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The integration processes of the distributional patterns in the Mexican Transition Zone: Phyletic, paleogeographic and ecological factors of a case study

GONZALO HALFFTER[1,4], MARIO ZUNINO[2], VICTOR MOCTEZUMA[1] & JOSÉ L. SÁNCHEZ-HUERTA[3]

[1]*Instituto de Ecología A.C., Red de Ecoetología, Carretera antigua a Coatepec 351, 91070 Xalapa, Veracruz, Mexico. E-mail: gonzalo.halffter@inecol.mx; abadonjvpm@hotmail.com*

[2]*Instituto de Ecología A.C., Invited researcher, Carretera antigua a Coatepec 351, 91070 Xalapa, Veracruz, Mexico. E-mail: mariozunino@hotmail.it*

[3]*Calle Enrique César Velarde 14, Colonia María Esther, 91030 Xalapa, Veracruz, Mexico. E-mail: jlshbeetle@hotmail.com*

[4]*Corresponding author*

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Abstract

In this study, we take the *Onthophagus chevrolati* species group, likely a monophyletic species group as an example to analyze the processes that led to the biogeographic integration of the Holarctic fauna in the mountains of the Mexican Transition Zone to test our biogeographic hypotheses. We propose a change from the status of subspecies to species for *O. oaxacanus* Zunino & Halffter, 1988 **new status**; *O. howdeni* Zunino & Halffter, 1988 **new status**; *O. jaliscensis* Zunino & Halffter, 1988 **new status**; *O. longecarinatus* Zunino & Halffter, 1988 **new status**; *O. omiltemius* Bates, 1889 **revised status**; and *O. retusus* Harold, 1869 **revised status**. Consequently, the *O. chevrolati* group of species is currently made up of 47 species belonging to four species lines: *O. vespertilio, O. hippopotamus, O. cyanellus* and *O. chevrolati*. The diversification of the *Onthophagus chevrolati* species group in this region resulted from three hypothetical stages of evolution. In the first, the penetration and expansion of the ancestor of the *O. chevrolati* species group occurred before the Miocene and the Trans-Mexican Volcanic Belt arose. During the second stage, the *O. hippopotamus* species line expanded and evolved, integrating with the paleogeographic changes and the formation of the Trans-Mexican Volcanic Belt, as a consequence of volcanism during the Miocene-Pliocene. In the third and most recent stage, the *O. chevrolati* species line used the existing mountain systems and interglacial climate fluctuations of the Pleistocene to expand and diversify. Thus, the mountains of the Mexican Transition Zone are not simply periglacial refugia. The entomofauna of Holarctic origin present in the region evolved while the Earth's geological processes were underway.

Key words: *Onthophagus*; Paleoamerican; Onthophagini; Scarabaeinae, dung beetles, Mountain Diversity

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Resumen

En el presente estudio tomamos como ejemplo al grupo de especies *Onthophagus chevrolati*, un grupo aparentemente monofilético, para analizar los procesos que llevaron a la integración biogeográfica de la fauna holártica en las montañas de la Zona de Transición Mexicana para probar nuestras hipótesis. Proponemos el cambio de status de subespecie a especie para *O. oaxacanus* Zunino & Halffter, 1988 **nuevo estatus**; *O. howdeni* Zunino & Halffter, 1988 **nuevo estatus**; *O. jaliscensis* Zunino & Halffter, 1988 **nuevo estatus**; *O. longecarinatus* Zunino & Halffter, 1988 **nuevo estatus**, *O. omiltemius* Bates, 1889 **estatus revisado**; *O. retusus* Harold, 1869 **estatus revisado**. Como consecuencia, el grupo de especies *O. chevrolati* se encuentra integrado por 47 especies incluidas en cuatro linajes: *O. vespertilio, O. hippopotamus, O. cyanellus* y *O. chevrolati*. La diversificación del grupo de especies *O. chevrolati* en la región fue resultado de tres etapas hipotéticas de evolución. En la primera tuvo lugar la penetración y expansión del ancestro del grupo de especies *O. chevolati* antes del Mioceno y de la elevación del Sistema Volcánico Transversal. Durante la segunda etapa, la línea *O. hippopotamus* se expande y evoluciona integrándose con los cambios paleogeográficos y la formación del Sistema Volcánico Transversal, como consecuencia del vulcanismo durante el Mioceno-Plioceno. En la tercera y más moderna etapa, el linaje *O. chevrolati* utiliza los sistemas montañosos existentes y las fluctuaciones climáticas interglaciares del Pleistoceno para expandirse y diversificarse. Como consecuencia, las montañas de la Zona de Transición Mexicana no son simplemente refugios periglaciales. La entomofauna de origen holártico presente en la región evolucionó junto con los procesos geológicos de la tierra.

Introduction

As indicated by Halffter & Morrone (2017; see also Halffter 2017) in their recent analysis of the patterns of distribution and dynamics in the Mexican Transition Zone (MTZ), the genus *Onthophagus* Latreille, 1802 (Coleoptera: Scarabaeidae: Scarabaeinae) is the example *par excellence* of the ecological and geographic diversification that a phyletic line of northern origin can attain in the MTZ. As such, it is suitable for the analysis of the processes that have shaped the integration of the distributional patterns, namely, the origin and phyletic relationships, paleogeographic and geographic scenarios, ecological requirements and changes in them. Currently, the genus *Onthophagus* in the Americas is comprised of more than 180 species (Delgado & Howden 2000; Pulido-Herrera & Zunino 2007; Kohlmann & Solís 2012; Delgado & Curoe 2014; Génier & Howden 2014; Arriaga-Jiménez *et al*. 2016; Moctezuma *et al*. 2016; Génier 2017; Sanchéz-Huerta *et al*. 2018; Gasca-Alvarez *et al*. 2018; Rossini *et al*. 2018a, b). All of the American *Onthophagus* have a common monophyletic origin: a group of the subgenus *Onthophagus*, that has spread out starting from the eastern part of the Palearctic region and the Chinese Transition Zone (Zunino & Halffter 1988a; Breeschoten *et al*. 2016). From this group several penetrations into America have occurred via what is now Bering Strait and have led to a series of lines distributed throughout the biogeographic provinces of the MTZ and even extend into South America. This migration process was first pointed out by Zunino & Halffter (1981), widely discussed by Zunino & Halffter (1988a), and confirmed with studies of the genitalia (Halffter 1991, 2003; Palestrini & Zunino 1986; Zunino & Halffter 1997) and phylogenetic studies (Tarasov & Solodovnikov 2011; Breeschoten *et al.* 2016).

Prior to the work of Zunino & Halffter (1997) five groups of *Onthophagus* were recognized in the Americas, with more than 130 species. Other studies (Génier & Howden 1999; Kohlmann & Solís 2001; Génier 2017; Rossini *et al*. 2018a) have increased the number of American groups to seven. It is interesting to note that although they all have the same geographic origin in what is today the Palearctic region, their distribution in the MTZ and in Central and South America follows completely different patterns: one species group is exclusive to the mountains (*O. chevrolati*) and mountain systems at the highest elevations; another is typical of the Mexican High Plateau (*O. mexicanus*); the ecological description of two others is less defined, with one typical of tropical forests (*O. clypeatus*); two other groups (*O. gazellinus* and *O. dicranius*) mainly found in cloud forest, and the last two (*O. hircus* and *O. landolti*) with a broad distribution (Génier & Howden 1999; Howden & Gill 1993; Kohlmann & Solís 2001; Génier 2017; Rossini *et al*. 2018a, 2018b).

The process of penetration by the northern biota into the Americas (and their consequent integration into the existing biota, their extinctions and displacement) has been interpreted by Zunino (Zunino and Zullini 2003 and literature cited therein) in terms of dynamic vicariance. The changing configuration of land connections between northeastern Asia and the current northwestern corner of America (currently the Bering Strait) and changing climate conditions from subtropical to the present boreal, for extended periods of time, allowed the biota from different climates (from subtropical to temperate cold) to disperse to North America and then southwards. In more than one stage of the previous process, it is highly probable that different species of *Onthophagus sensu* Zunino (1979) were involved; their evolution in the Americas have given rise to groups, whose biogeographic and ecological distribution fall into distinct distributional sub-patterns within the Paleoamerican pattern (Halffter 2017; Halffter & Morrone 2017).

The subgenus *Onthophagus sensu stricto*, absent from sub-Saharan Africa, is present in the western Palearctic with two species and very well represented in the eastern Old World. Of the Onthophagini, it is the group that has the greatest dispersal capacity. In addition to the American *Onthophagus* fauna, that of Australia has been included into the same subgenus by Palestrini (1985; Fig. 1). According to Matthews (1972) the Australian *Onthophagus* fauna is derived from several ancestors from the northeast that colonized the continent in different stages. Recently, Breeschoten *et al*. (2016), based on a molecular phylogenetic analysis, have stated that "all New World species of *Onthophagus* formed a monophyletic group, and the Australian taxa are confined to a single or two closely related clades, one of which forms the sister-group of the New World species". Moreover, quoting Tarasov & Solodnikov (2011), the authors emphasize "grouping these clades with Oriental taxa in the *Onthophagus* subgenus *Onthophagus*".

The evolution of the Earth and of the biota it hosts are manifestations of the same phenomenon, but the usual approach is to treat both processes independently, leading to separate conclusions. Over the course of our research (Zunino & Halffter 1988a, 1997; Sánchez-Huerta *et al*. 2015, 2018; Arriaga *et al.* 2016; Moctezuma *et al.* 2016; Joaqui *et al*. 2019), we have studied one of the great lines of insects that originated in the Old World and that penetrated the Americas via a northern route: the *O. chevrolati* species group (Figs. 2–8). The aim of these studies has been to achieve a global perspective of the evolution of the geographical distribution of the faunal elements of northern origin.

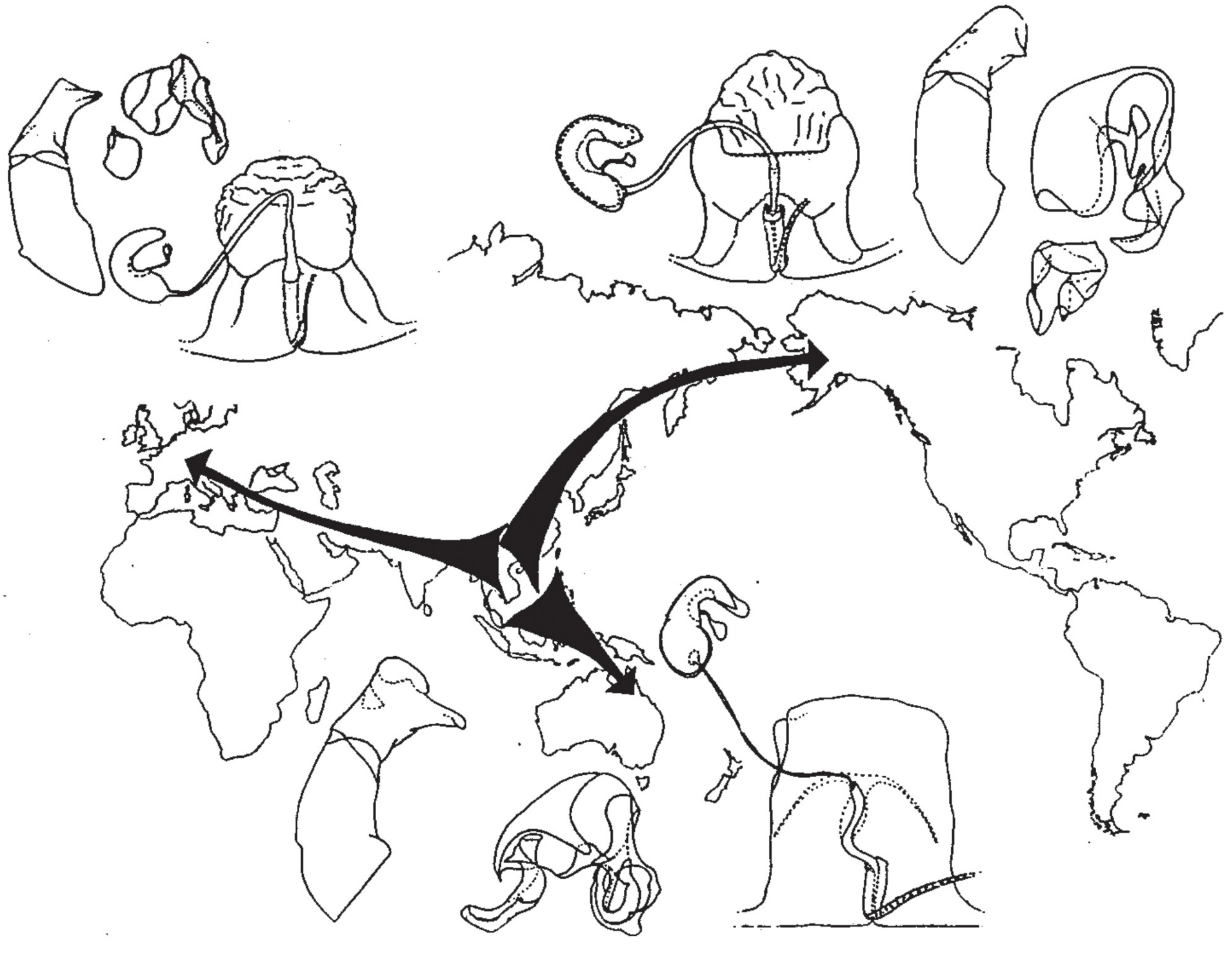

FIGURE 1. The origins of the American *Onthophagus* modified from Palestrini (1985).

With the present study, we aim: 1) to present a synthesis of the previous taxonomic studies on the *O. chevrolati* species group, and a taxonomic view of the geographical distribution of this group; 2) to evaluate the geological proposals of evolution of the Trans-Mexican Volcanic Belt (TMVB), as a context for the evolution of the *O. chevrolati* species group, both in relation to this group's morphology and its ecological requirements; and 3) to discuss the expansion of the *O. chevrolati* species group in the MTZ through at least three major stages of evolution.

From its beginnings, up to phenomena that are occurring today, the distribution of the fauna of northern origin in the MTZ has occurred hypothetically over a period of about 23 million years. During this long period of time, the factors that determine the distributional patterns have not always been equal. In this study, we propose that the expansion of the *O. chevrolati* species group in the MTZ (and possibly that of other groups of northern origin) has undergone at least three major stages of evolution. The first stage corresponds to the arrival of the ancestral line prior to the Miocene and prior to the rise of the TMVB; the line that would eventually become the *O. chevrolati* species group. *Onthophagus vespertilio* Howden, Cartwright & Halffter, 1956 (Fig. 2) and *O. cyanellus* Bates, 1887 (Figs. 7, 8) are witnesses of this stage.

