae classification with some investigators considering this taxon as a subfamily (Howden 2003), while others have suggested that the Bolboceratini and Athyreini should be elevated and considered as one family (Bolboceratidae), and thus separate from the Geotrupidae (Scholtz & Browne 1996).

For the genus *Geotrupes* Latreille 1796 (Geotrupini), a problem is encountered in the hierarchy of Mexican species. Based on observed genital differences among species, Zunino (1984a) raised to the genus level many subgenera of the time (*Onthotrupes* Howden 1964, *Haplogeotrupes* Nikolaev 1979) and described other new genera (*Megatrupes* Zunino 1984, *Geohowdenius* Zunino 1984, *Halffterius* Zunino 1984). Howden (2003) proposed a new classification similar to that of Zunino, but keeping the genera as subgenera. These classification differences emphasize the need to study and clarify the taxonomic relations among these groups of insects.

While it is important to characterize such insects' reproductive systems for systematic and phylogenetic reasons, data available on Geotrupinae are few.

The male reproductive system has been described for *Geotrupes (Megatrupes) cavicollis* (Bates, 1887) (Pluot-Sigwalt & Martínez, 1998) and for *Geotrupes (Halffterius) rufoclavatus* (Jekel 1965) (Trotta-Moreu et al. 2007). Histological studies have been made of the testis follicles of various species along with studies of sperm size, for two Palearctic and six Mexican species (Virkii 1957, López-Guerrero 1987, Martínez & Cruz 1999). The aedeagus and the internal sac had been comparatively studied in some Coleoptera groups including Geotrupinae (Hieke 1966, d'Hotman & Scholtz 1990). Genital musculature has been studied as well in different Scarabaeoidea species (Hieke 1966, Krell 1996).

The female has been less studied. In G. (M.) cavicollis, ovary state of maturity was related to different nesting behaviors (Halffter et al. 1985), and the reproductive system of *G. (H.) rufoclavatus* has been described (Trotta-Moreu et al. 2007). Recently, Dupuis (2005) described the female genitalia for various Palearctic Scarabaeoidea species, including Geotrupinae.

The present work compares the reproductive systems of both sexes, in various Mexican species of the Geotrupini, following the classification of Howden (2003), which is the latest classification for America, to gather basic data for subsequent systematic and phylogenetic studies. The genital musculature and the descriptive anatomy of the aedeagus are not refered in this work.

#### **MATERIALS AND METHODS**

The female and male reproductive systems were characterized for 10 Geotrupini species belonging to two genera (sensu Howden 2003) and collected from various Mexican sites, as follows. Genus *Geotrupes: G. (Onthotrupes) sobrinus* Jeckel 1865 (Cuiyachapa, Veracruz), *G. (O.) nebularum* Howden 1964 (Las Vigas, Veracruz), *G. (O.) herbeus* Jekel 1865 (San José de Aguazuelas, Veracruz), *G. (O.) viridiobscurus* Jeckel 1865 (Llano de las Flores, Oaxaca) *G. (Halffterius) rufoclavatus* (Paso de Cortés, Puebla), *G.(Megatrupes) fisheri* Howden 1974 (Los Azufres, Michoacán), *G.(M.) cavicollis* Bates 1887 (La Michilía, Durango), *G.(Geohowdenius cnephosus* Howden 1964 (Creel, Chihuahua), and *G. (Haplogeotrupes) guatemalensis unidentatus* Howden 1974 (Rancho Viejo, Chiapas). Genus *Ceratotrupes: C. fronticornis* (Ericsson 1879) (Mil Cumbres, Michoacán).

All individuals were maintained alive until immediately before dissection. Reproductive apparatus from each sex and species was obtained in Ringer saline solution for insects, fixed with AFATD, and stained with Feulgen-green light or chlorazol black (Martínez 2002). For each species, two to eight pairs were dissected, except in the case of *G*. *(G.) cnephosus*, for which only one pair was found. Scale drawings were made after fixation and before staining.

Anatomical terms employed here are those of Snodgrass (1935) and Matsuda (1976), taking into account the work of Bovo & Zunino (1983) and Dupuis (2005).

#### RESULTS

**Females:** The female reproductive apparatus has the same general anatomy across species, although some differences are found. We describe first here one of the species in detail, and thereafter compare the differences found among the group.

In *G. (O.) sobrinus*, the female reproductive system (Fig. 1) is formed by two ovaries, each with six ovarioles, and each ovariole with two oocytes of quite different size. Each ovariole ends in a pedicel, and the six pedicels of each ovary issue into the lateral oviduct. The two lateral oviducts lead to the common oviduct, which issues into the genital chamber or vagina. The spermatheca also leads into the vagina, dorsally, at the mouth of the common oviduct. The vagina is a voluminous sacular organ with a thick muscular wall. Joined to its anterior region is the common oviduct and spermatheca. In the medial dorsal region, a large, muscled pleat forms, covering the mouth of the spermathecal duct and common oviduct. In lateral and posterior regions, between the muscles, the palpi vaginalis almost cover the entry to the genital orifice. The genital orifice is found in the ventral region, as a fairly large and visible opening, delimited by notable, thick cuticular pleats, without muscles, and giving on the large anogenital chamber.

The palpi vaginalis are extended cuticular structures, found in almost symmetrical pairs, which form part of the lateral and posterior vaginal walls. The anterior of these structures is found in the lateral vaginal wall among the muscles, while the posterior part is pleated and more sclerotized presenting large bristles in the terminal region, and being located outside the muscular vaginal wall toward the anogenital chamber.

The spermatheca is formed by the seminal receptacle, spermathecal duct, and spermathecal gland. The seminal receptacle is pyriform, with transverse striations from the base. The spermathecal duct is short, thin, and with a smooth wall, a wall thicker than that of the seminal receptacle ending in the anterior, dorsal region of the vagina, close to the base of the oviduct. The gland of the seminal receptacle is rounded.



Figures 1 to 5. Schemata of the female reproductive system in various Geotrupini species: dorsal view (d) and ventral view (v). Feulgen-green light stain. 1, *G. (Onthotrupes) sobrinus.* 2, *G. (O). nebularum.* 3, *G. (O) viridiobscurus.* 4, *G. (O). herbeus.* 5, *G. (Halffterius) rufoclavatus.* (bo, basal oocyte; co, common oviduct; df, dorsal fold; ge, germarium; go, genital orifice; lo, lateral oviduct; ov, ovary; pv, palpi vaginalis; sp, spermatheca; va, vagina)



Figures 6 to 10. Schemata of the female reproductive system of various Geotrupini species: dorsal view (d) and ventral view (v). Feulgen-green light stain. 6, *G. (Haplogeotrupes) guatemalensis.* 7, *G. (Geohowdenius) cnophosus.* 8, *G. (Megatrupes) fisheri.* 9, *G. (M.) cavicollis.* 10, *Ceratotrupes fronticornis.* (bo, basal oocyte; co, common oviduct; df, dorsal fold; ge, germarium; go, genital orifice; lo, lateral oviduct; ov, ovary; pv, palpi vaginalis; sp, spermatheca; va, vagina)

Comparative characteristics in females.- Ovaries are similar in all species examined. Each ovary contains six ovarioles (Figs. 1 to 10). Ovary morphology depends on female state of maturity. The ovaries are small and without oocytes in immature females, as seen in *G. (G.) cnephosus* (Fig. 7), thereafter developing basal oocytes, as seen in *G. (O.) sobrinus* (Fig.1), *G. (O.) viridiobscurus* (Fig. 3), *G. (H.) rufoclavatus* (Fig. 5), *G. (M.) fisheri* (Fig. 8), *G. (M.) cavicollis* (Fig. 9), and finally, developing mature oocytes prior to oviposition, as seen in *G. (O.) nebularum* (Fig. 2), *G. (O.) herbeus* (Fig. 4), *G. (H.) guatemalensis* (Fig. 6), and *C. fronticornis* (Fig. 10). In the species examined, basal oocytes do not mature simultaneously in all ovarioles; rather, one oocyte is more mature than the others. Immediately before oviposition, the mature basal oocyte is very large, larger than the vagina in all species studied. The laterial oviducts and common oviduct are similar in most species, except in G. (M.) fisheri (Fig. 8), a species in which these structures are longer and covered with strong circular muscles.

