



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

Facultad de Ciencias

Análisis filogenético del género
Pantomorus Schoenherr (Coleoptera:
Curculionidae: Entiminae)

T E S I S

QUE PARA OBTENER EL GRADO ACADÉMICO DE

DOCTORA EN CIENCIAS

P R E S E N T A

MA. VENTURA ROSAS ECHEVERRÍA

TUTOR PRINCIPAL DE TESIS: DR. JUAN JOSÉ MORRONE LUPI

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MÉXICO, D.F.

NOVIEMBRE, 2011



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“Lo que verdaderamente importa en la educación -la que se supone obtenemos en un lugar como éste- no vendría a ser aprender a pensar, sino a elegir cómo vamos a pensar”
(David Foster Wallace, 2005)

*Solo cuando se haya talado el último árbol,
sólo cuando se haya envenenado el último río,
sólo cuando se haya pescado el último pez;
sólo entonces descubrirás que el dinero no es comestible.*
(Profecía de los Indios Cree)

Penetrar en el corazón de las cosas -incluso en el de las más pequeñas, en el de una brizna de hierba, como dijera Walt Whitman- produce un tipo de excitación y alegría que parece muy posible que, de todos los seres que pueblan este planeta, solo puedan experimentarla los seres humanos.
(Carl Sagan, Cerebro de broca)

*El más sabio de los hombres parece un mono al comparárselo con Dios en sabiduría,
en belleza y en todas las otras cosas.*
(Heráclito, Fragmentos)

Está en poder de todos los hombres conocerse a sí mismos y ser sensatos.
(Heráclito, Fragmentos)

*Erase dos peces jóvenes que nadaban juntos cuando de repente se toparon con un pez viejo, que los saludó y les dijo, "Buenos días, muchachos ¿Cómo está el agua?" Los dos peces jóvenes siguieron nadando un rato, hasta que eventualmente uno de ellos miró al otro y le preguntó,
"¿Qué demonios es el agua?"*
(Osho, Conciencia, David Foster Wallace, 2005)

Una persona creativa es aquella que tiene percepción, puede ver cosas que no ha visto nadie antes, oye cosas que no ha escuchado nadie antes; entonces hay creatividad.
(Osho, Creatividad)

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Resumen

Pantomorus Schoenherr (Curculinidae: Entiminae: Naupactini) es un género erigido con base en la especie mexicana *P. albosignatus* Boheman. *Pantomorus* usualmente se separa de *Naupactus* Dejean, por poseer antenas y rostro más cortos, hombros y alas posteriores ausentes y fémures anteriores iguales a los posteriores o ligeramente más anchos. Debido a que no había una clara distinción entre *Pantomorus* y *Naupactus*, se propuso el complejo *Pantomorus-Naupactus* para incluir 250 especies.

En este trabajo se evaluó la hipótesis que *Pantomorus sensu stricto* es monofilético. Los objetivos de este estudio fueron: determinar si el género *Pantomorus sensu stricto* es monofilético; reconocer grupos monofiléticos dentro del mismo; elaborar una clave para separar los géneros *Naupactus*, *Pantomorus* y *Phacepholis* Horn distribuidos en América del Norte y Central. Además, generar una clave y diagnosis para separar a las especies incluidas en *Pantomorus*, y finalmente inferir la historia biogeográfica de *Naupactus*, *Pantomorus* y *Phacepholis*, distribuidos en América del Norte y Central.

En el capítulo uno de esta tesis se presenta un análisis cladístico del complejo *Pantomorus-Naupactus* (Coleoptera: Curculionidae) de América del Norte y Central, basado en 35 especies y 61 caracteres morfológicos, más 1151 bp de los genes mitocondriales COI y Cyt b. Se obtuvo un cladograma que permitió reconocer dos linajes principales dentro del complejo. Un linaje representado por las especies incluidas en *Phacepholis* y *Pantomorus* grupo II, este último comprende a las especies que tienen un mucro grande en la tibia anterior y un mucro mediano en la tibia media de los machos. El otro linaje conformado por las especies de *Naupactus* y *Pantomorus* grupo I; *Pantomorus* grupo I incluye a las especies con mucro mediano en la tibia anterior y

macro ausente en la tibia media de los machos. Se recomendó utilizar el nombre de *Pantomorus* para aproximadamente 22 especies de *Pantomorus* grupo I. *P. stupidus* (Boheman) y *P. femoratus* Sharp fueron transferidas a *Naupactus*. Se amplió el concepto de *Phacepholis* para incluir las especies de *Pantomorus* grupo II (de cinco a 13 especies). Se estableció la sinonimia de *Athetetes* Pascoe 1886 bajo *Phacepholis* Horn 1876.

En el capítulo dos se presenta una sinopsis taxonómica del género *Pantomorus* de acuerdo con la circunscripción sugerida en el capítulo uno, ésta comprende una clave para separar los géneros *Naupactus*, *Pantomorus* y *Phacepholis* distribuidos en América del Norte y Central, además de una clave y diagnóstico de las especies de *Pantomorus*. En el capítulo tres se presenta un análisis panbiogeográfico para las especies del complejo *Pantomorus-Naupactus* distribuidas en América del Norte y Central, para proponer un escenario biogeográfico que explique su diversificación biótica. Con base en los trazos individuales de 30 especies, se obtuvieron seis trazos generalizados y dos nodos. Se concluyó que 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.

Abstract

Pantomorus Schoenherr (Entiminae: Naupactini) is a genus based on the Mexican species *P. albosignatus* Boheman. *Pantomorus* usually separates from *Naupactus* Dejean by the shorter antennae and rostrum, the lack of humeri and hind wings, and the front femora being as wide as to slightly wider than the hind femora. Because there was not a clear distinction between *Pantomorus* and *Naupactus*, was proposed the *Pantomorus-Naupactus* complex for include about 250 species.

Currently there are two main concepts of *Pantomorus*, expressed in the most recent checklists: a) *Pantomorus sensu lato*, it is distributed in the Neotropical region, with the highest species diversity in tropical areas of South America, including species from Mexico and Central America, and b) *Pantomorus sensu stricto* restricted to the Mexican and Central American species, with all the South American species included in the genus *Naupactus*.

In chapter one of this thesis we undertook the cladistic analysis of the *Pantomorus-Naupactus* complex (Coleoptera: Curculionidae) from North and Central America, based on 35 species and 61 morphological characters, plus 1151 bp of the mtDNA COI and Cyt b genes. Was obtained a cladogram that allowed to recognize two main lineages within of complex. One is represented by the species placed in *Phacepholis* and the *Pantomorus* species group II. This latter includes species with front tibia bearing a large mucro, and middle tibia with a medium-sized mucro in the males. The other lineage is represented by the species of *Naupactus* and *Pantomorus* species group I. *Pantomorus* species group I includes species with the front tibia bearing a medium mucro, and the middle tibia lacking mucro in the males. We recommend retaining the name *Pantomorus* for approximately 22 species of the *Pantomorus* group I.

P. stupidus (Boheman) and *P. femoratus* Sharp which should be transferred to *Naupactus*. We enlarge the concept of *Phacepholis* to include species of the *Pantomorus* group II (from five to 13 species). We establish the synonymy of *Athetetes* Pascoe 1886 with *Phacepholis* Horn 1876.

Chapter two presents a taxonomic synopsis of the genus *Pantomorus* according to the circumscription suggested in the chapter one; it includes a key to separate the genera *Naupactus*, *Pantomorus* and *Phacepholis* from North and Central America, besides a key and diagnosis of each species of *Pantomorus*. Chapter three presents a panbiogeographic analysis of the species of *Pantomorus*-*Naupactus* complex from North and Central America, in order to propose a biogeographic scenario to explain their biotic diversification. Based on individual tracks of 30 species we obtained six generalized tracks and two nodes. We conclude that the 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.

INTRODUCCIÓN GENERAL

El orden Coleoptera es el de mayor diversidad específica conocida dentro del reino animal. En este orden se ubican los gorgojos de la superfamilia Curculionoidea, la cual incluye alrededor de 62,000 especies y 6,000 géneros descritos (Thompson, 1992; Kuschel, 1995; Marvaldi et al., 2002; Oberprieler et al., 2007). Dado que Curculionoidea es uno de los grupos taxonómicos con mayor riqueza de especies, es uno de los más desafiantes en cuanto a su clasificación (Marvaldi et al., 2002). Muchas de sus especies son fitófagas y pueden llegar a constituir plagas agrícolas y forestales (Sauvard et al., 2010). Sus larvas constituyen el estado de desarrollo generalmente más dañino, alimentándose de raíces, vástagos, hojas, flores, frutos o semillas de las plantas. Pueden ser especialistas en diferentes tipos de tejidos vivos o alimentarse de restos de plantas muertas (Farrell et al., 2001; Lanteri et al., 2002; Marvaldi et al., 2002).

La familia Curculionidae es de las más diversas, con 51,000 especies descritas (Oberprieler et al., 2007), sólo superada por Staphylinidae que registra 55,440 (Grebennikov & Newton, 2009). Esta riqueza de especies es en gran medida responsable de la diversidad de Phytophaga (superfamilias Chrysomeloidea y Curculionoidea) y, de hecho, la de Coleoptera (Oberprieler et al., 2007). Sus especies se distribuyen en todo el mundo, desde las zonas árticas en el norte, hasta las islas subantárticas en el sur, desde las playas hasta las montañas y desde el desierto hasta los bosques lluviosos. Aunque se alimentan principalmente de angiospermas, las especies de Curculionidae hacen uso extensivo de las monocotiledóneas como plantas huéspedes. Es probable que las monocotiledóneas constituyan un hospedero ancestral de Curculionidae y podrían haber jugado un papel fundamental en la diversificación de la familia (Marvaldi et al., 2002; Oberprieler et al., 2007).

Dentro de la familia Curculionidae, los “gorgojos de rostro corto” pertenecen a la subfamilia Entiminae. Esta subfamilia es la de mayor diversidad, reuniendo 1,350 géneros (Alonso-Zarazaga & Lyal, 1999; Yunakov & Nadein, 2006; Marvaldi et al., en prensa) y alrededor de 12,200 especies a nivel mundial (Morrone, 1999; Oberprieler et al., 2007; Lanteri & Del Río, 2008; Marvaldi et al., en prensa). Análisis filogenéticos recientes, basados en evidencia morfológica (del estado adulto y larval) y molecular, señalan que se trata de un grupo natural (Marvaldi, 1997; Marvaldi et al., 2002). Los entiminos se caracterizan por la presencia de un rostro corto y robusto y un proceso mandibular deciduo, el cual deja una cicatriz, denominada escara, en la superficie externa de la mandíbula (Thompson, 1992; Oberprieler et al., 2007; Marvaldi et al., en prensa). La subfamilia Entiminae reúne 55 tribus según la clasificación de Curculionoidea del catálogo mundial de géneros de gorgojos más reciente (Alonso-Zarazaga & Lyal, 1999), entre las cuales se encuentra Naupactini, con una distribución casi exclusivamente Neotropical (Lanteri & Del Río, 2008).

Naupactini es una de las tribus con mayor número de especies y la más diversificada en la región Neotropical. Presenta gran importancia fitosanitaria, ya que varias de sus especies se han señalado como plagas de distintos cultivos. Tal es el caso de *Naupactus cervinus* (“fuller rose weevil”), *N. leucoloma* (gorgojo de la alfalfa), *N. minor* y *N. peregrinus* (“white fringed weevils”) y *N. xanthographus* (burrito de la vid) (Lanteri et al., 2002; Lanteri & Del Río, 2008; Del Río et al., 2010). Naupactini incluye aproximadamente 500 especies, agrupadas en alrededor de 65 géneros (Wibmer & O’Brien, 1986; Alonso-Zarazaga & Lyal, 1999), descritos en su gran mayoría en la obra *Genera et species Curculionidum* (Schoenherr, 1833-1840).

Las hembras de Naupactini no utilizan su rostro corto y ancho para la oviposición, la cual es exofítica y se realiza a menudo en lugares cercanos al suelo. Las larvas son subterráneas y se alimentan de los tejidos externos de las raíces. La pupación ocurre dentro de una celda de tierra construida por la larva y los adultos se alimentan sobre las hojas dejando en sus bordes incisiones semicirculares características (Marvaldi, 1999; Lanteri et al., 2002; Lanteri & Del Río, 2008). El rango de plantas huéspedes suele ser muy amplio, de modo que se habla de especies polífagas, aunque con ciertas preferencias por determinadas familias de plantas, sobre todo leguminosas (Lanteri et al., 2002).

El complejo *Pantomorus-Naupactus*

El complejo *Pantomorus-Naupactus* es un grupo neotropical de gorgojos de rostro corto, pertenecientes a la tribu Naupactini (Coleoptera: Curculionidae). Comprende especies distribuidas desde los Estados Unidos hasta la Argentina. Buchanan (1939) afirmó que *Pantomorus* Schoenherr y *Naupactus* Dejean son géneros vagamente definidos, y debido a esto, propuso el complejo *Pantomorus-Naupactus*, para incluir 250 especies asignadas a siete géneros: *Alceis* Billberg, 1820, *Naupactus* Dejean, 1821, *Pantomorus* Schoenherr, 1840, *Pantoplanes* Schoenherr, 1840, *Symmalthetes* Schoenherr, 1847, *Pantopactus* Jekel, 1876 y *Athetetes* Pascoe, 1886; con cuatro subgéneros pertenecientes a *Pantomorus*: *Phacepholis* Horn, 1876, *Atrichonotus* Buchanan, 1939, *Graphognathus* Buchanan, 1939 y *Asynonychus* Crotch, 1867. El estatus taxonómico de estos géneros y subgéneros ha cambiado a través del tiempo. Algunos autores los han considerados como géneros independientes, otros como sinónimos de *Pantomorus* o *Naupactus*, o como subgéneros de los anteriores (Sharp, 1891; Champion, 1911; Dalla

Torre et al., 1936; Buchanan, 1939; Emden, 1944; Blackwelder, 1947; Hustache, 1947; Voss, 1954; Kuschel, 1955; O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986; Lanteri, 1986; 1990; Lanteri & O'Brien, 1990; Alonso-Zarazaga & Lyal, 1999; Morrone, 1999).

Pantomorus (Entiminae: Naupactini) es un género erigido con base en la especie mexicana *P. albosignatus* Boheman, descrita en el trabajo clásico *Genera et species Curculionidum* junto con algunas especies de Brasil (Schoenherr 1833-1840). El género más cercano a *Pantomorus* es probablemente *Naupactus* Dejean, descrito con base en la especie *N. rivulosus* Olivier de Brasil, y con más de 150 especies distribuidas principalmente en América del Sur (sólo siete especies ocurren en México y América Central). Aunque hasta el presente no hay un concepto claro de *Pantomorus*, éste usualmente se separa de *Naupactus* por poseer antenas y rostro más cortos, hombros y alas posteriores ausentes y fémures anteriores iguales a los posteriores o ligeramente más anchos (Pascoe, 1886; Sharp, 1891; Champion, 1911; Buchanan, 1939; Emden, 1944; Hustache, 1947; Lanteri & Normark, 1995; Scataglini et al., 2005; Lanteri et al., 2010), y por algunos caracteres únicos del ovipositor (Lanteri, 1981).

Muchas de las especies de *Pantomorus* distribuidas en México y América Central fueron descritas por Sharp (1891) y Champion (1911) en la *Biologia Centrali-Americana*. Sharp (1891) y Champion (1911) reunieron a más de 30 especies que ocurren en esta parte de América y las dividieron en dos grupos: el grupo I incluye las especies con un mucro grande en la tibia anterior y un mucro pequeño o ausente en la tibia media de los machos; el grupo II comprende a las especies que tienen un mucro grande en la tibia anterior y un mucro mediano en la tibia media de los machos.

Por otra parte, hay otros dos nombres genéricos tradicionalmente considerados como sinónimos de los *Pantomorus* de México y América Central, *Pantopactus* Horn,

cuya especie tipo es *Naupactus stupidus* Boheman y *Athetetes* Pascoe, con *A. globicollis* Pascoe como especie tipo (O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986; Alonso-Zarazaga & Lyal, 1999; Morrone, 1999). Las especies tipo de *Pantomorus* y *Pantopactus* están incluidas en el grupo I, mientras que la especie tipo de *Athetetes* está incluida en el grupo II. El nombre de *Pantopactus* se refiere a los caracteres intermedios entre *Pantomorus* y *Naupactus* (Sharp, 1891; Champion, 1911; Buchanan, 1939; Lanteri, 1990; Lanteri & Morrone, 1995; Lanteri & Normark, 1995; Scataglini et al., 2005; Lanteri et al., 2010).

Hustache (1947) estudió los *Pantomorus* de la Argentina y regiones limítrofes. Van Dyke (1953) describió las especies de *Pantomorus* para las islas Galápagos, actualmente incluidas en el género *Galapaganus* Lanteri, 1992. Los *Pantomorus* de América del Sur han sido revisados por Lanteri y colaboradores, quienes revalidaron algunos de sus sinónimos con base en el criterio de monofilia. Lanteri adoptó la propuesta de Buchanan (1939), respecto del complejo *Pantomorus-Naupactus* (Lanteri, 1990; Lanteri & O'Brien, 1990; Lanteri & Díaz, 1994) y elevó a rango genérico los grupos monofiléticos bien soportados dentro de éste (e. g. *Aramigus* Horn, *Phacepholis* Horn y *Atrichonotus* Buchanan).

En el presente hay dos principales conceptos de *Pantomorus* expresados en los últimos catálogos: a) *Pantomorus sensu lato*, que se distribuye en la región Neotropical, con su mayor diversidad específica en las áreas tropicales de América del Sur, incluyendo las especies de México y América Central (O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986; Lanteri & O'Brien, 1990; Lanteri & Morrone, 1995; Alonso-Zarazaga & Lyal, 1999; Scataglini et al., 2005); b) *Pantomorus sensu stricto*, que está restringido a las especies distribuidas en México y América Central, con las especies sudamericanas

incluidas en el género *Naupactus* (Morrone, 1999).

Las contribuciones realizadas por Lanteri y colaboradores en años recientes han permitido una mejor caracterización de los grupos del complejo *Pantomorus-Naupactus* mediante el aporte de nuevos caracteres, principalmente de las estructuras genitales de machos y hembras, y además han establecido las bases para interpretar su filogenia (Lanteri, 1986; 1990; Lanteri & O'Brien, 1990; Lanteri & Díaz, 1994; Lanteri & Marvaldi, 1995). Lanteri & Morrone (1995), Lanteri & Normark (1995) y Scataglini et al. (2005) propusieron que *Naupactus* es probablemente parafilético y *Pantomorus sensu lato* es polifilético. Este último género incluiría linajes independientes asociados con ambientes similares, que pudieron haber evolucionado a partir de diferentes grupos de *Naupactus*. Lanteri et al. (2010) realizaron un análisis con 70 especies del complejo *Pantomorus-Naupactus* incluyendo muchas especies sudamericanas de *Pantomorus* y algunas especies de América Central y México, y llegaron a una conclusión similar.

Hasta el momento no se cuenta con un trabajo taxonómico que incluya las 34 especies del género *Pantomorus sensu stricto* (Morrone, 1999) mucho menos con un análisis cladístico para poner a prueba la monofilia o determinar las relaciones filogenéticas de este grupo. En este trabajo se evalúa la hipótesis de que el género *Pantomorus sensu stricto* (Morrone, 1999) es monofilético, además de identificar grupos monofiléticos dentro del mismo, por medio de caracteres morfológicos de adultos y secuencias de DNA mitocondrial (genes Citocromo Oxidasa I y Citocromo B). La utilidad de este tipo de análisis en el estudio filogenético de especies cercanamente emparentadas ha sido demostrada ampliamente durante los últimos años, inclusive en el caso de taxones de la tribu Naupactini (Normark & Lanteri, 1998; Sequeira et al.,

2000; 2008a,_b). Asimismo, se pretende inferir la historia biogeográfica de los taxones mediante un análisis panbiogeográfico.