Currently, *O. vespertilio* is limited to two caves that are close together in the state of Guerrero (the caves of Acuitlapán and El Mogote). These caves are located in the Balsas River Basin, south of the TMVB, on limestone dating from the Albian-Cenomanian (Cretaceous). Its origin appears to have been in the Plio-Pleistocene (Bonet 1971). *Onthophagus vespertilio* could be much older than the caves it currently inhabits. The association of *O. vespertilio* with the caves of Acuitlapán and El Mogote represent an endemism, but not a paleoendemism. In the section "The association with caves, burrows and rodent nests" the general association of *Onthophagus* with caves is discussed.

The other species line that we have identified as having supposedly primitive characteristics is that of *O. cyanellus* with O. *chiapanecus* Zunino & Halffter, 1988 and *O. salvadorensis* Zunino & Halffter, 1988; while Joaqui *et al*. (2019) suggest there is a close relationship between *O. semiopacus* Harold, 1869 and the species mentioned above. The *O. cyanellus* species line has a very broad, though not continuous, distribution, in eastern Mexico and Central America from Tamaulipas to Panama (Zunino & Halffter 1988a; Kohlmann & Solís 2001).

The second stage in the evolutionary history of the *O. chevrolati* species group in the MTZ occurs with the penetration of the *O. hippopotamus* species line (see "The *Onthophagus hippopotamus* species line and species complex"; Figs. 3–5). The *O. hippopotamus* species line has two species complexes: *O. hippopotamus* (Fig. 3) and *O. brevifrons* (Figs. 4, 5). The *O. hippopotamus* species complex evolved in and with the TMVB. Its current distribution is centered on the TMVB, with some expansion at its edges. Its evolution occurred in synchrony with the configuration of the TMVB in the Miocene-Pliocene. The volcanism of the Pliocene and Pleistocene and the glaciations of the Pleistocene fragmented distribution areas and created barriers within them for the *Onthophagus*, with the consequent processes of speciation. The species within the *O. hippopotamus* species complex are much more distinct in their morphology than the species of the *O. chevrolati* species line are (Fig. 6). Thus, as high mountain species, they can withstand strong daily oscillations in the weather by inhabiting Geomyidae burrows (pocket gophers), the nests of the rat *Neotoma* Say & Ord, 1825 or even caves. None of these associations occurs in the *O. chevrolati* or in the *O. cyanellus* species lines. The aforementioned associations are not occasional, as they are even reflected in some of the morphological characteristics of the male genitalia, and in the distribution areas of these species, which coincide with the distribution of Geomyidae burrows (a group of intermediate age in the MTZ). The other set of species within the *O. hippopotamus* species line is the *O. brevifrons* species complex. It has five species from northwestern Mexico and the United States of America that are closely related to each other. Three of them are associated with caves and the other two with the burrows of the rodent *Neotoma*.

The third and most modern stage of evolution is represented by the *O. chevrolati* species line, the third major set of species of the *O. chevrolati* species group (see "The *Onthophagus chevrolati* species line"). The geographic and ecological distributions of this species line are broader than those of *O. hippopotamus*. It is more modern and though its species are montane, they depend to a lesser degree on the physical configuration of the TMVB. Several pieces of evidence indicate that the dispersion and diversification of the *O. chevrolati* line occurred in the Pleistocene, taking advantage of the mountain systems that already existed. These beetles are adapted to the ecological conditions of high mountain elevations; they do not seek out burrows or caves.

FIGURE 2. *Onthophagus vespertilio*, male dorsal view.

FIGURE 3. *Onthophagus halffteri*, male dorsal view.

FIGURE 4. *Onthophagus brevifrons*, male dorsal view.

FIGURE 5. *Onthophagus moroni*, male dorsal view.

FIGURE 6. *Onthophagus chevrolati*, male dorsal view.

FIGURE 7. *Onthophagus cyanellus*, male dorsal view.

FIGURE 8. *Onthophagus mesoamericanus*, male holotype dorsal view, currently a synonym of *O. cyanellus*.

In summary (and this is a critical point for our hypothesis) the *O. chevrolati* species line has a more modern distribution and one that is geographically and ecologically broader than that of the *O. hippopotamus* species line. Its distribution has not been shaped by the paleogeographic changes of the TMVB, but rather it has used the mountain systems that already exist. Above, we have outlined a reconstruction in time and space of the evolution of the different phyletic lines that make up the *O. chevrolati* species group. This is our working hypothesis. In the sections that follow, we will outline the orogenic evolution of the TMVB. We will present the taxonomy of the units of different levels that comprise the *O. chevrolati* species group, and we will try to reach a conclusion about the relationship between the distributions, the time of penetration into the MTZ by *Onthophagus* and the paleogeography of the TMVB.

It is not common to consider simultaneously for a given time and space the evolution of the terrestrial surface and that of the organisms that inhabit it. The ideas of Léon Croizat, and above all the basic principle of panbiogeography that "flesh and rocks evolve together" (Croizat 1964) have become part of biogeographical discourse (see Zunino & Zullini 2003; Morrone 2009; Lomolino *et al.* 2010), but rarely makes its way into our daily work. Land and biota are usually treated as though they operated separately, even by different authors who use different methods and who later try to compare their conclusions. In this article, using the mountains of the MTZ with elevations greater than 2000 m as the physical setting, and working with a relatively ancient group of beetles, we synthesize five years of work by five researchers, plus the relevant literature.

The physical setting: The Trans-Mexican Volcanic Belt (TMVB)

In a way comparable only to island fauna, the distribution of mountain fauna depends on both the current structure and the history of its geological base: the mountains (Mastretta-Yanes *et al.* 2015). These have determined and determine the possibility of dispersal across its structures and their ecological conditions. The MTZ is a mega-space of mountains (Figs. 9, 10), with more than 70% at elevations above 1800 m. The TMVB is the most important east-west mountain system in the Americas. It crosses Mexico from west to east, between parallels 19 ° to 21 ° N, spanning elevations of 1500 to 3000 m and whose volcanic cones are even higher, especially in the central and eastern sectors. The biota of this mountain system is almost entirely northern in origin. The role of the TMVB as a dispersal path that connects the southern ends of the Sierra Madre Oriental and Occidental mountain systems (Eastern and Western), and the mountains of Guerrero, Oaxaca and Puebla, has been mentioned many times (see Luna *et al*., 2007).

In this paper, we propose that the TMVB is also a large mountane space where a cenocron with Paleoamerican lines and their own distribution processes come together. This confers a central role to the TMVB in the biogeographic structuring of MTZ mountain lines. Mastretta-Yanes *et al*. (2015) call attention to the effects of changes in climate, especially the Pleistocene glaciations, on the distribution of organisms in the TMVB. The coldest periods have caused organisms to move to lower elevations and consequently horizontally as well. As the climate warm and organisms increase the elevation mountain system of their distribution some ecosystems and species may be left isolated. These offer suitable conditions for the processes of allopatric speciation and vicariance that, together, appear to be a result of the horizontal colonization process (Lobo & Halffter 2000).

At the end of the Cretaceous the Laramidian orogeny began, a process that would determine the main physiographic features of the mountains of Mexico and northern Central America, with the exception of the TMVB. By the Mid-Miocene, the Mexican High Plateau had probably reached its full elevation, though its modern topography was shaped during the Miocene-Pliocene. The TMVB began to be formed in the Oligocene, later reaching its full development. Of great importance in geographic-evolutionary processes, the latitudinal layout of the TMVB favors fragmentation and vicariance over dispersion. There has been volcanic activity along the TMVB from the time of its origin to present. This activity has repeatedly caused fragmentation to a greater extent than it has caused catastrophic extinctions. Fragmentation has promoted vicariance, and this is the dominant phenomenon in the biogeography of the TMVB. Few mountain systems in the world highlight the different biogeographic possibilities of a tropical mountain system as the TMVB does. The ancient lines have shaped their distribution areas following the contours of the mountains, whereas the distribution areas of the new lines more strongly reflect their ecological requirements than the geography of the mountain system. In extreme cases, the mountain systems have served as highways for the expansion of the newer lines within certain ecological limits.

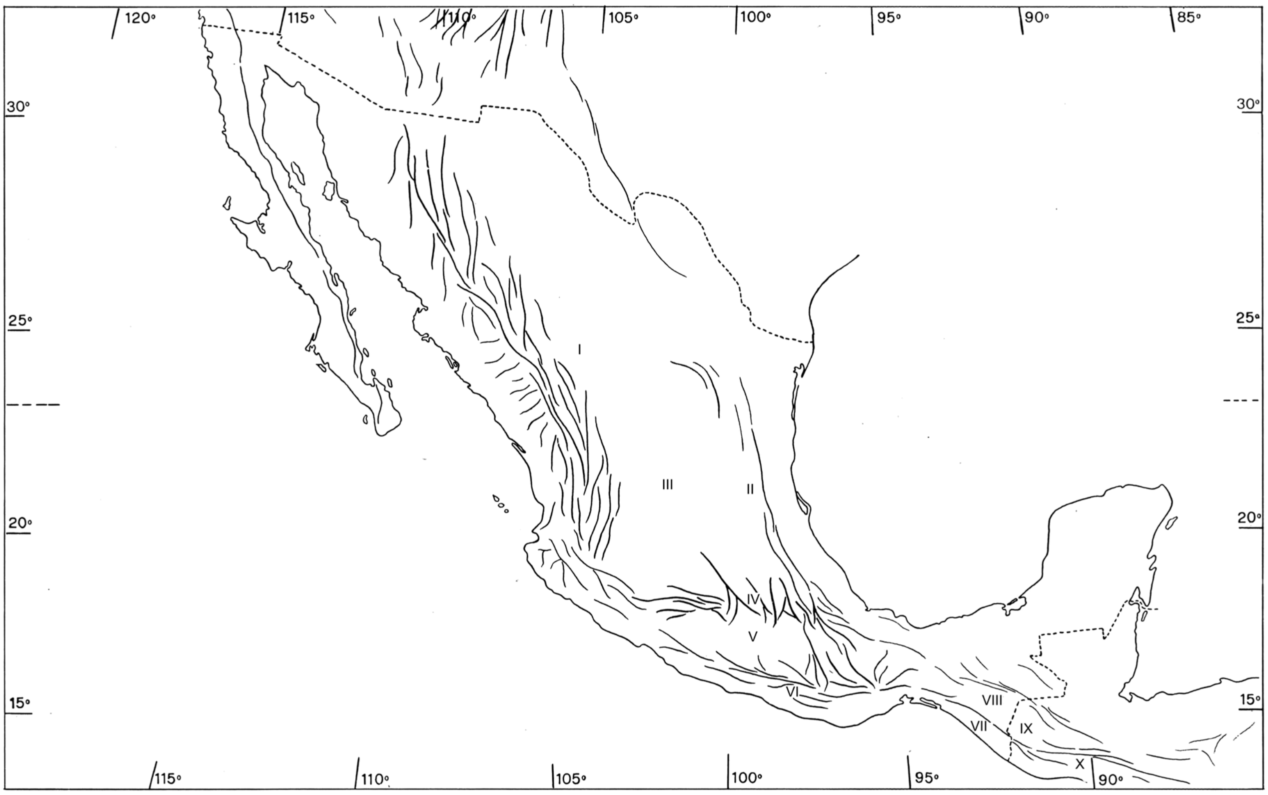

FIGURE 9. Main orographic formations of Mexico. Original map prepared by Violeta Halffter and used on many occasions in the biogeographic studies of the Mexican Transition Zone. I, Sierra Madre Occidental; II, Sierra Madre Oriental; III, Mexican Plateau; IV, Trans-Mexican Volcanic Belt; V, Balsas Basin; VI, Sierra Madre del Sur; VII, Sierra Madre de Chiapas; VIII, Chiapas Highlands; IX, Guatemalan Plateau; X, Central American Nucleous.

The *Onthophagus chevrolati* species group

Venturing into a new kind of biogeographical-phyletic discussion, in which the processes of speciation are properly compared with the geological history of the mountains, requires an adequate knowledge of the taxonomy of the group to be studied. Zunino & Halffter (1988a), based on the morphology of copulation apparatuses and external morphological characters, established the *O. chevrolati* species group, which they consider to be one of the best taxonomically studied of the American fauna of *Onthophagus*. These authors included in the group 39 species and subspecies, and later discoveries increased its number of species.

Based on the monograph by Zunino and Halffter (1988a), whose approaches continue to be valid, we have updated some details of this group's taxonomy using the results of recent studies (Delgado & Capistan 1996; Delgado 1999; Sánchez-Huerta *et al*. 2015, 2018; Arriaga *et al*. 2016; Moctezuma *et al*. 2016; Gasca-Álvarez *et al*. 2018; Joaqui *et al*. in press). We have also studied the morphology of the genitalia in depth, carrying out a detailed, comparative analysis of the characters of all the species of the *O. hippopotamus* species complex, except for *O. padrinoi* of which we have not yet been able to examine the anatomy.

With respect to Zunino & Halffter (1988a) we consider the following changes. All formerly recognized subspecies are elevated to species status. *Onthophagus mesoamericanus* Zunino & Halffter, 1988 (Fig. 9) is provisionally considered a synonym of *O. cyanellus* (Fig. 8). We consider *O. cyanellus* to be a species line, with the same rank as the *O. chevrolati* species line in which it was previously included. Within *Onthophagus*, the *O. chevrolati* species group is the model example of the Paleoamerican Mountain distributional sub-pattern, with the exception of *O. cyanellus* and related species that conform very well to the Paleoamerican Mesoamerican sub-pattern. The graphic representation of our taxonomic ideas (manually drawn in an intuitive manner, based on morphological similarity and supposed evolution) combined with the distribution of the lines is shown in Fig. 11.