While the vagina appears generally similar in all species, differences are seen in its components among the different species. The longitudinal pleats in the cuticular intima in the dorsal region, which cover the spermatheca opening and part of the basal oviduct region (Figs. 11 to 19) are transverse in most species, except in *G. (M.) fisheri* and above all *G. (M.) cavicollis*, in which they are longitudinal, very large, and very notable (Figs. 17 and 18).



**Figures 11 to 15.** Schemata of the vaginal cuticular intima, common oviduct, and spermatheca of various Geotrupini species: dorsal view (d) and ventral view (v). Chlorazol black stain, following treatment with potash. 11. *G. (Onthotrupes) sobrinus.* 12, *G. (O.) nebularum.* 13, *G. (O.) viridiobscurus.* 14, *G. (O.) herbeus.* 15, *G. (Halffterius) rufoclavatus.* (co, common oviduct; df, dorsal fold; go, genital orifice; pv, palpi vaginalis; sp, spermatheca; va, vagina)



**Figures 16 to 19.** Schemata of the vaginal cuticular intima, common oviduct, and spermatheca of various Geotrupini species: dorsal view (d) and ventral view (v). Chlorazol black stain, after treatment with potash . 16, *G. (Haplogeotrupes) guatemalensis.* 17, *G. (Megatrupes) fisher*i. 18, *G. (M.) cavicollis.* 19, *Ceratotrupes fronticornis.* (co, common oviduct; df, dorsal fold; go, genital orifice; pv, palpi vaginalis; sp, spermatheca; va, vagina)

The genital orifice differs in form from one species to another (Figs. 11 to 19). Few pleats are seen in *G. (O.) sobrinus* (Fig. 11), *G. (O.) viridiobscurus* (Fig. 13), or *G. (H.) guatemalensis* (Fig. 16); marked pleats are seen in *G. (H.) rufoclavatus* (Fig. 15), *G. (M.) fisheri* (Fig. 17), *G. (M.) cavicollis* (Fig. 18), and *C. fronticornis* (Fig. 19); and very notable, very large pleats are seen in *G. (O.) nebularum* (Fig. 12) and *G. (O.) herbeus* (Fig. 14).

The palpi vaginalis are the structures whose morphology varies most among the different species. The anterior region, given its position and morphology, could function as an apodeme, since it is found among the abundant muscles of the vaginal wall. The posterior

region, which is generally more sclerotized, is outside the vaginal wall, is bristled, and may serve a tactile function at times of oviposition and copulation.

In the *G. (Onthotrupes)* species examined, the palpi vaginalis vary from species to species. *In G. (O.) sobrinus* (Fig. 20), the anterior region of these structures is flat, almost triangular, being wider and then narrowing. The posterior region is pleated lengthwise, forming a peak, with many long bristles on the point. In *G. (O.) nebularum* (Fig. 21), the palpi vaginalis are flat, with a sharp point in the anterior region, but widening toward the posterior. At the very end of the posterior region, these structures narrow again, with a less sclerotized aspect and many long bristles on the point. In *G. (O.) viridiobscurus* (Fig. 22), the anterior region is almost triangular, modestly sclerotized, with a large striated zone at the beginning. The posterior region is wide, flat, and with a posterior pleat that is only modestly sclerotized, and with many short and long bristles on the point. In *G. (O.) herbeus* (Fig. 23), the anterior part is level, narrowing and then widening to form the posterior region. In the posterior region is found a very small pleat, and the point is marked by numerous long bristles.

In G. (H.) rufoclavatus (Fig. 24), the anterior region is flat and engorged, with a small striated zone initially, and the structure narrowing toward the posterior. The posterior part is larger and more sclerotized, pleated in two at its end, where both long and short bristles are seen. In *G. (H.) guatemalensis* (Fig.25), the palpi vaginalis are almost triangular, with a very small striated zone in the anterior region. The posterior part engorges greatly at the end, forming a pleat and presenting short bristles in the terminal region. These structures are similar to those of *G. (O.) viridiobscurus* (Fig. 22) and *G. (H.) rufoclavatus* (Fig. 24).

In *G. (G.) cnephosus*, the palpi vaginalis (Fig. 26) are quite different, almost triangular, forming a sharp point in the anterior region, while becoming wide and bifurcated in the posterior region, which presents small bristles.



Figures 20 to 24. Schemata of palpi vaginalis of various Geotrupini species: lateral views. Chlorazol black stain, after treatment with potash. 20, *G. (Onthotrupes) sobrinus*. 21, *G. (O.) nebularum*. 22, *G. (O.) viridiobscurus*. 23, *G. (O.) herbeus*. 24, *G. (Halffterius) rufoclavatus*.

In *G.* (*M.*) *fisheri*, the palpi vaginalis (Fig. 27) show a flat, engorged anterior region, with two anterior lobes and little sclerotized. The posterior region is more sclerotized, almost pleated in two longitudinally, and with many very long bristles on the point. In *G.* (*M.*) *cavicollis* (Fig. 28), the structures are longer, pointed, and pleated lengthwise almost their entire length, with many long terminating bristles.



Figures 25 to 29. Schemata of palpi vaginalis of various Geotrupini species: lateral views.
Chlorazol black stain, after treatment with NaOH (10% solution). 25. *G. (Haplogeotrupes) guatemalensis.*26, *G. (Geohowdenius) cnophosus.* 27. *G. (Megatrupes) fisheri.* 28, *G. (M.) cavicollis.* 29, *Ceratotrupes fronticornis.*

In *C. fronticornis* (Fig. 29), the palpi vaginalis differ from those of all other species. They are long, flat, without pleats, and with long bristles in the terminal region. The anterior region is rounded, while the posterior part is pointed.

Species differences are seen in the spermatheca, both in the seminal receptacle and spermathecal gland, although these differences are not marked. The seminal receptacle is pyriform and long in almost all species, except in *G. (O.) viridiobscurus* (Fig. 32), in which it is more rounded. It shows greater striations in *G. (O.) sobrinus* (Fig. 30) and *G. (G.) cnephosus* (Fig. 36) than in other species.