Introducción a los capítulos

Los resultados de esta investigación se presentan en tres capítulos. En el capítulo uno se refiere a la filogenia del complejo *Pantomorus-Naupactus* para América del Norte y Central, este trabajo tiene como objetivo general analizar las relaciones entre las especies del complejo *Pantomorus-Naupactus*, distribuidas en América del Norte y Central, con base en evidencia morfológica y molecular. Para tal análisis fueron utilizadas algunas especies de *Naupactus* y *Galapaganus* de América del Sur como grupos externos. Los objetivos particulares fueron poner a prueba la monofilia del grupo *Pantomorus sensu stricto*, reconocer grupos monofiléticos dentro del mismo y proponer un escenario biogeográfico que pudiera explicar su diversificación.

El capítulo dos comprende una sinopsis del género *Pantomorus* de acuerdo con la circunscripción sugerida en el capítulo uno; los objetivos son proveer una clave para separar los géneros *Naupactus*, *Pantomorus* y *Phacepholis* (Coleoptera: Curculionidae) distribuidos en América del Norte y Central y proporcionar una clave y diagnóstico de cada una de las especies incluidas en el género *Pantomorus* (Rosas et al., 2011).

En el capítulo tres se llevó a cabo un análisis biogeográfico de trazos para las especies del complejo *Pantomorus-Naupactus* distribuidas en América del Norte y Central. Se empleó el método panbiogeográfico para establecer un escenario posible sobre la evolución de este complejo de géneros y de este modo se expone una hipótesis que explique la diversificación biótica de estos taxones en el área donde las

regiones Neártica y Neotropical se sobrelapan. De esta forma se aporta información para al entendimiento de la evolución histórica de la Zona de Transición Mexicana (Morrone, 2006, 2010).

Hipótesis

El género *Pantomorus sensu stricto* es un linaje monofilético dentro del complejo *Pantomorus-Naupactus*, sustentado por una combinación de caracteres moleculares y morfológicos.

Objetivos

1. Determinar si el género *Pantomorus sensu stricto* es monofilético y si así fuera, señalar cuáles son las sinapomorfias que permiten identificarlo y separarlo de los géneros más cercanos, *Naupactus* y *Phacepholis*.
2. Sí el género fuera monofilético, reconocer grupos monofiléticos dentro del el género *Pantomorus sensu stricto*, usando caracteres morfológicos y moleculares de adultos.
3. Elaborar una clave para separar los géneros *Naupactus*, *Pantomorus* y *Phacepholis* (Coleoptera: Curculionidae) distribuidos en América del Norte y Central.
4. De acuerdo con los resultados obtenidos, generar una clave para separar las especies incluidas en *Pantomorus* con diagnosis de las mismas.
5. Inferir la historia biogeográfica de los géneros *Naupactus*, *Pantomorus* y *Phacepholis*, distribuidos en América del Norte y Central, mediante un análisis panbiogeográfico.

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CAPÍTULO 1

Phylogenetic analysis of the *Pantomorus-Naupactus* complex
(Coleoptera: Curculionidae: Entiminae) from North and Central
America

Phylogenetic analysis of the *Pantomorus*-*Naupactus* complex (Coleoptera: Curculionidae: Entiminae) from North and Central America

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Abstract

We undertook the first cladistic analysis of the *Pantomorus*-*Naupactus* complex (Coleoptera: Curculionidae) from North and Central America, based on 35 species and 61 morphological characters, plus 1151 bp of the mtDNA COI and Cyt b genes. The morphological and the combined matrices analyzed with TNT yielded a single most parsimonious cladogram that allows recognition of two main lineages within the *Pantomorus*-*Naupactus* complex in North and Central America. One is represented by the species formerly placed in *Phaeopholis* and the *Pantomorus* species group II *sensu* Sharp, ranging along the Pacific coast of Central America and Mexico and reaching the Great Plains of North America in the United States, yet not occurring in South America. The other lineage is represented by the species of *Naupactus* and *Pantomorus* species group I, with closer relationships to the South American species of these genera. The *Pantomorus* group I includes the type species of the genus (*P. albosignatus* Boheman) whereas the *Pantomorus* group II includes the type species of *Athetetes* Pascoe, 1886 (*A. globicollis* Pascoe). Based on the results of our phylogenetic analysis, we recommend retaining the name *Pantomorus* Schoenherr for most species of the *Pantomorus* group I, except *P. stupidus* (Boheman) and *P. femoratus* Sharp which should be transferred to *Naupactus* Dejean. Moreover, we enlarge the previous concept of *Phaeopholis* to include most species of the *Pantomorus* group II, and we establish the synonymy of *Athetetes* Pascoe, 1886 with *Phaeopholis* Horn, 1876, being the latter the valid name, by priority.

Key words: biogeography, classification, phylogenetics, Naupactini, Central America, Mexico, North America

Introduction

Pantomorus Schoenherr, 1840 (Entiminae: Naupactini) is a broad-nosed weevil genus based on the Mexican species *P. albosignatus* Boheman, 1840, and described in the classic work *Genera et species Curculionidum* along with several Brazilian species (Schoenherr, 1833–1845). The most closely related genus to *Pantomorus* is probably *Naupactus* Dejean, 1821 (Sharp, 1889–1891; Scataglini *et al.*, 2005), based on the type species *N. rivularis* (Olivier, 1790) from Brazil. *Naupactus* consists of more than 150 species distributed mainly in South America and only five species occurring in Mexico and Central America (O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986). *Pantomorus* has been traditionally separated from *Naupactus* by the smaller body size, the shorter antennae and rostrum, the lack of humeri and hind wings, and the front femora being as wide as to slightly wider than the hind femora (Lanteri & Normark, 1995; Scataglini *et al.*, 2005; Lanteri *et al.*, 2010); however, there is no clear distinction between both genera, and several species show intermediate characters between them. For this reason, Buchanan (1939) proposed the concept of *Pantomorus*-*Naupactus* complex, with about 250 species ranging from North to South America.

The North American species of *Pantomorus* were studied by Buchanan (1939). He recognized four subgenera (in addition to the nominotypic *Pantomorus*): *Phaeopholis* Horn, 1876, native to the Nearctic region, *Archonotus* Buchanan, 1939, *Graphognathus* Buchanan, 1939, and *Asymonechus* Crotch, 1867 (= *Aramégus* Horn, 1876).

native to South America and introduced into North America and other countries throughout the world. For South America, Hustache (1947) described several species of *Pantomorus* from Argentina and neighboring countries, and Van Dyke (1953) studied the *Pantomorus* species from the Galapagos Islands, currently classified in *Galapagamus* Lanteri, 1992. The species of *Pantomorus* and *Naupactus* from South America are being revised by Lanteri and colleagues who adopted Buchanan's proposal of the *Pantomorus*-*Naupactus* complex (see Scataglini *et al.*, 2005). These authors resurrected *Phaecepholis* Horn, *Arichonotus* Buchanan and *Acanthigys* Horn (Lanteri, 1990; Lanteri & O'Brien, 1990; Lanteri & Diaz, 1994), thus maintaining the name *Pantomorus* for the South American species which are not clearly separated from the type *P. albosignatus* and allied Mexican-Central American species, at least until a taxonomic study and a robust phylogeny of the complex are accomplished (Lanteri & Loiácono, 1990; Lanteri *et al.*, 1991; Morrone & Lanteri, 1991; Lanteri *et al.*, 2010).

Besides a contribution by Kuschel (1956), most Mexican and Central American species of *Pantomorus* were described in the *Biologia Centrali-Americana* (Sharp, 1889–1911; Champion, 1911). The characters of the female and male genitalia have not been studied for the majority of them, and a detailed taxonomic revision is needed. Sharp (1889–1911) separated the *Pantomorus* species from Mexico-Central America into two main groups: group I includes species with the front tibiae of the males bearing a medium to small-sized macro, and the middle tibiae lacking macro; and group II includes species with front tibiae bearing a large macro, and middle tibiae with a medium-sized macro. The type species of *Pantomorus* (*P. albosignatus*) and *Pantopactus* Jeckel, 1876 (type species *Naupactus stupidus* Boheman, 1840, from Mexico) are included in group I, whereas the type species of *Athetetes* Pascoe, 1886 (*A. globicollis* Pascoe, 1886, from Mexico) is included in group II. Both *Pantopactus* and *Athetetes* are currently considered synonyms of *Pantomorus* (O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986; Alonso-Zarazaga & Lyal, 1999; Morrone, 1999).

There are two main concepts of *Pantomorus* expressed in the most recent weevil checklists. *Pantomorus sensu lato* includes species from Mexico, Central America and South America (O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986; Alonso-Zarazaga & Lyal, 1999). On the other hand, *Pantomorus sensu stricto* is restricted to the Mexican and Central American species, with all the South American species of the *Pantomorus*-*Naupactus* complex being assigned to *Naupactus* (Morrone, 1999).

Our main objective is to analyze the relationships among most North and Central American species of the *Pantomorus*-*Naupactus* complex, based on morphological and molecular evidence (i.e., sequences of two mitochondrial genes), using some South American species of *Naupactus* and *Galapagamus* as outgroups. We aim to test the monophyly of *Pantomorus sensu stricto*, recognize monophyletic groups within this narrower concept of the genus, and propose a biogeographic scenario that may explain its diversification.

Material and methods

This study was based upon the examination of 1249 adult specimens borrowed from the following entomological collections:

AMNH	American Museum of Natural History, New York, USA (Lee Herman).
CMNC	Canadian Museum of Nature, Ottawa, Canada (Robert Anderson).
CWOB	Charles W. O'Brien Private Collection, Arizona, USA (Charles O'Brien).
EBCC	Estación de Biología "Chamela" San Patricio, Universidad Nacional Autónoma de México, Jalisco, México (Jorge Vega).
FSCA	Florida State Collection of Arthropods, Florida, USA (Michael C. Thomas).
IBUNAM	Instituto de Biología, Universidad Nacional Autónoma de México, México City, México (Santiago Zaragoza).
MLP	Museo de la Plata, La Plata, Argentina (Analia A. Lanteri).
MZFC	Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, México City, México (Juan J. Morrone).
TAMU	Texas A and M University, Texas, USA (John D. Oswald).
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (David Furth).

For dissections of genitalia, dry specimens were submerged in distilled water to soften the tissues and to extract the abdomen. After dissection, genitalia were treated with KOH 10%, washed with distilled water and 70% alcohol, and finally placed in glycerin in plastic vials, pinned beneath the specimens. Drawings of the genitalia were made using a lucid camera adapted to a stereoscopic microscope Nikon.

Specimens assayed for molecular analyses were collected in Mexico (see Table 1) and they were preserved at -20°C in 100% ethanol. The corresponding vouchers were deposited in the MZFC.

TABLE 1. References of the DNA sequences used in the combined analysis, including names of the species, Genbank accession numbers and geographic locations of the material assayed for molecular analyses.

Species	Genbank accession numbers		Locations of specimens assayed for molecular analyses
	COI	Cyt B	
<i>Galapagamus homoleuca</i>	AF211485	EU265284	Santa Cruz Island, Galápagos, Ecuador
<i>G. galapagoensis</i>	AF015914	EU265220	San Cristóbal Island, Galápagos, Ecuador
<i>Naupactus xanthographus</i>	AF211490	EU265322	Punta Lara, Buenos Aires, Argentina
<i>N. cineritarsium</i>	AY770388	Not available	Córdoba, Argentina
<i>N. leucoloma</i>	AY790880	EU265325	Buenos Aires, Argentina
<i>N. sulvianus</i>	GU565270	GU565279	La Ventosa, Salina Cruz, Oaxaca, Mexico
<i>Pantomorus stupidus</i>	GU565275	GU565283	La Ventosa, Salina Cruz, Oaxaca, Mexico
<i>P. globicollis</i>	GU565273	GU565285	La Ventosa, Salina Cruz, Oaxaca, Mexico
<i>P. albicans</i>	GU565278	GU565282	Tecpan, Guerrero, Mexico
<i>P. viridicars</i>	GU565277	GU565286	Chamela, Jalisco, Mexico

Morphological analysis. Morphological features were scored for 35 species formerly placed in *Pantomorus*, *Phaeopholis*, *Naupactus*, and *Galapagamus*, including those used as outgroups. The complete list of species herein studied, with their respective distributions, is shown in Table 2. The list of morphological characters and their states is included in Table 3. From a total of 61 characters, 47 belong to the external morphology, nine to the female genitalia, and five to the male genitalia. Five external morphological characters are continuous and the remaining 56 are discrete (binary or multistate). Continuous characters correspond to averages of ratios between measurements taken from the specimens with an ocular micrometer. TNT deals with continuous characters as such, avoiding the use of *ad hoc* methods to establish ranges (Goloboff *et al.*, 2008). The data matrix is shown in Table 4.

Molecular analysis.

DNA preparation, polymerase chain reaction amplification and sequencing. DNA was extracted following the protocols of Reiss *et al.* (1995) and the Qiagen DNeasy animal tissue kit (Qiagen GmbH, Germany). For the amplification of partial sequences of Cytochrome c Oxidase I (COI) we followed Normark (1994, 1996) and Scatagliini *et al.* (2005), and for Cytochrome b we followed Keargeat *et al.* (2004).

Typical PCRs were prepared in 25 µl volumes using 0.5 U Taq-polymerase and 1 µl of genomic DNA at 1.75 µl MgCl₂, 0.5 µl dNTP, 0.5 µl of each primer (10 pm/µl) 100X. PCR cycling conditions for COI started with an initial 1 min denaturing step at 96°C followed by 35 amplification cycles of 1 min denaturing at 96°C, annealing at 60°C for 1 min, and extension at 72°C for 1 min, with a final extension at 72°C for 4 min. The cycling conditions for Cyt b started with an initial 5 min denaturing step at 92°C, followed by 35 amplification cycles of 1 min denaturing at 92°C, annealing at 52°C for 30 seconds, and extension at 72°C for 1 min, with a final extension at 72°C for 10 min. PCR products were purified using a millipore PCR purification kit and recovered in 25 µl elution buffer. A negative control with no template was included for each series of amplifications to eliminate the possibility of contamination.

Sequences were obtained using an Applied Biosystem 3100 Automated sequencer and were compiled and edited with Bioedit (Hall, 1999). Alignments were performed with Clustal W (Thompson *et al.*, 1994). To avoid the possibility of amplification of COI and Cyt b pseudogenes (Bensançon *et al.*, 2000; Song *et al.*, 2008), nucleotide sequences were translated to amino acid sequences, according to the invertebrate mitochondrial genetic code obtained from several insect orders (Lunt *et al.*, 1996).

TABLE 2. List of species with data of distribution and biogeographic provinces according to the schemes of Morrone (2005, 2006, 2010) and Udvardy (1975).

Species	Distribution	Altitude (m)	Biogeographic provinces
<i>Galapaganus howlandi</i> Lanteri, 1992	Ecuador (Guayas, Manabí, Los Ríos, and Pichincha). Introduced in the Galápagos Islands (Santa Cruz Island)	700–1400	Western Ecuador, Arid Ecuador and Galápagos Islands
<i>G. galapagoensis</i> (Linell, 1898)	Ecuador, Galápagos Islands (San Cristóbal Island)	0–100	Galápagos Islands
<i>Nanpactus xanthographus</i> Germar, 1824	Argentina, Brazil, Paraguay, and Uruguay. Introduced into Chile (incl. Juan Fernández islands)	Sea level	Parana Forest, Cerrado, Chaco, Monte and Pampa
<i>N. cinereolorsum</i> Hustache, 1947	Argentina	Sea level	Chaco
<i>N. leucoluma</i> Boheman, 1840	Argentina, Brazil, Paraguay, and Uruguay. Introduced into Chile (incl. Easter and Juan Fernández islands), Perú, Australia, USA (California to Florida and Texas to Illinois), New Zealand, and South Africa	Sea level	Parana Forest, Yungas, Cerrado, Chaco, Monte and Pampa
<i>N. laticeps</i> Champion, 1911	Costa Rica (Cartago and Guanacaste), Honduras (Comayagua, Choluteca, El Paraíso, and Francisco Morazán) and Nicaragua (León)	120–1200	Chiapas and Mexican Pacific Coast
<i>N. virescens</i> Champion, 1911	Mexico (Chiapas and Oaxaca)	25–1000	Chiapas and Mexican Pacific Coast
<i>N. sulfuratus</i> Champion, 1911	Mexico (Chiapas and Oaxaca)	30–620	Chiapas and Mexican Pacific Coast
<i>Pantomorus stupidus</i> (Boheman, 1840)	Mexico (Chiapas and Oaxaca)	25–760	Chiapas and Mexican Pacific Coast
<i>P. femoratus</i> Sharp, 1891	Costa Rica (Alajuela, Guanacaste, Puntarenas, and San José), El Salvador (San Andrés), Honduras (Comayagua), Nicaragua (most departments) and Trinidad Island	120–1600	Chiapas, Mexican Pacific Coast and Western Panamanian Isthmus
<i>P. picturatus</i> Sharp, 1891	Costa Rica, El Salvador (San Salvador), Guatemala (Baja Verapaz, Escuintla, Guatemala and Quetzaltenango), Honduras (Comayagua and Totonicapán) and Mexico (Chiapas)	480–880	Chiapas
<i>P. circumcinctus</i> Sharp, 1891	El Salvador (Chalatenango), Guatemala (Baja Verapaz) and Honduras (Copán and Ocotepeque)	850–1250	Chiapas
<i>P. salvini</i> Sharp, 1891	Guatemala (Chimaltenango Guatemala, Sacatepéquez and Zacafo)	1560–2000	Chiapas
<i>P. dorsalis</i> Sharp, 1891	Guatemala (Chimaltenango) and Honduras (Comayagua, El Paraíso, Choluteca and Francisco Morazán)	820–1760	Chiapas
<i>P. salvadorensis</i> Kuschel, 1956	El Salvador (Cuzcatlán and La Libertad)	500–1000	Chiapas
<i>P. picipes</i> Sharp, 1891	Mexico (Oaxaca)	1220–1860	Chiapas and Sierra Madre del Sur
<i>P. subrimus</i> Sharp, 1891	Guatemala (Sacatepéquez)	1760	Chiapas
<i>P. subcinctus</i> Sharp, 1891	Guatemala (Baja Verapaz)	900–1070	Chiapas
<i>P. longulus</i> Sharp, 1891	Mexico (Chiapas and Oaxaca)	870–2256	Chiapas and Sierra Madre del Sur

continued next page

TABLE 2. (continued)

Species	Distribution	Altitude (m)	Biogeographic provinces
<i>P. rufus</i> Sharp, 1891	Guatemala (Chimultenango and Baja Verapaz) and Honduras (Comayagua)	940–2440	Chiapas
<i>P. horrius</i> Champion, 1911	Mexico (Nayarit, Jalisco, and Sinaloa)	0–700	Mexican Pacific Coast
<i>P. comes</i> Kuschel, 1956	El Salvador (San Salvador) and Guatemala (Quetzaltenango)	400–800	Chiapas and Mexican Pacific Coast
<i>P. parvulus</i> Sharp, 1891	Mexico (Oaxaca)	0–500	Mexican Pacific Coast
<i>P. albosignatus</i> Boheman, 1840	Mexico (Aguascalientes, Coahuila, Chihuahua, Distrito Federal, Durango, Guanajuato, Hidalgo, Monterrey, Oaxaca, Puebla, Querétaro, San Luis Potosí and Zacatecas)	1090–2255	Mexican Plateau, Transmexican Volcanic Belt and Sierra Madre del Sur
<i>P. globicollis</i> (Pascoe, 1886)	Mexico (Chiapas, Oaxaca and Veracruz)	25–680	Chiapas, Mexican Pacific Coast and Mexican Gulf
<i>P. brevis</i> Sharp, 1891	Mexico (Chiapas, Morelos, Oaxaca and Puebla)	1000–1980	Chiapas and Sierra Madre del Sur
<i>P. albicans</i> Sharp, 1891	Mexico (Guerrero)	30–680	Mexican Pacific Coast and Balsas Basin
<i>P. viridicinctus</i> Sharp, 1891	Mexico (Jalisco, Nayarit and Sinaloa)	0–760	Mexican Pacific Coast
<i>P. strabus</i> Sharp, 1891	Costa Rica (Alajuela and Guanacaste), Honduras (Comayagua and Choluteca), and Nicaragua (Carazo, León, Managua, Masaya and Nueva Segovia)	90–950	Chiapas, Mexican Pacific Coast and Western Panamanian Isthmus
<i>P. sulfureus</i> Champion, 1911	Mexico (Oaxaca)	0–215	Mexican Pacific Coast
<i>Phaeopholis elegans</i> Horn, 1876	USA (Arizona, Arkansas, California, Colorado, Iowa, Kansas, Missouri, Nebraska, Nevada, Oklahoma, South Dakota and Texas)	Sea level	Grasslands
<i>Ph. comulifer</i> Horn, 1876	USA (Colorado, Kansas, Nebraska, South Dakota, Texas and Wyoming)	Sea level	Grasslands
<i>Ph. plumitanus</i> (Buchanan, 1939)	USA (Colorado, Kansas and Nebraska)	Sea level	Grasslands
<i>Ph. obscurus</i> Horn, 1876	USA (Oklahoma and Texas)	Sea level	Grasslands
<i>Ph. viridis</i> (Champion, 1911)	USA (Louisiana and Texas)	Sea level	Grasslands

TABLE 3. List of morphological characters used in the cladistic analyses. Multistate characters treated as additive are indicated in bold.