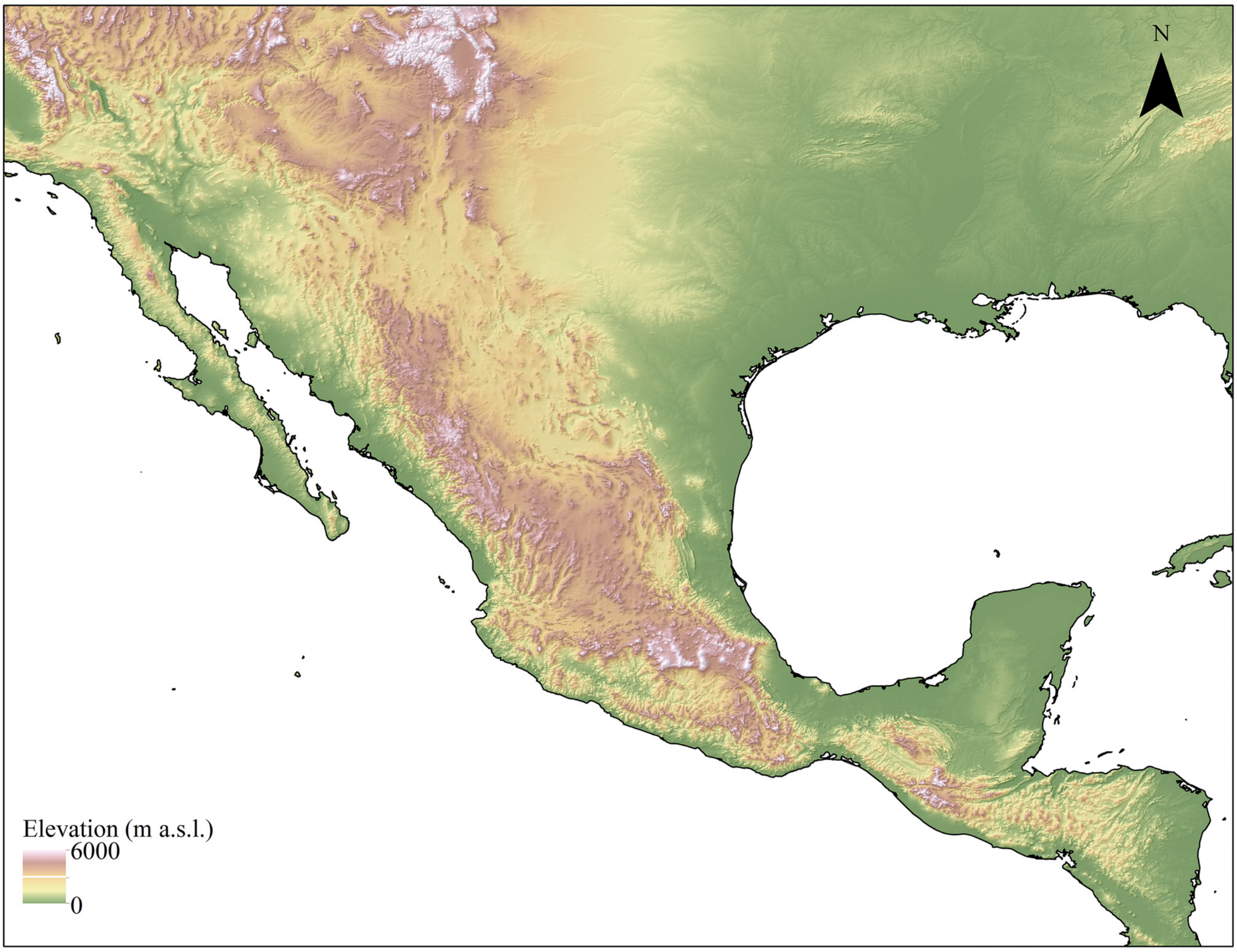

FIGURE 10. Digital Elevation Model of the Mexican Transition Zone.

To distinguish and delimit species, in this work we are following the phylogenetic species concept as defined by Wheeler & Platnick (2000): "The smallest aggregation of (sexual) populations or (asexual) lines diagnosable by a unique set of character states". Consequently, all of the taxa considered as subspecies in the revision by Zunino & Halffter (1988a) are raised to the rank of species, since each has a set of diagnostic characters that allow it to be distinguished from the others, potentially representing different evolutionary histories.

Taxonomy of the *Onthophagus chevrolati* species group, updated from Zunino & Halffter (1988a)

Genus *Onthophagus* Latreille, 1802
Subgenus *Onthophagus* Latreille, 1802 *sensu stricto*
O. chevrolati species group
O. vespertilio species line
O. vespertilio Howden, Cartwright & Halffter, 1956 (Figs. 2, 12)
O. hippopotamus species line
O. hippopotamus species complex (Fig. 13)
O. bassariscus Zunino & Halffter, 1988
O. coproides Horn, 1881
O. cuboidalis Bates, 1887
O. halffteri Zunino, 1981 (Fig. 3)

O. hippopotamus Harold, 1869
O. padrinoi Delgado, 1999
O. skelleyi Sánchez-Huerta, Zunino & Halffter, 2018
O. brevifrons species complex (Fig. 14)
O. brevifrons Horn, 1881 (Fig. 4)
O. cavernicollis Howden & Cartwright, 1963
O. cuevensis Howden, 1973
O. subtropicus Howden & Cartwright, 1963
O. moroni Zunino & Halffter, 1988 (Figs. 5, 15)
O. chevrolati species line
O. chevrolati species complex (Fig. 16)
O. chevrolati Harold, 1869 (Fig. 6)
O. longecarinatus Zunino & Halffter, 1988 **new status**
O. omiltemius Bates, 1889 **revised status**
O. retusus Harold, 1869 **revised status**
O. coahuilae Zunino & Halffter, 1988
O. cochisus Brown, 1927
O. hidalgus Zunino & Halffter, 1988
O. fuscus species complex (Fig. 17)
O. clavijeroi Moctezuma, Rossini & Zunino, 2016
O. fuscus Boucomont, 1932
O. canescens Zunino & Halffter, 1988
O. mycetorum Zunino & Halffter, 1988
O. parafuscus Zunino & Halffter, 2005
O. navarretorum Delgado & Capistan, 1996
O. orizabensis Moctezuma, Joaqui & Sánchez-Huerta, 2019
O. undulans species complex (Fig. 18)
O. howdenorum Zunino & Halffter, 1988
O. undulans Bates, 1889
O. oaxacanus Zunino & Halffter, 1988 **new status**
O. pseudoundulans Zunino & Halffter, 1988
O. howdeni Zunino & Halffter, 1988 **new status**
O. reyesi Zunino & Halffter, 1988
O. aureofuscus species complex (Fig. 19)
O. aureofuscus Bates, 1887
O. gilli Delgado & Howden, 2000
O. inflaticollis Bates, 1889
O. totonicapamus Bates, 1887
O. chilapensis Gasca-Álvarez, Zunino & Deloya, 2018
O. aztecus species complex (Fig. 20)
O. aztecus Zunino & Halffter, 1988
O. bolivari Moctezuma, Rossini & Zunino, 2016
O. tarascus Zunino & Halffter, 1988
O. jaliscensis Zunino & Halffter, 1988 **new status**
O. cyanellus species line (Fig. 21)
O. cyanellus species complex
O. cyanellus Bates, 1887 (Figs. 7, 8)
O. semiopacus species complex
O. semiopacus Harold, 1869
O. chiapanecus Zunino & Halffter, 1988
O. salvadorensis Zunino & Halffter, 1988

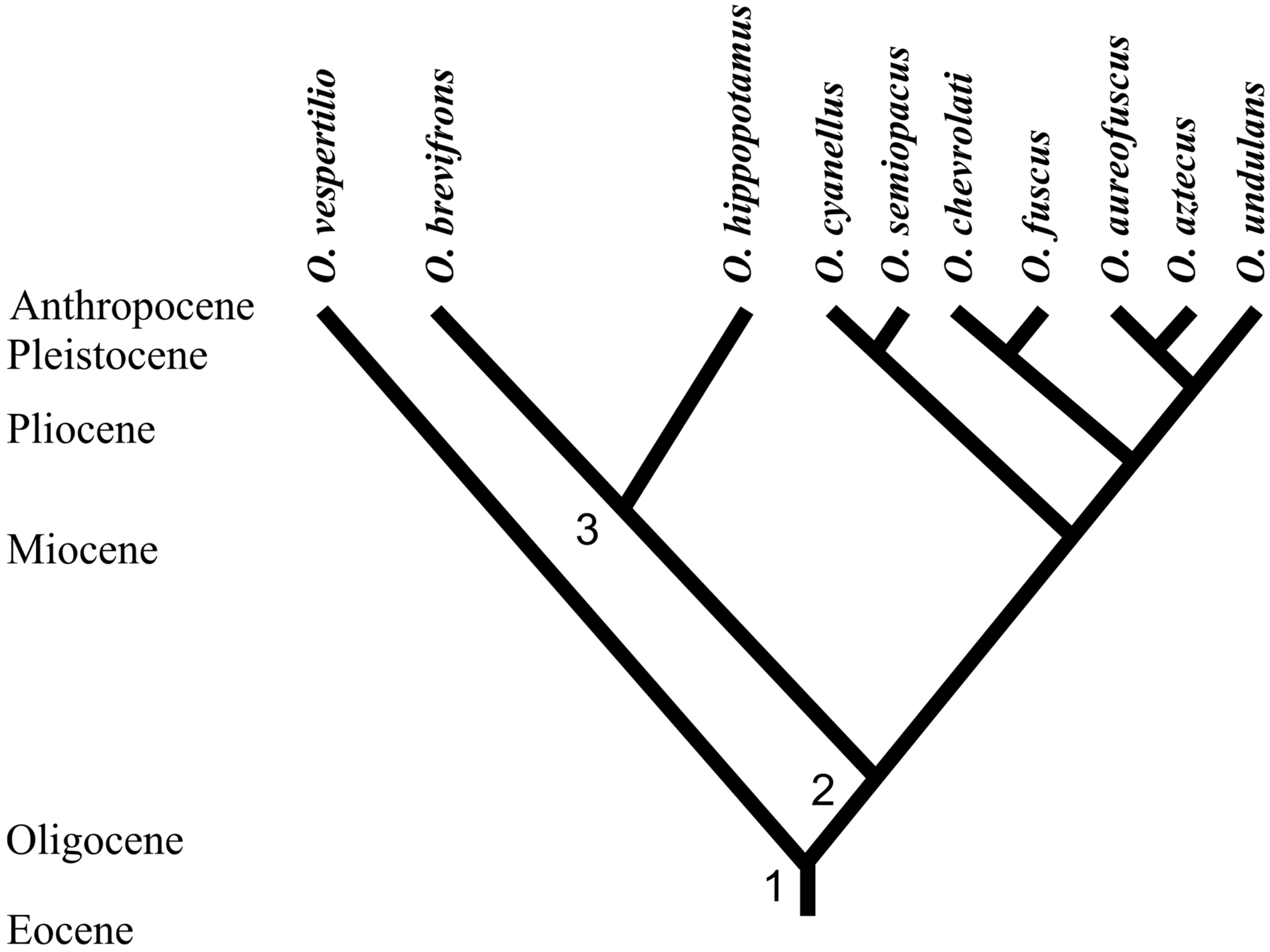

FIGURE 11. Graphic hypothesis of the phyletic diversification and relationships of the *O. chevrolati* species group in the Mexican Transition Zone. Tip names are the species complexes. The figure elucidates our ideas of the taxonomical relationships and evolution of this species group based on the male and female genitalia, external morphology and geographic distribution: 1. The ancestral line of the *O. chevrolati* species group must have arrived in what is now Mexico between the Eocene and the Miocene, as part of the most ancient fauna of northern origin. The ancestor of *O. vespertilio* early separated from the ancestral trunk (plesiomorphic genitalia characters). 2. The ancestral species of the *O. hippopotamus* species line and of the *O. hippopotamus* species complex dispersed throughout the Trans-Mexican Volcanic Belt prior to its current conformation (Miocene to Pliocene). The geomorphological evolution of this mountain system drived the processes of speciation in this complex. Its descendants adapted to the burrows of Geomyidae in the mountains. 3. Separation of the *O. hippopotamus* and *O. brevifrons* species complexes. The first evolved with the TMVB, with some expansion southwards and northwards (*O. coproides* reaching New Mexico and Arizona). The *brevifrons* species complex is found in the southeastern United States of America and north-northeastern Mexico. Both complexes are found in the mountains and associated with the protected environments of rodent nests: Geomyidae in the case of the *O. hippopotamus* and *Neotoma* species complexes, plus three species in caves in the case of the *O. brevifrons* species complex.

The oldest stages of evolution of the *Onthophagus chevrolati* species group

According to our position ("Introduction", "The *Onthophagus chevrolati* species group", and "Taxonomy of *Onthophagus chevrolati* species group, updated from Zunino & Halffter (1988a)"; Fig. 18) the *O. chevrolati* species group has four lines. Dispersal times and thus the distributional patterns of each line are different. For the *O. vespertilio* species line, we only have one known species from localities that are very close together, so a distributional pattern cannot be assigned to it. The *O. cyanellus* species line is an element of ancient northern origin within the Mesoamerican Paleoamerican distributional sub-pattern (see Halffter & Morrone 2017; Fig. 21). The *O. hippopotamus* and *O. chevrolati* species lines clearly correspond to the Paleoamerican Mountain distributional sub-pattern, though there are differences between them (Fig. 22). Of these two species lines, *O. hippopotamus* seems to represent the oldest diversification stage. Its current distributional is the result of a historical interaction between the dispersal of the beetles (strongly influenced by their association with the protected environments within nests and caves), and the geomorphological dynamics of the TMVB mountains. For the *O. chevrolati* species line, the mountains in their Pleistocene-Anthropocene conformation were routes for the active dispersion of beetles ecologically fully adapted to high mountain conditions (i.e., those that do not take refuge in burrows or nests).

