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Track analysis of the North and Central American species of the *Pantomorus–Naupactus* complex (Coleoptera: Curculionidae)

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Abstract

We undertook a panbiogeographic analysis of the broad-nosed weevils of the genera *Naupactus* Dejean, 1821, *Pantomorus* Schönherr, 1840 and *Phacepholis* Horn, 1876 (Coleoptera: Curculionidae) from North and Central America to propose a biogeographic scenario to explain their biotic diversification. Based on individual tracks of 30 species, we obtained six generalized tracks: Mesoamerican, Chiapas, Sierra Madre del Sur, Mexican Pacific Coast, Southern Great Plains and Northern Great Plains tracks. The Sierra Madre del Sur generalized track is the best supported, based on 10 species of the three genera. We found two nodes, one at the intersection of the Mesoamerican and Chiapas tracks, and another at the intersection of the Chiapas and Sierra Madre del Sur tracks. Species of *Naupactus* are primarily distributed in lowlands, associated mostly with dry forests and xeric environments. Species of *Pantomorus* and *Phacepholis* would have diversified from South American *Naupactus*-like ancestors, mainly in montane habitats and lowlands of North and Central America, between sea level to about 2500 m of altitude.

Key words: Panbiogeography – weevils – Naupactini – Mexican Transition Zone

Introduction

The *Pantomorus–Naupactus* complex is a group of broad-nosed weevils belonging to the tribe Naupactini (Coleoptera: Curculionidae). It consists of approximately 250 species distributed from the Great Plains of the United States of America to Central Argentina and Chile (Lanteri 1990; Scataglini et al. 2005; Rosas et al. 2011). Its highest diversity is found in the Neotropical region, particularly in the tropical forests of the Amazonian subregion. Some species, especially those with apomictic parthenogenesis (Lanteri and Normark 1995; Normark and Lanteri 1998; Rodriguero et al. 2010), have been introduced into other countries outside the Americas along with different crops, becoming agricultural pests (Lanteri and O'Brien 1990; Lanteri and Diaz 1994; Lanteri and Marvaldi 1995).

Most species of the *Pantomorus–Naupactus* complex occurring in Mexico and Central America have been assigned to *Pantomorus* Schönherr (O'Brien and Wibmer 1982), a genus that based on a recent phylogenetic analysis (Rosas et al. 2011) is restricted to some species formerly placed in *Pantomorus* group I *sensu* Sharp (1889–1911). They are flightless species (metathoracic wings reduced to absent), usually inhabiting dry forests and other xerophytic environments above 700 m of altitude (Rosas et al. 2011). The usually fully winged species of *Naupactus* Dejean have been recorded from the tropical and subtropical forests of South America, especially Brazil (Wibmer and O'Brien 1986). This genus also occurs in dry forests of southern Mexico and Central America, mainly at lower altitudes than *Pantomorus*. *Phacepholis* Horn, currently considered a distinct monophyletic genus (Lanteri 1990; Rosas et al. 2011), includes flightless forms, some occurring in the Great Plains of North America (*Phacepholis sensu stricto* or *sensu* Lanteri 1990), others distributed along the Pacific coast of Mexico and Central America (*Ph. globicollis* species group) (Rosas et al. 2011). The former species inhabit grasslands at sea level, the latter occur from sea level to about 2000 m of altitude, usually in dry forests and environments characterized by xerophytic shrubs.

Our main objective is to undertake a panbiogeographic analysis of the species of *Pantomorus, Naupactus* and *Phacepholis* from North America, Mexico and Central America. We propose a biogeographic scenario that explains the biotic diversification of these taxa in the area where the Neotropical and the Nearctic biotas overlap (Halffter 1964, 1987; Morrone and Márquez 2001). This way we will contribute to the understanding of the historical evolution of one of the most interesting transition zones in the Americas, the Mexican Transition Zone (Morrone 2006, 2010).