External morphology- Continuous characters

0. Width of frons between anterior margins of eyes, over width of rostrum at apex ($\bar{\nu}$).
1. Maximum width over maximum length of pronotum ($\bar{\nu}$).
2. Maximum length over maximum width of elytra ($\bar{\nu}$).
3. Maximum length of elytra, over maximum length of pronotum (σ).
4. Maximum width of front femora, over maximum width of hind femora (σ).

External morphology- Discrete characters

5. Body length in dorsal view, from apex of rostrum to apex of elytra: medium to large (over 1 cm long) (0); small (less than 1 cm long) (1).
6. Rostral apex: V-shaped, epistome impressed, well defined (0); slightly emarginated, epistome slightly impressed, not well defined (1).
7. Pair of longitudinal lateral carinae of rostrum: absent to slight (0); moderate to strong (1).

8. Longitudinal central sulcus of rostrum: not widened towards apical end (0); widened towards apical end (1).
9. Rostral setae: not forming semicircles towards sulcus (0); forming semicircles (1).
10. Mandibular scar: strongly protruding (0); slightly protruding (1).
11. Eyes: strongly to moderately convex (0); slightly convex (1); flat (2).
12. Postocular constriction: indistinct (0); slight to moderate (1); strong (2).
13. Vertex: scarcely squamose (0); glabrous (1).
14. Antennae: moderately stout (0); slender (1).
15. Antennal scape ($\bar{\nu}$): largely exceeding hind margin of eyes (0); reaching to slightly exceeding hind margin of eyes (1); not reaching hind margin of eyes (2).
16. Antennomere 2: distinctly longer than 1 (0); slightly longer to about as long as 1 (1).
17. Gular angle in lateral view, between venter of rostrum and head ($\bar{\nu}$): strongly obtuse (near 180°) (0); almost right (near 90°) (1).
18. Shape of pronotum: subcylindrical (0); slightly subconical, with curved flanks (1); strongly subconical, with straight flanks (2).
19. Pronotum (σ^7): narrower than elytra (0); as wide as, to slightly wider than elytra (1).
20. Surface of pronotal disc (σ^7): flat to slightly convex (0); strongly convex (1).
21. Texture of pronotal disc: smooth to slightly rugose (0); granulose (1); irregularly punctate (2).
22. Pronotal scales: not arranged in radial clusters (0); arranged in radial clusters (1).
23. Scutellum size: large (0); small (1); indistinct (2).
24. Elytral humeri: broad (0); reduced (1); absent (2).
25. Elytral base: bisinuate (0); slightly bisinuate (1); straight (2).
26. Elytral disc: flat to slightly convex (0); moderately, evenly convex (1); strongly convex, and elevated toward beginning of the declivity (2).
27. Size of elytral punctures (σ^7): about 1/3 width of intervals (0); about 1/2 width of interval (1); about same width of intervals (2).
28. Elytral intervals: flat (0); slightly convex (1).
29. Vestiture of elytra: composed of scales and setae (0); composed of scales and seta-like scales (1); composed of setae (2).
30. Elytral setae or seta-like scales: long, suberect to erect (0); short, recumbent (1).
31. Elytral scales: uniformly distributed (0); restricted to flanks (1).
32. Color of elytral vestiture: uniform (0); with longitudinal stripes (1); with brown design of irregular stripes and maculae over light background (2).
33. Metathoracic wings: well developed (0); reduced to absent (1).
34. Vestiture of legs: composed of round scales (0); composed of elongate scales or appressed setae (1).
35. Color of integument of femora: dark-brown (0); front femora dark-brown, middle and hind femora reddish (1); all femora reddish (2).
36. Front tibiae (σ^7): slender, moderately curved near apex (0); very stout, strongly curved near apex (1).
37. Mucro of front tibiae (σ^7): large (about as long as tarsal claws) (0); medium-sized to small (shorter than tarsal claws) (1).
38. Mucro of middle tibiae (σ^7): medium-sized (0); small (1); absent (2).
39. Mucro of hind tibiae (σ^7): present (0); absent (1).
40. Row of denticles on inner margin of middle tibiae (σ^7): absent (0); present (1).
41. Row of denticles on inner margin of hind tibiae (σ^7): absent (0); present (1).
42. Metatibial apex of hind tibiae: with broad outer bevel (0); with moderate outer bevel (1); with slender outer bevel (2); simple (3).
43. Dorsal comb of setae at apex of hind tibiae: longer than apical comb (0); about as long as apical comb (1); shorter than apical comb (2).
44. Ventrite II (σ^7): lacking tubercles (0); with two large tubercles (1); with three large tubercles (2); with four or more medium-sized tubercles (3).
45. Apex of ventrite V ($\bar{\nu}$): straight (0); slightly emarginated (1).
46. Abdominal tergites: membranose (0); slightly sclerotized (1); moderately sclerotized (2); strongly sclerotized (3).

Female genitalia

47. Shape of plate of sternite VIII: subrhomboidal, about 3x longer than wide (Fig. 14) strongly elongate (0); subrhomboidal, about 2x longer than wide (Fig. 15) (1); subcircular (Fig. 16) (2); subtriangular (Fig. 17) (3).
48. Apodeme of sternite VIII: less than 2.5x longer than plate (0); 2.5 to 4x longer than plate (1); more than 4x longer than plate (2).
49. Ovipositor: about as long as to distinctly longer than abdomen (0); shorter than abdomen (1).
50. Rows of setae along sides of baculi of ovipositor: absent (0); present (1).
51. Shape of spermathecal body: subcylindrical (Fig. 18–20) (0); subglobose (Fig. 21) (1); globose (Fig. 22) (2).

- 52. Nodus of spermatheca: indistinct (Fig. 18) (0); short (Figs. 21–22) (1); moderately long (Figs. 19–20) (2).
- 53. Position of nodulus of spermatheca: parallel to opening of spermathecal gland (Figs. 18–19, 21–22) (0); oblique regarding opening of gland (Fig. 20) (1).
- 54. Ramus of spermatheca: distinct (Fig. 20) (0); indistinct (Figs. 18–19, 21–22) (1).
- 55. Cornu of spermatheca: long (Fig. 18) (0); medium length (Figs. 19–20) (1); short (Figs. 21–22) (2).

Male genitalia

- 56. Setae around apex of median lobe: absent (0); present (1).
- 57. Median lobe: slightly shorter to about as long as its apodemes (0); slightly longer than its apodemes (1); about twice longer than its apodemes (2).
- 58. Shape of apex of median lobe: acute to subacute (Fig. 28) (0); rounded (Fig. 24) (1); rounded with two lateral points (arrow shaped) (Fig. 26) (2).
- 59. Apex of median lobe: not dorsally incurved in lateral view (0); slightly incurved (1); strongly incurved (2).
- 60. Angle formed between median lobe and its apodemes: almost right (near 90°) (Fig. 23) (0); obtuse (Fig. 25) (1); almost flat (near 180°) (Fig. 27) (2).

A molecular matrix of 1151 characters (691bp for COI and 460bp for Cyt b) was compiled for ten species. Five sequences were downloaded from Genbank and the complete set of five new sequences was submitted to Genbank under the accession numbers listed in Table 1. Nucleotide diversity was estimated using MEGA, version 2.1 (Kumar *et al.*, 2001).

Phylogenetic analyses. The outgroups used in the analyses were the South American species *Galapagamus howdenae* Lanteri, 1992; *G. galapagoensis* (Linell, 1898); *Naupactus cinereidorsum* Hustache, 1947; *N. leucoloma* Boheman, 1840; and *N. xanthographus* (Germar, 1824) (see Tables 1 and 2). The most parsimonious trees were rooted with *G. howdenae* Lanteri, which belongs to a different species group than *G. galapagoensis*, and has never been classified in any genus of the ingroup (Lanteri, 2004; Sequeira *et al.*, 2008 a b). Sequences of COI and Cyt b are available for all of them, except the sequence of Cyt b for *N. cinereidorsum* (see Table 1).

Morphological characters were analyzed separately and combined with the molecular data set (Nixon & Carpenter, 1996). Character states corresponding to species that could not be assayed for DNA sequences or scored for the morphology of the male genitalia were completed with “?” and treated as missing data. Data matrices were analyzed using TNT, version 1.1 (Goloboff *et al.*, 2008), either (1) with 17 multistate characters coded as ordered or additive and the remaining characters coded as unordered, or (2) with all characters as unordered or non-additive (see Table 3).

Searches of the most parsimonious trees were performed using the heuristic “traditional search” algorithm of TNT, with 100 replications, and tree-bisection-reconnection branch-swapping (TBR), holding 10 trees during each replication. To evaluate branch support we calculated bootstrap values with 1000 replicates (Felsenstein, 1985) as well as Bremer support (Bremer, 1990), though the latter only for the morphological trees. For each cladogram we provide the following parameters: total length (L), consistency index (CI) (Kluge & Farris, 1969) and retention index (RI) (Farris, 1989).

Results

Molecular analysis

A combined 1151 bp segment of mtDNA COI and Cyt b gene sequences (positions 1662–2352 and 10693–11152, respectively) was amplified, yielding 250 parsimony informative characters. The alignments of translated sequences show the same distributional patterns of variation and the same aminoacid sequences within the conserved regions of the corresponding genes. These patterns, along with the absence of stop codons or frame shifts, exclude the possibility of having amplified pseudogenes (Bensanson *et al.*, 2000; Song *et al.*, 2008). The total proportions of nucleotides are 37.6% T, 17.6% C, 30.3% A and 14.6% G, with a strong A + T bias (67.9%), and observed in other Curculionidae (Langor & Sperling, 1997; Scataglini *et al.*, 2005).

TABLE 4. Data matrix of 35 species and 61 morphological characters. The first five characters are continuous and the remaining, discrete. Missing data and no comparable states are coded with “?”.

	0	1	2	3	4	5/6/7/8	1	2	3	4	5	6
<i>G. hirsutula</i>	1.35	1.46	1.5	2.03	1.6	00111	0010100010	0101012200	0100110001	0010000010	0120011010	0
<i>G. galapagosensis</i>	1.31	1.27	1.35	2.16	1.67	00010	0010010100	0001011202	0701105011	0010000010	0020001000	0
<i>N. xanthographa</i>	1.33	1.12	1.66	2.63	1.33	00110	0010100010	0000110101	1011000000	0101000111	0000110120	1
<i>N. curvicastrum</i>	1.35	1.34	1.55	2.91	1.36	00010	0010020110	0000011001	1000000111	0031000201	1000110000	1
<i>N. leucostoma</i>	1.35	1.24	1.46	2.68	1.55	00111	1100010110	0000121000	0011100111	0031000201	1000100200	2
<i>N. laticeps</i>	1.33	1.31	1.51	2.75	1.42	00011	1021020010	0000001001	1010100111	0011043101	0020010101	1
<i>N. strabus</i>	1.36	1.38	1.49	2.7	1.38	00011	1111010020	0000001001	1010100111	0001002111	0020010101	1
<i>N. alifornica</i>	1.3	1.3	1.64	2.59	1.4	01011	1010010010	0000011011	1010110121	0020012111	0020110020	0
<i>P. zapida</i>	1.47	1.24	1.41	2.6	1.37	11010	1010010010	0001221011	1011110121	0011000211	0020110020	0
<i>P. flavicatus</i>	1.35	1.23	1.46	2.21	1.3	01010	1010010000	0001111000	0001000100	0020001111	0020010001	0
<i>P. picturatus</i>	1.33	1.26	1.44	2.6	1.41	11010	1010010010	0001220200	1111110111	0011000221	0020110202	2
<i>P. chrysostictus</i>	1.3	1.21	1.75	2.46	1.46	11010	0010010110	0001220200	1111110121	0012000221	0020110202	2
<i>P. sabini</i>	1.33	1.32	1.52	2.6	1.2	11010	0010010110	0001220200	0111120121	0012000221	0020110101	1
<i>P. oberholzi</i>	1.37	1.27	1.47	2.1	1.38	11010	1010010110	0001221200	0111100121	0011000221	0020110202	2
<i>P. subadriensis</i>	1.35	1.2	1.8	2.12	1.25	11010	1010010010	0001220200	1111100121	0011000221	0020110202	2
<i>P. phidippi</i>	1.47	1.25	1.48	2.11	1.23	11000	1010021110	0001221200	0011120121	0012000211	0021010002	1
<i>P. subviesi</i>	1.34	1.32	1.52	2.27	1.18	11000	1010010110	0001220000	1001100121	0021000211	0020110101	1
<i>P. subclivata</i>	1.32	1.22	1.56	2.21	1.2	11000	1010010110	0001221200	0001120121	0021000211	0020110001	1
<i>P. longipes</i>	1.36	1.36	1.8	2.71	1.3	11000	1010010110	0001220000	1001120121	0022000311	0021117777	?
<i>P. nalis</i>	1.44	1.35	1.28	2.13	1.3	11110	1011020100	0201221200	1001100121	0021000111	0021010000	1
<i>P. horridus</i>	1.45	1.3	1.28	2.22	1.2	11000	1111010100	0201221200	0001000121	0012000111	0021010001	0
<i>P. comis</i>	1.33	1.3	1.4	2.17	1.3	11000	1010120110	0001121100	0001000121	0011000111	0020010000	1
<i>P. parvulus</i>	1.45	1.2	1.37	2.24	1.11	11000	1010021110	0201221100	0021000121	0011000101	0020110000	1
<i>P. orbicollis</i>	1.45	1.31	1.29	2.52	1.1	11000	1010021110	0201221100	0021000121	0011000101	0020117777	?
<i>P. gibbicollis</i>	1.25	1.13	1.36	1.6	1.65	00100	0010100101	1002222001	1021001001	1102200000	0110120000	1
<i>P. bespian</i>	1.36	1.19	1.43	1.69	1.6	00100	0010100111	1202222001	1021001001	1102200000	0110120000	1
<i>P. albicans</i>	1.29	1.12	1.46	1.76	1.54	00100	0010100111	1002222001	1001001001	1102200000	0110120000	1
<i>P. strabus</i>	1.35	1.15	1.48	1.75	1.6	00100	0010100101	1002222001	1001001001	1102200000	0110120000	1
<i>P. strabus</i>	1.33	1.21	1.37	1.75	1.44	00100	0200100100	1002222001	1021001001	1102100000	0110120000	1
<i>P. subviesi</i>	1.45	1.17	1.43	1.7	1.33	10000	1200010100	1002222001	1001001111	0002000110	0110120000	1
<i>Ph. elegans</i>	1.43	1.1	1.47	2.29	1	10000	0010110110	0012221001	1001000001	1002000000	0210120000	1
<i>Ph. sandrita</i>	1.49	1.12	1.44	2.23	1.18	10000	0100110110	0011111001	1001000001	1102310000	0210120010	1
<i>Ph. plantator</i>	1.49	1.16	1.46	2.26	1.13	10000	0100120110	0011111000	0001000001	1102310000	0210120010	1
<i>Ph. subviesi</i>	1.56	1.17	1.34	2.13	1.14	10000	1010121110	0011221000	0001000001	1002010000	0210120000	1
<i>Ph. viridis</i>	1.39	1.24	1.34	2.23	1.1	10000	0010110110	0002221001	1001000001	1002000000	0210120000	1

Morphological phylogenetic analyses

1. Additive coding scheme

The analysis of the morphological data matrix (35 species, 61 characters) with 17 multistate characters run as additive yielded a single most parsimonious cladogram 256.39 steps long, with a CI = 0.352 and a RI = 0.697 (Fig. 1). The clade including *Pantonomus*, *Nanxarctus* and *Phacopholis* is recovered with a bootstrap support of 71% and a Bremer support of 3, the latter being grounded in several morphological characters such as the dorsal comb of setae at the apex of the hind tibiae nearly as long as or shorter than the apical comb (characters 43.1 and 43.2).

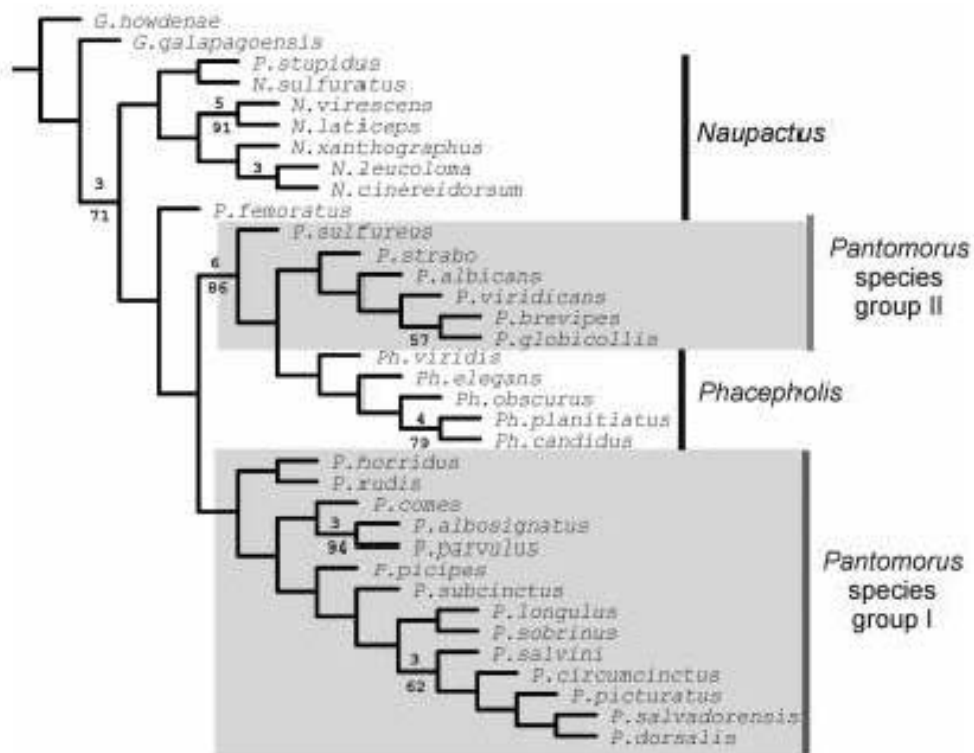


FIGURE 4. Most parsimonious morphological tree under equal weights, with 17 morphological characters coded as additive. Bremer support values over 3 are given above each corresponding branch and bootstrap values over 50% are below the branches.