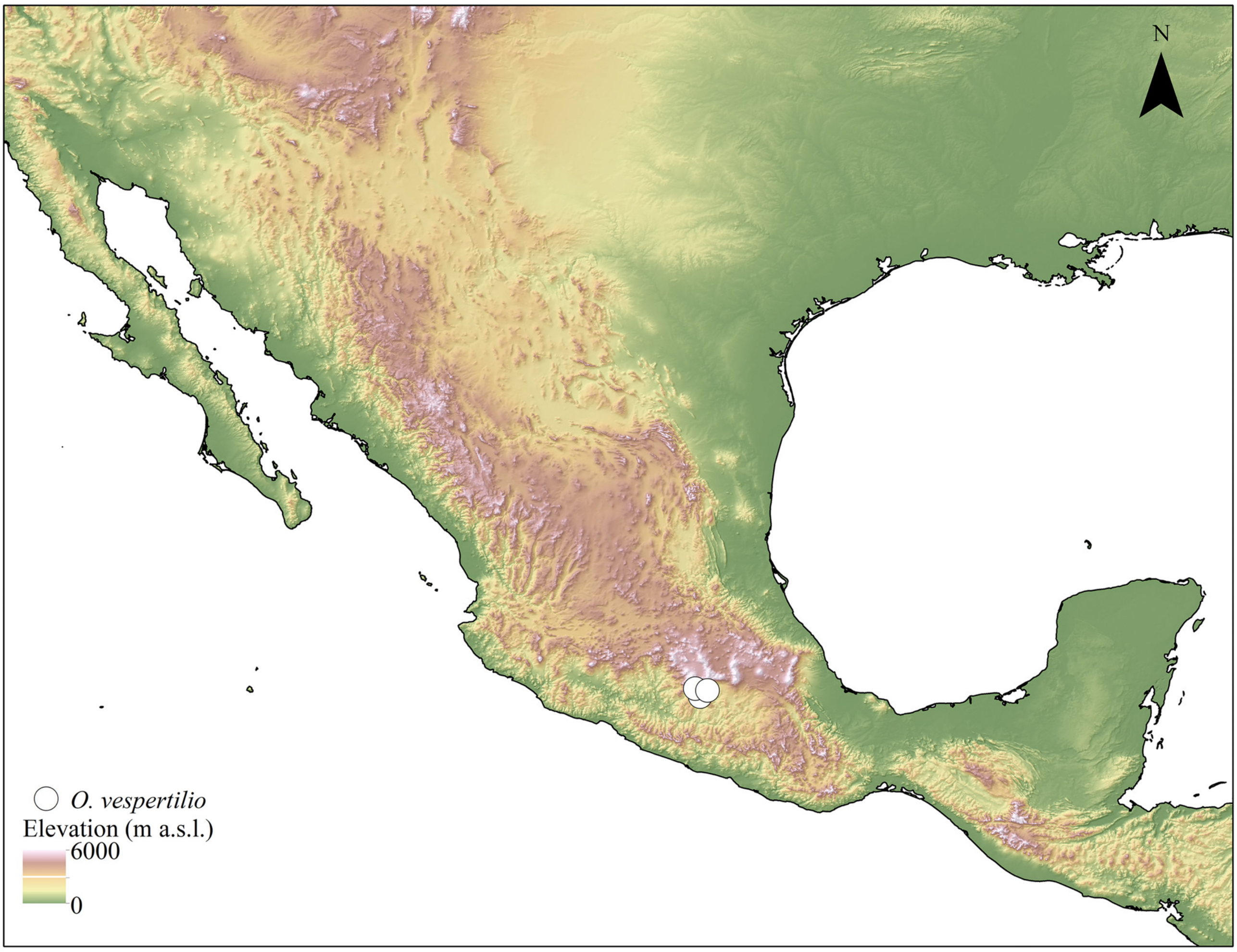

FIGURE 12. Distribution of *O. vespertilio*.

Of the entire *O. chevrolati* species group, the two species lines that hipotethically have diversified in older geological times are the *O. vespertilio* and *O. cyanellus*, which are quite distinct in their morphology, distributional patterns and ecological requirements. *Onthophagus vespertilio* was described from the Acuitlapán cave, state of Guerrero. Zunino & Halffter (1988b) state: "*O. vespertilio* occupies a very isolated position in the *O. chevrolati* species group"; by itself it represents a species line equivalent to the two species lines *O. chevrolati* + *O. hippopotamus*. Genital sclerotized structures especially that of the male, reveal a very marked separation between *O. vespertilio* and all the other species of the species group. The copulatory lamella and the parameres exhibit putatively autapomorphic characteristics, along with others, that we consider putatively plesiomorphic: the internal keel of the copulatory lamella, very important within the *O. chevrolati* species group whose left and right parts are attached but not completely fused.

Based on the characteristics of the genitalia and its external morphology, *O. cyanellus* with closely related species (*O. chiapanecus*, *O. salvadorensis,* and *O. semiopacus*) constitutes a fourth species line with a particular geographical distribution and specific ecological requirements (Figs. 7, 8, 21). The distribution of the *O. cyanellus* species line extends from the Sierra Madre Oriental (in the states of Tamaulipas and Hidalgo) and follows the eastern mountains of this mountain system into the states of Puebla and Veracruz. South of the TMVB, the *O. cyanellus* species line is found in Oaxaca, in the Sierra Madre del Sur and in the Chimalapas region, where it reappears in the intermontane valley of San Cristobal de las Casas, Chiapas. It has been collected in the mountains of Guatemala, Nicaragua, Costa Rica and Panama (between 1000–2500 m; Fig. 21).

Kohlmann & Solís (2001) synonymized *O. mesoamericanus* (Fig. 8) with *O. cyanellus* (Fig. 7), a synonymy that we maintain for this work. The lamella copulatrix of the holotype was broken during the original preparation, preventing its study to confirm the synonymy. As a consequence, the remaining type material need to be revised, and additional male specimens of *O. mesoamericanus* need to be collected and studied. As first suggested by Joaqui *et al*. (2019), we incorporate into the *O. cyanellus* line *O. semiopacus* of the Puebla-Oaxaca Mountain System, *O. chiapanecus* of the mountains of Chiapas (surroundings of San Cristóbal de Las Casas and Soconusco) at elevations between 1850–2800 m, and *O. salvadorensis* from Monte Cristo, Matapan, El Salvador at 2300 m.

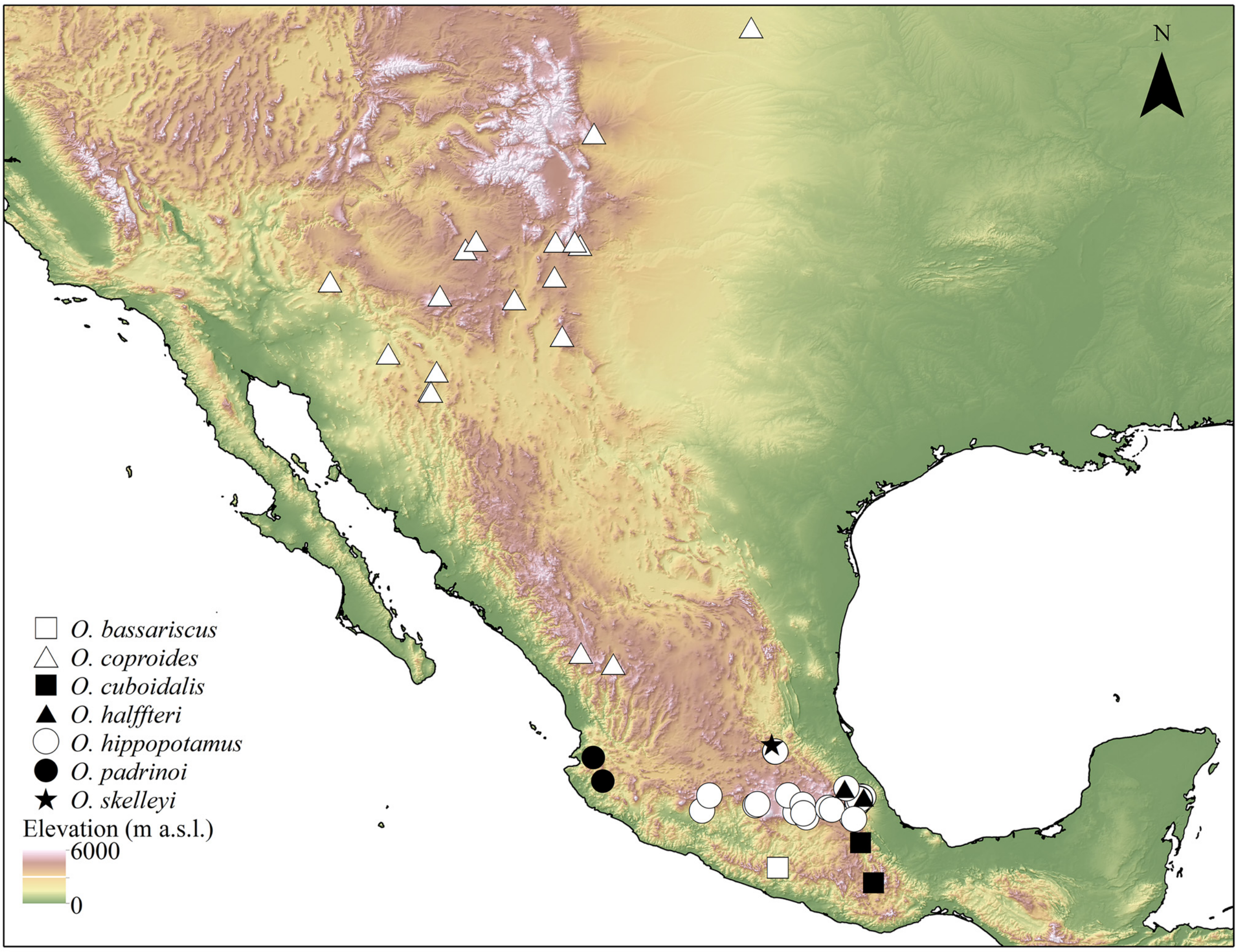

FIGURE 13. Distribution of the *O. hippopotamus* species complex.

A new distributional sub-pattern: The Paleoamerican Mesoamerican

Identifying whether a group of organisms has a northern or southern origin is the first step in distinguishing a distributional pattern in the MTZ. In the Mountain Mesoamerican distributional pattern, characterization is essentially geographical-ecological: this pattern encompasses lines of ancient South American origin, found in the tropical mountains of the MTZ, on the slope that receives the humid, oceanic winds between 1200 and 2000 m, where conditions allow cloud forest to grow (Halffter 1987; Halffter & Morrone 2017). Historically, these forests and the pattern corresponding to their distribution were integrated from Miocene onwards with Neotropical elements and an important amount of evolution occurring *in situ*. Ruiz-Sánchez & Ornelas (2014) reported a genetic break between the United States and Mesoamerican populations of *Liquidambar styraciflua* L., 1753 (a typical element of the Mountain Cloud Forest) from the late Miocene to the early Pleistocene. Palynological records of *Liquidambar* L., 1953 from Miocene floras in southern Mexico support this result (Chávez 1993; Palacios-Chávez & Rzedowski 1993; Graham 1999; Martínez-Hernández & Ramírez-Arriaga 1999). Due to the strong association between *L. styraciflua* and the Mesoamerican cloud mountain forest, palynological and phylogenetic studies help us support the hypothesis of the Mountain Mesoamerican distributional pattern dispersing throughout the Mexican Transition Zone during the Oligocene-Miocene (Halffter 1987; Halffter & Morrone 2017). Examples of some insect lines will help us understand the integration of the Mountain Mesoamerican distributional pattern. This pattern is followed by several genera of Proculini (Coleoptera: Passalidae) of Neotropical origin as *Proculus* Kaup, 1868; *Vindex* Kaup, 1871; and *Pseudacanthus* Kaup, 1869 (Reyes-Castillo & Halffter 1978); the genus *Chrysina* Kirby, 1828 (Coleoptera: Melolonthidae; Morón 1991); and the *Phanaeus amethystinus* species group (Coleoptera: Scarabaeidae; Edmonds & Zídek 2012), which clearly diversified in the Central American Nucleus.

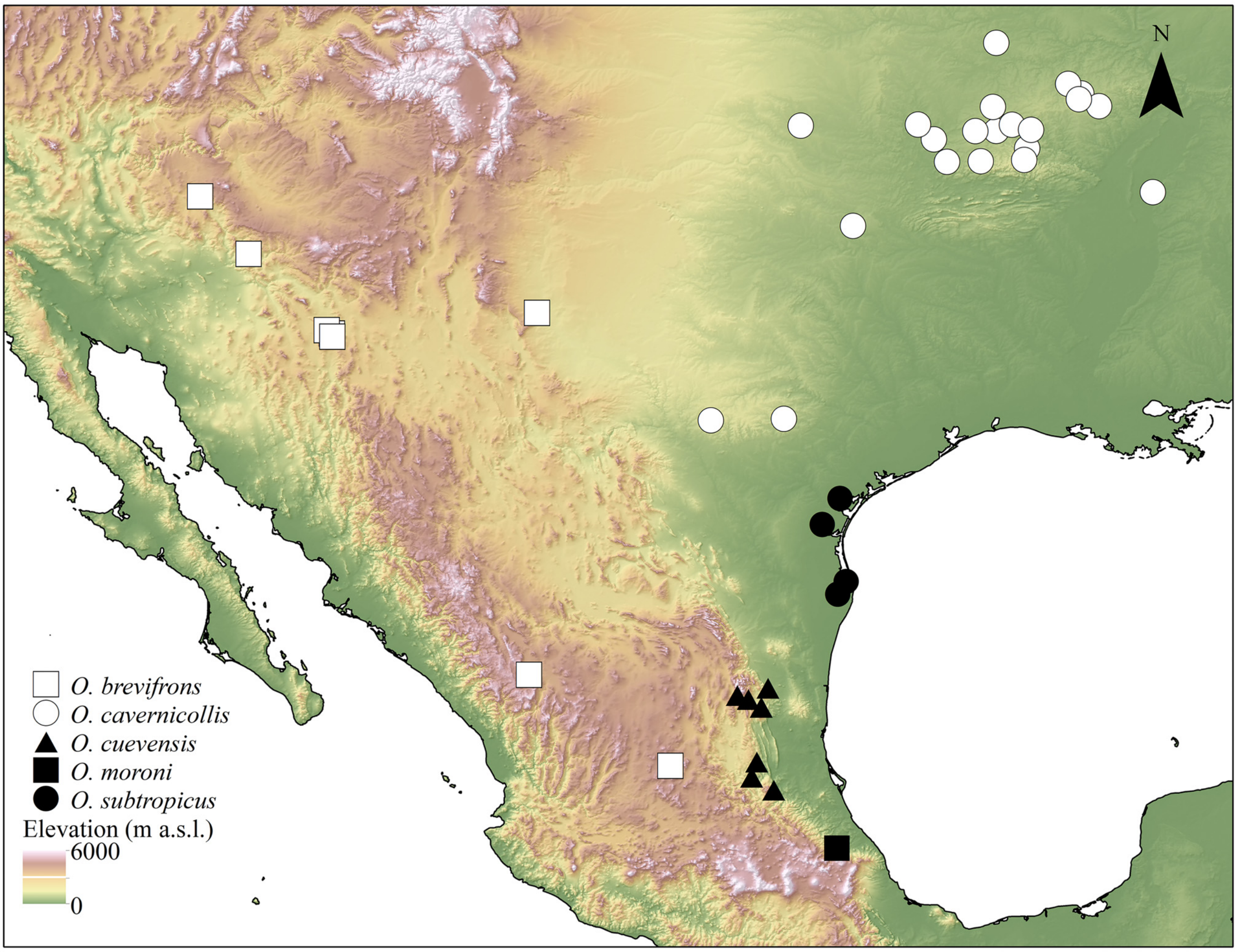

FIGURE 14. Distribution of the *O. brevifrons* species complex.