Material and Methods

We analysed distributional data of 30 species of the *Pantomorus–Naupactus* complex from North and Central America, previously treated in a phylogenetic analysis by Rosas et al. (2011) and assigned to the genera *Phacepholis* (11 species), *Pantomorus* (14 species) and *Naupactus* (five species). Geographical records were obtained mainly from specimens examined in Rosas et al. (2011) and from the literature (Sharp 1889–1911; Champion 1911; Buchanan 1939; Maes and O'Brien 1990; Salas-Araiza et al. 2001; Jones and Luna-Cozar 2007).

The panbiogeographic method (Croizat 1958, 1964) consists in plotting localities of different taxa on maps and connecting them throughout lines termed individual tracks. When superimposed, individual tracks result in summary lines called generalized or standard tracks, which indicate the pre-existence of ancestral biotas subsequently fragmented by tectonic and/or climate changes. If two or more generalized tracks intersect in a given area, they determine a node, which indicates that different ancestral biotic and geological components interrelate in space/time (Morrone and Crisci 1995; Craw et al. 1999; Morrone 2009).

Localities, individual and generalized tracks, and nodes were represented on maps using ARCVIEW 3.2 (ESRI 1999). Localities were connected according to their geographical proximity, using a minimum

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spanning tree method. Generalized tracks and nodes were characterized following the biogeographic regionalizations of Morrone (2006, 2010) for Mexico and Central America and Udvardy (1975) for the USA.

Results

Based on the overlap of 30 individual tracks (Figs 1–12), we identified six generalized tracks (Fig. 13), herein called Mesoamerican, Chiapas, Sierra Madre del Sur, Mexican Pacific Coast, Southern Great Plains and Northern Great Plains.

The Mesoamerican generalized track is supported by the individual tracks of *Phacepholis strabo* (Sharp 1891) (Fig. 6), *Pantomorus rudis* (Sharp 1891) (Fig. 7), *Naupactus laticeps* Champion 1911 (Fig. 9) and *N. femoratus* (Sharp 1891) (Fig. 11). It is distributed in Costa Rica, Nicaragua and Honduras, along the Mexican Pacific Coast, Chiapas and Western Panamanian Isthmus biogeographic provinces, from sea level to about 2400 m of altitude.

The Chiapas generalized track is supported by the individual tracks of *Pantomorus comes* Kuschel 1956 (Fig. 4), *P. dorsalis* Sharp 1891 (Fig. 5), *P. sobrinus* (Sharp 1891) (Fig. 6), *P. circumcinctus* Sharp 1891 (Fig. 9), *P. subcinctus* (Sharp 1891) (Fig. 10), *P. salvini* (Sharp 1891) (Fig. 11) and *P. salvadorensis* Kuschel 1956 (Fig. 12). It is distributed in Guatemala, El Salvador and Honduras, in the Chiapas biogeographic province, usually over 500 m up to about 2000 m of altitude.

The Sierra Madre del Sur generalized track is supported by the individual tracks of *Naupactus virescens* Champion 1911 (Fig. 7), *N. stupidus* Boheman 1840 (Fig. 11), *N. sulfuratus* Champion 1911 (Fig. 12), *Phacepholis globicollis* (Pascoe 1886) (Fig. 4), *Ph. sulfureus* (Champion 1911) (Fig. 5), *Ph. brevipes* (Sharp 1891) (Fig. 6), *Pantomorus parvulus* (Sharp 1891) (Fig. 8), *P. picturatus* (Sharp 1891) (Fig. 8), *P. longulus* Sharp 1891 (Fig. 9) and *P. picipes* Sharp 1891 (Fig. 10). This track is distributed in Mexico (Chiapas, Puebla and Oaxaca states), in the Sierra Madre del Sur, Mexican Pacific Coast and Chiapas biogeographic provinces, between sea level to about 2000 m of altitude.

The Mexican Pacific Coast generalized track is supported by the individual tracks of *Phacepholis viridicans* (Sharp 1891) (Fig. 4), *Ph. albicans* (Sharp 1889–1911) (Fig. 5) and *Pantomorus horridus* Champion 1911 (Fig. 8). It is distributed in Mexico, in the states of Guerrero, Michoacán, Colima, Jalisco, Nayarit and Sinaloa, along the Mexican Pacific Coast biogeographic province, from sea level to about 700 m of altitude.