Naupactus, including *P. stupidus* (Fig. 7) as the sister species of *N. sulfuratus* (Fig. 8), is corroborated as monophyletic, based mainly on characters of the vestiture composed of scales and short seta-like scales (characters 29.1 and 30.1), and forming longitudinal stripes of different color patterns along the elytra (character 32.1). The relationship of *N. sulfuratus* and *P. stupidus* is supported by the slightly convex elytral intervals (character 28.1) and the arrow-shaped apex of the aedeagus (character 58.2), also present in some South American species of *Naupactus* such as *N. xanthographus* (Figs. 24–25). The color patterns of *N. sulfuratus* and *P. stupidus* are virtually identical (see Figs. 7–8). *Naupactus virescens* and *N. laticeps* are sister species (bootstrap 91%, Bremer 5), based on the glabrous vertex (character 13.1), the strongly bisinuate elytral base (character 25.0), the moderately to strongly sclerotized abdominal tergites (characters 46.2 and 46.3), and the slightly incurved apex of the median lobe (character 59.1). *Naupactus xanthographus* is closely related to the sister species *N. leucoloma* and *N. cinereidorsum* (Bremer support 3), the other two species of *Naupactus* native to South America. The relationship of these species is supported by the simple metatibial apex of the hind tibiae (character 42.3) and the presence of rows of setae along sides of the baculi of the ovipositor (character 50.1), characters that are not present in any species of the *Pantomorus*-*Naupactus* complex native to North or Central America.

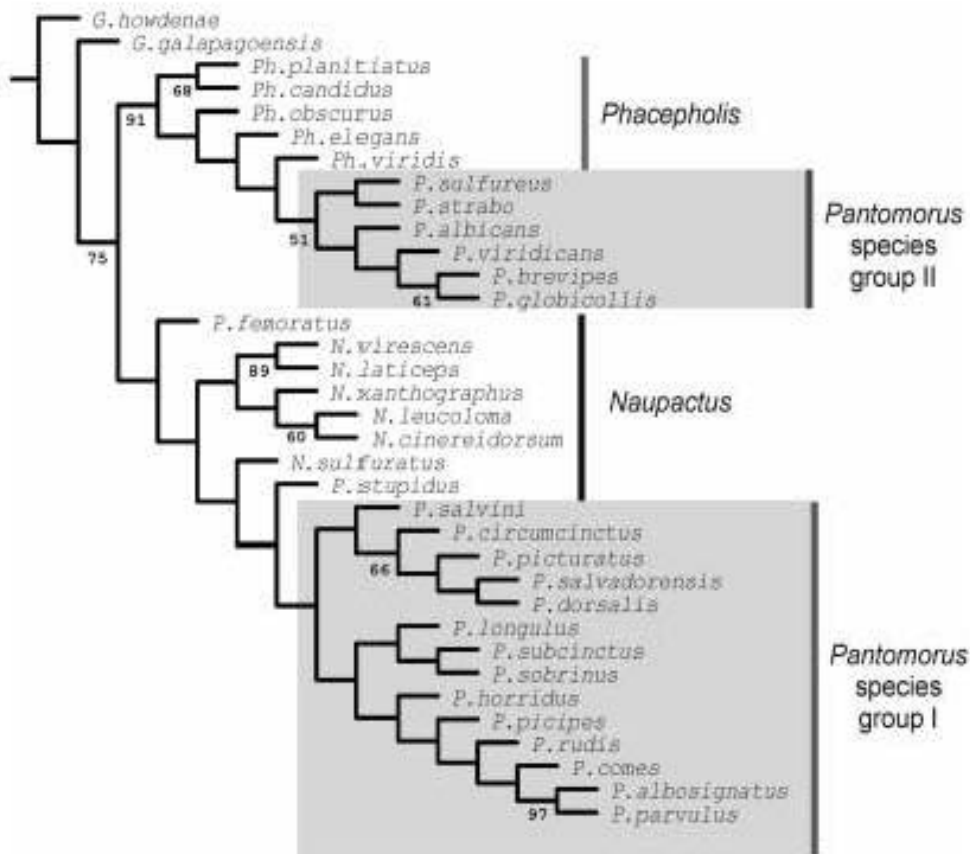


FIGURE 2. Most parsimonious combined tree under equal weights, with 17 morphological characters coded as additive. Bootstrap values over 50% below the corresponding branches.

Pantomorus femoratus is the sister taxon of the clade formed by *Phacepholis* (Fig. 3) and *Pantomorus* (Fig. 5). This species shows "intermediate" character states between *Naupactus* and *Pantomorus*, e.g. it is larger than most *Pantomorus* and its front femora are widened in comparison to the hind femora.

Pantomorus plus *Phacepholis* are recovered as a monophyletic group based on several morphological synapomorphies, e.g. the small body length (character 5.1), the nearly 90° gular angle (character 17.1), the absent elytral humeri (character 24.2), and the straight elytral base (character 25.2).

Phacepholis plus *Pantomorus* group II (= *P. globicollis* species group *sensu* Lanteri 1990) are recovered as a strongly supported clade (bootstrap 86%, Bremer 6), grounded, e.g., in the indistinct scutellum (character 23.2), the ovipositor being about as long as to longer than the abdomen (character 49.0), and the globose to subglobose spermatheca with an indistinct ramus and short nodulus (characters 51.1, 54.1, and 55.2) (Figs. 20–21). The species of this clade also have a maximum width over the maximum length of the pronotum ratio usually lower than 1.20 (character 1), whereas in most other species examined the values of this continuous character are higher. Furthermore, males usually have a row of denticles on the inner margin of the hind tibiae (character 41.1) and the abdominal ventrite II bears different numbers of tubercles (character 44). *Pantomorus sulfureus* is the sister taxon of the remaining species of this clade as it lacks some of their synapomorphies, e.g. the presence of tubercles on the abdominal ventrite II of males (character 44).

The clade including all species of *Pantomorus* group II except *P. sulfuratus* is characterized by slender antennae with a long scape largely exceeding the hind margin of the eyes (character 15.0), a strongly convex surface of the pronotal disc (character 20.1), a strongly convex elytral disc which is elevated toward the onset of the declivity (character 26.2) (Figs. 4 and 9), and very stout front tibiae that are curved near the apex (character 36.1). Males within this group show widened front femora, their width usually being 1.50 times that of the hind femora. *Pantomorus globicollis* and *P. brevipennis* are inferred sister species (bootstrap 57%).

Pantomorus group I – i.e. the “true” *Pantomorus* clade which includes the type species *P. albosignatus*—shows low values of branch support. It is recognized by the presence of large elytral punctures (character 27.2) and by the absence of a mucro at the apex of the middle tibiae (character 38.2; (the mucro of the front tibiae is medium-sized to small). It is precisely this character of the mucro that was used by Sharp (1889–1911) to separate this group from *Pantomorus* group II which includes species with a large mucro on the front tibiae whereas the middle tibia always have a medium-sized mucro.

The species with shortest elytra (e.g. *P. albosignatus*, see Fig. 5) and not widened front femora are placed near the root of the *Pantomorus* group I, whereas the species with elongate elytra and front femora much wider than hind femora are located near its tip (e.g. *P. picturatus*, see Figs. 6 and 10). *Pantomorus salvini*, *P. circumcinctus*, *P. picturatus*, *P. salvadorensis* and *P. dorsalis* form a strongly supported group (bootstrap 62%, Bremer 3), herein called *P. circumcinctus* group supported by having the elytral scales restricted to flanks (character 31.1), the presence of longitudinal stripes (character 32.1), the apodeme of the sternum VIII of the female more than 4x longer than the plate (character 48.2), and the median lobe twice longer than its apodemes (character 57.2).

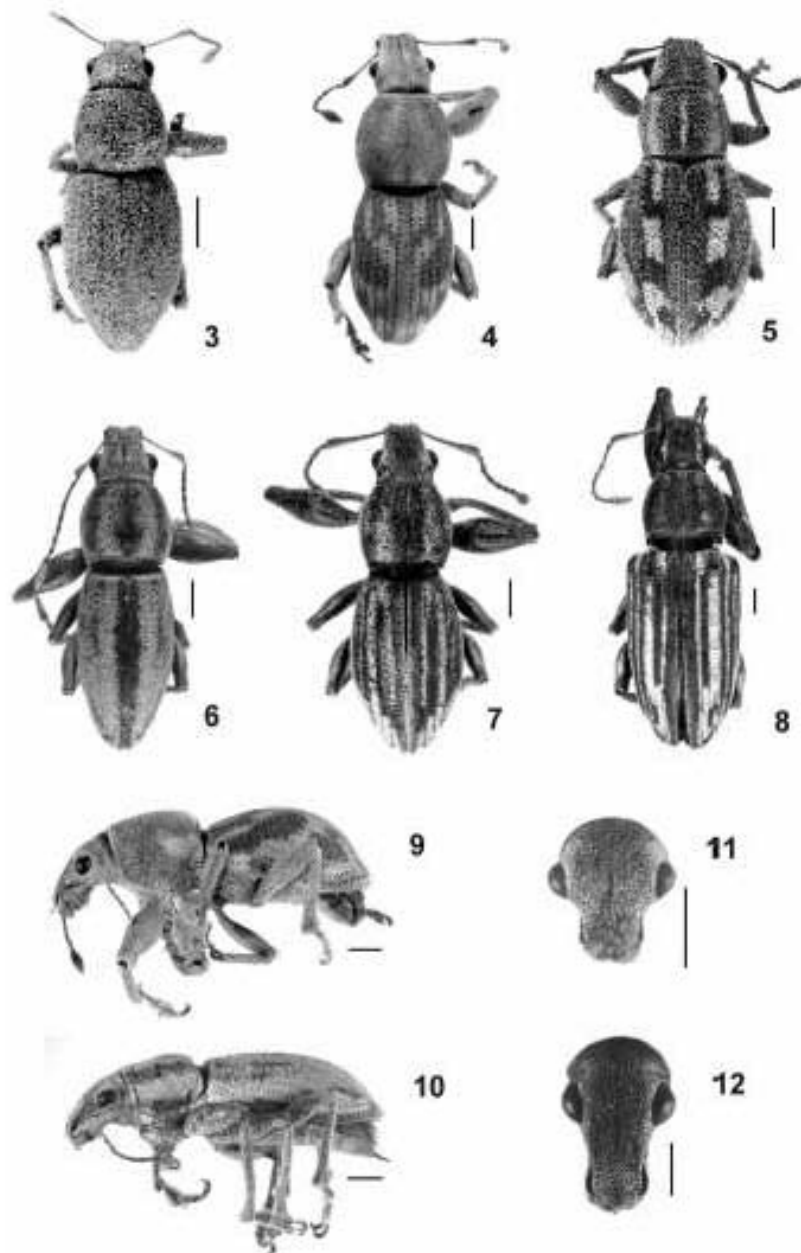
2. Non-additive coding scheme

The analysis of the morphological matrix with all characters treated as non-additive yielded a single most parsimonious tree 248.69 steps long, with a CI = 0.363 and a RI = 0.697 (not shown), yielding a topology that is very similar to that of Fig. 1. The main difference is that under the non-additive scheme *Pantomorus femoratus* follows *Galapaganus* in phylogenetic sequence, thus being the putative sister taxon of all remaining species. Within *Naupactus*, *N. sulfuratus* and *P. stupidus* are sister species (as in Fig. 1), but *N. xanthographus* is placed as the sister taxon of the remaining species of this genus. The clade *Phaecepholis* plus *Pantomorus* group II is strongly supported and shows the same species relationships as in Fig. 1. *Pantomorus* group I is weakly supported and shows slight differences in the phylogenetic sequence of its species, with the *P. circumcinctus* group situated at the tip of this clade (as in Fig. 1).

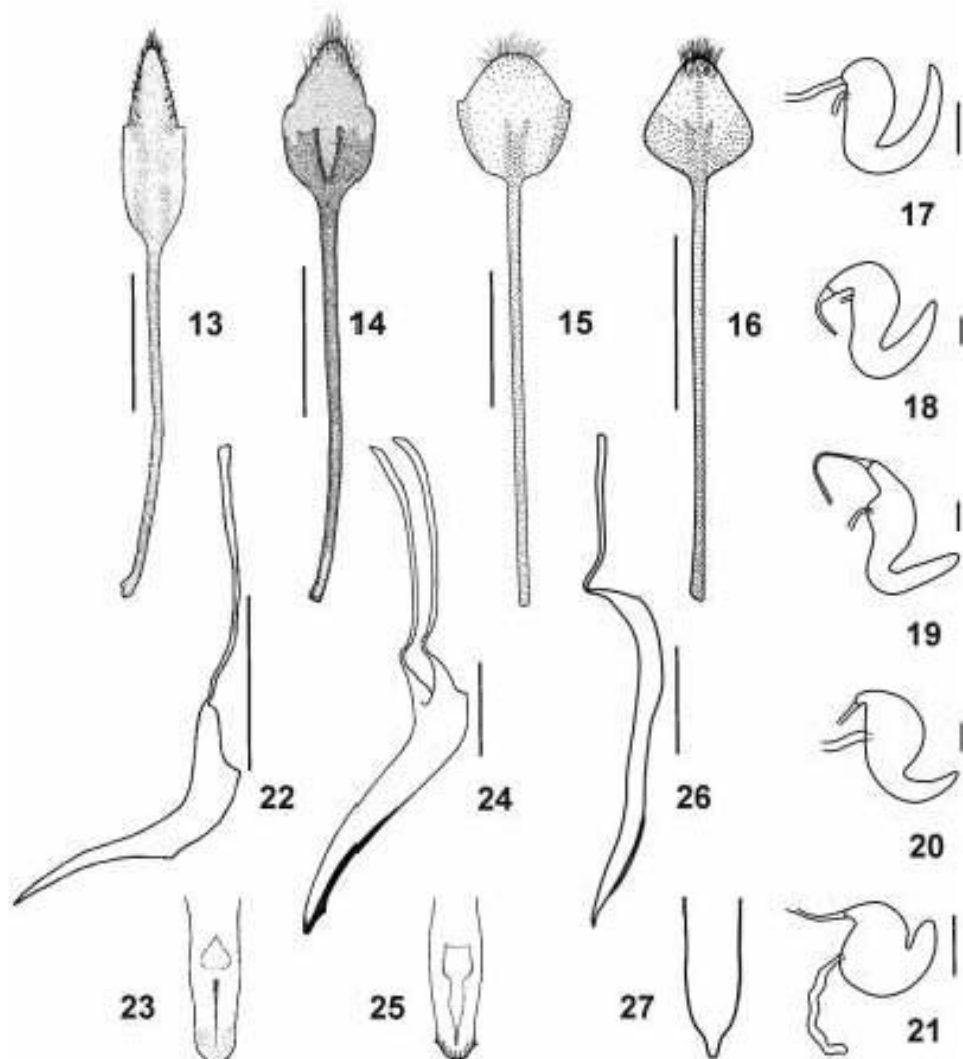
Combined phylogenetic analyses

The analysis of a combined data matrix of 1212 characters (61 morphological plus 1151 bp of the mtDNA COI and Cyt b genes), with 17 multistate characters run as additive, yielded a single most parsimonious cladogram 1363.68 steps long, with a CI = 0.564 and a RI = 0.611 (Fig. 2). Two main clades are recovered, one including the species of *Phaecepholis* plus *Pantomorus* group II, and the other including those of *Naupactus* plus *Pantomorus* group I. In the former clade, which is strongly supported (bootstrap 91%), *Phaecepholis* is paraphyletic with regards to *Pantomorus* group II. In the second clade, which is not strongly supported, *Naupactus* is paraphyletic with respect to *Pantomorus* group I. *Naupactus sulfuratus* and *Pantomorus stupidus* are not sister species, but they follow one another in phylogenetic sequence, and the *P. circumcinctus* group is congruently recovered as the sister clade of the remaining species of *Pantomorus* group I.

The combined matrix with all characters run as non-additive yielded a single most parsimonious cladogram 1150.70 steps long, with a CI = 0.588 and a RI = 0.528 (not shown), in which *P. femoratus* follows *Galapaganus galapagoensis*. *Naupactus* (including *P. stupidus* as sister species of *N. sulfuratus*) is recovered as monophyletic—as in the cladogram based on morphology with all the characters run as non-additive—but *Pantomorus* group I and *Phaecepholis sensu* Lanteri (1990) are paraphyletic with regards to a monophyletic *Pantomorus* group II which is placed at the tip of this clade.



FIGURES 3–12. Species diversity within the *Pantomorus-Nanpactus* complex in North and Central America. 3–8, Habitus, dorsal views: 3, *Phaecephala elegans* Horn; 4, *Pantomorus globicollis* (Pascoe); 5, *P. albosignatus* Boheman; 6, *P. picturatus* Sharp; 7, *P. stipitatus* (Boheman); 8, *Nanpactus sulfuratus* Champion. 9–10, Habitus, lateral views: 9, *P. globicollis* (Pascoe); 10, *P. picturatus* Sharp. 11–12, Heads, frontal views: 11, *P. albosignatus* Boheman; 12, *N. sulfuratus* Champion. Scales: 1 mm.



FIGURES 13–27. Female genitalia. 13–16, Sternites VIII of females: 13, *Phaecepholis elegans* Horri; 14, *Nanpactus xanthographus* (Germar); 15, *N. sulfuratus* Champion; 16, *Pantomyia longulus* Sharp. 17–21, Spermathecae: 17, *N. leucoloma* Boheman; 18, *N. sulfuratus* Champion; 19, *P. princeps* Sharp; 20, *P. globicollis* (Pascoe); 21, *Phaecepholis elegans* Horri. 22–27, Male genitalia, medial lobe (lateral view and apex). 22–23, *Ph. candidus* Horri; 24–25, *N. xanthographus* (Germar); 26–27, *P. circumvinctus* Sharp. Scales: 1 mm.

Discussion

Phylogenetics. The results of our phylogenetic analyses demonstrate that *Galapagosmias galapagoensis*, a species originally described in *Pantomyia* (see Lanteri, 1992), is consistently placed outside this genus as it does not share

the synapomorphies of the group including *Pantomorus*, *Naupactus* and *Phaecepholis*. *Galapagamus* includes two species groups, (1) the *G. darwini* group to which *G. galapagoensis* and other species lacking metathoracic wings pertain, and (2) the *G. femoratus* group with two fully winged species (*G. femoratus* Lanteri and *G. howdenae* Lanteri) (Lanteri, 2004; Sequeira *et al.*, 2008a, 2008b). Similarly, in the *Pantomorus*-*Naupactus* complex there are both apterous species with reduced to absent elytral humeri, usually classified as *Pantomorus* and *Phaecepholis* (see Figs. 3–7), and species with well developed humeri and wings, usually classified as *Naupactus* (see Fig. 8). The characters of the wings are likely subject to environmental influences and thus not optimal for separating genera. Indeed, according to our results *Naupactus* also includes species with reduced or absent humeri and hind wings (*N. xanthographus* and *N. leucoloma*).

Most cladograms herein presented indicate that *Naupactus* is monophyletic, although the tree resulting from the combined matrix with some multistate characters treated as additive (Fig. 2) would indicate that it is paraphyletic regarding *Pantomorus* group I. We believe that the number of species of *Naupactus* included in this study is too small to draw a definitive conclusion about this genus, especially because most *Naupactus* occur in South America.

In the morphological trees and the combined tree with all characters run as non-additive, *N. sulfuratus* is the sister species of *P. stupidus* (see Fig. 1); however, in the combined tree with some morphological characters treated as additive (Fig. 2), *P. stupidus* is placed in a phylogenetic sequence after *N. sulfuratus*, "between" a paraphyletic *Naupactus* and a monophyletic *Pantomorus* group I. Indeed, *P. stupidus* was originally described in *Naupactus*, then subsequently designated as the type species of *Pantopactus* (a generic name that refers to its dubious position between *Pantomorus* and *Naupactus*), and finally placed in *Pantomorus* group I (Sharp 1889–1911). The cladogram of Fig. 2 illustrates this dubious position and complex taxonomic history of this species. Moreover, it is worth mentioning that Champion (1911: 232) suggested the possibility that *N. sulfuratus* and *P. stupidus*, occurring in the same localities of Oaxaca and Chiapas from sea level to about 750 meters, correspond to a single dimorphic species, "being *N. sulfuratus* the winged form of *P. stupidus*".