In the montane cloud forests there is a noteworthy presence of lines of ancient northern or Paleoamerican origin that have also undergone an *in situ* radiation process and are mixed with Neotropical affinity lines to make up the typical fauna of the Mesoamerican mountains. The *O. cyanellus* species line is a clear example of a Paleoamerican line that has successfuly colonized the Central American mountains (Fig. 21). It has made it through two tropical portals: the Isthmus of Tehuantepec and the region of Lake Nicaragua; and it is one of the few insects of northern origin that has colonized the Costa Rica-Panama mountain systems. According to Kohlmann & Solís (2001), it has a wide distribution in the Pacific slope of the Central Mountain system in Costa Rica, between 1000 and 2750 m a.s.l. This distribution coincides with that of the cloud forest and other forests of intermediate elevations and that are very humid. Thus, the distribution of *O. cyanellus* corresponds to that of the tree species shared with the east-southeast of the United States of America, forming an important part of the montane cloud forest.

For the lines of northern origin (Holarctic) with a distribution similar to that of the Mountain Mesoamerican pattern, we decided to establish herein a new distributional sub-pattern: the Paleoamerican Mesoamerican. Unlike the rest of the *O. chevrolati* species group that follow the Mountain Paleoamerican sub-pattern, the distribution of the *O. cyanellus* species line fits in the Paleoamerican Mesoamerican sub-pattern. Other examples of lines that follow the Mesoamerican Paleoamerican sub-pattern are the *O. dicranius* species group that are present from the humid mountains of Puebla-Oaxaca-Veracruz to Ecuador (Howden & Gill 1993, Génier & Howden 1999; Kohlmann & Solís 2001; Génier 2017) and the *Copris remotus* species complex (Matthews 1961; Marchisio & Zunino 2012; Mora-Aguilar & Delgado 2015). The other distributional patterns of the entomofauna in the MTZ are detailed in Halffter & Morrone (2017).

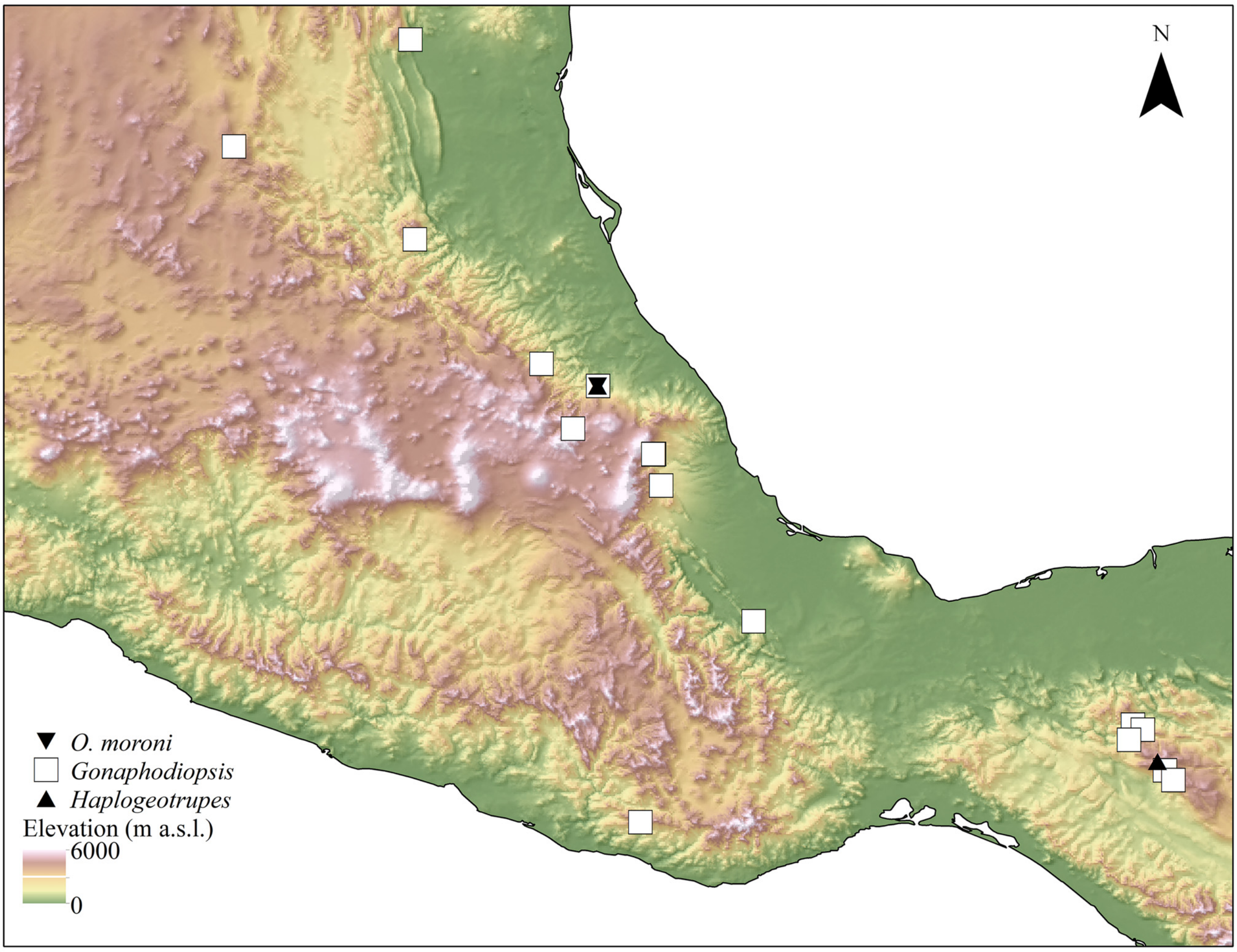

FIGURE 15. Location of the Cuetzalan cave associated fauna.

The *Onthophagus hippopotamus* species line and species complex

Within the *O. chevrolati* species group, the *O. hippopotamus* species line is one of the two main phyletic sets of species. It can be distinguished by the characters of its external morphology, the male and female genitalia, the time and way in which its geographical distribution occurred, and as previously mentioned, by its ecological requirements. Our hypothesis is that in composition, the distribution and evolution of this line is perfectly differentiated and is associated with the orogenesis of the TMVB. The *O. hippopotamus* species line comprises (see "Taxonomy of *Onthophagus chevrolati* species group, updated from Zunino & Halffter (1988a)") 12 species compared to the 29 species of the other central species line of the *O. chevrolati* species group, and most modern *O. chevrolati* species line. All the species of this species line live in Geomyidae burrows, *Neotoma* nests, and three of them in caves (one of them in both caves and *Neotoma* nests).

Within the *O. hippopotamus* species line, the *O. brevifrons* species complex comprises five closely related species found in the southwestern United States of America, and in the north and northwest of Mexico. The other species complex (*O. hippopotamus*) comprises seven species associated with pocket gopher nests. One of these species is distributed in the mountains and plains of Nebraska, Arizona, New Mexico and Colorado (Slay *et al.* 2012), another in the Sierra Madre Occidental (SMO) in the state of Durango (*O. coproides* Horn). The rest of the species are found along the TMVB and in the Sierra Madre del Sur mountains. Given the major interspecific differences and its fragmented distribution, this species complex is considered by Zunino & Halffter (1988a) to has elderly diversified than other species lines of the *O. chevrolati* species group that have a continuous distribution in the mountains of the MTZ (e.g., the *O. chevrolati* species line).

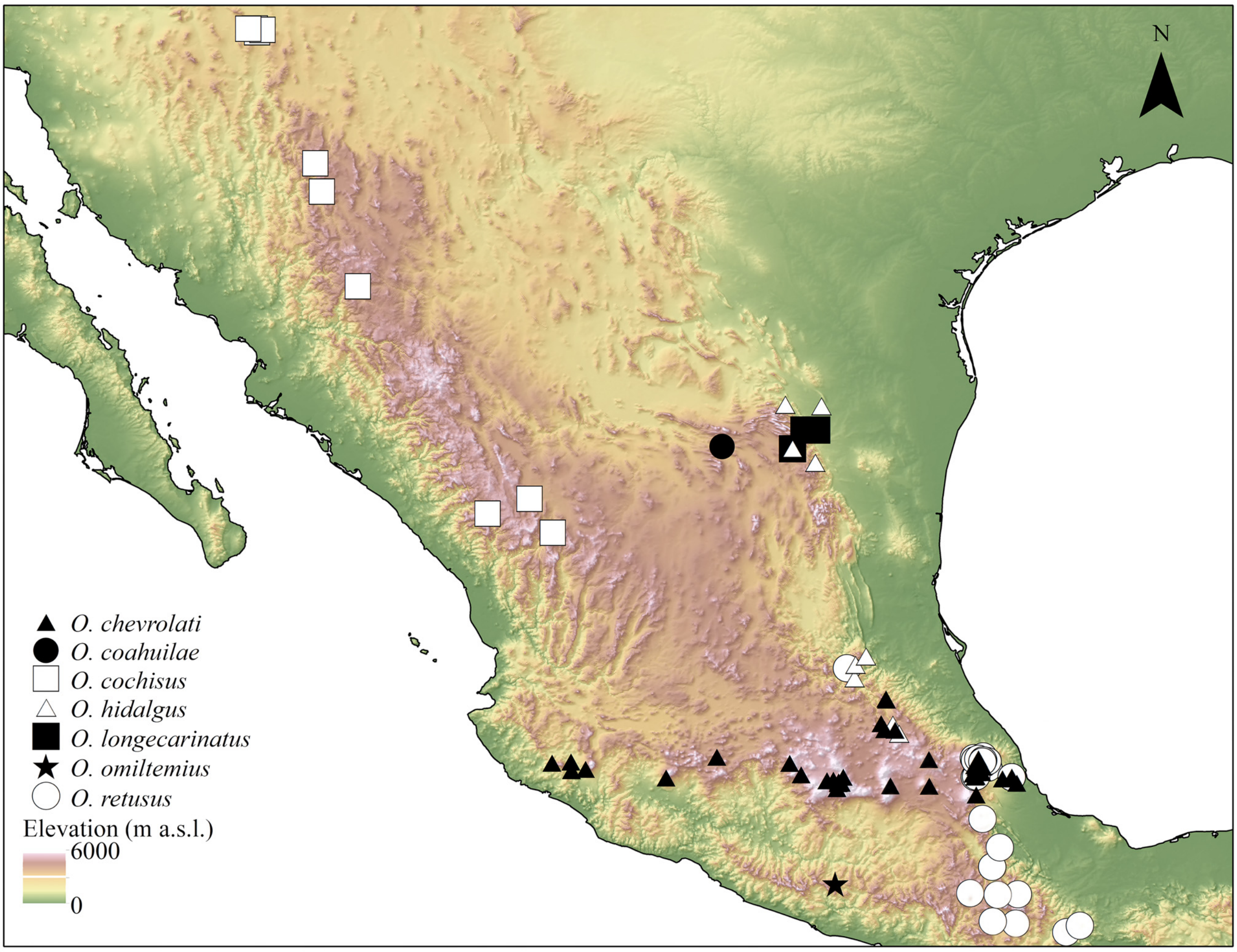

FIGURE 16. Distribution of the *O. chevrolati* species complex.

Comparative analysis of the genitalia

The importance of genital characters in taxonomy and phylogeny, and the history of the studies of such structures in the Scarabaeoidea beetles, have been summarized in a recent paper (Zunino 2012). Also, Tarasov & Solodovnikov (2011) highlight the importance of the male genitalia of the Onthophagini as phylogenetic markers. Philips (2016) discussed the same topic, analyzing the phyletic relationship between Oniticellini and Onthophagini. Song (2009) highlighted the great importance of the structure of the aedeagus in phylogenetic reconstructions. We attempt an evolutionary-biogeographic approach by comparing the male and female genitalia in the species of the *O. hippopotamus* species complex. Several authors have emphasized that the characters of the genitalia elucidate phylogenetic relationships more clearly than other characters do, as they are less subject to selection by environmental phenomena (Zunino 1983, 1987; Zunino & Palestrini 1988; Medina *et al*. 2013).

Our taxonomical hypotheses have been based specifically on the comparative observation of genitalia. From a theoretical point of view, we continue to think that the genitalia are part of the so-called "SMRS" (Specific Mate

Recognition System, Paterson 1985), e.g., the set of characters that maintain the cohesion of species. The interruption of panmixis that arises when some type of barrier intervenes and fragments an initially whole population group, causes a rapid divergence in the genital characters that can be empirically verified (see Arnqvist 1997 and bibliography reviewed; also Zunino & Palestrini 1991; Papavero & Llorente-Bousquets 1992).

The detailed observation of male and female genitalia has thus allowed us to establish a first approximation of the taxonomy within the *O. hippopotamus* species complex. Essentially, for genital characters there are two lines: the first includes *O. coproides*, *O. skelleyi* Sánchez-Huerta, Zunino & Halffter, and *O. padrinoi* Delgado, which occupy an area in the northern and eastern regions of the TMVB. The second one includes *O. halffteri* Zunino, *O. bassariscus* Zunino & Halffter and is distributed in the TMVB and especially in the mountains to the south of it. *O. hippopotamus* Harold, the species with the widest distribution (throughout the entire TMVB) also has an intermediate morphology relative to that of the other species, and genital traits that can be considered as basal and general to these two branches. The species closest to *O. hippopotamus* is *O. halffteri*, as well as *O. bassariscus* is closely related to *O. cuboidalis* Bates.