Figures 30 to 34. Schemata of spermatheca of two Geotrupini genera . Chlorazol black stain, after treatment with NaOH (10% solution). 30, *G. (Onthotrupes) sobrinus*. 31, *G. (O.) nebularum*. 32, *G. (O.) viridiobscurus*. 33, *G. (O.) herbeus*. 34, *G. (Halffterius) rufoclavatus*. (sd, spermathecal duct; sg, spermathecal gland; sr, seminal receptacle)

The spermathecal gland is rounded in *G. (O.) sobrinus* (Fig. 30), *G. (O.) viridiobscurus* (Fig. 32), *G. (G.) cnephosus* (Fig. 36), and *C. fronticornis* (Fig. 39), while it is very elongated in *G. (O.) nebularum* (Fig. 31) and *G. (O.) herbeus* (Fig. 33), and pyriform in *G. (H.) rufoclavatus* (Fig. 34), *G. (H.) guatemalensis* (Fig. 35), *G. (M.) fisheri* (Fig. 37), and *G. (M.) cavicollis* (Fig. 38).



Figures 35 to 39. Schemata of spermatheca of two Geotrupini genera . Chlorazol black stain, after treatment with NaOH (10% solution). 35, G. (Haplogeotrupes) guatemalensis. 36, G. (Geohowdenius) cnophosus. 37, G. (Megatrupes) fisheri. 38, G. (M.) cavicollis. 39, Ceratotrupes fronticornis. (sd, spermathecal duct; sg, spermathecal gland; sr, seminal receptacle )

**Males:** In general, males of the various species studied showed very similar anatomy, though some differences were seen at the species level.

In *G. (O.) sobrinus*, the reproductive system (Fig. 40) is formed by a pair of testicles, each with six spherical testis follicles leading to the respective vas deferens, which is found rolled up on itself under each testicle. The two vas deferentia lead into the ejaculatory bulb, which continues as the ejaculatory duct, which discharges into the aedeagus.

Two pairs of accessory glands, very different from one another, are also seen; of mesodermic origin, they are known as mesadenia. The longer mesadenia have a very long glandular region, which is rolled up on itself and issues in the glandular reservoir. Both reservoirs continue with the glandular ducts, which issue into the ejaculatory bulb. The

shorter mesadenia are small, straight, and without glandular reservoir; and they issue directly in the ejaculatory bulb to the side of each of the longer mesadenia and each of the vas deferentia.

The ejaculatory bulb is very small relative to the entire reproductive system. It is formed by thick muscular walls, and engorged in its anterior region, into which the two pairs of mesadenia and vasa deferentiae are inserted. In the posterior region, the ejaculatory bulb leads to the internal sac within the aedeagus.



Figures 40 to 44. Schemata of the male reproductive system in various Geotrupini species: dorsal views. Feulgen-green light stain. The aedeagus is shown only for the first species; figures below illustrate the aedeagus in other Geotrupini species. 40, *G. (Onthotrupes) sobrinus*. 41, *G. (O.) nebularum*. 42, *G. (O.) viridiobscurus*. 43, *G. (O.) herbeus*. 44, *G. (Halffterius) rufoclavatus*. (ae, aedeagus; eb, ejaculatory bulb, ed, ejaculatory duct: gd, glandular duct; gr, glandular reservoir; lm, large mesadenia; sm, small mesadenia; te,

testis; vd, vas deferens)

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Figures 45 to 49. Schemata of the male reproductive system in various Geotrupini species: dorsal views. Feulgen-green light stain. 45, *G. (Haplogeotrupes) guatemalensis.* 46, *G. (Geohowdenius) cnophosus.* 47, *G. (Megatrupes) fisheri.* 48, *G. (M.) cavicollis.* 49, *Ceratotrupes fronticornis.* (ae, aedeagus; eb, ejaculatory bulb, ed, ejaculatory duct: gd, glandular duct; gr, glandular reservoir; lm, large mesadenia; sm, small mesadenia; te, testis; vd, vasa deferentia)

The aedeagus of this species consists of two short parameres of complex design. The right paramere is straight and long, while the left is more rounded and planar. The phallobase has two dorsal lobes of unequal size, and two smaller ventral lobes, also unequal, and of greater complexity. Inside the aedeagus is found the medial lobe, to which the median struts and internal sac of the endophallus are attached.

**Comparative characteristics in males:** The male reproductive system is similar among all the species studied. All observed species have two testicles with six testis follicles each, regardless of the subgenus and genus to which they belong (Figs. 40 to 49).

The accessory glands, both the longer and shorter mesadenia, are seen in all the species studied (Figs. 40 to 49). In *G. (G.) cnephosus* (Fig. 46), the glandular ducts of the longer mesadenia have transversally wrinkled walls; and the shorter mesadenia are the longest, thinnest, and most twisted of all those observed. In *G. (M.) fisheri* and *G. (M.) cavicollis* (Figs. 47 and 48), the shorter mesadenia are also much longer than those of the other species.

The ejaculatory bulb is very small compared to other reproductive system organs and has a very similar morphology in all species, including the short ejaculatory duct (Figs. 40 to 49). *G. (Megatrupes) fisheri* and *G. (Megatrupes) cavicollis* (Figs. 47 and 48) have the smallest ejaculatory bulb observed.

The aedeagus is the organ that varies most according to species, and hence is most used to distinguish them. The aedeagus of *G. (O.) herbeus* (Fig. 53) is very similar to that of *G. (O.) sobrinus* (Fig. 50), although in *G. (O.) herbeus*, in the left region of the parameres' ventral suture, there is a rounded depression much more pronounced than in *G. (O.) sobrinus*. The right paramere is less rounded and presents two spines on its left side in *G. (O.) nebularum* (Fig. 51), while *G. (O.) viridiobscurus* (Fig. 52) shows a narrowing in the posterior part.

The aedeagus in *G. (H.) rufoclavatus* (Fig. 54) differs from that of the other species in that the dorsal lobes of the phallobase are of similar size. The right paramere is wider and more squared than in the other species, and the parameres' ventral suture is straighter.

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Figures 50 to 54. Schemata of the aedeagus in various Geotrupini species: dorsal view (d), ventral view (v), and right lateral view, following treatment with NaOH (10% solution). 50, *G. (Onthotrupes) sobrinus*. 51, *G. (O.) nebularum*. 52, *G. (O.) viridiobscurus*. 53, *G. (O.) herbeus*. 54, *G. (Halffterius) rufoclavatus*. (pa, parameres; ph, phallobase; dl, dorsal lobe of the parameres; ml, median lobe; vl, ventral lobe of the parameres; vs, ventral suture of the parameres).



Figures 55 to 59. Schemata of the aedeagus in various Geotrupini species: dorsal view (d), ventral view (v), and right lateral view, following treatment with NaOH (10% solution. 55, *G. (H.).guatemalensis.* 56, *G. (Geohowdenius) cnophosus.* 57, *G. (Megatrupes) fisheri.* 58, *G. (M.). cavicollis.* 59, *Ceratotrupes fronticornis.* (pa, parameres; ph, phallobase; dl, dorsal lobe of the parameres; ml, median lobe; vl, ventral lobe of the parameres; vs, ventral suture of the parameres).

In *G. (H.) guatemalensis* (Fig. 55), the right dorsal lobe of the phallobase is very narrow and fine. This species can also be distinguised by its right paramere, which is finer than in other species.

In *G. (G.) cnephosus* (Fig. 56), the aedeagus is long and straight. The dorsal lobes of the phallobase are of different sizes, with the right lobe longer than the left, and asymmetrical parameres. This species is distinguished by its right paramere, which has a triangular form.