In our phylogenetic analyses, *N. virescens* is always recovered as the sister species of *N. laticeps*, another typical *Naupactus* from the Pacific coasts of Mexico. However, Champion (1911: 335) had hypothesized that "*N. virescens* would be the winged form of *P. unifornis*", similarly to the sister species *N. sulfuratus*-*P. stupidus*. We have studied samples of *N. virescens* from several localities of Chiapas and Oaxaca (800–1000 m), and also from Michoacán, including specimens smaller than those of the typical form, with reduced humeri, that could correspond to *P. unifornis*. Detailed studies of population-level and geographic variation of *N. sulfuratus*-*P. stupidus* and *N. virescens*-*P. unifornis*, including molecular analyses, will be necessary to understand the mechanisms of speciation and evolution of wings in these groups of weevils.

The species of *Naupactus* from South America, i.e. *N. xanthographus*, *N. leucoloma* and *N. cinereidorsum*, are recovered as a monophyletic group, usually separated from the Central American species of the same genus (Figs. 1–2). The support of this group is not very high, probably because each species is more closely related to other South American *Naupactus* not included in this study than to each other (Lanteri & Marvaldi, 1995; Lanteri *et al.*, 2010). *Naupactus leucoloma* and *N. cinereidorsum* show rows of setae along the ovipositor which are also present in the type species *N. rivulosus* and allied South American species yet absent in all Mexico and Central American ones.

Pantomorus femoratus (synonymized with *P. robustus* Sharp by O'Brien & Wibmer, 1982) showed a variable position in the obtained cladograms. In those trees with all characters coded as non-additive it is placed near the root, in sequence after *Galapagamus galapagoensis*, but when some multistate characters are treated as additive it is either the sister taxon of *Phaecepholis* plus *Pantomorus* (Fig. 1) or the sister taxon of *Naupactus* plus *Pantomorus* (Fig. 2). This ambiguous position is probably due to a particular combination of morphological characters that appear somewhat intermediate between *Pantomorus* and *Naupactus*, and/or to the absence of a closely related species among those selected for the current analyses. Sharp (1889–1911) placed this species in *Pantomorus* group II; however, our phylogenetic analyses clearly demonstrate that *P. femoratus* does not belong to this group.

The clade including the species of *Phaecepholis* and those of the *Pantomorus* group II is recovered in all the cladograms (Figs. 1–2). The similarity between *Phaecepholis* and *Pantomorus* group II was noticed by Champion (1911, page 333) who stated that "*P. globicollis*, type of *Athetes* Pascoe, has the tips of the hind tibiae squamose as in *Phaecepholis*, and the second ventral segment of the male armed with two or three small transversely placed tubercles". Using similar criteria, Lanteri (1990) used this group as the outgroup for her cladistic analysis of *Phae-*

pholis. Both *Phaecepholis* and *Pantomorus* group II share not only features of the external morphology but also characters of the female genitalia, such as the elongate plate of the sternite VIII, the very long ovipositor (exceeding the length of the abdomen), and the globose to subglobose spermathecae, with short nodulus and cornu (Figs. 13, 20–21). In the remaining species, the plate of the sternite VIII, as well as the ovipositor are shorter, and the spermathecae are subcylindrical, with a longer cornu and usually longer nodulus (Figs. 14–16, 17–19). Moreover, the corresponding males are unique within the tribe Naupactini for having tubercles on the second ventrite; moreover, their aedeagi are distinctly rounded at apex (Figs. 22–23) and in the species of *Pantomorus* group II there is a strong sexual dimorphism in the characters of the pronotum and front legs.

Phaecepholis is corroborated as monophyletic in the cladograms based on morphology (Fig. 1), but paraphyletic regarding *Pantomorus* group II in the combined trees (Fig. 2). Molecular characters are available for three species of the latter group but not for those of *Phaecepholis*, and the presence of several missing data affects the inference of relationships of these taxa.

Pantomorus, including the two main groups recognized by Sharp (1889–1911), is not recovered as monophyletic in the cladograms based on morphology nor in the combined trees (Figs. 1–2). However, it is possible to recognize a weakly supported *Pantomorus* group I, related either to *Phaecepholis* plus *Pantomorus* group II (Fig. 1) or to *Naupactus* (Fig. 2).

Pantomorus group I includes the type species of the genus, *P. albosignatus* (Fig. 5), which is closely related to *P. parvulus* and *P. comes*. All aforementioned species have short, somewhat globose elytra, front femora that are about as wide as the hind femora, and female and male genitalia of the generalized type *sensu* Lanteri & del Río (2008). In a few species (e.g. *P. picipes* and *P. horridus*) the spermathecae have a moderately long nodulus, positioned obliquely to the opening of the spermathecal gland (Fig. 19); whereas in the remaining species the nodulus is oriented in parallel to the opening of the gland (Fig. 18). The ovipositor is always shorter than the abdomen and the plate of the VIII sternite is subrhomboidal to subcircular or subtriangular (Figs. 14–16).

The strongly indicated sister relationship of *P. albosignatus* and *P. parvulus*, together with the fact that the samples of the former species include only females, suggest that *P. parvulus* is a sexual lineage of *P. albosignatus*. The samples of *P. parvulus* studied herein, coming from localities of Oaxaca at lower altitudes (0–500 m), have females and males, whereas those of *P. albosignatus*, collected along the Mexican Plateau (1000–2000 m) (see Table 2), include only females. It is possible that *P. albosignatus* is parthenogenetic, as observed in other South American species of the *Pantomorus*-*Naupactus* complex inhabiting marginal areas (Lanteri & Normark, 1995; Scatagliini *et al.*, 2005; Rodríguez *et al.*, 2010).

Another stable clade within *Pantomorus* group I includes *P. circumcinctus*, *P. dorsalis*, *P. salvadorensis*, *P. picturatus* and *P. salvini*. This clade, herein called *P. circumcinctus* group, is easily recognized by the elongate and slender body, covered with usually long and erect setae, and having the scaly vestiture restricted to the margins of the elytra, thus leaving the central area glabrous (Figs. 6 & 10). The front femora are wider than those of the hind legs, as in most species of *Naupactus* and *Pantomorus* group II. The characters of the male genitalia provide strong support for this group; the median lobe is twice as long as the aedeagal apodemes, strongly incurved at the apex and forming an angle of about 180° in relation to the apodemes in lateral view (Figs. 26–27). Similar characters are present in males of *Naupactus hirtellus* from Brazil (Lanteri, 1981).

Taxonomy and nomenclature. Based on the results of our phylogenetic analyses we recommend undertaking some taxonomic and nomenclatural changes:

1. *Pantomorus stupidus*, originally described in *Naupactus*, should be classified in this genus, even though *Naupactus* is not always recovered as monophyletic. Further decisions about the status of *Naupactus* should be taken based on larger samples of species, including the type, *N. rivulatus*. A similar decision applies to *P. femoratus*. It is possible that with the inclusion of more species of *Naupactus* the position of *P. femoratus* will be resolved.
2. Even though the species of *Phaecepholis sensu* Lanteri (1990) are easy to distinguish from *Pantomorus* group II, and it was corroborated as monophyletic in the morphological trees (see Fig. 1), its leaves a paraphyletic *Pantomorus* group II. Consequently, we propose to treat *Phaecepholis* Horn, 1876 (type *P. elegans* Horn, 1876) as the senior synonym of *Athetetes* Pascoe, 1886, since its type species *A. globicollis* Pascoe, 1886 pertained to *Pantomorus* group II.

The species to be transferred from *Pantomorus* to *Phaecepholis* are: *P. globicollis* (Pascoe), *P. brevipes* Sharp, *P. albicans* Sharp, *P. viridicans* Sharp, *P. strabo* Sharp, and *P. sulfureus* Champion. Other species not included in the present study that should be classified in *Phaecepholis* are: *P. annectens* Sharp and *P. trituberculatus* Champion. *Pantomorus distans* Sharp, placed by its author in *Pantomorus* group II, is probably not a *Phaecepholis*, since it resembles *P. picturatus* (Sharp 1889–1911: 162).

3. All species formerly placed in *Pantomorus* group I *sensu* Sharp, in which the type species *P. albosignatus* belongs, will remain in *Pantomorus*, at least until there is a definite solution for the *Pantomorus*-*Naupactus* complex.

Biogeography

There is a strong correlation between the main groups recovered in the cladistic analyses and the geographic distribution of the species.

The species of *Naupactus* from Central America range from sea level to about 1000 m, along the Mexican Pacific Coast biogeographic province (Neotropical region) and the Chiapas biogeographic province (Mexican transition zone) (Morrone, 2006, 2010).

Phaecepholis sensu Lanteri (1990) is distributed in the Nearctic region, being the only genus of the *Pantomorus*-*Naupactus* complex that naturally occurs outside the Neotropics. Its species occur throughout the Great Plains of North America, from Arizona, Louisiana and Texas to North Dakota, Montana and Wyoming (Table 2). This distribution corresponds to the Grassland province *sensu* Udvardy (1975). The species of *Phaecepholis* are apterous, steppe or prairie-adapted, showing subtle sexual dimorphism. *Phaecepholis viridis*, reaches the southernmost distribution (Texas and Louisiana, USA) and its natural occurrence in Mexico should be confirmed. Champion (1911) stated that he saw three females from Mexico, similar to those collected in San Antonio, Texas. Lanteri (1990) studied a single specimen deposited at the National History Museum of London, labeled as Guanajuato, Mexico; however, in the large series of specimens herein revised, we have not seen any *Phaecepholis viridis* from Mexico.

The species of *Pantomorus* group II occur along the Pacific coast of Central America, from Costa Rica to the Sinaloa State in Mexico (see Table 2) on the western side of the Sierra Madre Occidental, from sea level to 1000 meters. Their distribution corresponds to the lowlands of the Mexican Pacific Coast, Western Panamanian Isthmus and Balsas Basin biogeographic provinces of the Neotropical region (Morrone, 2006, 2010), as well as higher altitudes (1000–2000 m) in the Chiapas and Sierra Madre del Sur provinces of the Mexican transition zone (Halffter, 1987; Morrone, 2010).

Pantomorus femoratus shows the broadest altitudinal and latitudinal range among the studied species (Costa Rica, El Salvador, Honduras, Nicaragua and Trinidad island), from 120 to 1600 m, in the Mexican Pacific Coast, Chiapas and Western Panamanian Isthmus biogeographic provinces (see Maes & O'Brien, 1990, for more details on distribution and host plants).

Most species of *Pantomorus* group I usually range from southern Mexico to Central America (Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua and Panama), from 500 to 2000 m altitude, in the Chiapas and Sierra Madre del Sur biogeographic provinces, except *P. horridus* which inhabits lower altitudes and higher latitudes in the Mexican Pacific Coast biogeographic province *sensu* Morrone (2006).

Pantomorus albosignatus diverges from the general biogeographic pattern of this genus, given that it occurs throughout the Mexican Plateau biogeographic province (Morrone, 2006), from 1000 to 2000 m altitude (see Table 2), and furthermore in the Transmexican Volcanic Belt and Sierra Madre del Sur provinces. The Mexican Plateau is assigned to the Nearctic region, whereas the Transmexican Volcanic Belt and Sierra Madre del Sur provinces belong to the Mexican transition zone (Morrone, 2005, 2010), inhabited by several Neotropical and Nearctic taxa. The broad distribution of *P. albosignatus* in one biogeographic province not inhabited by other species of the *Pantomorus*-*Naupactus* complex, could have been favored by a parthenogenetic mode of reproduction.

Finally, we hypothesize on the cenocrons involved, namely, the sets of taxa that share the same biogeographic history, constituting identifiable subsets within the biogeographic provinces by their common origin and evolutionary history (Morrone, 2009). Within the taxa distributed in the Nearctic region, *Phaecepholis* probably belongs to the ancient Neotropical cenocron which dispersed to North and Central America in the Palaeocene and diversified in that area, prior to the Pliocene closure of the Isthmus of Tehuantepec (Halffter, 1964; Morrone, 2005). In turn,

the presence of *P. albosignatus* in the Mexican Plateau may be a more recent event, as suggested by an ongoing panbiogeographic analysis of this group (Rosas *et al.*, 2010). The remaining taxa, distributed in the Neotropical region and the Mexican transition zone (Morrone, 2010), belong to the Mountain Mesoamerican and Tropical Mesoamerican cenocrons (Morrone, 2005) which evolved in the Mexican and Central American mountains and lowland habitats, respectively.

Conclusions and future directions

The species traditionally classified in *Pantomorus* share several characters mainly associated with the loss of flight which likely evolved several times in the history of the *Pantomorus-Naupactus* complex. In South and North America, the flightless species appear to have evolved in areas of open vegetation whereas in southern Mexico and Central America they usually occur at higher altitudes than their winged relatives.

This contribution does not provide a definitive solution for the classification of the *Pantomorus-Naupactus* complex, because the abundance of homoplastic characters makes it very difficult to recognize monophyletic groups. The recognition of well supported clades will require the addition of gene sequences for more species and the inclusion of a larger sample of species of *Pantomorus*, *Naupactus* and other related genera from Central and South America. The results of our phylogenetic analysis nevertheless constitute a step forward, in particular with regards to the North and Central America species of this difficult group.

We were able to recognize two main lineages of the *Pantomorus-Naupactus* complex: one includes the species of *Pantomorus* group II and *Phaecepholis*, occurring along the Pacific coast of Central America and Mexico and reaching the Great Plains of North America in the United States, and the other is represented by the species of *Naupactus* and *Pantomorus* group I with a southern geographic distribution and closer relationships to the South American species of the *Pantomorus-Naupactus* complex.

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CAPÍTULO 2

Synopsis of the genus *Pantomorus* (Coleoptera: Curculionidae:
Entiminae)

Synopsis and a key of the genus *Pantomorus* (Coleoptera: Curculionidae: Entiminae)

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Abstract. According to its present circumscription, *Pantomorus* Schoenherr (Coleoptera: Curculionidae) includes approximately 22 species of broad-nosed weevils of the tribe Naupactini distributed in Mexico and Central America. It is closely related to *Naupactus* Dejean, which is probably paraphyletic regarding to the latter, and it is mainly distributed in South America (only seven species would occur in Mexico and Central America). A key for separating the broad-nosed weevils of the genera *Naupactus*, *Pantomorus* and *Phacepholis* Horn from North and Central America is presented. In addition diagnoses as well as a key that allows to recognize each species of *Pantomorus* are provided.

Key words: key to genera and species, diagnosis, *Pantomorus*, Central and North America.

Resumen. De acuerdo a su actual circunscripción, *Pantomorus* Schoenherr (Coleoptera: Curculionidae) incluye aproximadamente 22 especies de gorgojos de rostro corto, distribuidos en México y América Central. *Naupactus* Dejean es un género parafilético, cercanamente relacionado, que se distribuye principalmente en América del Sur (solo siete especies se han registrado hasta el presente en México y América Central). Se presenta una clave para separar los gorgojos de la tribu Naupactini de los géneros *Naupactus*, *Pantomorus* y *Phacepholis* Horn de América del Norte y Central. Además se proporciona una clave y diagnosis para la identificación de las especies del género *Pantomorus*.

Palabras clave: claves para géneros y especies, diagnosis, *Pantomorus*, América Central, América del Norte.

Introduction

Pantomorus Schoenherr, 1840 (Entiminae: Naupactini) is a broad-nosed weevil genus based on the Mexican species *P. albosignatus* Boheman, 1840. The most closely related genus to *Pantomorus* is probably *Naupactus* Dejean, based on the type species *N. rivulosus* Olivier from Brazil (Sharp, 1889-1911; Scataglini et al., 2005). *Pantomorus* has been traditionally separated from *Naupactus* because of its smaller body size, the shorter antennae and rostrum, the lack of humeri and hind wings, and the front femora as wide as to slightly wider than the hind femora (Lanteri and Normark, 1995; Scataglini et al., 2005; Lanteri et al., 2010). However, there is no clear distinction between both genera and several species show intermediate characters between them. Buchanan (1939) also stated that there is not a clear distinction between *Pantomorus* and *Naupactus*, and he established the *Pantomorus*-*Naupactus* complex, with about 250 species distributed from North to South America (Scataglini et al., 2005; Rosas et al., 2011). He recognized seven genera for this complex: *Alceis* Billberg, 1820, *Naupactus* Dejean, 1821, *Pantomorus* Schoenherr, 1840, *Pantoplanes* Schoenherr, 1840, *Symmathetes* Schoenherr, 1847, *Pantopactus* Jekel, 1876, and *Athetetes* Pascoe, 1886, and four subgenera (in addition to the nominotypic *Pantomorus*): *Phacepholis* Horn, 1876, *Atrichonotus* Buchanan, 1939, *Graphognathus* Buchanan, 1939, and *Asynonychus* Crotch, 1867 (= *Aramigus* Horn, 1876).

Most Mexican and Central American species of *Pantomorus* were described in the *Biologia Centrali-Americana* (Sharp, 1891; Champion, 1911). Sharp (1891) separated the *Pantomorus* species from Mexico-Central America into two main groups: group I includes species lacking mucro on the middle tibiae; and group II includes species with a medium-sized

muco on the middle tibiae. The type species of *Pantomorus* (*P. albosignatus*) and *Pantopactus* (*P. stupidus*) are included in group I, whereas the type species of *Athetetes* is included in group II. Both *Pantopactus* and *Athetetes* were considered synonyms of *Pantomorus* (O'Brien and Wibmer, 1982; Wibmer and O'Brien, 1986; Alonso-Zarazaga and Lyal, 1999; Morrone, 1999). A recent phylogenetic analysis has established that *Pantopactus* is a synonym of *Naupactus*, and *Athetetes* is a synonym of *Phacepholis* (Rosas et al., 2011).

Lanteri and Morrone (1995), Lanteri and Normark (1995) and Scataglioni et al. (2005) proposed that *Pantomorus sensu lato* is a polyphyletic genus which includes species from Mexico, Central America and South America (O'Brien and Wibmer, 1982; Wibmer and O'Brien, 1986; Alonso-Zarazaga and Lyal, 1999; Lanteri et al., 2010). On the other hand, Morrone (1999) proposed that *Pantomorus sensu stricto* includes the species from Mexico and Central America, and all the South American species of *Pantomorus* should be assigned to *Naupactus*. A recent phylogenetic analysis has shown that the species assigned to *Pantomorus* are recognized by the presence of large elytral punctures and by the absence of a muco at the apex of the middle tibia (Rosas et al., 2011).

The objective of this study is to provide a key to separate the genera *Naupactus*, *Pantomorus* and *Phacepholis* (Coleoptera: Curculionidae) from North and Central America. Besides, a key and diagnoses to separate the species of the genus *Pantomorus* are provided (Rosas et al., 2011).

Material and methods

This study is based on borrowed material of 16 species from different institutions collections (see Rosas et al., 2011) and from the descriptions from literature (Sharp, 1891; Champion, 1911; O'Brien and Wibmer, 1982; Wibmer and O'Brien, 1986; Morrone, 1999). Unfortunately, no

specimens of *P. asperatus*, *P. faber*, *P. facialis*, *P. mollis*, *P. maculosus* and *P. nobilis* were available for this study.

Dissections of genitalia were made according to standard entomological techniques (Lanteri and O'Brien, 1990). Drawings of genitalia were done with a camera lucida adapted to a stereoscopic microscope. Measurements were taken with an ocular micrometer and have used to calculate length of abdomen and wide of femora.