The Southern Great Plains generalized track is supported by the individual tracks of *Phacepholis viridis* (Champion 1911) (Fig. 1) and *Ph. obscurus* Horn 1876 (Fig. 2). It is distributed in the USA (Texas), in the Grasslands biogeographic province, at sea level.

The Northern Great Plains generalized track is supported by the individual tracks of *Phacepholis planitiatus* (Buchanan

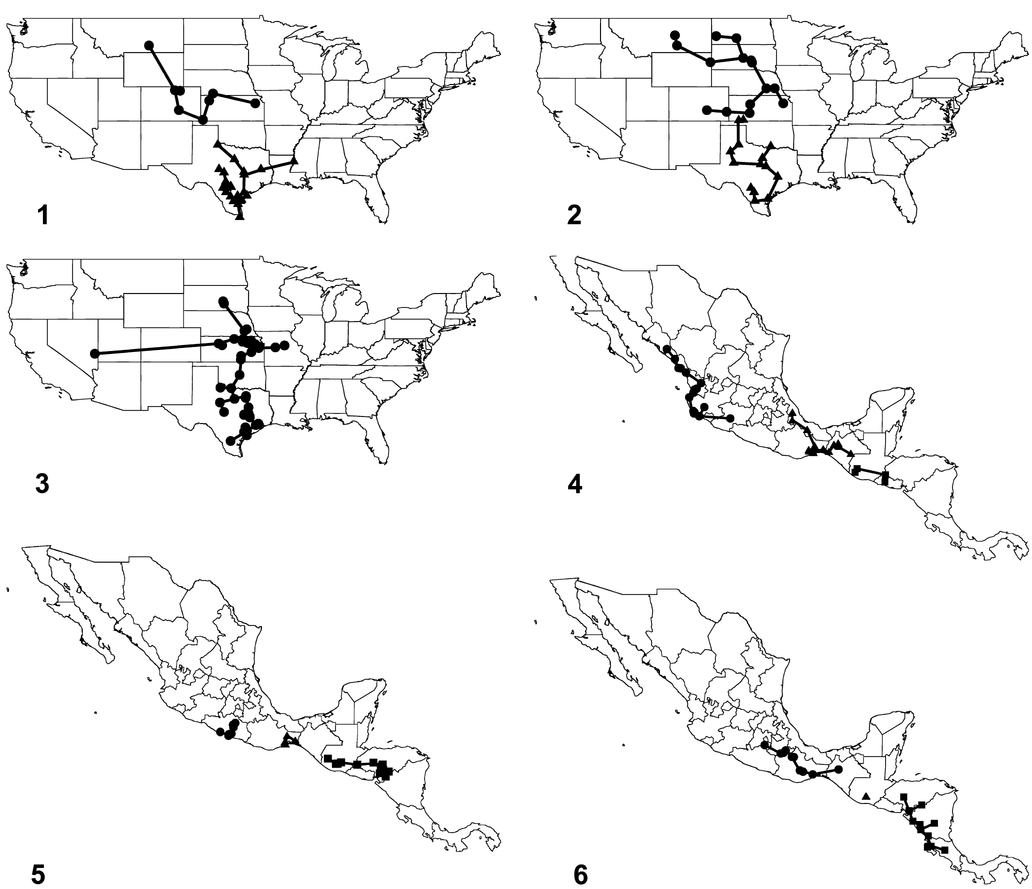

Fig. 1–6. Individual tracks. (1) *Phacepholis planitiatus* (circles), *Phacepholis viridis* (triangles); (2) *Phacepholis candidus* (circles), *Phacepholis obscurus* (triangles); (3) *Phacepholis elegans* (circles); (4) *Phacepholis viridicans* (circles), *Phacepholis globicollis* (triangles), *Pantomorus comes* (squares); (5) *Phacepholis albicans* (circles), *Phacepholis sulfureus* (triangles), *Pantomorus dorsalis* (squares); (6) *Phacepholis brevipes* (circles), *Pantomorus sobrinus* (triangles), *Phacepholis strabo* (squares).