In *G. (M.) fisheri* and *G. (M.) cavicollis,* the aedeagus is very similar (Figs. 57, 58). In *G. (M.) cavicollis,* the ventral lobes are rounded and less slender than those of *G. (M.) fisheri.* The dorsal lobes of the phallobase tend to merge with the ventral lobes in *G. (M.) cavicollis,* which is not seen in *M. (M.) fisheri.* 

The aedeagus in *C. fronticornis* (Fig. 59) is robust and wide, while the dorsal right lobe of the phallobase is fine, with a sharp point. The parameres are asymmetrical, with the right paramere wider and more robust. The parameres' dorsal suture is more open on its left side.

#### DISCUSSION

The reproductive systems of females and males in the examined *Geotrupes* and *Ceratotrupes* species are similar within gender, although some differences are seen between species.

The females of all the species studied have the same number of ovarioles. In all species as well, the basal oocytes do not mature simultaneously, which suggests that egg laying occurs egg by egg and fecundity is therefore low — but none of the species of this group has actually been studied in these regards.

The dung beetles grouped under Aphodiinae, Scarabaeinae, and Geotrupinae are known to have developed an extremely reduced number of ovarioles (Robertson 1961, Ritcher & Baker 1974) and their fecundity is low (Halffter & Edmonds 1982, Cambefort & Hanski 1991). In Geotrupinae, seven European species are known to oviposit from 1 to 17 eggs, in field or laboratory conditions (Brussaard 1983). Under laboratory conditions, females of *G. (Megatrupes) cavicollis* have laid up to five eggs (Halffter et al. 1985).

The vaginal sac is similar in all Geotrupini females, as Willimzik (1930) already described for Geotrupinae and Scarabaeinae. In Aphodiinae, the bursa copulatrix is well developed, ending in a very small vagina (Martínez et al. 2001). Nevertheless, Dupuis (2005) does not consider this bursa copulatrix as such, arguing that Geotrupinae, Scarabaeinae, and Aphodiinae females do not have this organ. Thus, further study is needed of Aphodiinae females, including Old World species, before coming to general conclusions about this group. Morphology and ventral position of the genital orifice in Geotrupini females are quite different than in Aphodiinae and Scarabaeinae.

The palpi vaginalis are the structures that show the greatest morphological differences among the species studied, exhibiting many features that can be used in species identification. They are cuticular, form part of the vaginal wall, and surely function as apodemes for the muscles that carpet the vaginal wall. The palpi vaginalis, like many other anatomical structures, have been variously named depending on the author: vaginal palpen (Ritterhaus, 1927), palpen (Willimzik, 1930), coxite (Snodgrass, 1935), hemisternite (Tuxen, 1970), gonocoxite (Jameson, 1997), palpes génitaux (Zunino, 1983), genital plates (Morón, 1995), and recently Dupuis (2005) named them coxosucoxites, as result of the fusion of the two basal articles of the gonopode, the coxite and subcoxite. These sclerites are seen in Aphodiidae, but not in Scarabaeidae, which show no trace of the 9th segment (Dupuis, 2005).

In describing various Geotrupinae species, Zunino (1984a) presents sagital schemes of the genital cuticular intima; these schemes identify the genital orifice as the ostium vaginal, the dorsal vaginal wall as the tectum, and the ventral wall and genital palps as the pavimentum.

The spermathecae of the Geotrupini species examined showed some inter-species differences, but they were not very marked. As has been previously observed, the spermathecae of Geotrupini and Lethrini species are elongated, while in Taurocerastini and Bolboceratini they take the form of an anphora (Zunino 1984b, López-Guerrero & Halffter 2000, Martín-Piera & López-Colón 2000). In Aphodiidae and Scarabeidae, they are curved like the letter C, except in species of Sisyphus Latreille, 1807 (Scarabaeidae), in which they take a spiral form (Barbero et al. 1991, Vaz de Mello 2007)

In males of the Mexican Geotrupini species studied, the number of testicular follicles is consistent with the observations of Pluot & Martínez (1998) of five European species. Each testicle presents six testis follicles, as in Scarabaeinae (with the exception of Digitonthophagus gazella (F.), which presents twelve). Aphodiinae species show seven equal follicles, or two larger and five smaller follicles (Aphodiini), or only two follicles (Eupariini) (Martínez & Cruz 1999).

The Geotrupini especies examined do not have a seminal vesicle. None are seen in any Scarabaeinae or Aphodiinae species, except for species in the genus *Cephalocyclus* (Aphodiinae) (Martínez et al. 2001).

With regard to accessory glands, elongated mesadenia are seen in all the Geotrupini species studied and are similar to the single pair observed in Scarabaeinae and Aphodiinae (Pluot & Martínez 1998). Short mesadenia are seen only in Geotrupinae species.

The ejaculatory bulb is small and the ejaculatory duct is short in the species examined, in contrast to the structures observed in Scarabaeinae and Aphodiinae (Pluot & Martínez 1998). Nevertheless, the pumping action achieved during copulation would be the same as in other species during the formation of the spermatophore.

In studied Geotrupini, the aedeagus is seen to have multiple species variations, chiefly in the parameres, the pallobase lobes, and the ventral suture of the parameres, structures that have great taxonomic value. The aedeagus of Coleoptera, including Geotrupinae, Scarabaeinae and Aphodiinae, have been the subject of comparative studies above all characters that have systemic and phylogenetic significance (Sharp & Muir 1912, Nikolaev 1977, Krikken 1981, Bovo & Zunino 1983, Zunino 1984a,b, D'Hotman & Scholtz 1990, Krell 1996), and for this reason not discussed in this work.

The differences observed in female reproductive anatomy of the examined Geotrupini species are valuable for taxonomic and phylogenetic purposes, just as features of the aedeagus are in the male. It would be instructive to compare additional species of this tribe and compare them to Bolboceratini and Athyreini species.

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### LITERATURE CITED

- Barbero, E., Palestrini, C. & Zunino, M. 1991. Filogenesi, biogeografia e sistematica generica dei Sisyphini (Coleoptera: Scarabaeidae). Congresso nazionale italiano di Entomologia Bari. Martina Franca: 837-844.
- Bovo, B. & Zunino, M. 1983. Nuovi generi di Geotrupini asiatici. Bolletino del Museo Regionale de Scienze Naturali. Torino 1(2):397-416.
- **Brussaard, L. 1983.** Reproductive behavior and development of the dung beetle Typhaeus typhoeus (Coleoptera, Geotrupidae). *Tijdschrift voor Entomologie* 126:203-231.
- Cambefort, Y. & Hanski, I. 1991. Dung beetle population biology. In Hanski I. & Cambefort Y. (eds.): Dung Beetle Ecology. *Princeton University Press*, New Jersey. pp. 36-50.
- D'Hotman, D. & Scholtz, C.H. 1990. Phylogenetic significance of the structure of the external male genitalia in the Scarabaeoidea (Coleoptera). Entomology Memoir of the Department of Agricultural Development of the Republic of South Africa 77:1-51.
- **Dupuis, F. 2005.** L'abdomen et les genitalia des femelles de coléoptères Scarabaeoidea (Insecta, Coleoptera). *Zoosystema* 27(4):733-822.
- Halffter, G. & Edmonds, W.D. 1982. The nesting behaviour of dung beetles (Scarabaeinae). An ecological and evolutive approach. *Publicaciones del Instituto de Ecología*, México D.F., México. 176 pp.
- Halffter, V., López-Guerrero, Y. & Halffter, G. 1985. Nesting and ovarian development in Geotrupes cavicollis Bates (Coleoptera: Scarabaeidae). Acta Zoológica Mexicana (n.s.) 7:1-28.
- Hieke, F. 1966. Vergleichende funktionelle Anatomie der Abdominalmuskulatur einiger männlicherColeopterenunterbesondererBerücksichtigungdesGenitoanalkomplexes. Deutsche Entomologische Zeitschrift, N.F. 13:1-168.
- Howden, H. F. 2003. Geotrupinae. In Morón M.A. (ed.): Atlas de los escarabajos de México (Coleoptera: Lamellicornia: Scarabaeidae, Trogidae, Passalidae y Lucanidae) Vol. II (4):95-106.