Description

Key to *Pantomorus* and related genera

1. Body length in dorsal view medium to large (over 1 cm long); scutellum generally large; elytral humeri broad; elytral base bisinuate to slightly bisinuate and metathoracic wings generally well developed (Fig. 1)*Naupactus*
- 1'. Body length in dorsal view small (≤ 1 cm); scutellum small to indistinct; elytral humeri reduced to absent; elytral base straight; metathoracic wings2
2. Scutellum indistinct; small elytral punctures, about 1/3 width than intervals; mucro of middle tibiae (male) generally present (Fig. 4); metatibial apex of hind tibiae with broad outer bevel; ventrite II (male) generally with tubercles (Figs. 6-7); spermatheca globose to subglobose (Fig. 2).....*Phacepholis*
- 2'. Scutellum small; large elytral punctures, about 1/2 width of interval or the same width of the interval; mucro of middle tibiae (male) generally absent (Fig. 5); metatibial apex of hind tibiae with moderate or slender outer bevel; ventrite II (male) lacking tubercles (Figs. 8-9); spermatheca subcylindrical (Fig. 3).....*Pantomorus*

Pantomorus Schoenherr, 1840

Pantomorus Schoenherr, 1840:942

Body length in dorsal view, from apex of rostrum to apex of elytra small (less than 1 cm long); scutellum small, elytral humeri absent, metathoracic wings absent; the front femora being as wide as to slightly wider than the hind femora. *Pantomorus* has been traditionally separated from *Naupactus* by the smaller body size and shorter antennae and rostrum.

Original key to species of *Pantomorus*

1. Elongate and slender body; elytral scales restricted to flanks, elytral vestiture with longitudinal stripes; front femora wider than hind femora.....*P. circumcinctus* species group.....2
1. Small and oval body; elytral scales uniformly distributed, elytral vestiture uniform or with brown design of irregular stripes and maculae over light background; front femora as wide as to slightly wider than hind femora6
2. Gular angle in lateral view, between venter of rostrum and head, strongly obtuse (near 180°).....3
- 2'. Gular angle in lateral view, between venter of rostrum and head, almost right (near 90°).....4
3. Sutural stripe black and mucro of middle tibiae (male) small.....*P. picturatus*
- 3'. Sutural stripe absent and mucro of middle tibiae (male) absent..... *P. salvadorensis*
4. Elytral setae or seta-like scales short and recumbent; front femora dark brown; middle and hind femora reddish*P. circumcinctus*
- 4'. Elytral setae or seta-like scales long and erect; all femora reddish or dark brown5
5. Sutural stripe green and all femora reddish.....*P. salvini*
- 5'. Suture blackish and all femora dark brown.....*P. dorsalis*

6. Elytra somewhat globose; elytral punctures medium, about 1/2 width of interval.....	7
6'. Elytra flat to slightly convex; elytral punctures as width as the interval or 1/3 of width of interval.....	9
7. Antennae stout; pronotal disc irregularly punctuate; elytral humeri absent; elytral vestiture with brown design of irregular stripes and maculae over light background.....	8
7'. Antennae slender; pronotal disc irregularly smooth to slightly rugose; elytral humeri reduced; elytral vestiture uniform.....	<i>P. comes</i>
8. Antennomere 2 longer than 3; parthenogenetic reproduction (Fig. 3.....	<i>P. albosignatus</i>
8'. Antennomere 3 twice as long as 2; sexual reproduction	<i>P. parvulus</i>
9. Nodulus of spermatheca oblique regarding opening of gland.....	10
9'. Nodulus of spermatheca parallel to opening of spermathecal gland.....	13
10. Vertex glabrous.....	11
10'. Vertex scarcely squamose.....	12
11. Eyes slightly convex; elytral anterior margin straight, not thickened.....	<i>P. horridus</i>
11'. Eyes strongly convex; elytral anterior margin straight and thickened.....	<i>P. rudis</i>
12. Elytral setae or seta-like scales long, suberect to erect; without lateral stripes.....	<i>P. longulus</i>
12'. Elytral setae or seta-like scales short, recumbent; with lateral stripes of pales scales	<i>P. picipes</i>
13. Dorsal comb of setae at apex of hind tibiae about as long as apical comb; apex of ventrite V (male) slightly emarginated.....	14
13'. Dorsal comb of setae at apex of hind tibiae shorter than apical comb; apex of ventrite V (male) straight	15
14. Elytral setae or seta-like scales short, recumbent; all femora dark brown	<i>P. sobrinus</i>

- 14'. Elytral setae or seta-like scales long, suberect to erect; all femora reddish
*P. subcinctus*
15. Scutellum distinctly black; body vestiture covering uniformly with golden-green or blue
 scales.....*P. uniformis*
- 15'. Scutellum scarcely black; only elytral vestiture greenish-grey or yellowish-grey with metallic
 sides or pallid grey with brown spots.....*P. crinitus*

Species of *Pantomorus*

P. albosignatus Boheman, 1840

Fig. 3

Pantomorus albosignatus Boheman, 1840:943

Diagnosis. Antennomere 2 slightly longer to about as long as 1; pronotal disc irregularly punctuate; elytral punctures about 1/2 width of interval, elytral setae or seta-like scales long, suberect to erect, elytral vestiture with brown design of irregular stripes and maculae over light background; parthenogenetic reproduction.

Distribution. Mexico (Aguascalientes, Coahuila, Chihuahua, Distrito Federal, Durango, Guanajuato, Hidalgo, Monterrey, Oaxaca, Puebla, Querétaro, San Luís Potosí, Veracruz and Zacatecas).

Material examined: MEXICO. *Chihuahua*. Chihuahua, 1933, coll Wickman (5 USNM); Sta. Barbara, 6300 ft, VII-15-1947 (1 AMNH). *Durango*. Durango, coll Wickham (7 USNM), 1933, coll Wickham (1 USNM); El Tascate, 6400 ft, VII-28-1947 (1 AMNH); Guadalupe Victoria, 8 mi ENE VII-14-1959, coll R. B Selander (2 USNM); Nombre de Dios, 5900 ft, VIII-13-1947 (2 AMNH), 63 mi N, 6000 ft, VI-25-1952 (4 CMNC); San Juan del Río, 5200 ft, VII-30-1947 (1 AMNH); Villa Madero, 6700 ft, VIII-18-1947 (1 AMNH). *Hidalgo*. Santiago de Anaya, 2030 m,

VII-19-1999, coll A. M. Corona (1 EBCC); Tasquillo, 8.5 km S, 1830 m, VII-20-1999, coll A. M. Corona (4 EBCC). *Oaxaca*. Oaxaca, 5043 ft, VI-30-1955, coll Vaurie (2 AMNH), VII-14-1955 (3 AMNH), VII-16-1955 (2 AMNH); 10 km al NE, Hwy 175, 1800 msnm, VI-11-1979, coll H. and A. Howden (8 CMNC); 8 km SW, 1450 msnm, VII-05-1983 coll R. Anderson, Acacia thorn scrub (1 CMNC); 5 mi SW, 4700 ft, VIII-04-1983, coll R. Anderson and Maddison, Acacia thorn scrub (7 CMNC); Mitla, 3.5 mi SW, 5200 ft, VIII-04-1983, coll R. Anderson and Maddison, Acacia thorn shrub (3 CMNC); Quiotepec, 5.7 mi SE, Hwy 131, 2100 ft, VII-21-1987 coll Kovarik and Schaffner (4 CMNC); Teotitlán del Camino, 39.1 km SE of, 518 msnm, VII-21-1987, coll R. Anderson, Acacia scrub (6 CMNC). *Puebla*. Tlacotepec, VII-02-1955, coll RB & JR Selander (3 USNM). *San Luis Potosí*. San Luis Potosí, 19 mi N, IX-01-1958 (1 CMNC), 43.8 mi S on # 57, 5600 ft, VIII-08-1983, coll R. Anderson, Acacia/cactus desert (2 CMNC), 70 km S on 57, 1700 m, VIII-08-1983, coll R. Anderson, Acacia/cactus desert (3 CMNC), 11.6 km E, 1945 m, VII-03-1987, coll R. Anderson, Acacia scrub (1 CMNC); La Calzada, 1 mi al SE on # 80, 3900 ft, VI-08-1983, coll R. Anderson, on mezquite (1 CMNC). *Zacatecas*. Fresnillo, 7000 ft, VIII-15-1947 (1 AMNH).

P. circumcinctus Sharp, 1891

Pantomorus circumcinctus Sharp, 1891:160

Diagnosis. Mandibular scar strongly protruding; elytra elongate, elytral scales restricted to flanks, lateral stripes of green scales very distinct; front femora dark brown, middle and hind femora reddish, front femora much wider than hind femora.

Distribution. El Salvador, Guatemala and Honduras.

Material examined: GUATEMALA. *Baja Verapaz*. Purulha, 54.4 km S, 850 m, VII-01-1993, coll F. Génier (3 CMNC); San Gerónimo 5 km S, 20-V-1991, coll R. Anderson, dry pine/oak scrub (5

CMNC). *Quetzaltenango*. Zunil, 14.4 km, 1520 m, VI-21-1993, coll R. Anderson, second growth (4 CMNC), 12.9 km SW, 1340 m, VI-18-1993 coll F. Génier, hand coll (4 CMNC), 14.4 km, 1340 m, VI-18-1993, coll Is Ashe, beating vegetation (1 CMNC), 14.4 km, 1520 m, VI-21-1993, coll F. Génier, beating vegetation (9 CMNC). HONDURAS. *Ocotepeque*. Ocotepeque, 12.7 km E and 2.4 km S, 1450 m, VI-15-1994 coll R. Anderson (1 CMNC).

P. comes Kuschel, 1956

Pantomorus comes Kuschel, 1956:335

Diagnosis. Antennae slender, antennomere 2 distinctly longer than 1; pronotal disc smooth to slightly rugose; elytral punctures about 1/2 width of interval, elytral humeri reduced.

Distribution. El Salvador and Guatemala.

Material examined: GUATEMALA. *Quetzaltenango*. Zunil, 25.2 km SW, 800 m, VI-20-1993, coll F. Genier (1 CMNC).

P. crinitus (Boheman, 1840)

Naupactus crinitus Boheman, 1840:20

Pantomorus crinitus; Chevrolat, 1879:cxxx

Pantomorus affinis Sharp 1891:157; Morrone, 1999:162 (= *P. crinitus*)

Diagnosis. Antennae slender; scales small and neatly arranged; elytral vestiture greenish-grey or yellowish-grey with metallic sides or pallid grey with brown spots; mucro of middle tibiae (male) small. Sharp (1891) states that: "this I look as a very variable species, not being able to find any good distinctive characters for separating some examples of it".

Distribution. El Salvador, Guatemala and Mexico (Chiapas and Veracruz).

Material examined: MEXICO. *Chiapas*. Villaflores, Los Ángeles, campo CONANP, R. de La Biosfera, La Sepultura, 16°15'49.7''N, 93°37'01.3'' W, 1000 m, VII-30-31-2005, coll R. Anderson, open-oak-pine forest, beating oaks (6 CMNC).

P. dorsalis Sharp, 1891

Pantomorus dorsalis Sharp, 1891:159

Diagnosis. Elytral setae long, erect and fine, suture blackish; elytra elongate, elytral scales restricted to flanks, lateral stripes of pale scales, all femora dark brown, front femora much wider than hind femora.

Distribution. Guatemala and Honduras.

Material examined: HONDURAS. *El Paraíso*. Cerro Monserrat, 6.9 km W Yucaran, 1760, VI-10-1994, m coll Ashe and Brooks, cloud forest (1 CMNC). *Francisco Morazán*. El Espinido, 3250 ft, V-25-1993, coll R. Turnbow (4 CMNC); El Zamorano, 6 km SE, 850 m, V-17-1994, V-20-1994, coll H. and A. Howden, thorn scrub (6 CMNC), 6 km SE, V-21-1994, V-22-1994, coll H. and A. Howden, thorn scrub (17 CMNC), 4 km W, 1.7 km SE, 1010 m, VI-10-1994, coll R. Anderson, dry oak forest (1 CMNC), 4 km W, 1.7 km SE, 900 m, VI-12-1994, coll R. Anderson, dry oak forest (5 CMNC), 30 km ESE, 830 m, V-14-1994, VI-05-1994, VI-06-1994, coll H. and A. Howden (8 CMNC), 4 km E, 900 m, VI-06-1994, coll VI-06-1994, thorn scrub (4 CMNC), 2 km S, 820 m, VI-09-1994 coll Ashe and Brooks (1 CMNC), 5 km E, VI-02-1993, coll R. Turnbow (1 CMNC); El Zamorano, 4 km W, El Macuelis, V-27-1994, VI-02-1994 coll H. and A. Howden, oak forest (3 CMNC); El Zamorano, 15 km N, San Juan del Rancho, 1400 m, V-26-1994, coll H. and A. Howden (4 CMNC); Güinope, 7 km N, 1200 m, VI-08-1994, coll H. and A. Howden (1 CMNC); Talanga, 25 km SE, Finca la Archaga, 900 m, V-19-1994, coll H. and A.

Howden (2 CMNC). *Ocotepeque*. Ocotepeque 12. 7 km E, 2.4 km S, 1450 m, VI-15-1994, coll R.

Anderson (1 CMNC).

P. horridus Champion, 1911

Pantomorus horridus Champion 1911:334

Diagnosis. Eyes slightly convex; vertex glabrous; body vestiture with pale bluish-grey scales; elytral vestiture with green and golden scales, setae long, erect and bristly.

Distribution. Mexico (Jalisco, Nayarit and Sinaloa)

Material examined: MEXICO. *Jalisco*. Chamela, VII-12-1985, coll R. Ayala (1 CMNC), Estación de Biología, X-04-1986, coll Rosa A. Usela V. (1 EBCC); El Tuito, IX-12-1986, coll Rosa A. Usela V. (1 EBCC); Puerto Vallarta, Hwy 200, 21 mi S, 2310 ft, VII-9-10-1984, coll McCleve and P. Jump (2 CMNC). *Nayarit*. Bucerías, 11 km NW, VII-07-1983 (1 CMNC); San Blas, VII-05-1972, coll K. F. Stephan (2 CMNC); Tepic, VII-20-24-1952, F. W. and F. G. Werner (1 CMNC), VII-28-1953, coll C. and P. Vaurie (4 AMNH); 20 mi N, VIII-05-1956, coll Vincent D. Roth (14 AMNH); Hwy 54W Junction Hwy 15, VIII-30-1971, coll T. F. Halstead (2 ex CMNC); San Blas, VII-05-1972, coll K. F. Stephan (2 CMNC). *Sinaloa*. Escuinapa, 18 mi SE, VIII-26-1965, Coll C. D. Jonson (1 CMNC).

P. longulus Sharp, 1891

Pantomorus longulus Sharp, 1891:154

Diagnosis. Pronotum broad, short and dark brown, elytra elongate, elytral scales uniformly distributed and the same color than pronotum; elytral punctures about 1/3 width of intervals; all femora reddish.

Distribution. Mexico (Chiapas and Oaxaca).

Material examined: MEXICO. *Chiapas*. Cinco Cerros, 860 m, VI-31-1990, coll H. and A. Howden (1 CMNC). *Oaxaca*. Díaz Ordaz, 8 km NW, 2400 m, VI-15-1979, coll H. and A. Howden (1 CMNC); Guelatao, 22.9 km S, 2256 m, VII-17-1987, coll R. Anderson, oak-Acacia woodland (1 CMNC); Juchitán, 10.8 km N of Jct, 1859 m, VII-19-1987, coll R. Anderson (1 CMNC); Mitla, 13-14 km E, 2100 m, VIII-02-1986, coll H. and A. Howden (7 CMNC); Oaxaca, 20.5 mi NW, 5500 ft, VIII-06-1983, coll Anderson and Maddison (3 CMNC); Teotitlan del Valle, 9 km N, 2045 m, VII-10-1992, coll R. L. Westcott (2 CMNC).

P. parvulus Sharp, 1891

Pantomorus parvulus Sharp, 1891:153

Diagnosis. Antennomere 2 slightly longer to about as long as 1, antennomere 3 twice as long as 2; pronotal disc irregularly punctuate; sutural region dark brown; elytral punctures about 1/2 width of interval; elytral setae or seta-like scales long, suberect to erect; sexual reproduction.

Although *P. parvulus* has stout antennae, these are slender than *P. albosignatus* and the former is smaller than the latter.

Distribution. Mexico (Oaxaca).

Material examined: MEXICO. *Oaxaca*. Candelaria, 10.9 km N, 991 m, VII-12-1987, coll R. Anderson, cloud forest (1 CMNC); San Gabriel Mixtepec, 7.6 km S, 762 m, VII-10-1987, coll R. Anderson (2 CMNC), 24.3 km N, 1174 m, VII-11-1987, coll R. Anderson (2 CMNC); Teotitlán del Camino, 39.1 km SE, 518 m, VII-21-1987, coll R. Anderson, Acacia scrub (1 CMNC).

P. picipes Sharp, 1891

Pantomorus picipes Sharp, 1891:154

Diagnosis. Elytral setae or seta-like scales long, suberect to erect, elytral scales uniformly distributed, lateral stripes of pale scales; all femora reddish.

Distribution. Mexico (Oaxaca).

Material examined: MEXICO. *Oaxaca*. Juchitán, 10.8 km N, 1859 m, VII-19-1987, coll R.

Anderson, oak-acacia Woodland (1 CMNC), 5 km NW, 1783 m, VII-20-1987, coll R. Anderson, oak-acacia grassland (2 CMNC); Mitla, 3.5 mi SW, 5200 ft, VIII-04-1983, coll R. Anderson and Maddison, Acacia grassland (1 CMNC); Oaxaca, 20.5 mi NW, 5500 ft, VIII-06-1983, coll Anderson and Maddison (3 CMNC); 12.4 km SE, 1219 m, VII-16-1987 coll R. Anderson (1 CMNC); 11 km NW, 1800 m, VII-27-1992, coll R. Anderson (1 CMNC), VII-29-1992, coll R. Anderson, oak-acacia woodland on *Quercus* (1 CMNC).

P. picturatus Sharp, 1891

Pantomorus picturatus Sharp, 1891:160

Diagnosis. Gular angle in lateral view, between venter of rostrum and head, strongly obtuse (near 180°); sutural stripe black; longitudinal stripes of greenish-yellow scales very distinct; front femora dark brown, middle and hind femora reddish, front femora much wider than hind femora; mucro of middle tibiae (male) small.

Distribution. Costa Rica, El Salvador, Guatemala Honduras and Mexico (Chiapas and Oaxaca).

Material examined. GUATEMALA. *Escuintla*. Finca Variedades, 500 ft, VII-02-1947, coll F.

Johnson (2 AMNH); *Guatemala*. Guatemala city, VI-00-1945, coll E. J. Hambleton (1 USNM).

Quetzaltenango. Zunil, 12.9 km SW, 1340 m, 18-V-1993 coll F. Genier (5 CMNC), coll R.

Anderson (1 CMNC); 14.4 km SW, 1340 m, 18-VI-1993, coll J. S. Ashe, beating vegetation (1

CMNC), 12.5 km SW, 1520 m, VI-21-1993, coll F. Genier (8 CMNC), coll R. Anderson (6

CMNC). *Sacatepéquez*. San Miguel Dueñas, 4.5 km W, 1760 m, VI-12-1991 coll H T Howden (2

CMNC), coll R. Anderson (1 CMNC), Capetillo, 3 km S of Ciudad Vieja, VI-03-1993, coll A. T. Howden (1 CMNC). HONDURAS. Siguatepequez, 10 km S, VI-02-1994, coll H. and A. Howden (1 CMNC). *Francisco Morazán*. Cataramas, 3.2 km S, VI-01-1993, coll R. Turnbow (1 CMNC); *Tegucigalpa*. VII-01-1948, coll W. D. Clarke (1 CMNC). MEXICO. *Chiapas*. Cinco Cerros, 860 m, V-30-1990, coll H. and A. Howden (1 CMNC). *Oaxaca*. Yosocuta, 1660 m, VIII-09-2008, coll A. Casasola and M.V. Rosas, *Acacia* sp. (1 MZFC).

P. rudis Sharp, 1891

Pantomorus rudis Sharp, 1891:162

Diagnosis. Vertex glabrous; longitudinal lateral carinae of rostrum strongly distinct; elytral anterior margin straight and thickened.

Distribution. Costa Rica, Guatemala and Honduras.

Material examined: GUATEMALA. *Baja Verapaz*. San Gerónimo, 100 m, V-28-1991, coll H. and A. Howden (1 CMNC). HONDURAS. *Comayagua*. Siguatepéquez, 10 km S, VI-02-1994, coll H. and A. Howden (4 CMNC).