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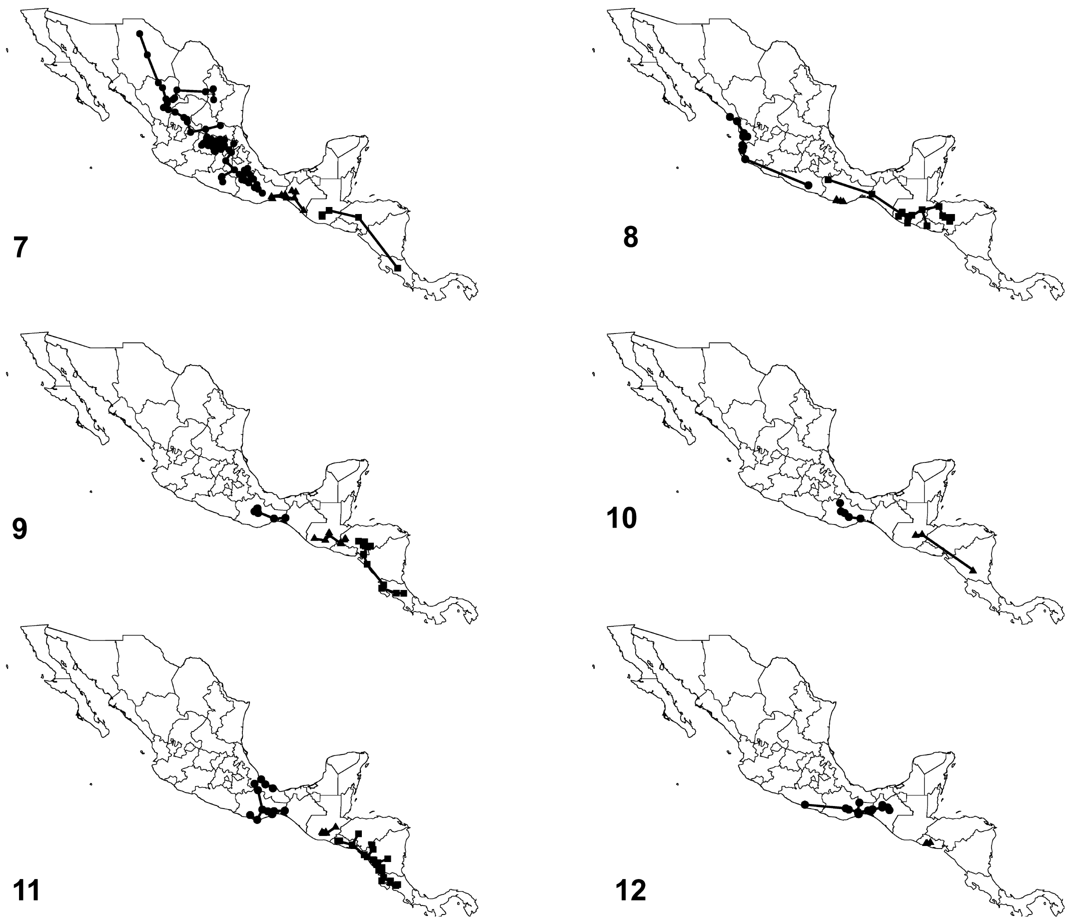

Fig. 7–12. Individuals tracks. *Pantomorus albosignatus* (circles), *Naupactus virescens* (triangles), *Pantomorus rudis* (squares); (8) *Pantomorus horridus* (circles), *Pantomorus parvulus* (triangles), *Pantomorus picturatus* (squares); (9) *Pantomorus longulus* (circles), *Pantomorus circumcinctus* (triangles), *Naupactus laticeps* (squares); (10) *Pantomorus picipes* (circles), *Pantomorus subcinctus* (triangles); (11) *Naupactus stupidus* (circles), *Pantomorus salvini* (triangles), *Naupactus femoratus* (squares); (12) *Naupactus sulfuratus* (circles), *Pantomorus salvadorensis (triangles)*.

1939) (Fig. 1) and *Ph. candidus* Horn 1876 (Fig. 2). This track is distributed in the USA (Kansas, Nebraska, South Dakota, Wyoming and Montana), in the Grasslands biogeographic province, at sea level.