Jameson, M. L. 1997. Phylogenetic analysis of the subtribe Rutelina and revision of the

Rutela generic groups (Coleoptera: Scarabaeidae: Rutelinae: Rutelini). *Bulletin of the University of Nebraska State Museum* 14:1-184.

- Krell, F.T. 1996. Die Kopulationsorgane des Maikäfers Melolontha melolontha (Insecta: Coleoptera: Scarabaeidae). Ein Beitrag zur vergleichenden und funktionellen Anatomie der ektodermalen Genitalien der Coleoptera. *Stuttgarter Beiträge zur Naturkunde*, Serie A 537. 101 pp. Stuttgart.
- Krikken, J. 1981. Geotrupidae from the Nepal Himalayas. New flightless species of Geotrupes Latreille, with a biogeographical discussion. *Senckenbergiana Biologica* 61(5-6):369-381.
- López-Guerrero, Y. 1987. Análisis de la estructura del testículo y de las células neurosecretoras de la pars intercerebralis de Halffterius rufoclavatus (Jekel) (Coleoptera: Geotrupinae: Ceratotrupini). Bolletino del Museo Regionale de Scienze Naturali Torino 5(2):433-445.
- López-Guerrero, Y. & Halffter, G. 2000. Evolution of the spermatheca in the Scarabaeoidea (Coleoptera). *Fragmenta Entomologica* 32:225-285.
- Martínez, M.I. 2002. Técnicas básicas de anatomía microscópica y de morfometría para estudiar los insectos. *Boletín de la Sociedad Entomológica Aragonesa* 30:187-195
- Martínez, M. I. & Cruz, R. M. 1999. Comparative morphological analysis of testis follicles in dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae, Aphodiinae, Geotrupinae). *Proceedings of the Entomological Society of Washington* 101:804-815.
- Martínez, M. I., Deloya, L.C. & Dellacasa, M. 2001. Anatomical and functional data on female and male reproductive systems of some dung beetles species of Aphodiinae and Eupariinae inhabiting México (Coleoptera Scarabaeoidea: Aphodiidae). *Proceedings* of the Entomological Society of Washington 103(1):227-248.
- Martín-Piera, F. & López-Colón, J.I. 2000. Coleoptera, Scarabaeoidea I. Fauna Ibérica14. Museo Nacional de Ciencias Naturales, CSIC, Madrid, España. 526 pp.
- Matsuda, R. 1976. Morphology and evolution of the insect abdomen. Pergamon Press, Oxford, 534 pp.

- Morón, M. A. 1995. Review of the Mexican species of Golofa Hope (Coleoptera: Melolonthidae: Dynastinae). *The Coleopterist Bulletin* 49(4):343-384.
- Nikolaev, G.V. 1977. Materialy k izučenju plastinčatousykh žukov podroda Odontotrupes Fairm. Roda Geotrupes Latr. (Coleoptera, Scarabaeidae). *Entomologicheskoye obozreniye* 61(2):375-382.
- Pluot-Sigwalt, D. & Martínez, M. I. 1998. Anatomie morpho-fonctionnelle de l'appareil génital mâle des Coléopteres Scarabaeoidea coprophages: Données comparatives. *Annales de la Société Entomologique de France* 34(4):419-444.
- Ritcher, P.O. & Baker, C.W. 1974. Ovariole numbers in Scarabaeoidea (Coleoptera: Lucanidae, Passalidae, Scarabaeidae). Proceedings of the Entomological Society of Washington 76:480-494.
- Ritterhaus, K. 1927. Studien zur Morphologie und Biologie von Phyllopertha horticola L. und Anomala aenea Geer. (Coleopt). Zeitschrift für Morphologie und ökologie der Tiere 8:282-408.
- Robertson, J.G. 1961. Ovariole numbers in Coleoptera. *Canadian Journal of Zoology* 39: 245-263.
- Sharp, D. & Muir, F. 1912. The comparative anatomy of the male genital tube in Coleoptera. *Transactions of the Royal Entomological Society of London* 60:477-642.
- Scholtz, C. H. & Browne, D. J. 1996. Polyphyly in the Geotrupidae (Coleoptera: Scarabaeoidea): A case for a new family. *Journal of Natural History* 30:597-614.
- Snodgrass, R.E. 1935. Principles of insect morphology. MacGraw-Hill Book Company, Inc., New York and London. 667 pp.
- Tuxen, S.L. 1970. Taxonomist's Glossary of Genitalia of Insects. 2nd ed. Munksgaard, Copenhagen. 359 pp.
- Trotta-Moreu, N., Montes de Oca, E. & Martínez, M. I. 2007. Ecological and reproductive characteristics of Geotrupes (Halffterius) rufoclavatus Jekel, 1865 (Coleoptera: Scarabaeoidea: Geotrupinae) on the Cofre de Perote volcano (Veracruz, México). *The Coleopterists Bulletin* 61:435-446.

- Trotta-Moreu, N., Lobo, J. & Cabrero-Sañudo, F. J. 2008. Distribución conocida y potencial de Geotrupinae (Coleoptera: Scarbaeoidea) México. Acta Zoológica Mexicana (nueva serie) 24(2):39-65.
- Vaz de Mello, F. Z. 2007. Revisión taxonómica y análisis filogenético de la tribu Ateuchini (Coleoptera: Scarabaeidae: Scarabaeinae). *Tesis de Doctorado*. Instituto de Ecologia A. C., Xapala, Veracruz, México. 238 pp.
- Virkki, N. 1957. Structure of the testis follicle in relation to evolution in the Scarabaeidae. *Canadian Journal of Zoology* 35:265-277.
- Willimzik, E. 1930. Über den Bau der Ovarien verschiedener coprophager Lamellicornier und ihre Beziehungzur Brutpflege. Zeitschrift für Morphologie und Ökologie der Tiere 18:669-700.
- Sharp, D. & F. Muir, F. 1912. The comparative anatomy of the male genital tube in Coleoptera. Transactions of the Royal Entomological Society of London 60:477-642
- Zunino, M. 1983. Essai préliminaire sur l'evolution des armures genitales des Scarabaeinae, par rapport à la taxonomie du groupe et à la l'évolution du comportement de nidificacion. Bulletin de la Société Entomologique de France 88:531-542.
- Zunino, M. 1984 a. Sistematica generica dei Geotrupinae (Coleoptera, Scarabaeoidea: Geotrupidae), filogenesi della sottofamiglia e consideración biogeografiche. *Bolletino del Museo Regionale di Scienze Naturali Torino* 2(1):9-162.
- **Zunino, M. 1984 b.** Analisi sistematica e zoogeografica della sottofamiglia Taurocerastinae Germain. *Bolletino del Museo Regionale di Scienze Naturali Torino* 2(2): 445-464.