P. salvadorensis Kuschel, 1956

Pantomorus salvadorensis Kuschel, 1956:339

Diagnosis. Gular angle in lateral view, between venter of rostrum and head strongly obtuse (near 180°); elytral setae or seta-like scales short and recumbent; elytral scales restricted to flanks; all femora dark brown, front femora much wider than hind femora.

Distribution. El Salvador.

P. salvini Sharp, 1891

Pantomorus salvini Sharp, 1891:155

Diagnosis. Mandibular scar strongly protruding; sutural stripe green; elytral scales restricted to flanks; lateral stripes of green scales very distinct and regular; all femora reddish, front femora much wider than hind femora.

Distribution. Guatemala.

Material examined: GUATEMALA. *Guatemala*. Puerta Parada, 1790 m, VI-12-1991, coll R.

Anderson, cutover oak forest (2 CMNC). *Sacatepequez*. Santa Lucía, Milpas Altas, 1800 m, VI-

24-1993, H. and A. Howden (15 CMNC). *Zacapa*. San Lorenzo, 1800 m, VII-09-1986, VII-11-

1986, VII-17-1986, coll L. LeSage, sweeping mainly oak in clearing (6 CWOB), 1067 m, VI-17-

1983, coll B. D. Gill, sweeping mainly oak in clearing (9 CMNC), 950 m, 1067 m, VI-17-1983,

coll J. M. Cambell, sweeping mainly oak in clearing (18 CMNC), 7 km S, 900 m, 1560 m, VI-18-

1993, coll H. and A. Howden (29 CMNC).

P. sobrinus Sharp, 1891

Pantomorus sobrinus Sharp, 1891:158

Diagnosis. Elytral intervals black and shining, body vestiture dark brown; elytral punctures about 1/3 width of intervals; apex of ventrite V (male) slightly emarginated.

Distribution. Guatemala.

Material examined: GUATEMALA. *Sacatepéquez*. Ciudad Vieja, 3 km S, V-03-1993, coll A. T.

Howden (1 CMNC); San Miguel Dueñas, 4.5 km NW, 1760 m, VI-12-1991, coll H. and A.

Howden (4 CMNC).

P. subcinctus Sharp, 1891

Pantomorus subcinctus Sharp, 1891:158

Diagnosis. Elytra elongate, elytral setae or seta-like scales long, suberect to erect; elytral punctures about same width of intervals; all femora reddish; apex of ventrite V (male) slightly emarginated.

Distribution. Guatemala and Nicaragua.

Material examined: GUATEMALA. *Zacapa*. San Lorenzo, 1067m, VI-17-1983, coll B. D. Gill (8 CMNC), 950 m, 1067m, VI-17-1983, coll J. M. Campbell (18 CMNC), 13 km, 950 m, VI-17-1993, coll J. M. Campbell (12 CMNC), 7 km S, 900 m, VI-18-1993, coll H. and A. Howden (23 CMNC).

P. uniformis Sharp, 1891

Pantomorus uniformis Sharp, 1891:161

Diagnosis. Club very slender; scutellum black; elytral punctures about 1/3 width of intervals; body vestiture covering uniformly with golden-green or blue scales.

Distribution. Mexico (Chiapas, Guanajuato, Querétaro, Oaxaca and Veracruz).

Material examined: MEXICO. *Chiapas*. Cinco Cerros, X-22-1988, coll R. Turbow (1 CMNC); Tapanatepec, 4 km NO, 27-VIII-1990, F. A. Noguera (1 EBCC). *Oaxaca*. Rincón Antonio, Fredk Knab (3 USNM). Veracruz. Veracruz, VII-1955, NLH Kraus, on *Lantana camara* (1 USNM), VII-1965 (1 USNM).

Conclusions

This study presents a most precise data about distinction of three genera of broad-nosed weevils of the tribe Naupactini. Herein an illustrated key to differentiate the genera *Naupactus*, *Pantomorus* and *Phacepholis* (Coleoptera: Curculionidae) from North and Central America is proposed.

According to its currently circumscription, the genus *Pantomorus* includes approximately 22 species distributed mainly in Mexico and Central America, although, the shared characters are not enough to recognize it as a monophyletic group, as these are homoplastic. This genus includes a monophyletic group named *P. circumcinctus* group. This group is conformed by five species: *P. circumcinctus*, *P. dorsalis*, *P. salvadorensis*, *P. picturatus* and *P. salvini*. An original key to separate the species as well as the diagnoses that allow recognize the species in *Pantomorus* are provided.

Although this study was based upon the examination of 1249 adult specimens borrowed from ten entomological collections, it is important to continue with collecting and examination of specimens of the species, including the types, in order to improve the accuracy of the data. So it is crucial generate further information about the complex *Pantomorus-Naupactus* in Mexico and Central America for future researches.

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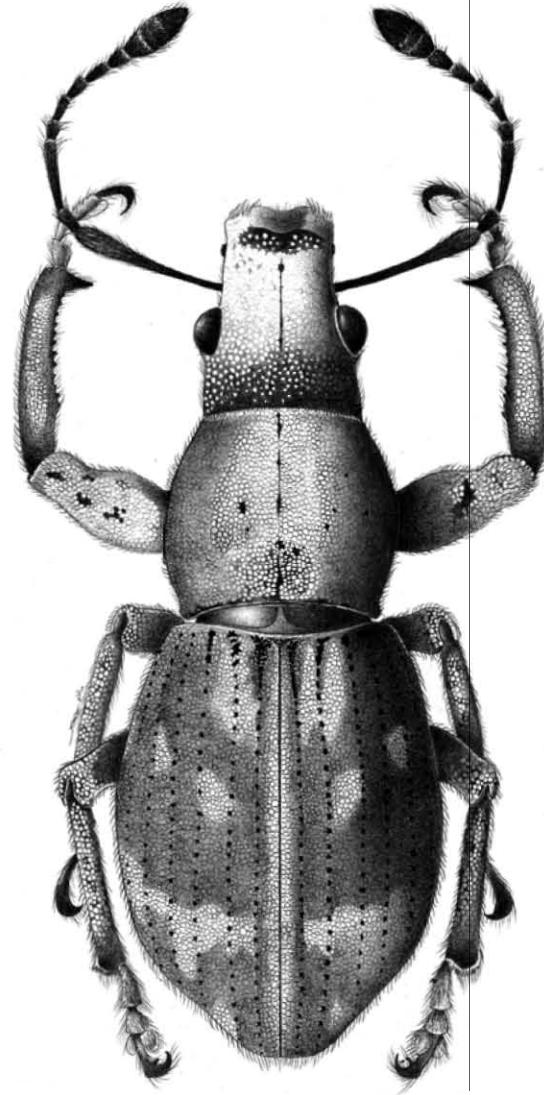
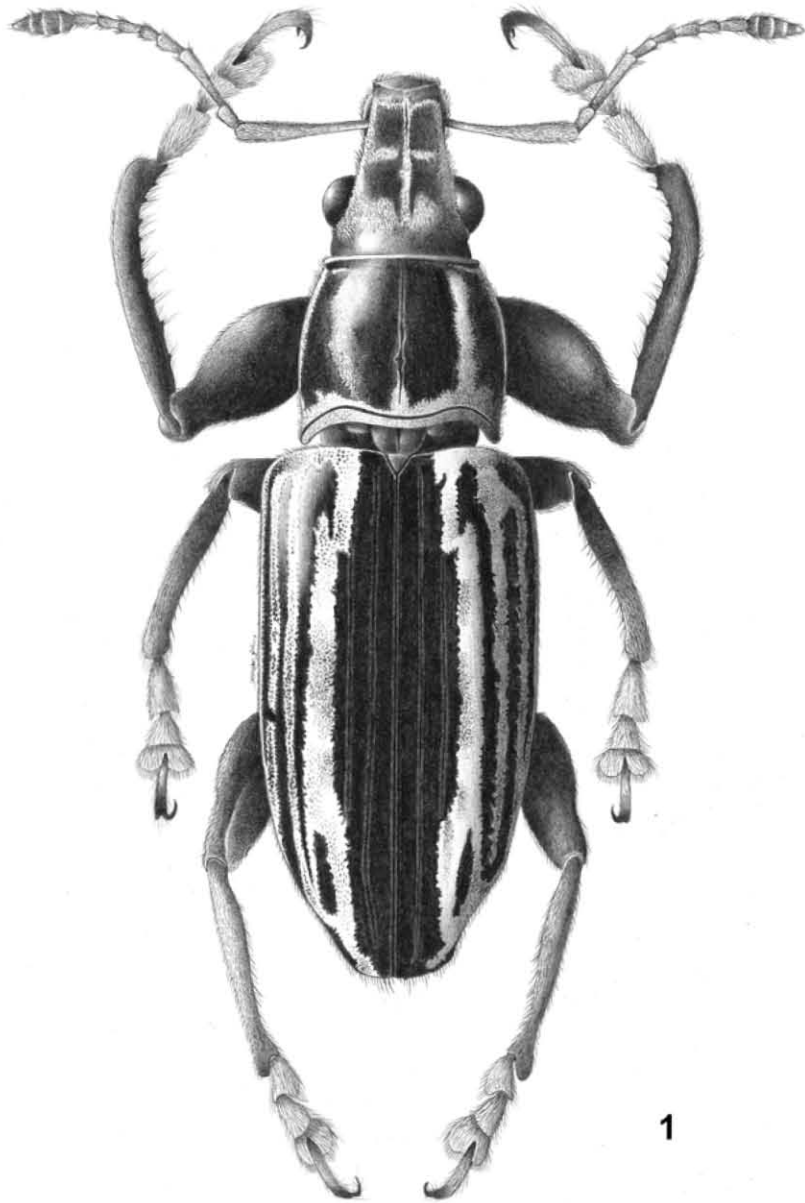
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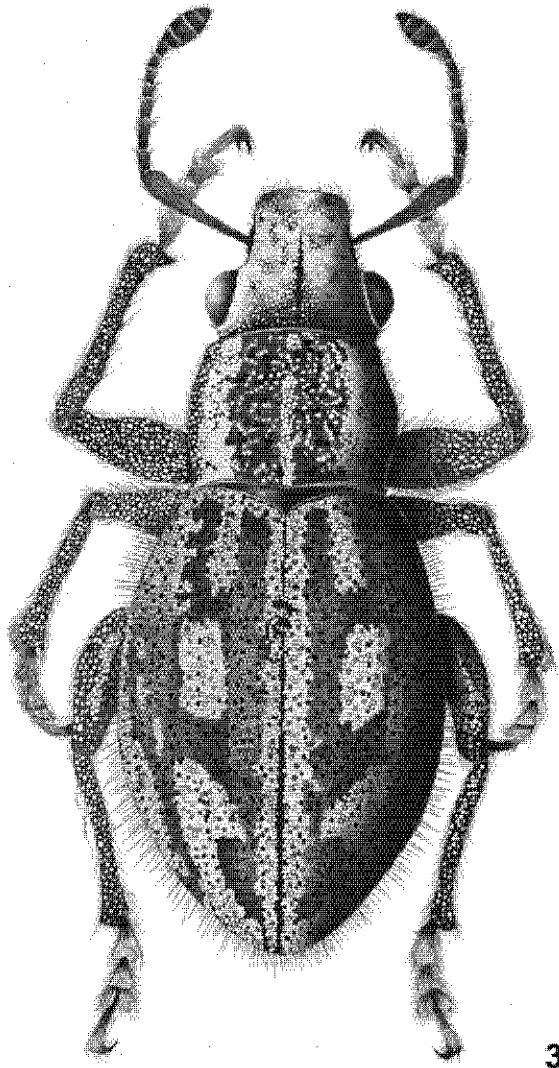
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Figure captions

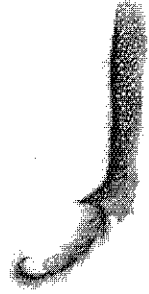
Figures. **1-2**, Habitus, dorsal view: **1**, *Naupactus sulfuratus* (Champion). 120 mm; **2**, *Phacepholis globicollis* (Pascoe). 93 mm.

Figures. **3-9**, Habitus, dorsal view: **3**, *Pantomorus albosignatus* Boheman. 80 mm. **4-5**, Legs: middle tibiae with large mucro **4**, *Ph. globicollis*; middle tibiae lacking mucro, **5**, *P. albosignatus* Boheman. **6,8**, ventral view: ventrite II (male) with tubercles; **6**, *Ph. globicollis* (Pascoe); ventrite II (male) lacking tubercles, **8**, *P. albosignatus*. **7,9**, lateral views: ventrite II (male) with tubercles; **7**, *Ph. globicollis* (Pascoe); ventrite II (male) lacking tubercles, **9**, *P. albosignatus*.

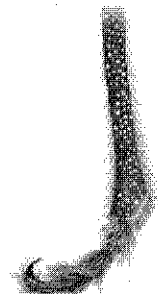




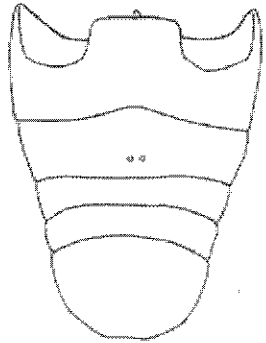
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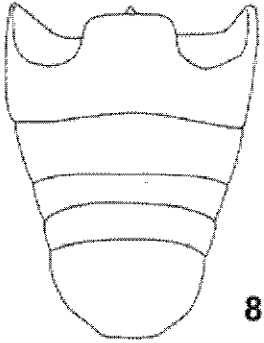
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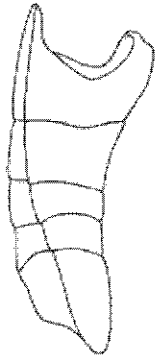
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CAPÍTULO 3

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

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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 conducted a paleogeographic analysis of the broad-winged weevils of the genera *Naupactus* Dejean, 1821, *Pantomorus* Schöenherr, 1846 and *Phaeoporus* Horn, 1870 (Coleoptera: Curculionidae) from North and Central America to propose a biogeographic scenario to explain their distribution. Based on individual tracks of 30 species, we obtained six generalized tracks: Mesoamerica, 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 first generalized track for all species of the three genera. We found two tracks, one at low altitudes of the Mesoamerica and Chiapas tracks, and another at the extension of the Chiapas and Sierra Madre del Sur tracks. Species of *Pantomorus* are possibly distributed in lowlands, associated mostly with dry forests and terra firme environments. Species of *Pantomorus* and *Phaeoporus* would have diversified from South American Amazonian lowlands (mostly Amazonian habitats and lowlands of North and Central America) between one level to about 2000 m of altitude.

Key words: Paleogeography, weevils, Neotamara, Mexico, Transisthmian Zone

Introduction

The *Pantomorus*–*Naupactus* complex is a group of broad-winged 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 (Lantini 1990; Santiago et al. 2007; 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 apomorphic paleogeographic (Lantini and Normark 1992; Normark and Lantini 1999; Rodrigues et al. 2010), have been introduced into other countries outside the Americas along with different crops, including agricultural pests (Lantini and O'Brien 1995; Lantini and Diaz 1996; Lantini and Martynoff 1997).

Most species of the *Pantomorus*–*Naupactus* complex occurring in Mexico and Central America have been assigned to *Pantomorus* Schöenherr (O'Brien and Wilmer 1982), a genus that based on recent phylogenetic analysis (Rosas et al. 2011) is restricted to some species formerly placed in *Pantomorus* from Lacroix Sharp (1889–1913). They are flightless species (metathoracic wings reduced to absent), usually inhabiting dry forests and other xerophilic environments above 500 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 (Wilmer and O'Brien 1986). This genus also occurs in dry forests of southern Mexico and Central America, mainly at lower altitudes than *Pantomorus*. *Phaeoporus* Horn, currently considered a distinct monophyletic genus (Lantini 1990; Rosas et al. 2011), includes flightless forms, some occurring in the Great Plains of North America (*Phaeoporus* *sonoriensis* in

form Lantini 1990), others distributed along the Pacific coast of Mexico and Central America (*P. gibbivittis* 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 xerophilic shrubs.

Our main objective is to undertake a paleogeographic analysis of the species of *Pantomorus*, *Naupactus* and *Phaeoporus* from North America, Mexico and Central America. We propose a biogeographic scenario that explains the broad diversification of these taxa in the area where the Neotropical and the Nearctic biotas overlap (Hallgrím 1964, 1987; Morrison and Klapálek 2001). This way we will contribute to the understanding of the historical evolution of one of the most interesting invasion zones in the Americas, the Mexican Transisthmian Zone (Marrino 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 *Phaeoporus* (11 species), *Pantomorus* (14 species) and *Naupactus* (10 species). Distributional records were obtained mainly from specimens deposited in Rosas et al. (2011) and from the Smithsonian (1889–1911), Chicago (1911), Berkeley (1939), Mexico and O'Brien (1986) herbaria (Rosas et al. 2001; Jones and Lantini 2002).

The paleogeographic method (Crisci 1980, 1984) consists in plotting locations at different times on maps and connecting these distributions from current individual tracks. When superimposed individual tracks result in similar lines when generalized to individual tracks, which indicate the presence of associated forms subsequently fragmented by tectonic shift or climatic changes. When or more generalized tracks overlap in a given area, they determine a node, which indicates that different ancestral taxa and phylogenetic components diversified in such area (Morrison and Crisci 1987; Crisci et al. 1989; Crisci 1996, 2000).

Locations, individual and generalized tracks, and nodes were represented on maps using the view 3.2 (ENVI 1999). Locations were represented according to their geographical coordinates, using a reference

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opting tree method). Generalized tracks and nodes were characterized following the biogeographic regionalizations of Matzou (2006, 2010) for Mexico and Central America and Gilinsky (1977) for the USA.

Results

Based on the overlap of 30 individual tracks (Figs 1–12), we identified six generalized tracks (Fig. 13), hereinafter 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 *Phaeophloeus atralis* (Sharp 1891) (Fig. 6), *Pantomorus rufus* (Sharp 1891) (Fig. 7), *Nasoputis latipes* Champion 1911 (Fig. 9) and *N. jennisoni* (Sharp 1891) (Fig. 11). It is distributed in Costa Rica, Nicaragua and Honduras, along the Mexican Pacific Coast, Chiapas and Western Panamanian hillmass biogeographic provinces, from sea level to about 2400 m of altitude.

