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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 *Phacepholis* 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 *Phacepholis* to include most species of the *Pantomorus* group II, and we establish the synonymy of *Athetetes* Pascoe, 1886 with *Phacepholis* 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, 1889–1991; Scataglini *et al.*, 2005), based on the type species *N. rivulosus* (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*): *Phacepholis* Horn, 1876, native to the Nearctic region, *Atrichonotus* Buchanan, 1939, *Graphognathus* Buchanan, 1939, and *Asynonychus* Crotch, 1867 (= *Aramigus* Horn, 1876),

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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 *Galapaganus* 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 *Phacepholis* Horn, *Atrichonotus* Buchanan and *Aramigus* Horn (Lanteri, 1990; Lanteri & O'Brien, 1990; Lanteri & Díaz, 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 mucro, and the middle tibiae lacking mucro; and group II includes species with front tibiae bearing a large mucro, and middle tibiae with a medium-sized mucro. 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 *Galapaganus* 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 Mexico, Jalisco, Mexico (Jorge Vega).
FSCA	Florida State Collection of Arthropods, Florida, USA (Michael C. Thomas).
IBUNAM	Instituto de Biología, Universidad Nacional Autónoma de Mexico, Mexico City, Mexico (Santiago Zaragoza).
MLP	Museo de la Plata, La Plata, Argentina (Analía A. Lanteri).
MZFC	Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de Mexico, Mexico City, Mexico (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 accesion numbers		Locations of specimens assayed for molecular analyses
	COI	Cyt B	
Galapaganus howdenae	AF211485	EU265284	Santa Cruz Island, Galápagos, Ecuador
G. galapagoensis	AF015914	EU265220	San Cristóbal Island, Galápagos, Ecuador
Naupactus xanthographus	AF211490	EU265322	Punta Lara, Buenos Aires, Argentina
N. cinereidorsum	AY770388	Not available	Córdoba, Argentina
N. leucoloma	AY790880	EU265325	Buenos Aires, Argentina
N. sulfuratus	GU565270	GU565279	La Ventosa, Salina Cruz, Oaxaca, Mexico
Pantomorus stupidus	GU565275	GU565283	La Ventosa, Salina Cruz, Oaxaca, Mexico
P. globicollis	GU565273	GU565285	La Ventosa, Salina Cruz, Oaxaca, Mexico
P. albicans	GU565278	GU565282	Tecpan, Guerrero, Mexico
P. viridicans	GU565277	GU565286	Chamela, Jalisco, Mexico