We recognized two nodes: one in the intersection of the Mesoamerican and the Chiapas generalized tracks and another in the intersection of the Chiapas and Sierra Madre del Sur generalized tracks. Both are located in the Chiapas biogeographic province (Fig. 13), which has been included in the Mexican Transition Zone (Halffter 1964, 1987; Morrone 2010).

Discussion

The Mesoamerican, Chiapas and Sierra Madre del Sur generalized tracks correspond to the Southern Mesoamerican generalized track of Abrahamovich et al. (2004), based on species of *Bombus* (Hymenoptera: Apidae), and to the Sierra Madre del Sur, Northern and Southern Mesoamerican generalized tracks of Márquez and Morrone (2003), based on species of *Heterolinus* and *Homalolinus* (Coleoptera: Staphylinidae). The Mexican Pacific Coast generalized track is partially coincident with the Center South Pacific generalized track of Escalante et al. (2004), based on mammal species, and partially coincident with the generalized track 11 of Corona and Morrone (2005), based on Buprestidae (Coleoptera) of the genus *Lampetis*. The Northern and Southern Great Plains generalized tracks are coincident with the North American Prairies pattern of Katinas et al. (2004), based on plant species of the tribes Epilobieae, Gongylocarpeae and Onagrae (Onagraceae), and with the geographical range of the black-tailed prairie dog (*Cynomys ludovicianus*) (Lomolino and Smith 2001).

The *Pantomorus–Naupactus* complex is mostly distributed in the Neotropical region and the Mexican Transition Zone, but five species of *Phacepholis* are found in the Great Plains of central USA, which correspond to the Nearctic region. These prairie-adapted species occur in grasslands and are distributed from Texas to Montana. The other species of *Phacepholis*, belonging to the *Ph. globicollis* species group (Rosas et al. 2011), occur mainly on lowlands of the Pacific coast and are associated with dry forests, not exceeding 900 m of altitude. They are part of the Mesoamerican, the Sierra Madre del Sur and the Mexican Pacific Coast generalized tracks. A single species of *Phacepholis (Ph. brevipes)* is distributed between 1000 and 2000 m of altitude on the slopes of the Sierra Madre del Sur and Chiapas. Other steppe- or prairie-adapted species

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Fig. 13. Individual tracks. Generalized tracks and nodes obtained from the biogeographic analysis of 30 species belonging to *Phacepholis, Pantomorus* and *Naupactus,* distributed in North and Central America. A, Mesoamerican generalized track; B, Chiapas generalized track; C, Sierra Madre del Sur generalized track; D, Mexican Pacific Coast generalized track; E, Southern Great Plains generalized track; F, Northern Great Plains generalized track

of the *Pantomorus–Naupactus* complex occurring in the Great Plains of North America, belonging to the genera *Aramigus* Horn, *Atrichonotus* Buchanan and *Naupactus* (Lanteri and O'Brien 1990; Lanteri and Diaz 1994; Lanteri and Marvaldi 1995; Lanteri and Morrone 1995; Scataglini et al. 2005), have been introduced into the USA along with different crops. Their dispersal and establishment might have been facilitated by their parthenogenetic mode of reproduction (Lanteri and Normark 1995; Normark and Lanteri 1998; Rodriguero et al. 2010). Species of *Phacepholis* are not parthenogenetic, and they are not as harmful for crops as the invasive species.

Most *Pantomorus* species from Mexico and Central America contribute to support four of the six generalized tracks herein recovered, mainly the Chiapas and Sierra Madre del Sur tracks. These species usually occur above 700 m of altitude, except *P. parvulus* and *P. horridus*, the latter inhabiting the coastal plains of the Mexican Pacific Coast biogeographic province. The Chiapas generalized track is mainly supported by the *Pantomorus* species previously assigned to a very distinct monophyletic group, the *P. circumcinctus* species group (Rosas et al. 2011), that is distributed above 1000 m of altitude.