The Chiapas generalized track is supported by the individual tracks of *Pantomorus conus* Kuschel 1936 (Fig. 4), *P. dorsalis* Sharp 1891 (Fig. 3), *P. sobrius* (Sharp 1891) (Fig. 6), *P. coahuilensis* Sharp 1891 (Fig. 9), *P. subvittatus* (Sharp 1891) (Fig. 10), *P. salteri* (Sharp 1891) (Fig. 11) and *P. rubrodorsatus* Kuschel 1936 (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 *Nasoputis straminea* Champion 1911 (Fig. 7), *N. nigula* Boheman 1840 (Fig. 11), *N. ruficornis* Champion 1911 (Fig. 12), *Phaeophloeus globosus* (Pavane 1866) (Fig. 4), *Ph. albicans* (Champion 1911) (Fig. 5), *Ph. brevipalpis* (Sharp 1891) (Fig. 6), *Pantomorus parvulus* (Sharp 1891) (Fig. 8), *P. pizarator* (Sharp 1891) (Fig. 8), *P. longior* Sharp 1891 (Fig. 9) and *P. pilipes* 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 *Phaeophloeus ruficornis* (Sharp 1891) (Fig. 4), *Ph. albicans* (Sharp 1891–1911) (Fig. 5) and *Pantomorus Azevedo* 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 *Phaeophloeus 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 *Phaeophloeus plumbeus* (Buchanan

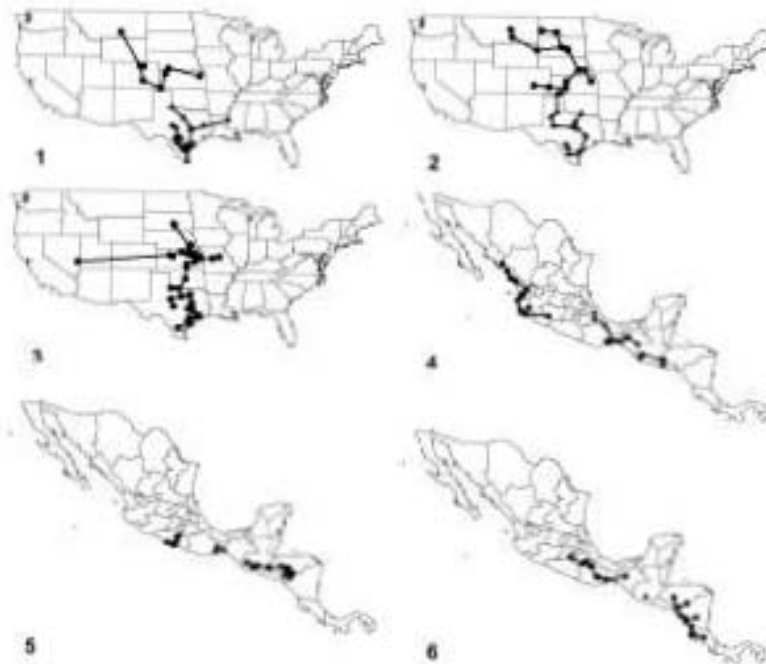


Fig. 1–6. Individual tracks: (1) *Phaeophloeus plumbeus* (circle), *Phaeophloeus viridis* (triangle), (2) *Phaeophloeus obscurus* (circle), *Phaeophloeus albicans* (triangle), (3) *Phaeophloeus ruficornis* (circle), (4) *Phaeophloeus ruficornis* (circle), *Phaeophloeus globosus* (triangle), *Pantomorus conus* (square), (5) *Phaeophloeus albicans* (circle), *Phaeophloeus albicans* (triangle), *Pantomorus dorsalis* (square), (6) *Phaeophloeus brevipalpis* (circle), *Pantomorus sobrius* (triangle), *Phaeophloeus atralis* (square).

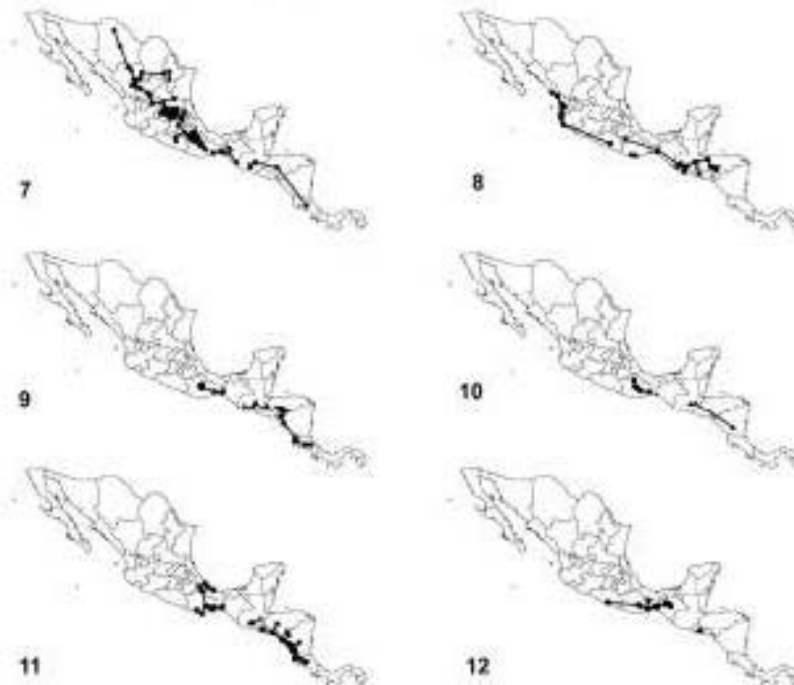


Fig. 7–12. Individual tracks. *Pantonomus albicinctus* (circles), *Naupactus viverris* (triangles), *Pantonomus rufus* (squares) (8) *Pantonomus auratus* (circles), *Pantonomus parvulus* (triangles), *Pantonomus picturatus* (squares), (9) *Pantonomus longulus* (circles), *Pantonomus circumscriptus* (triangles), *Naupactus laticeps* (squares) (10) *Pantonomus pictus* (circles), *Pantonomus subvittatus* (triangles); (11) *Naupactus asaphus* (circles), *Pantonomus varius* (triangles), *Naupactus brevicornis* (squares); (12) *Naupactus subvittatus* (circles), *Pantonomus subvittatus* (triangles).

1939) (Fig. 1) and *Ph. cosidulus* 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 Mesamerican 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 (Hallgr 1964, 1987; Morrison 2010).

Discussion

The Mesamerican, Chiapas and Sierra Madre del Sur generalized tracks correspond to the Southern Mesamerican generalized track of Abrahamovich et al. (2004), based on species of *Bombus* (Hymenoptera: Apidae), and to the Sierra Madre del Sur, Northern and Southern Mesamerican generalized tracks of Márquez and Morrison (2003), based on species of *Heterostelus* and *Bomboloma* (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 Morrison (2005), based on Buprestidae (Coleoptera) of the genus *Larytus*. The Northern and Southern Great Plains generalized tracks are coincident with the North American Prairies pattern of Kutinas et al. (2004), based on plant species of the tribes Epilobieae, Gongylocepsae and Onagreae (Onagraceae), and with the geographical range of the black-tailed prairie dog (*Cynomys ludovicianus*) (Lomolino and Smith 2001).

The *Pantonomus*-*Naupactus* complex is mostly distributed in the Neotropical region and the Mexican Transition Zone, but five species of *Phaeophobus* 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 *Phaeophobus*, 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 Mesamerican, the Sierra Madre del Sur and the Mexican Pacific Coast generalized tracks. A single species of *Phaeophobus* (*Ph. brevicornis*) 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



Fig. 11. Individual tracks. Generalized tracks and nodes obtained from the biogeographic analysis of 30 species belonging to *Phaeophobos*, *Pantonomus* and *Naupactus*, distributed in North and Central America. A, Mesosamerican generalized track; B, Chiapas generalized track; C, Sierra Madre del Sur generalized track; D, Mexican Pacific Coast generalized track; E, Southern Green Plains generalized track; F, Northern Great Plains generalized track.

of the *Pantonomus*-*Naupactus* complex occurring in the Great Plains of North America, belonging to the genera *Araonopus* Horn, *Archaeonopus* Bachtanz and *Naupactus* (Lanteri and O'Brien 1990; Lanteri and Diaz 1994; Lanteri and Marvaldi 1995; Lanteri and Moreno 1995; Scatignati 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 Norrmann 1995; Norrmann and Lanteri 1998; Rodriguez et al. 2010). Species of *Phaeophobos* are not parthenogenetic, and they are not as harmful for crops as the invasive species.

Most *Pantonomus* 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. jordanii* 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 *Pantonomus* species previously assigned to a very distinct monophyletic group, the *P. circumvectus* species group (Rosas et al. 2011), that is distributed above 1000 m of altitude.

Pantonomus albispinus 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 (Hallgr 1964, 1987) and where there are also Neartic elements above 3000 m of altitude (Escalante et al. 2004). In general, Mesamerican taxa are not found above 2200-2300 m (Hallgr 1987, 2003). *Pantonomus albispinus*, 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 arid 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. jordanii*, 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. albispinus* throughout the Mexican Plateau could be a recent event, as happens with other recent immigrants to this area (Hallgr 1964).

The species of *Naupactus* contribute to two generalized tracks, the Mesosamerican and the Sierra Madre del Sur tracks. They are more frequent at lower elevations than those of *Pantonomus*, 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. laevipes* and *N. viverrus*) (Maes and O'Brien 1990; Rosas et al. 2011). The absence of species of *Naupactus* and of the *Ph. globosus* 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 Mesosamerican lineages across the lowlands of the Panamanian Isthmus to the north (Hallgr 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 Mesosamerican distributional pattern of Hallgr (1987).

When comparing the distributional pattern of the *Pantonomus*-*Naupactus* complex with that of the genus *Erycinus* 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 Rio and Lanteri 2010) also supports this hypothesis. Moreover, the highest species diversity of *Erycinus* 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*, *Pantonomus* and the *Phaeophobos globosus* species group). Montane environments with altitudinal gradients, such as those of the Sierra Madre del Sur, usually restricted dispersal and favoured speciation (Hallgr 1987). *Erycinus* is much less diversified than the *Pantonomus*-*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 *Erycinus* usually do not occur.

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

are frequently associated with xerophytic shrubs of the genus *Larrea* (Lanteri 1995). Within the *Pantonomus-Nasopactus* complex, the species of *Phaeophobus 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 *Pantonomus* (e.g. *P. horridus*) and the *Phaeophobus globicollis* group (e.g. *Ph. albivitta* and *Ph. vividus*) 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 *Ericyodes* in North America is partially coincident with the western generalized track of Kallias et al. (2004), and the range of *Phaeophobus 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; Rojas et al. 2011), we hypothesize that the ancestors of *Pantonomus* and *Phaeophobus* probably expanded their ranges into Central and North America from South America, sometime between Late Cretaceous and Early Tertiary, as other insect groups (Hoffler 1964, 1987), although following different northward pathways of dispersal. *Ericyodes* was able to colonize and to diversify in the xeric environments of the Sonora and Mohave deserts, whereas *Pantonomus* was able to colonize and diversify in the same environments, dry forests and montane habitats of Mexico and Central America. *Nasopactus* and the *Ph. globicollis* species group are distributed primarily in lowlands, as most South American species of *Nasopactus*, and are associated with dry forests and xeric environments.

Lanteri and Morrone (1995) and Lanteri and Norrmark (1995) proposed that *Nasopactus* is paraphyletic (Scatagliari et al. 2005). We hypothesize herein that the species of *Pantonomus* and *Phaeophobus* have different *Nasopactus*-like ancestors and belong to two different clades. 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). *Phaeophobus* belongs to this ancient Neotropical clade and diversified mainly in the Mexican coasts, Central America and the lowlands of North America. *Pantonomus* might belong to a younger clade, the Mountain Mesoamerican clade, 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 tracks de las especies mesoamericanas y centroamericanas del complejo *Pantonomus-Nasopactus* (Coleoptera: Curculionidae)

Se realizó un análisis parabiogeográfico de los gorgojos de nuestro complejo pertenecientes a los géneros *Nasopactus* Dejean, *Pantonomus* Schölkner

y *Phaeophobus* Horn (Coleoptera: Curculionidae) de América del Norte y Central, para proponer un escenario biogeográfico que explique su diversificación histórica. Se obtuvieron seis tracks generalizados (Mesoamericano, Chiapas, Sierra Madre del Sur, Costa Pacífica Mexicana, Grandes Planicies del Sur y Grandes Planicies del Norte) a partir de los tracks individualizados de 30 especies. El track generalizado Sierra Madre del Sur es el mejor sustentado por 10 especies de los tres géneros. Se obtuvieron diez tracks, uno en la intersección de los tracks Chiapas y Mesoamericano, y otro en la intersección de los tracks Chiapas y Sierra Madre del Sur. Las especies de *Nasopactus* están distribuidas principalmente en tierras bajas y están asociadas, generalmente, con selvas secas y ambientes xerófilos. Las especies de *Pantonomus* y *Phaeophobus* se han diversificado a partir de ancestros similares a *Nasopactus* 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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DISCUSIÓN, CONCLUSIONES Y PERSPECTIVAS

De acuerdo con los resultados obtenidos en la presente investigación, se descarta la hipótesis que *Pantomorus sensu stricto* (Morrone, 1999) es monofilético, sin embargo, a partir del análisis filogenético se obtuvo un cladograma que permite reconocer dos linajes principales. Un linaje está representado por las especies incluidas en *Phacepholis* y *Pantomorus* grupo II, distribuidas a lo largo de la costa de América Central, pasando por México y alcanzando las grandes planicies de América del Norte en los Estados Unidos. Otro linaje está representado por las especies de *Pantomorus* grupo I y *Naupactus*, distribuidas principalmente en hábitats montañosos y tierras bajas de América Central y del Sur, con una relación cercana a las especies de América del Sur. *Pantomorus* grupo I incluye la especie tipo del género (*P. albosignatus* Boheman), mientras que *Pantomorus* grupo II incluye a la especie tipo de *Athetetes* Pascoe (*A. globicollis* Pascoe).

El clado que incluye las especies de *Phacepholis* y de *Pantomorus* grupo II fue recuperado en ambos cladogramas (morfológico y combinado). Los caracteres que comparten (sinapomorfías) estas especies son: corbículas de las tibias posteriores escamosas en hembras y machos, y segundo ventrito de los machos armado con dos o tres tubérculos transversales, fila de dentículos en el margen interno de la tibia posterior de los machos. En el caso de las hembras, los caracteres de los genitalia que comparte este clado son: la placa del esternito VIII elongada; ovipositor muy alargado (excede el largo del abdomen), espermateca de globosa a subglobosa, cornu y nodulus cortos.

Los resultados obtenidos permitieron ampliar el concepto previo de *Phacepholis* (*sensu stricto* o *sensu* Lanteri, 1990) para incluir las especies de *Pantomorus* grupo II (*Ph. globicollis* (Pascoe), *Ph. brevipes* (Sharp), *Ph. albicans*

(Sharp), *Ph. viridicans* (Sharp), *Ph. strabo* (Sharp), *Ph. sulfureus* (Champion), *Ph. annectens* (Sharp) y *P. trituberculatus* (Champion)). También se estableció la sinonimia de *Athetetes* Pascoe 1886 con *Phacepholis* Horn, 1876, siendo este último el nombre válido por prioridad.

El otro linaje está representado por las especies de *Pantomorus* grupo I y *Naupactus*. Dentro de *Pantomorus* grupo I se observa la existencia de un probable grupo monofilético, el grupo de especies *P. circumcinctus* que incluye a *P. circumcinctus*, *P. dorsalis*, *P. salvadorensis*, *P. picturatus* y *P. salvini*. Este grupo es fácilmente reconocido por las escamas elitrales restringidas a los márgenes de los élitros, dejando el área central glabra, la presencia de bandas longitudinales. El carácter compartido en los genitalia de las hembras es: el apodema del esternito VIII cuatro veces más largo que la lámina; en los machos: el lóbulo medio es dos veces tan largo como los apodemas del edeago. Tomando en cuenta el análisis filogenético, se recomienda utilizar el nombre *Pantomorus* para la mayoría de las especies de *Pantomorus* grupo I, estas especies permanecerán en *Pantomorus* hasta que haya una solución definitiva para el complejo *Pantomorus-Naupactus*. Las especies *P. stupidus* y *P. femoratus* fueron transferidas a *Naupactus*.

La abundancia de caracteres homoplásticos hace muy difícil determinar las especies y reconocer los grupos monofiléticos dentro del complejo *Pantomorus-Naupactus*, por esta razón se elaboró una clave, además de ilustraciones que permiten separar los géneros *Naupactus*, *Pantomorus* y *Phacepholis* distribuidos en América del Norte y Central; también, se generó una clave para separar las especies de *Pantomorus* con sus respectivas diagnósis.

Aunque esta contribución no proporciona una solución definitiva a la clasificación del complejo *Pantomorus-Naupactus*, los resultados de este trabajo

constituyen un avance en lo que se refiere a las especies pertenecientes a estos grupos, distribuidos en América del Norte y Central.

Finalmente, en el presente trabajo se empleó el método panbiogeográfico para establecer un escenario que explique la diversificación biótica de *Naupactus*, *Pantomorus* y *Phacepholis* de América del Norte y Central. De este modo se postula una hipótesis sobre el patrón de distribución geográfica actual de estos géneros. La panbiogeografía es uno de los métodos básicos de la biogeografía histórica (Morrone & Crisci, 1995), que enfatiza el análisis espacio temporal de los patrones de distribución de los organismos, para lograr un mejor conocimiento de los patrones y procesos evolutivos (Craw et al., 1999; Morrone, 2004). La dimensión espacial de los organismos es un pre-requisito para cualquier estudio evolutivo, ya que la geografía es el sustrato donde transcurre la vida (Morrone, 2004, 2009).

Los resultados del análisis panbiogeográfico de los géneros *Naupactus*, *Pantomorus* y *Phacepholis* de América del Norte y Central, muestran que de los seis trazos generalizados obtenidos (Mesoamericano, Chiapas, Sierra Madre del Sur, Costa Pacífica Mexicana, Grandes Planicies del Sur y Grandes Planicies del Norte), el trazo generalizado Sierra Madre del Sur es el mejor sustentado por 10 especies de los tres géneros. El área donde dos o más trazos generalizados diferentes se intersectan se denomina nodo. Para ellos se postula un origen biótico múltiple, en ocasiones, en tiempos geológicos diferentes. Un nodo se considera como una zona compleja y compuesta en el sentido geológico y biológico (Espinosa & Llorente, 1993; Morrone, 2009), e implica una conjunción de historias biogeográficas y ecológicas distintas (Craw et al., 1999; Morrone, 2009). En este trabajo 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 (Rosas et al., 2011a). Los nodos localizados (1 y 2) principalmente en la zona de Transición (Morrone, 2010), corroboran que las zonas de transición representan eventos de hibridación biótica favorecida por cambios históricos y ecológicos.

El complejo *Pantomorus-Naupactus* presenta su mayor distribución en la región Neotropical y en la Zona de Transición Mexicana, sin embargo, cinco especies de *Phacepholis* se encuentran distribuidas en las grandes planicies de América del Norte en los Estados Unidos, (región Neártica). Estas especies ocupan las grandes planicies desde Texas hasta Montana; en este trabajo estas especies contribuyen a formar los trazos generalizados Grandes Planicies del Sur y Grandes Planicies del Norte. Las otras especies de *Phacepholis*, pertenecientes al grupo de especies *Ph. globicolis* (Rosas et al., 2011b) contribuyen a formar los trazos generalizados Mesoamericano, Sierra Madre del sur y Costa Pacifica Mexicana. Estas especies ocupan principalmente las tierras bajas de la costa Pacífica y están asociadas con selvas secas.

La mayoría de las especies de *Pantomorus* distribuidas en México y América Central contribuyen a soportar cuatro de los seis trazos generalizados, principalmente los trazos generalizados Chiapas y Sierra Madre del Sur, estas especies se distribuyen principalmente a una altitud superior a los 700 msnm. El trazo generalizado Chiapas esta soportado principalmente por las especies de *Pantomorus* asignadas al grupo *P. circumcinctus* (Rosas et al., 2011b).

Las especies de *Naupactus* contribuyen a formar dos trazos generalizados, Mesoamericano y Sierra Madre del Sur. Estas especies se encuentran distribuidas

principalmente en tierras bajas y están asociadas, con selvas secas y ambientes xerófilos (Rosas et al., 2011a).

Los resultados del análisis permitieron generar una hipótesis en la cual las especies de *Pantomorus* y *Phacepholis*, pertenecen a dos cenocrones distintos, aunque poseen un ancestro similar a *Naupactus*. *Phacepholis* pertenece a un antiguo cenocrón neotropical que se diversificó en las costas mexicanas, América Central y en las tierras bajas de América del Norte; y *Pantomorus* pertenece a un cenocrón más joven, mesoamericano de montaña, que se distribuye básicamente en las tierras altas de Guatemala y América Central (Rosas et al., 2011a).

Al proponer un escenario biogeográfico que explique el origen y la diversificación biótica de estos taxones, en el área donde las biotas Neotropical y Neártica se superponen, se contribuye al entendimiento de la evolución histórica de la Zona de Transición Mexicana (Morrone, 2006, 2010).

Es fundamental seguir trabajando en las colectas de especímenes, así como en la obtención de secuencias de distintos genes de las especies pertenecientes a *Pantomorus*, *Phacepholis*, *Naupactus* y otros géneros relacionados en México, América Central y del Sur. Esta información nos permitirá obtener datos que aportarán más evidencia para el reconocimiento de grupos monofiléticos así como de sus distribuciones.

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