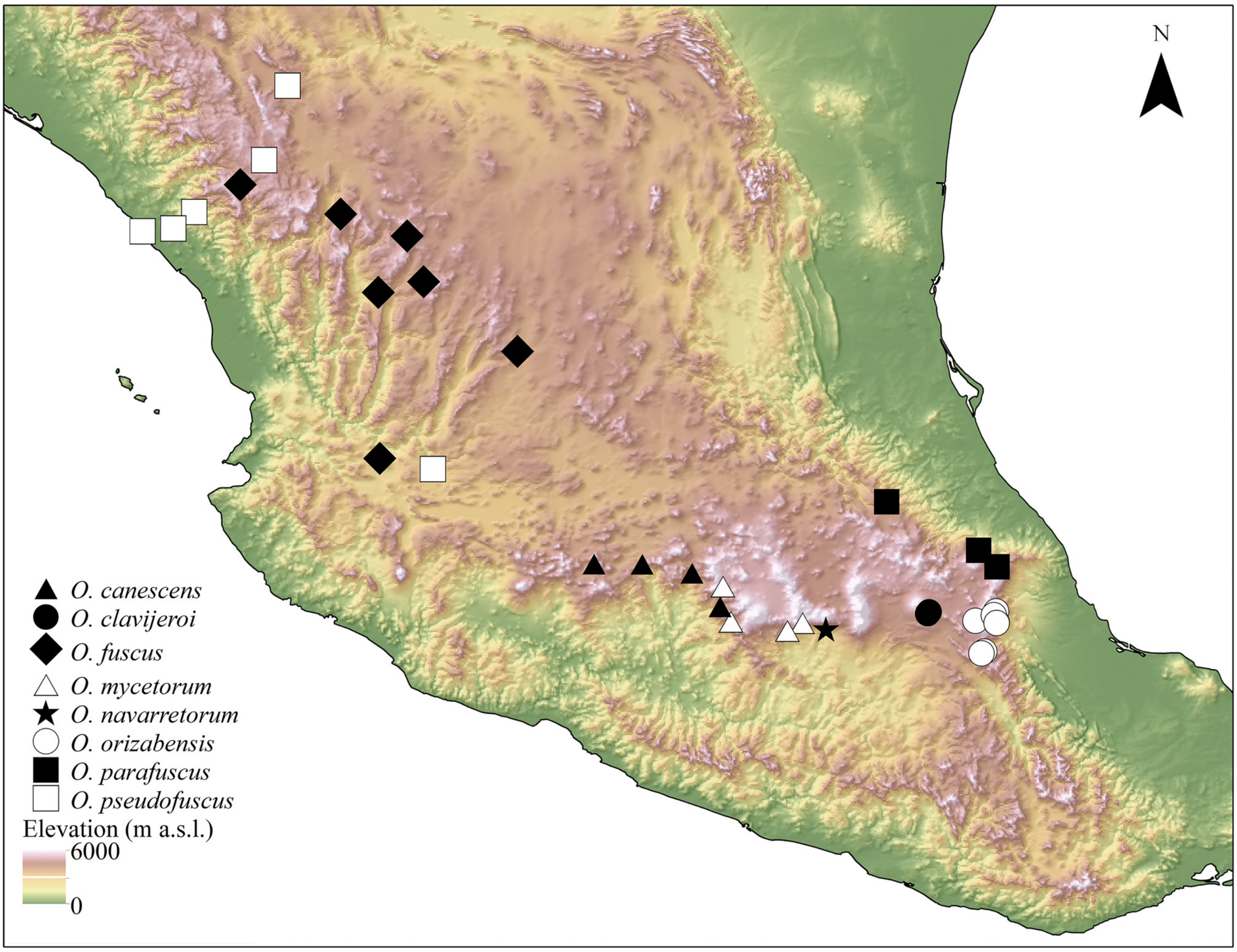

FIGURE 17. Distribution of the *O. fuscus* species complex.

The association with caves, burrows and rodent nests

The importance of the response of the Scarabaeinae to caves, burrows and rodent nests is very different. There is a relatively large number of Scarabaeinae associated with galleries and nests: 63 species worldwide, 52 of which belong to *Onthophagus* (Zunino & Halffter 2007). In contrast, regarding the association with caves, there are only two very specific citations of Scarabaeinae (Deltochilini) not *Onthophagus*, and the four species of this genus, *O. chevrolati* species group of the MTZ and North America.

We think that the association with caves is an extreme case of the same phenomenon that leads, in other cases and species, to burrows and nests of rodents. What are *O. vespertilio* (Fig. 2) and the three species of the *O. brevifrons* species complex (Figs. 4, 5) looking for in the caves? Likely, the same thing that other *Onthophagus* species seek in burrows: a stable environment with very few oscillations in temperature and humidity and abundant food (mounds of guano in different parts of the cave). Very occasionally, a specimen has been found outside. It is noteworthy that so far all of the captures in caves have been adult specimens. Neither larvae nor nests have been found.

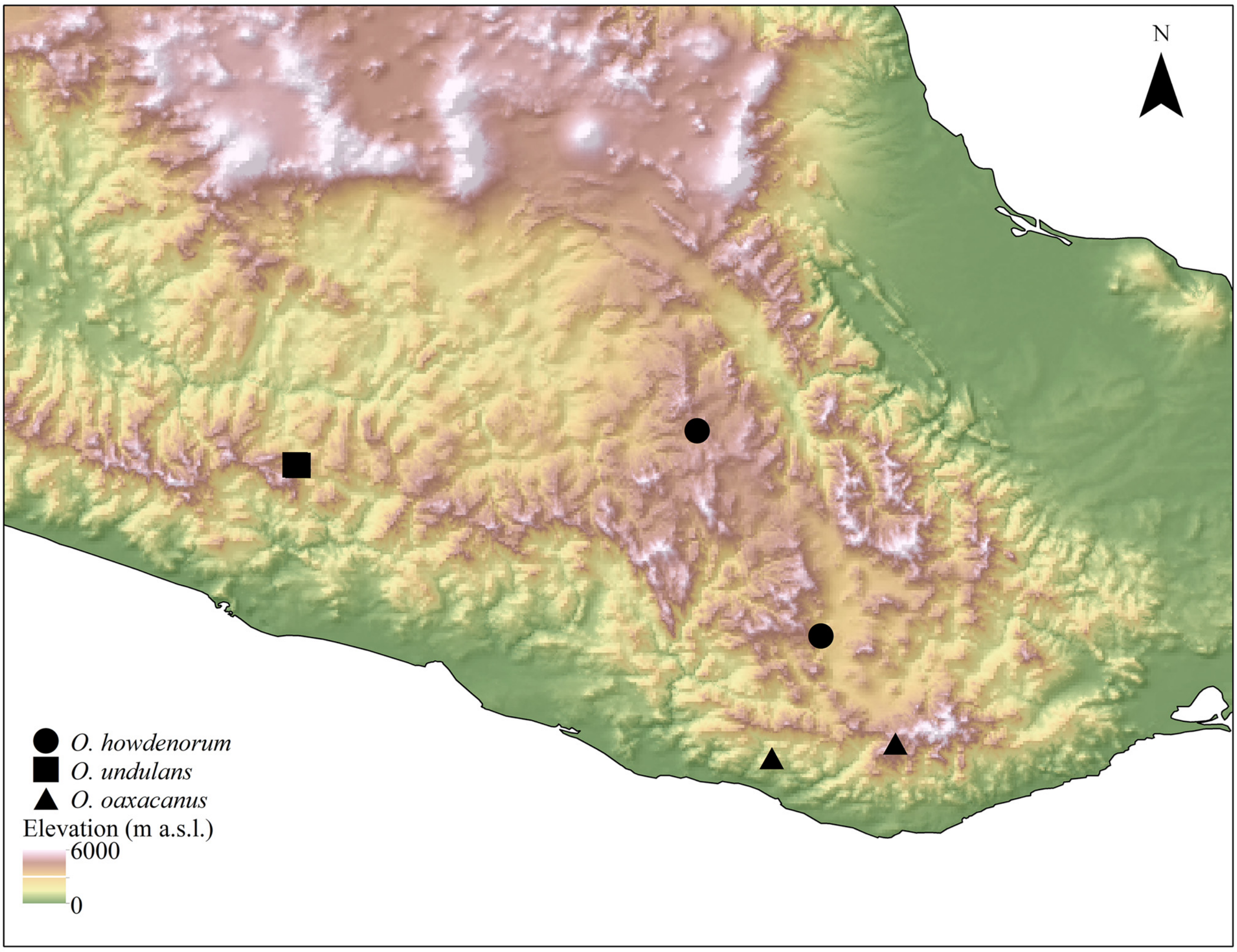

FIGURE 18. Distribution of the *O. undulans* species complex.

The association of *Onthophagus* with caves, along with equivalent associations with burrows and nests, has another perspective if we examine the ideas of Giachino & Vailati (2010, 2016) about what a cave is. They state that a cave is a crack in the rocky hypogeum whose dimensions allow humans to move within it. That is to say, the cave is a perception, a human appreciation of a fissure in the Earth. It is not a radically different environment. According to this criterion, ecologically and faunistically there is a sequence between fissures in the rock layer and caves. The burrows would be an initial stage in this sequence. Independently of the ecological mechanisms that make it possible (or even desirable) for a beetle to live in a cave or burrow, what biogeographic factors have favored the limited number of examples that we know of? The answer is important to understand the biogeographic history of the *O. chevrolati* species group, especially that of the *O. brevifrons* species complex.

The Cuetzalan cave in the state of Puebla, Mexico, has exceptional conditions that help us answer this question (Fig. 15). As far as we know it is the only cave in the world where three species of Scarabaeoidea occur (Zunino & Halffter 1988b; Halffter & Deloya 2007). Furthermore, its surroundings have been systematically collected, making it possible to compare what is inside and what outside the cave. The first Scarabaeoidea in the cave is the Ceratotrupini (Geotrupidae: Geotrupinae) *Haplogeotrupes reddelli* (Howden), known exclusively in the Cuetzalan cave (Zunino & Halffter 1988b) and the nearby Xochitl cave, located in the surroundings of Xochitlán (state of Puebla), where it was described (Howden 1980). *Haplogeotrupes reddelli* feeds on the bat guano, which it even stores in galleries dug into the floor of the cave. Geotrupine nests have been found in the cave floor (Halffter & Deloya 2007). In addition to *H. reddelli*, the genus *Haplogeotrupes* Nikolaev has another species with three vicariant subspecies (none of which are associated with caves) from the mountains of Chiapas (Mexico) and Guatemala (Fig. 15).

The second Scarabaeoidea is *Gonaphodiopsis deloyai* Dellacasa, Dellacasa & Gordon, originally cited as *Aphodius* sp. aff. *diminutus* Bates by Zunino & Halffter (1988b) and redescribed as *Aphodius diminutus* Bates by Zunino & Dellacasa (1989). Halffter & Deloya (2007) point out that while *G. deloyai* specimens were found in the mounds of bat guano, they were collected more frequently and abundantly in the nest-masses packed inside the *H. reddelli* galleries. In addition to Cuetzalan cave, *G. deloyai* has been collected in three additional locations (not caves) in the Sierra Madre Oriental mountains, in one location in the Sierra Madre in Puebla-Oaxaca and another in the Sierra Madre del Sur. The genus comprises four additional species that occur in the Sierra Madre Occidental and the Sierra Madre del Sur, all collected in forests. The third species, *O. moroni* Zunino & Halffter (Fig. 5), represents the southernmost presence of the *O. brevifrons* species complex (Figs. 14, 15).

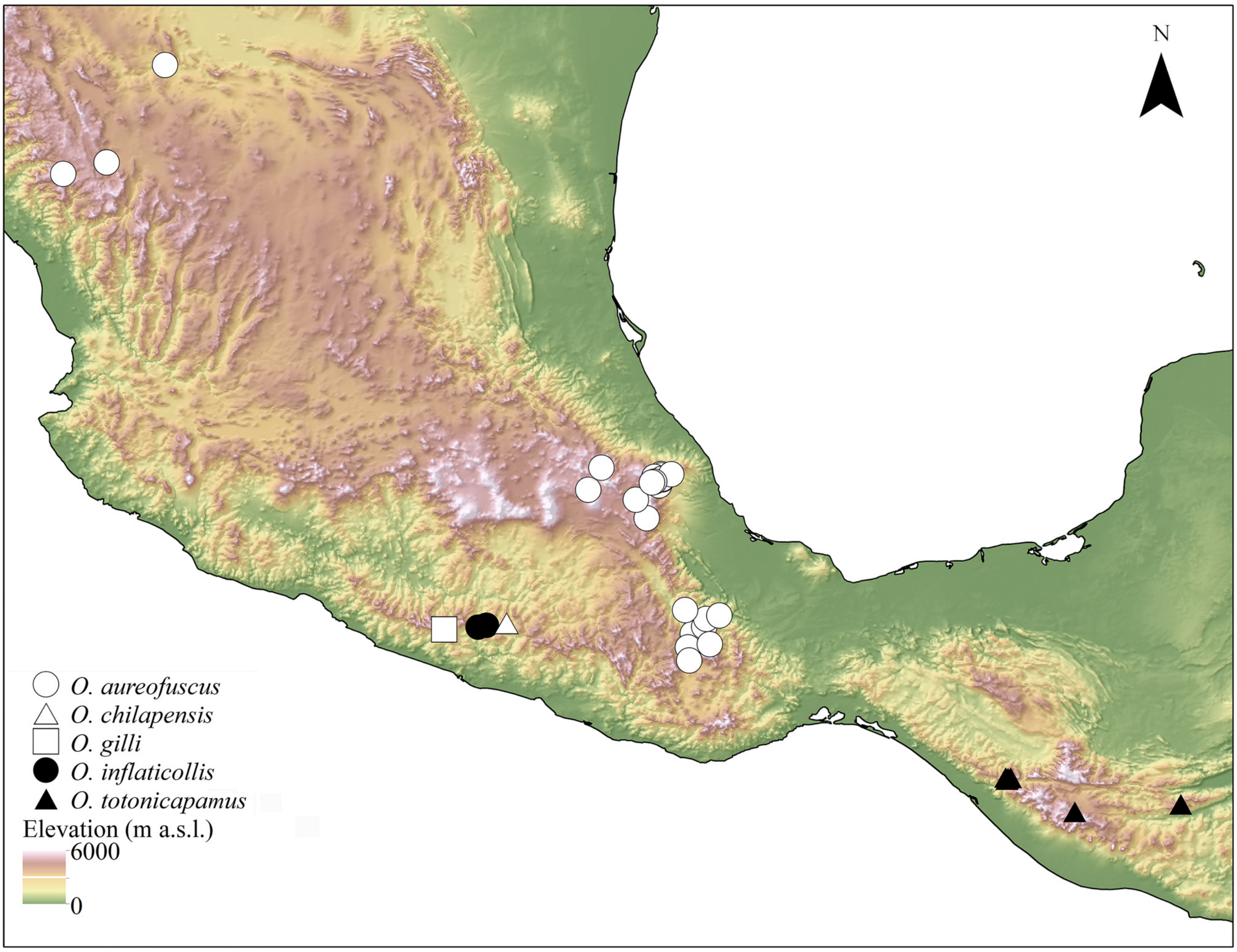

FIGURE 19. Distribution of the *O. aureofuscus* species complex.