Discusión Final

## DISCUSIÓN FINAL

Los Geotrupinae Mexicanos son un grupo muy poco estudiado en México, a pesar de que en este país ha habido una gran tradición en el estudio de los Scarabaeoidea (Onore *et al.*, 2003). En la presente tesis, se ha pretendido aumentar un poco más el conocimiento biológico existente sobre este grupo para México, presentando una serie de resultados básicos que pueden servir de apoyo para la realización de estudios posteriores.

De esta manera, se presentan por primera vez los mapas de distribución de cada una de las especies de Geotrupinae. Estos mapas nos muestran que, en general, los Geotrupinae pueden encontrarse por todo el territorio mexicano. Los Geotrupini tienen preferencia por zonas más altas y montañosas, los Bolboceratini por zonas bajas y, en general, por todo el territorio mexicano y los Athyreini también por zonas bajas, pero con distribuciones más meridionales.

El estado mexicano que presenta un mayor número de especies conocidas hasta ahora es Oaxaca, con quince especies, y los que presentan un menor número serían Aguascalientes y Quintana Roo, sin especies conocidas.

Los mapas de distribución potencial nos muestran las zonas nuevas donde podrían habitar las diferentes especies hasta ahora conocidas. Por otra parte, los análisis del proceso descriptivo muestran, también, que todavía quedarían nuevas especies por describir. Por lo tanto, a consecuencia de los análisis realizados en este campo, se abren nuevas líneas de investigación, como la búsqueda de nuevas especies y la localización de nuevas localidades de distribución para las especies conocidas. La búsqueda de nuevas localidades debería centrarse en las zonas señaladas por los modelos predictivos, lo que también nos permitiría a su vez corroborar la validez de dichos modelos. La búsqueda de nuevas especies estaría dirigida hacia los Geotrupinae, en general, y en concreto hacia los Geotrupini, en enclaves meridionales y buscando especies con rangos de distribución reducidos. En el caso de los Bolboceratini, estos esfuerzos deberían centrarse sobre zonas situadas más hacia el Norte tal y como han mostrado los análisis del proceso de descripción de especies.

Los estudios realizados sobre los Geotrupini a escala local (Cofre de Perote, Veracruz) también han servido para conocer más sobre la ecología de los Geotrupini. Los datos obtenidos en los muestreos y en los posteriores análisis estadísticos realizados nos muestran diferentes aspectos de la ecología de este grupo. Así, se ha observado que los Geotrupini encontrados en dicha zona empiezan a aparecer a partir de los 2200 metros de altitud, que las zonas de distribución de cada especie parecen estar muy delimitadas por la orientación de la montaña y, por último, que parece haber una relación significativa entre la altura, la preferencia de hábitat y la fenología. Estos resultados sugieren que es necesario estudiar las comunidades de estos escarabajos en las áreas de solapamiento entre las distintas especies del Cofre de Perote. También sería interesante estudiar en el futuro las preferencias de hábitat y la fenología de estas especies y la relación de estas características con las variaciones altitudinales y climáticas.

Otra parte importante de la tesis ha sido el estudio de los sistemas reproductivos masculino y femenino en diversas especies de Geotrupini. Se han estudiado especies pertenecientes a todos los subgéneros de geotrupini mexicanos. En la mayoría de los casos ha sido la primera vez que se han descrito, con detalle, estos sistemas reproductivos y que se han comparado unos subgéneros con otros. Así pues, el trabajo presentado es meramente descriptivo y comparativo.

A lo largo del desarrollo de la tesis se ha ido señalando la importancia que tienen dichos estudios para poder conocer y desarrollar la sistemática y la filogenia del grupo en un futuro. Es así, entonces, que este trabajo serviría como base o como apoyo para la realización de estudios posteriores sobre la filogenia y sistemática de dicho grupo. Actualmente, todavía hay muchos interrogantes sobre este tema, puesto que se han realizado diversas clasificaciones (ver segundo trabajo de la tesis) y alguna filogenia (Scholtz & Browne, 1996; Verdu *et al.,* 2004), pero, aún así, en este campo quedarían bastantes interrogantes por resolver.

Así pues, resumiendo, la presente tesis ha aportado nuevos datos del conocimiento
de los Geotrupidae en México, ha abierto nuevas líneas de investigación, pero también se ha servido para poner de manifiesto que todavía quedan muchos estudios por realizar para poder conocer a este grupo de insectos.





## **Conclusiones Finales**

## **CONCLUSIONES FINALES**

A lo largo de los diferentes capítulos en que hemos dividido la presente tesis hemos ido procurando alcanzar los objetivos propuestos en su inicio, a partir de las diferentes técnicas, nociones y procedimientos propios de cada disciplina considerada (Biogeografía, Ecología y Anatomía). No obstante, la consecución de estos objetivos no cierra, ni mucho menos, las posibilidades de investigación que ofrecen los Geotrupinae mexicanos, sino que, en realidad, abre nuevas vías de investigación para continuar en el estudio de dicho grupo de insectos.

La presente tesis aporta, por primera vez, mapas de distribución reales y potenciales para los Geotrupinae en el territorio mexicano. Se analiza por primera vez el proceso descriptivo de los Geotrupinae mexicanos comparándolo con el proceso descriptivo de las especies del Paleártico. Se ha realizado, también, el primer estudio ecológico básico sobre las especies encontradas en una zona de México (Cofre de Perote, Veracruz). Y, por último, se han descrito y comparado detalladamente los sistemas reproductores de los géneros de Geotrupini mexicanos. Considerando en su conjunto los resultados obtenidos, las conclusiones obtenidas por medios de estos estudios pueden resumirse en los siguientes apartados:

- La curva de acumulación de las especies de Geotrupinae descritas para el Norte y Centro-América parece poseer un carácter asintotico, de modo que, considerando la actual tasa de descripción de especies, quedarían por describir entre un 10 o un 20% del total de especies.
- 2. Según se extrae de los análisis estadísticos realizados, las variables más influyentes en el proceso descriptivo de estas especies fueron los efectos puros relacionados con la localización y el rango geográfico, así como el efecto combinado de ambos. El tamaño corporal no ha resultado ser un factor primordial a la hora de explicar el proceso de descripción taxonómica seguido por los Geotrupinae de Norte y Centro-America.

- 3. Comparando el proceso descriptivo de los Geotrupinae de Norte y Centro-America con el que se obtuvo para el Paleártico Occidental, se ha observado que en la fauna del Paleártico Occidental la curva de acumulación sí habría alcanzado la asíntota, por lo que se habrían descrito la mayoría de las especies. Las variables que más influyeron en el proceso descriptivo para ambas faunas son similares, aunque varíe su importancia comparada.
- 4. Los mapas obtenidos para los Geotrupinae mexicanos no sólo nos proporcionan una imagen razonable de la distribución de las especies, sino que constituyen una herramienta útil para el diseño y planificación de nuevas colectas.
- 5. Las distribuciones potenciales presentadas podrían considerarse imágenes que nos muestran, en general, cuáles serían las tendencias de distribución de estas especies si a lo largo de la historia evolutiva de estos taxones si no hubiera habido ninguna otra influencia que la climática.
- 6. La fauna de Geotrupinae mexicana está compuesta por grupos taxonómicos con diferentes orígenes e historias biogeográficas, los cuales han marcado la distribución actual de sus especies. Por lo tanto, el conocimiento de esta información biogeográfica complementa y da sentido a las distribuciones presentes en los mapas.
- 7. Los modelos predictivos tienden a sobrestimar la distribución de las especies, al no incluir las ausencias en los análisis. Por ello, es necesario incorporar una medida de fiabilidad usando combinadamente modelos predictivos con estimadores no paramétricos que reduzcan dichos errores y que puedan estimar la precisión de los modelos predictivos.