Pantomorus albosignatus Boheman, 1840 represents an example of a successful colonization of a biogeographic province out the geographical range where most of the species analysed occur, and it does not take part of any of the generalized tracks herein recovered. The individual track of this species is defined by numerous locality records extended mainly on the Mexican Plateau, although it also occurs in the Transmexican Volcanic Belt and Sierra Madre del Sur provinces. The Mexican Plateau consists of an extensive plateau in central Mexico situated between the Sierra Madre Occidental and the Sierra Madre Oriental, where many insect species of ancient Neotropical origin survived and diversified probably during the Eocene-Pliocene (Halffter 1964, 1987) and where there are also Nearctic elements above 3000 m of altitude (Escalante et al. 2004). In general, Mesoamerican taxa are not found above 2200–2300 m (Halffter 1987, 2003). *Pantomorus albosignatus,* occurring between 1000 and 2300 m of altitude, is the most common representative of the Naupactini in Mexico. It would have been capable of colonizing a broad area throughout the xeric environments of the Mexican Plateau (Nearctic region), probably due to a parthenogenetic mode of reproduction (Rosas et al. 2011). By contrast, its sister species, *P. parvulus*, has sexual populations and occurs only in the state of Oaxaca, below 500 m of altitude (Rosas et al. 2011). Based on this information, we propose that the dispersal of *P. albosignatus* throughout the Mexican Plateau could be a recent event, as happens with other recent immigrants to this area (Halffter 1964).

The species of *Naupactus* contribute to two generalized tracks, the Mesoamerican and the Sierra Madre del Sur tracks. They are more frequent at lower elevations than those of *Pantomorus*, although some of them show a broad altitudinal range, from sea level to about 1000 m or more, especially in montane habitats of Central America (*e.g. N. femoratus*, *N. laticeps* and *N. virescens*) (Maes and O'Brien 1990; Rosas et al. 2011). The absence of species of *Naupactus* and of the *Ph. globicollis* species group in the highlands of the Chiapas biogeographic province suggests that these groups are primarily lowland groups, as most of the South American species of *Naupactus*. South American lowland taxa have originated Mesoamerican lineages across the lowlands of the Panamanian Isthmus to the north (Halffter 1987). Most of the insects of the mountains south of the Isthmus of Tehuantepec evolved in the Central America Nucleus, which received an ancient and very important biotic contribution from South America. The biota that evolved in this area has expanded towards South America and the North through the Isthmus of Tehuantepec and corresponds to the Mesoamerican distributional pattern of Halffter (1987).

When comparing the distributional pattern of the *Pantomorus–Naupactus* complex with that of the genus *Ericydeus* Pascoe, another member of the Naupactini broadly distributed from the USA to Argentina (Lanteri 1995), we found interesting similarities as well as differences. The cladograms of both groups (Lanteri 1995; Rosas et al. 2011) show a southern–northern direction of evolutionary change, suggesting a South American origin of their ancestors. A preliminary phylogenetic tree for all the genera of Naupactini (del Río and Lanteri 2010) also supports this hypothesis. Moreover, the highest species diversity of *Ericydeus* is recorded for the Mexican Transition Zone, especially the Sierra Madre del Sur province, an area where we found the best supported generalized track of the group under study (10 species belonging to *Naupactus, Pantomorus* and the *Phacepholis globicollis* species group). Montane environments with altitudinal gradients, such as those of the Sierra Madre del Sur, usually restricted dispersal and favoured speciation (Halffter 1987). *Ericydeus* is much less diversified than the *Pantomorus–Naupactus* complex (16 species versus 250 species). We believe that the notorious morphological diversity seen on the latter group, along with the development of some adaptive traits (*e.g.* loss of flight due to the reduction in hind wings), would have favoured the colonization of higher altitudes, prairies and steppes, environments where species of *Ericydeus* usually do not occur.