In the same geographic area, Cuetzalan, Puebla (97°32'38.63"W; 20°00'47.88"N; 945 m a.s.l.), we found two distinct coprophagous Scarabaeoidea faunas: one inside and another outside of the cave. The inside fauna has three species of Paleoamerican mountain distribution, two of them exclusive to the cave, though with species very close to those outside. This group of beetles corresponds to colder conditions, more northern than those that are found outside the cave today, but both environmental conditions and northern affinities would have occurred during any of the last glacial periods.

In contrast, outside of the cave (collections by Carrillo-Ruiz & Morón 2003; Halffter & Deloya 2007) there is a set of 15 species of Scarabaeinae and Aphodiinae (but no Geotrupinae) clearly of Neotropical origin (the majority) of Tropical Paleoamerican origin and with tropical ecological requirements. The cave fauna may be a sample of what existed during the last glacial periods and refugiated in this environment. The fauna from the outside is evidence of the expansion of the Neotropical fauna. The cave and its surroundings are a living summary of the dispersal movements during the Pleistocene in the TMVB. The association of the Scarabaeinae with nests, burrows and caves is not taxonomically or geographically random (see Zunino & Halffter 2007). We have already pointed out that most of the examples correspond to the genus *Onthophagus*, which is geographically concentrated in North America and the MTZ. Even within the *Onthophagus* of North America there is a strong taxonomic concentration: all of the American *Onthophagus* associated with burrows and nests belong to two species groups (*O. chevrolati* and *O. mexicanus*), of the at least seven groups that comprise the genus in America.

The combined analysis of the taxonomy and of the evolution of the genitalia, the orographic evolution of the TMVB as well as the historical biogeography of the group and their ecological requirements, allow us to propose the following reconstruction of the relationship with burrows. The first ancestral element, whose descendants are today the *O. chevrolati* species group, reached the current central region of the TMVB towards the Miocene. The geographical space did not have the mountains it currently has, nor was there any Geomyidae beetle-burrow association (below, we refer to the historical biogeography of the rodents). The separation of *O. vespertilio* must have happened early (Miocene-Pliocene); its restriction to the Acuitlapán cave is rather a later occurrence of endemism.

The *O. hippopotamus* species complex is associated with the TMVB and with the burrows of Geomyidae. In the mountains and plains of northern Mexico and the southern United States of America, under more arid conditions, the *O. brevifrons* species complex is found in *Neotoma* nests or in caves. In the *O. hippopotamus* species complex, the process of diversification must have started in Plio-Pleistocene and is still ongoing. In the case of the *O. brevifrons* species complex, dispersion-speciation must have occurred later. It is also an ongoing process today. Geomyidae are a family of rodents endemic to the Americas, with highly developed fossorial habits: they make deep, extensive, branching burrows. The oldest fossils correspond to a subfamily from the late Oligocene-Early Miocene of southwestern North America that is now extinct. The second subfamily, Geomyinae, is diversified in the Central Mexican High Plateau, from where it expanded to North America in the early Pliocene. During the late Pliocene, the isolation and differentiation of the current genera occurred, with the TMVB as the primary and main diversification center of the species of the genus *Cratogeomys* Merriam during the Pleistocene. The line *Cratogeomys castanops* (Baird) extended to northeastern Mexico, penetrating up into the United States of America (Russell 1968). As noted by Lobo & Halffter (1994) knowledge of the chronology of rodents gives us another element to establish the chronology of these beetles.

What ecological elements determine the beetle-burrow-cave relationship? Beetles seek stability in environmental conditions (humidity and temperature), and the accumulation of excrement found in the nesting chambers and latrines of the burrows, or in the heaps of bat guano in the caves. This relationship is stronger at high mountain elevations (the area of the *O. hippopotamus* species complex) and in more arid climates (the area of the *O. brevifrons* species complex). For example, the association with burrows of the Mexican pocket gopher *C. merriami* (Thomas) allows *O. hippopotamus* and *O. halffteri* to be found above 3000 m a.s.l. in the central and eastern part of the TMVB.

The distribution of the fossorial Geomyidae is wider than that of the *O. hippopotamus* species complex. In the eastern part of the TMVB and in the nearby Mexican tropics, below 1800–1500 m a.s.l. there are no representatives of the *O. hippopotamus* species line. Its place in the burrows is occupied by the genus *Ateuchus* Weber, a Scarabaeinae of Neotropical origin. The rodent with which the beetles are associated can also change. Thus, within the *O. hippopotamus* species complex, *O. coproides* ocurrs in the north of the Sierra Madre Occidental (state of Durango), where it uses the burrows of *Thomomys* Wied-Neuwied instead of those of *Crateogeomys* in the central TMVB. In Arizona, *O. coproides* is found in *Cynomys* Rafinesque burrows.

Neither the *Onthophagus* that live in caves, nor those associated with burrows, have adaptations like those seen in other Coleoptera; however, Zunino & Halffter (2007) point out that in several of these species there is an alteration of sexual dimorphism with respect to what is usually seen in the genus. This phenomenon mainly involves the development of the horns of the frontal keel in both sexes. They raise an interesting problem in light of Emlen's interpretations (2008, 2014 and literature reviewed therein; Emlen *pers. comm.* to MZ). According to

Emlen & Philips (2006), the horns of the males would play an important role in the defense of the entrance of the nest tunnel, impeding access to a female by other males. In fact, both in the American line *O. chevrolati*, as in the Palearctic *Palaeonthophagus* Zunino, 1979 living in similar ecological niches in Eurasia, in at least two Afrotropical species of *Onthophagus sensu lato* (Zunino & Halffter 2007), neither the sexual dimorphism in the frontal keel, nor that of the prothorax, corresponds to the morphology that is considered general in the genus *Onthophagus*.

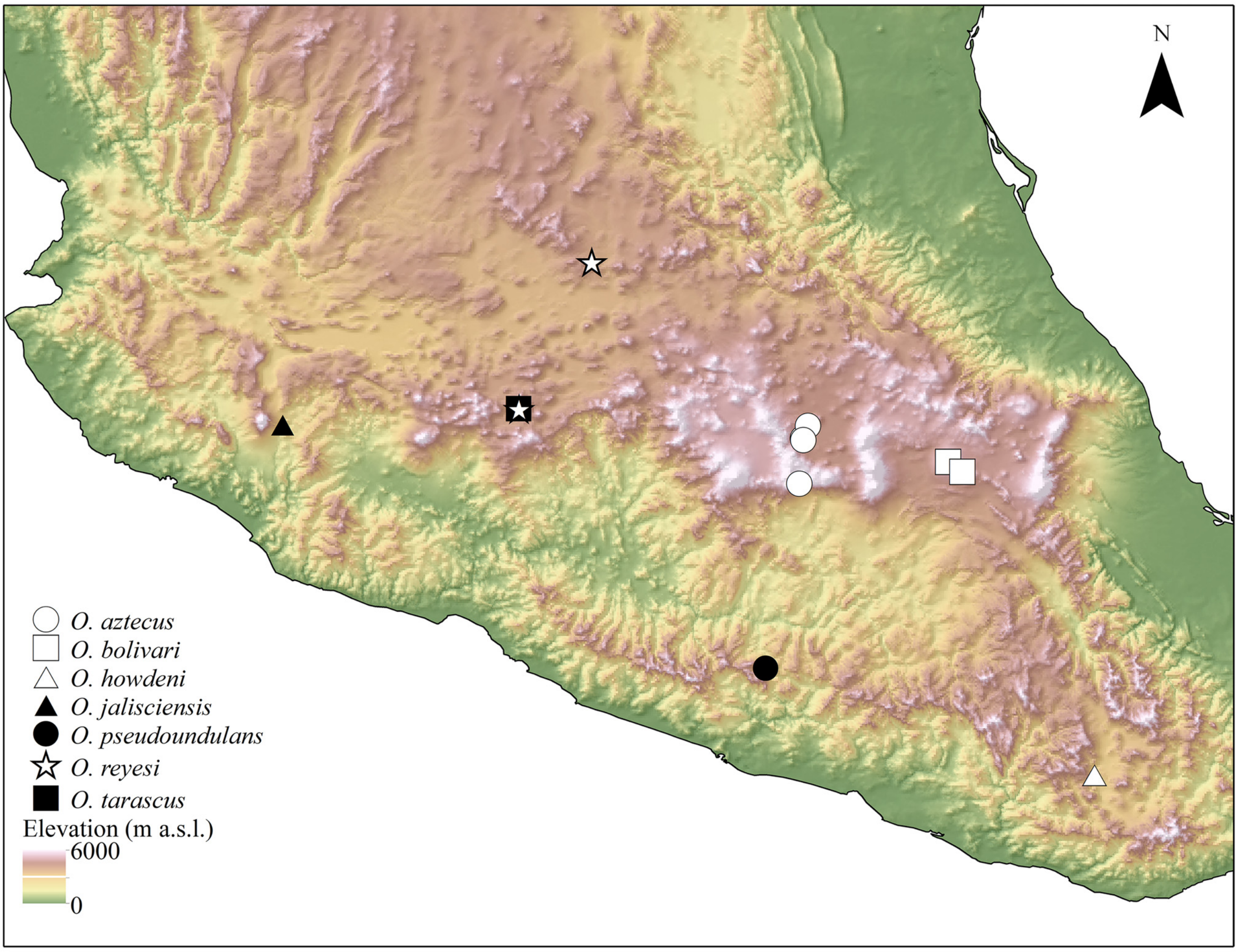

FIGURE 20. Distribution of the *O. aztecus* species complex.

To interpret in an evolutionary sense the phenomena that affect sexual dimorphism in cave and burrow species, we would need very detailed knowledge of their bionomics, which we do not have. We can assume that in *O. halffteri*, a very localized but abundant species, the extreme development of the prothoracic prominence in the males plays a role in the defense of the entrance to the tunnel from other males. That is, the role that the horns of the frontal keel play in other taxa. On the other hand, it should be noted that in the *O. hippopotamus* species complex there are species with unarmed males while the females have horns, both sexes are unarmed or both sexes with horns. There is also a reduction in the number of small teeth located between the teeth of the outer edge of the anterior tibia. The same phenomenon occurs in the non-American *Onthophagus* associated with burrows (see Montreuil & Ziani 2011; Ziani & Gudenzi 2009 and literature reviewed therein; Ziani *et al*. 2017; Ziani *pers. comm.* to MZ). In evolutionary terms, this reduction could be related to the lower fossorial effort required to move the soil of the burrows, already loosened by the rodent and constantly wetter, and the heaps of bat guano. An interesting essay on morphology and biomechanics of the fossorial foreleg of *Copris ochus* Motschulsky published by Zhang *et al*. (2018) could support the idea of maintaining greater digging efficiency in free-living pecies with respect to cave and burrow species within the framework of the *O. chevrolati* species group, and hence, our interpretations of the evolution of the group.

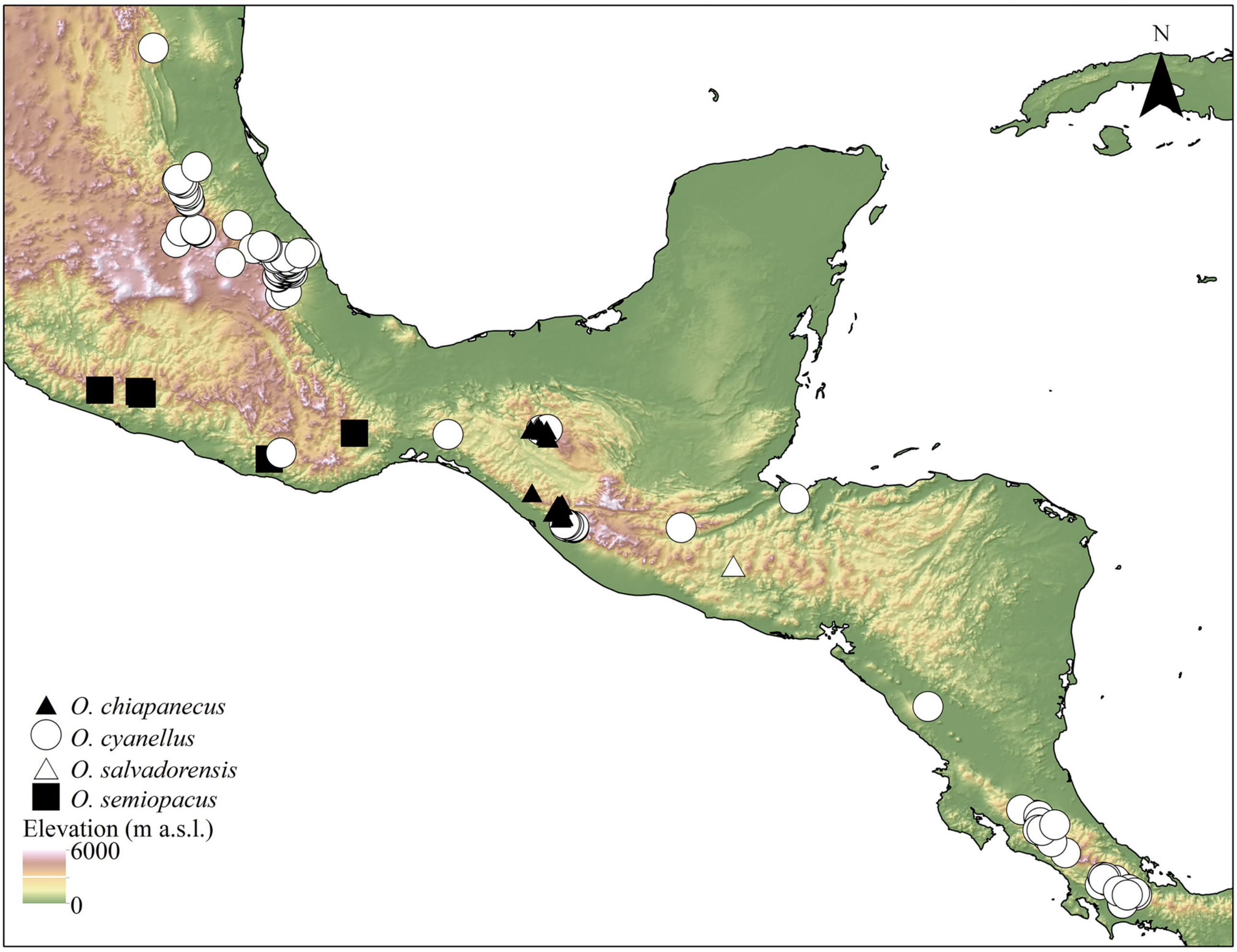

FIGURE 21. Distribution of the *O. cyanellus* species line, which hypothetically represents oldest stage of evolution of the *O. chevrolati* species group.