- 8. A partir de los datos obtenidos en el muestreo realizado en el Cofre de Perote, Veracruz, y los datos obtenidos en la bibliografía, se observa que la distribución de los Geotrupini en dicha zona parece ser muy regionalizada para cada especie.
- 9. La mayor parte de los individuos colectados en el muestreo corresponden a la especie *Geotrupes (Halffterius) rufoclavatus*. Esta especie aparece desde los 2200 metros de altitud, siendo más abundante a partir de los 3000 m. Por debajo de los 3000 m. de altitud, la mayor cantidad de individuos está en bosques de pinos y se presentan varios picos de abundancias altas al año. A más de 3000 m. de altitud, el número de individuos es mayor en campos de cultivo y en potreros, y se presenta un solo pico de abundancia alta al año.
- 10. En el estudio realizado en la localidad de Tonalaco (Cofre de Perote), se encontraron 7 hembras y 4 machos a lo largo del año. Todos los machos y las hembras encontrados estaban en proceso de maduración sexual, menos una hembra que se encontró ya madura en el mes de febrero.
- 11. El sistema reproductivo femenino en los ejemplares estudiados es bastante similar para todas las especies. Las hembras presentan dos ovarios con seis ovariolas cada uno. Cada ovario termina en un oviducto lateral. Los dos oviductos laterales desembocan en un oviducto común que, a su vez, desemboca en la vagina.
- Las principales diferencias morfológicas en las hembras se encuentran a nivel de los coxosubcoxitos.

- 13. El sistema reproductivo masculino es bastante similar en todas las especies estudiadas. El sistema reproductor está formado por un par de testículos, cada uno con seis folículos testiculares esféricos. De cada testículo sale un conducto deferente. Se presentan dos pares de glándulas accesorias, unas son muy largas y enrolladas sobre sí mismas y desembocan en su propio reservorio glandular, las otras son muy cortas y no tienen reservorio. Los dos conductos deferentes y los dos reservorios glandulares desembocan en la parte anterior del bulbo eyaculador. La parte posterior del bulbo eyaculador desemboca en el edeago.
- Las principales diferencias morfológicas en los machos se encuentran a nivel del edeago.









## **BIBLIOGRAFÍA ADICIONAL**

- Arellano, L. 1992. Distribución y abundancia de Scarabaeidae y Silphidae (Insecta: Coleoptera) en un transecto altitudinal en el Estado de Veracruz. *Tesis de Licenciatura*. *Universidad Nacional Autónoma de México*. 205 pp.
- Arellano, L. 2002. Evaluación de la diversidad alfa, beta y gamma de Scarabaeoidea y Silphidae (Insecta: Coleoptera) en la región Cofre de Perote, Veracruz, México. *Tesis de Maestria. Universidad Nacional Autónoma de México.* 197 pp.
- Balthasar, V., 1963. Monographie der Scarabaeidae undaphodiidae der Palaearktischen und Orientalischen Region (Coleoptera: Lamellicornia). Volume 1. Scarabaeidae. Verlag Tschechoslovakia Akademie Wissenschaft, Prague.
- Bartlein, P. J., Prentice, Y. C. & Webb, T., 1986. Climatic response surfaces from pollen data for some eastern North American taxa. *Journal of Biogeography* 13:35-37.
- Beattie, A. (Ed.), 1995. Australia's Biodiversity Living Wealth. Griffin Press, Netley, Australia.
- Bornemissza, G. F., & C. H. Williams. 1970. An effect on dung beetle activity on plant yield. *Pedobiologia* 10:1-7.
- Bornemissza, G. F. 1976. The Australian Dung Beetle Project 1965-1975. *Australian Meat Research Committee Review*. 30:1-30.
- Buckland, S. T. & D. A. Elston. 1993. Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology* 30:478-495.
- Clark, T. E. & Samways, M. J., 1993. Ecological landscaping for conservation of macroarthropod diversity in a southern hemisphere (Sourh African) urban botanic garden. En: Habitat Creation and Wildlife Conservation in Post-industrical and Urban Habitats. J. Rieley and S. Page eds. Packard. United Kingdom.
- **Fincher, G. T. 1981.** The potential value of dung beetle activity on the number of nematode parasitoid required by grazing cattle. *Journal of Parasitology* 61:759-762.
- Galante, E., & Verdú, J. R., 2000: Los artrópodos de la "Directiva Hábitat" en España.
   *Ministerio de Medio Ambiente*, Dirección General de Conservación de la Naturaleza, Madrid, España.

- Gaston, K. J., 1991. The magnitude of global insect species richness. *Conservation Biology* 5:283-296.
- Gaston, K. J., 1994. Spatial Patterns of species description: how is our knowledge of the global insect fauna growing? *Biological Conservation*. 67:37-40.
- Groombridge, B., & Jenkins, M. D., 2002: World atlas of biodiversity. Earth's living resources in the 21st century. Preparado por la UNEP World Conservation Monitoring Centre, University of California Press, Berkeley, EEUU.
- Halffter, G. & A. Martínez. 1962. Monografía del Género Ceratotrupes Jekel (Coleopt. Scarab. Geotrup.). *Ciencia* 11(4):145-159.
- Halffter,G. 1964. La Entomofauna Americana, ideas acerca de su origen y distribución. Folia Entomológica Mexicana 6:1-108
- Halffter, G. 1972. Eléments anciens de l'entomofaune Néotropicale: ses implications biogéographiques. Pages 1-40 in *Biogéographie et Liaisons Intercontinentales au Cours du Mésozoïque* (t. C. o. I. Zoology, ed.), Monte Carlo.
- Halffter, G. 1976. Distribución de los insectos en la zona de Transición Mexicana. Relaciones con la entomofauna de Norteamérica. *Folia Entomologica Mexicana* 35:1-64.
- Halffter, G. 1978. Un nuevo patrón de dispersión en la Zona de Transición Mexicana: el mesoamericano de montaña. *Folia Entomologica Mexicana* 39-40:219-226.
- Halffter, G., & W. D. Edmonds. 1982. The nesting behavior of dung beetles (Scarabaeinae).
  An ecological and evolutive approach. *Instituto de Ecología*, México D. F., México.
- Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. *Annual Review of Entomology* 32:95-114.
- Halffter, G. y Ezcurra, E. 1992. ¿Qué es la biodiversidad? En: La diversidad biológica en Iberoamérica I: (ed. Halffter, G.), pp 2-24, Acta Zoológica Mexicana (número especial), Xalapa, Veracruz, México.
- Halffter V., López-Guerrero, Y. & Halffter G. 1985: Nesting and ovarian development in Geotrupes cavicollis Bates (Coleoptera: Scarabaeidae). *Acta Zoológica Mexicana* (n.s.). 7:1-28.