Ericydeus and the *Pantomorus–Naupactus* complex, both groups of Neotropical origin, were able to colonize and diversify in the Nearctic region, but following different pathways. *Ericydeus* reached the deserts of north-western Mexico and south-western USA (California and Arizona), where the species endemic to this area [*E. forreri* (Champion 1911); *E. placidus* (Horn 1876) and *E. lautus* (LeConte 1854)]

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are frequently associated with xerophytic shrubs of the genus *Larrea* (Lanteri 1995). Within the *Pantomorus–Naupactus* complex, the species of *Phacepholis sensu stricto* diversified in the Great Plains of North America, on the eastern side of the Rocky Mountains, reaching a broad distribution throughout this grassland bioma. Even though some species of *Pantomorus* (*e.g. P. horridus*) and the *Phacepholis globicollis* group (*e.g. Ph. albicans* and *Ph. viridicans*) extended their ranges along the Mexican Pacific coast up to the states of Jalisco, Nayarit and Sinaloa, they were not able to overcome the barrier of the Sonoran desert. The distribution of *Ericydeus* in North America is partially coincident with the western generalized track of Katinas et al. (2004), and the range of *Phacepholis sensu stricto* (Lanteri 1990) agrees with the eastern North American generalized track of the same authors, based on plant species of the family Onagraceae.

Based on evidence of previous phylogenetic analyses (Lanteri et al. 2010; Rosas et al. 2011), we hypothesize that the ancestors of *Pantomorus* and *Phacepholis* probably expanded their ranges into Central and North America from South America, sometime between Late Cretaceous and Early Tertiary, as other insect groups (Halffter 1964, 1987), although following different northward pathways of dispersal. *Ericydeus* was able to colonize and to diversify in the xeric environments of the Sonora and Mohave deserts, whereas *Pantomorus* was able to colonize and diversify in the xeric environments, dry forests and montane habitats of Mexico and Central America. *Naupactus* and the *Ph. globicollis* species group are distributed primarily in lowlands, as most South American species of *Naupactus,* and are associated with dry forests and xeric environments.

Lanteri and Morrone (1995) and Lanteri and Normark (1995) proposed that *Naupactus* is paraphyletic (Scataglini et al. 2005). We hypothesize herein that the species of *Pantomorus* and *Phacepholis* have different *Naupactus*-like ancestors and belong to two different cenocrons. The oldest arrived in the late Cretaceous to early Palaeocene via a hypothesized proto-Antillean land bridge (Savage 1966; Rosen 1975; Savage and Myers 2002; Crawford and Smith 2005), formed at the leading edge of Caribbean tectonic plate as it moved east between North and South America (Crawford and Smith 2005). *Phacepholis* belongs to this ancient Neotropical cenocron and diversified mainly in the Mexican coasts, Central America and the lowlands of North America. *Pantomorus* might belong to a younger cenocron, the Mountain Mesoamerican cenocron, basically distributed in the highlands of Guatemala and Central America (Morrone 2005). A future phylogenetic analysis will allow falsifying this hypothesis.

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Resumen

Análisis de trazos de las especies norteamericanas y centroamericanas del complejo Pantomorus–Naupactus *(Coleoptera: Curculionidae)*

Se realizó un análisis panbiogeográfico de los gorgojos de rostro corto pertenecientes a los géneros *Naupactus* Dejean, *Pantomorus* Schönherr y *Phacepholis* Horn (Coleoptera: Curculionidae) de América del Norte y Central, para proponer un escenario biogeográfico que explique su diversificación biótica. Se obtuvieron seis trazos generalizados (Mesoamericano, Chiapas, Sierra Madre del Sur, Costa Pacífica Mexicana, Grandes Planicies del Sur y Grandes Planicies del Norte) a partir de los trazos individuales de 30 especies. El trazo generalizado Sierra Madre del Sur es el mejor sustentado por 10 especies de los tres géneros. Se obtuvieron dos nodos, uno en la intersección de los trazos Chiapas y Mesoamericano, y otro en la intersección de los trazos Chiapas y Sierra Madre del Sur. Las especies de *Naupactus* están distribuidas principalmente en tierras bajas y están asociadas, generalmente, con selvas secas y ambientes xerófilos. Las especies de *Pantomorus* y *Phacepholis* se han diversificado a partir de ancestros similares a *Naupactus* provenientes de América del Sur, principalmente en hábitats montañosos y tierras bajas de América del Norte y Central, entre el nivel del mar y los 2500 m de altitud.

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