The *Onthophagus brevifrons* species complex

Within the *O. hippopotamus* species line, the *O. brevifrons* species complex has five species whose distribution forms an arch (Fig. 4, 5, 14, 15) to the north of the Mexican High Plateau, from the Sierra Madre Occidental to the Sierra Madre Oriental. As mentioned, it is an equivalent line to the *O. hippopotamus* species complex, but it may have diversified in more recent geological times (see "The *Onthophagus hippopotamus* species line and species complex" and "Comparative analysis of the genitalia").

There is a series of morphological and ecological differences that support the idea of conserving both species complexes. The supposedly plesiomorphic characters present in the *O. brevifrons* species complex include the mid-keel of the lamella copulatrix lacking a sagittal suture and the orientation of the axis of the apexes of the parameres. Supposedly synapomorphic characters are the introflexion of the left lateral wall of the copulatory lamella, as well as the development of the caudal branches of the sclerotization of the vaginal support that is much larger than the cephalic branches. In this species complex, *O. brevifrons* Horn and *O. cuevensis* Howden show the supposedly plesiomorphic character states. The supposedly most apomorphic character states are present in *O. cavernicollis* Howden & Cartwright. *Onthophagus moroni* (Fig. 5) is supposed to be a closely related species to *O. cavernicollis*. The relationship of *O. subtropicus* Howden & Cartwright with the other species in the *O. brevifrons* complex is unclear, but this is the single species that occurs near sea level in tropical lowland habitats.

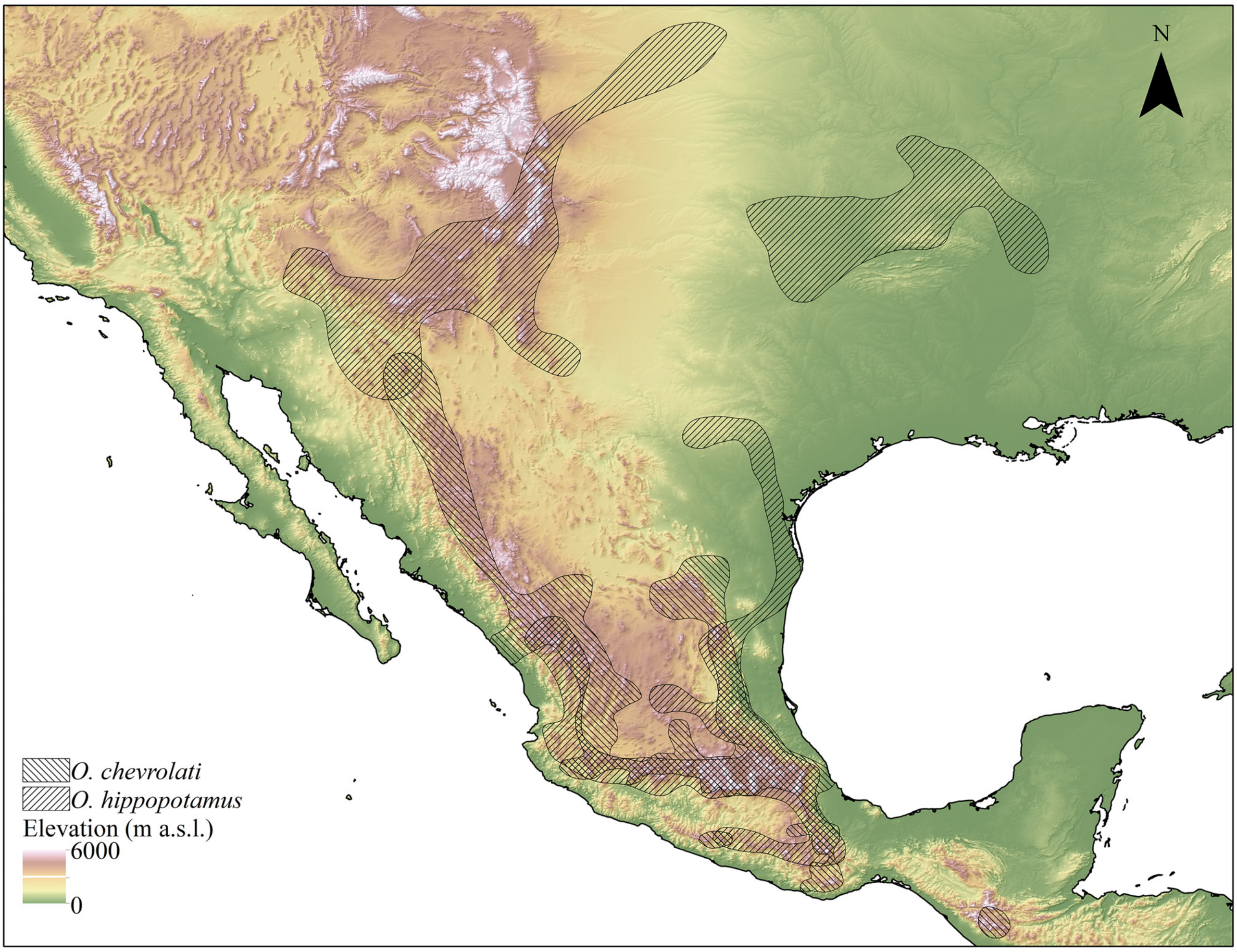

FIGURE 22. Comparison of the distribution areas of the *O. hippopotamus* and *O. chevrolati* species lines.

The *Onthophagus chevrolati* species line

In contrast to Zunino & Halffter (1988a), we think that *O. cyanellus* and closely related species deserve to be considered a species line that is distinct from the *O. chevrolati* species line (see "Taxonomy of *Onthophagus chevrolati* species group, updated from Zunino & Halffter (1988a)" and "The hipotetically oldest stages of evolution of the *Onthophagus chevrolati* species group"). This leaves the line *O. chevrolati* as the most recently difersified set of species within the *O. chevrolati* species group. Its geographic distribution is also the most modern (end of the Pliocene to the Anthropocene; Figs. 16–20, 22). As we have proposed ("Introduction" and "The *Onthophagus hippopotamus* species line and species complex"), the spatial distribution of the *O. hippopotamus* species line and the formation of the mountain systems of the TMVB are simultaneous phenomena. The dispersal and speciation of the *O. chevrolati* species line occurred when this mountain landscape already had its current configuration. Apart from its association with high mountains, the *O. chevrolati* species line does not have any special ecological characteristics. The morphology of its species is very uniform. These species probably originated during a recent radiation process, and only differ by very small characters. Taken together, we think that *O. chevrolati* is a much more modern species line than the *O. hippopotamus* species line.

The *O. chevrolati* species line is composed of several complexes that follow the Paleoamerican Mountain distributional sub-pattern, with distributions that correspond to different biogeographic times and settings, ranging from the Pleistocene to the Anthropocene. Thus, the *O. aureofuscus* species complex (for the taxonomic composition of this line and its complexes see "Taxonomy of *Onthophagus chevrolati* species group, updated from Zunino & Halffter (1988a)") expands in the Sierra Madre mountain systems (Fig. 19). The *O. chevrolati* and *O.*

fuscus species complexes have a u-shaped distribution in the cordilleras that surround the Mexican High Plateau, with a notable presence in the Oaxacan mountainous areas (Figs. 16, 17). To the west, the species of the *O. chevrolati* species complex that reaches the furthest north (Arizona) is *O. cochisus* Brown.

In the TMVB, the *O. chevrolati* species complex predominates. Several species have an aggressive distribution, certainly recent. Arriaga-Jiménez *et al*. (2018), studying the coprophagous beetles (Aphodinae, Geotrupinae, Scarabaeinae) of four mountains at the eastern end of the TMVB and that is in contact with the Sierra Madre Oriental, suggest that only "*O. chevrolati chevrolati* Harold" was found on all the mountains. Nevertheless, they mistakenly considered *O. chevrolati*, *O. retusus* Harold and *O. orizabensis* as the same species. As a matter of fact, both *O. chevrolati* and *O. retusus* are found in all the *high mountains* of the eastern TMVB. The general distribution of *O. chevrolati* includes the TMVB and the Sierra Madre Oriental, the mountainous areas of the southern Mexican High Plateau, while *O. retusus* occurs in the eastern TMVB, the southern Sierra Madre Oriental, and the sierras of Puebla-Oaxaca, both species with a broad elevation distribution from 1800 to more than 3000 m a.s.l (*O. retusus* occurs near the sea level in its southernmost distribution area). In the Sierra Madre Oriental, 900 km to the northeast is the northernmost species of the species complex, *O. coahuilae* Zunino & Halffter.

In the TMVB, the *O. fuscus* species complex is represented by several species, and has two species in the Sierra Madre Oriental. The *O. undulans* species complex is located in the Sierra Madre del Sur, with an expansion into the Puebla-Oaxaca Mountain System. In the western and central parts of the TMVB, but not in its eastern part or in the Sierra Madre Oriental, there is the *O. aztecus* species complex, at elevations around 2200 m a.s.l. It is clear that the different species complexes of the *O. chevrolati* species line occupy different mountain systems in the central part of the MTZ. It can be inferred that their dispersal occurred when the mountain systems already had their current conformation (end of the Pliocene to the Pleistocene).

Conclusions

The American *Onthophagus* all belong to the same subgenus (*Onthophagus*), a monophyletic group; however, their penetration into the Americas could be the result of several diachronic dispersion events by different lines of the same origin. This means that within their ancient and northern origin they have differences in their distributional patterns. Considering the whole genus, possibly the lines of oldest penetration are the *O. clypeatus* and *O. hircus* species groups, which today are widely distributed in Central and even South America.

Within the *O. chevrolati* species group, the *O. hippopotamus* species line but in a much more defined way the *O. hippopotamus* species complex, is separated from the general distribution scheme of the fauna of northern origin in the MTZ; i.e. the succession of species from north to south following the mountain systems structure and alignment. Speciation in the *O. hippopotamus* species complex (Fig. 13) could be directly related to the geological history of the TMVB. Starting in the Pliocene there has been active volcanism in this mountainous system, to which the effects of glaciation were later added. The TMVB is a geographic space where a significant degree of speciation via vicariance occurred.

The careful comparative examination of the microanatomy of the genitalia of the *O. hippopotamus* species line, together with the study of the distribution areas allows us to make some proposals. It is quite evident that the TMVB was not a place for displacement and dispersal of the *O. hippopotamus* species complex, but rather an area of diversification. Consistent with this, the first cladogenetic event would have been the separation of the *O. brevifrons* and *O. hippopotamus* species complexes, which probably occurred in the Miocene, or early Pliocene. The *hippopotamus* species complex is distinguished by two clearly defined ecological characteristics: its association with high mountain elevations and its occupation of gopher burrows. Morphologically, the anterior tibias of the male are elongated and thin with a pointed terminal spur, strongly curved medially; a character that we associate with the handling of excrement in the gopher burrows. The distribution of the *O. hippopotamus* species complex is even more striking when we consider that not only is it almost totally restricted to the TMVB, but it is also ecologically restricted to the nests of gopher (Rodentia: Geomyidae) of the genus *Cratogeomys* whose distribution center is the TMVB (Lobo & Halffter 1994). The Geomyidae expanded from the TMVB starting in the Early Pliocene.

The *high mountains*, i.e. those elevations where ecological conditions are very different from those of the surrounding lowlands, is of prime importance in the biogeography of some regions, among them the MTZ. This importance not only depends on the elevation, but more importantly the geographical location. The high mountains of Europe and North America that have been in contact with or near the great glaciers of the Pleistocene (and that had or have had their own glaciers) have acted as *refugia*. Tropical mountains do not have this role, or it is much less important. In the tropics, environments at high elevations on the mountains are very different from those at lower elevations. They are true islands. Their distribution is a striking example of what Mastretta-Yanes *et al.* (2015) call *sky islands*: an archipelago of temperate-cold or cold high mountain enclaves, isolated from the surrounding environment by unfavorable conditions. The changes associated with the Pleistocene glaciations did not cause horizontal expansions of specific distribution areas, but rather vertical displacement (Lobo & Halffter 2000). Under these conditions, the model of vertical colonization appears; very characteristic of mountains located in the tropics, characteristic of some tropical lands, but not all. In the MTZ, vertical colonization is the absolute exception.

The MTZ is first and foremost a transition zone. The colonization of the mountains as such is of minor importance, given the role of the mountains as a route of penetration and displacement. Hence the importance of horizontal colonization and its various manifestations. The formation and evolution of the distribution area of a species, and even more to the point, of a high mountain species is an active process of interactions between the physical environment and populations. In the coldest periods (for example, during glaciation), cold, humid conditions move to lower elevations so that the space available to the high mountain biota expands horizontally (i.e., as one descends the area increases). As the climate changes, warmer conditions bring with them, the forced ascent of biota adapted to the cold. If the preceding horizontal expansion was significant, there will not be one upward movement, but rather several, with the consequent fragmentation. In the TMVB, the process described above has been occurring since the Miocene, but it intensified in the Pleistocene and Recent.

Summaryzing the evolutionary history of the *O. chevrolati* species group, the ancestor of the *O. vespertilio* species line must have reached the MTZ early (Miocene). Its restriction to caves seems to be a later phenomenon. Equally, the expansion of the *O. cyanellus* species line must also have been Miocenic, at intermediate elevations in the mountains of eastern Mexico and Central America. The main line evolved in the TMVB, where the *O. hippopotamus* and *O. chevrolati* species lines exhibit a different relationship with the mountain systems: the *O. hippopotamus* species line evolved with the mountain system (TMVB); the *O. chevrolati* line used the mountain systems as a mean of expansion. With few exceptions, the mountains of the MTZ were not periglacial wildlife refuges. Nor were they enclaves colonized by the lowland fauna. These mountain systems were mainly routes of penetration for a fauna of northern origin. Some of the mountains represent very important areas of speciation, especially the TMVB, resulting in alpha diversity that is not very high, but notable beta values. There is a strong turnover even among nearby mountains.

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