- Howden, H. F. 1964. The Geotrupinae of North and Central America. Memoirs of the Entomological Society of Canada. 39:1-91.
- Howden, H. F. 2003. Geotrupinae in Atlas de los escarabajos de México (Coleoptera: Lamellicornia Vol. 2: Scarabaeidae, Trogidae, Passalidae y Lucanidae) (M. A. Morón, ed.) Argania, Barcelona, Spain.
- Huntley, B. Berry, P. M., Cramer, W & McDonald, A. P., 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography* 22:967-1001.
- Jones, P. G., Sthephen. E., Joe Thome, B, Galwey, N. W., 1997. The use of geographical information systems in biodiversity exploration and conservation. *Biodiversity Letters* 6:947-958.
- Kohlmann, B. 1991. Dung beetles in subtropical North America. Pages 116-132 in Dung beetle ecology (I. Hanski, & Y. Cambefort, eds.). *Princeton University Press*, New Jersey, USA.
- Krikken, J. 1981. Geotrupidae from the Nepal Himalayas. New flightless species of Geotrupes Latreille, with a biogeographical discussion. *Senckenbergiana Biologica* 61(5-6):369-381.
- López-Guerrero, Y. & Benitez, J. 1982. Análisis de la estructura de testículo y neurosecreción durante la etapa reproductora en Geotrupes cavicollis (Coleoptera-Geotrupinae). *Actas del VIII Congreso Latinoamericano de Zoología*, vol. 1, Tomo 2: 1039-1048.
- López-Guerrero Y. 1987: Análisis de la estructura del testículo y de las células neurosecretoras de la pars intercerebralis de Halffterius rufoclavatus (Jekel) (Coleoptera: Geotrupinae: Ceratotrupini). Estratto dal Bolletino del Museo Regionale de Scienze Naturali – Torino 5(2):433-445.
- Martín-Piera, F., & J. M. Lobo. 1995. Diversity and ecological role of dung beetles in Iberian grasslands biomes. Pages 147-153 in Farming on the edge: the nature of tradicional farmland in Europe (D. I. McCracken, E. M. Bignal, & S. E. Wenlock, eds.). *Joint Nature Conservation Committee*, Peterborough, UK.

Martín-Piera, F., 1997. Apuntes sobre biodiversidad y conservación de insectos: dilemas,

ficciones y ¿soluciones? Boletín de la Sociedad Entomológica Aragonesa 20: 1-31

- Martín-Piera, F., & J. I. López-Colón. 2000. Coleoptera, Scarabaeoidea I. Fauna Ibérica 14. Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain.
- Martínez, I., & M. Cruz. 1999. Comparative morphological analysis of testis follicles in dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae, Aphodiinae, Geotrupinae). *Proceedings of the Entomological Society of Washington* 101:804-815.
- McKay, R., 2002: The Penguin atlas of endangered species. A worldwide guide to plants and animals. *Penguin Books Ltd. Harmondsworth*, Middlesex, GB.

McQueen, A. 1975. Dung as insect food source: dung beetle as competitors of other coprophagous fauna and as targets for predators. *Journal of Applied Ecology* 12:821-827.

- McQueen, A., & B. P. Beirne. 1975. Influence of other insects on production of horn fly, Haematobia irritans (Diptera: Muscidae) from cattle dung in south-central British Columbia. *Canadian Journal of Plant Science* 107:1255-1264.
- Nikolaev, G.V. 1977. Materialy k izučenju plastinčatousykh žukov podroda Odontotrupes Fairm. Roda Geotrupes Latr. (Coleoptera, Scarabaeidae). *Entomologicheskoye obozreniye* 61(2):375-382.
- Norse, E. A., Rosenbaum, K. L., WilRove, D. S., Wilcox, B. A., Romme, W., H., Johnston,
   D. W., & Stout, M. L., 1986. Conserving biological diversity in our national forests.
   The Wilderness Society, Washington, EEUU.
- Onore, G., Reyes-Castillo, P., Zunino, E.M. 2003. Presentación. En: Escarabeidos de Latinoamérica: Estado del conocimiento (ed). Pp. 7-8. *Monografías Tercer Milenio*.
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995. The future of biodiversity. Science 269:347-350.
- Pluot-Sigwalt D. & Martínez M. I. 1998 : Anatomie morpho-fonctionnelle de L'appareil génital mâle des Coléopteres Scarabaeoidea coprophages : Données comparatives. Annales de la Société Entomologuique de France 34(4): 419-444.
- Rosas, G., Ramos, M. A. & García-Valdecasas, A., 1992. Invertebrados españoles protegidos por Convenios Internacionales. ICONA. Ed. Madrid. 250 pp
- Rougon, D., C. Rougon, J. Trichet, & J. Levieux. 1988. Enrichissement en matipre

organique d'un sol sah'Ulien au Niger par les insects coprophages (Coléoptères: Scarabaeidae): implications agronomiques. *Revue d'Ecologie et de Biologie du Sol* 25:413-434.

- Samways, M. J., 1993. A spatial and process sub-regional framework for insect and biodiversity conservation research and management. En: *Perspectives on Insect Conservation. Gaston*, K. J., New, T. R. & Samways, M. J. (Eds.)., pp. 1-28. Intercept ltd., Andover, U.K., 250 pp.
- Samways, M. J., 1994. Insect Conservation Biology. Chapman & Hall. London, 358 pp.
- Scholtz, C. H. & D. J. Browne. 1996. Polyphyly in the Geotrupidae (Coleoptera: Scaraboidea) a case for a new family. *Journal of Natural History* 30:597-614.
- Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco,
  F. D'Erchia, T. C. Edwards, J. Ulliman & R. G. Wright. 1993. Gap Analysis:
  A geographic approach to protection of biological diversity. *Wildlife Monographs* 123:1-41.
- Skov, F. & Borchsenius, F., 1997. Predicting plant species distributio patterns using simple climatic parameters: a case study of Ecuadorian palms. *Ecography* 20:347-355.
- Solbrig, O. T., 1991a. From genes to ecosystems: a research agenda for biodiversity. International Union of Biological Sciencies, Cambridge, EEUU.
- **Solbring, O. T., 1991b.** Biodiversity. A review of the scientific issues and a proposal for a collaborative program of research. UNESCO, MAB Digest, 9.
- Smith, P. A., 1994. Autocorrelation in logistic regression modelling of species' distributions. Global Ecology and Biogeography Letters 4:47-61.
- Verdú, J.R., Galante, E., Lumaret, J.P., and Cabrero-Sañudo, F.J. 2004. Phylogenetic analysis of Geotrupidae based on larval characters. *Systematic Entomology* 24:509-523.
- Waterhouse, D. F. 1974. The biological control of dung. Scientific American 230:101-109

Williams, C. B., 1964. Patterns in the Balance of Nature and related problems in quantitative ecology. *Academic Press London*.

- Williams-Linera, G., G. Halffter, & E. Ezcurra. 1992. Estado de la biodiversidad en México. Pages 285-312 in La diversidad biológica de Iberoamérica (G. Halffter, ed.) Acta Zoológica Mexicana, Xalapa, Veracruz, México.
- Wilson, E. O., 1988. The current state of biological diversity. En: Wilson, E. O., & Peter, F. M. (Eds.), Biodiversity. *National Academy Press*, Washington, EEUU, pps. 3-18.

Wilson, E. O., 1994. La diversidad de la vida. Edit. Crítica. Barcelona.

Zunino, M. 1984. Sistematica genérica dei Geotrupinae (Coleoptera, Scarabaeoidea: Geotrupinae) filogenesi della sottofamiglia e consideración biogeografiche. Bolletino del Museo *Regionale di Scienze Naturale di Torino* 2:9-162.