Morphological analysis. Morphological features were scored for 35 species formerly placed in *Pantomorus*, *Phacepholis, Naupactus,* and *Galapaganus*, 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 Scataglini *et al.* (2005), and for Cytochrome b we followed Keargoat *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 $MgCl_2$, 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 (Bensansson *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
Galapaganus howdenae 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
G. galapagoensis (Linell, 1898)	Ecuador, Galápagos Islands (San Cristóbal Island)	0–100	Galápagos Islands
Naupactus xanthographus Germar, 1824	Argentina, Brazil, Paraguay, and Uruguay. Introduced into Chile (incl. Juan Fernández islands)	Sea level	Parana Forest, Cerrado, Chaco, Monte and Pampa
N. cinereidorsum Hustache, 1947	Argentina	Sea level	Chaco
N. leucoloma 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
N. laticeps 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
N. virescens Champion, 1911	Mexico (Chiapas and Oaxaca)	25–1000	Chiapas and Mexican Pacific Coast
N. sulfuratus Champion, 1911	Mexico (Chiapas and Oaxaca)	30–620	Chiapas and Mexican Pacific Coast
Pantomorus stupidus (Boheman, 1840)	Mexico (Chiapas and Oaxaca)	25–760	Chiapas and Mexican Pacific Coast
P. femoratus 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
P. picturatus 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
P. circumcinctus Sharp, 1891	El Salvador (Chalatenango), Guatemala (Baja Verapaz) and Honduras (Copán and Ocopteque)	850–1250	Chiapas
P. salvini Sharp, 1891	Guatemala (Chimaltenango Guatemala, Sacatepéquez and Zacapa)	1560–2000	Chiapas
P. dorsalis Sharp, 1891	Guatemala (Chimaltenango) and Honduras (Comayagua, El Paraíso, Choluteca and Francisco Morazán)	820–1760	Chiapas
P. salvadorensis Kuschel, 1956	El Salvador (Cuzcatlán and La Libertad)	500–1000	Chiapas
P. picipes Sharp, 1891	Mexico (Oaxaca)	1220–1860	Chiapas and Sierra Madre del Sur
P. sobrinus Sharp, 1891	Guatemala (Sacatepéquez)	1760	Chiapas
P. subcinctus Sharp, 1891	Guatemala (Baja Verapaz)	900–1070	Chiapas
P. longulus 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
P. rudis Sharp, 1891	Guatemala (Chimaltenango and Baja Verapaz) and Honduras (Comayagua)	940–2440	Chiapas
P. horridus Champion, 1911	Mexico (Nayarit, Jalisco, and Sinaloa)	0–700	Mexican Pacific Coast
P. comes Kuschel, 1956	El Salvador (San Salvador) and Guatemala (Quetzaltenango)	400–800	Chiapas and Mexican Pacific Coast
P. parvulus Sharp, 1891	Mexico (Oaxaca)	0– 500	Mexican Pacific Coast
P. albosignatus 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
P. globicollis (Pascoe, 1886)	Mexico (Chiapas, Oaxaca and Veracruz)	25–680	Chiapas, Mexican Pacific Coast and Mexican Gulf
P. brevipes Sharp, 1891	Mexico (Chiapas, Morelos, Oaxaca and Puebla)	1000–1980	Chiapas and Sierra Madre del Sur
P. albicans Sharp, 1891	Mexico (Guerrero)	30–680	Mexican Pacific Coast and Balsas Basin
P. viridicans Sharp, 1891	Mexico (Jalisco, Nayarit and Sinaloa)	0–760	Mexican Pacific Coast
P. strabo 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
P. sulfureus Champion, 1911	Mexico (Oaxaca)	0–215	Mexican Pacific Coast
Phacepholis elegans Horn, 1876	USA (Arizona, Arkansas, California, Colorado, Iowa, Kansas, Missouri, Nebraska, Nevada, Oklahoma, South Dakota and Texas)	Sea level	Grasslands
Ph. candidus Horn, 1876	USA (Colorado, Kansas, Nebraska, South Dakota, Texas and Wyoming)	Sea level	Grasslands
Ph. planitiatus (Buchanan, 1939)	USA (Colorado, Kansas and Nebraska)	Sea level	Grasslands
Ph. obscurus Horn, 1876	USA (Oklahoma and Texas)	Sea level	Grasslands
Ph. viridis (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 characteres

0. Width of frons between anterior margins of eyes, over width of rostrum at apex (♀).
1. Maximum width over maximum length of pronotum (♀).
2. Maximum length over maximum width of elytra (♀)
3. Maximum length of elytra, over maximum length of pronotum (♂).
4. Maximum width of front femora, over maximum width of hind femora (♂).

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 (♀): 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 (♀): strongly obtuse (near 180º) (0); almost right (near 90º) (1).
18. Shape of pronotum: subcylindrical (0); slightly subconical, with curved flanks (1); strongly subconical, with straight flanks (2).
19. Pronotum (♂): narrower than elytra (0); as wide as, to slightly wider than elytra (1).
20. Surface of pronotal disc (♂): flat to slightly convex (0); strongly convex (1).
21. Texture of pronotal disc: smooth to slightly rugose (0); granulose (1); irregularly punctuate (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 (♂): 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 (♂): slender, moderately curved near apex (0); very stout, strongly curved near apex (1).
37. Mucro of front tibiae (♂): large (about as long as tarsal claws) (0); medium-sized to small (shorter than tarsal claws) (1).
38. Mucro of middle tibiae (♂): medium-sized (0); small (1); absent (2).
39. Mucro of hind tibiae (♂): present (0); absent (1).
40. Row of denticles on inner margin of middle tibiae (♂): absent (0); present (1).
41. Row of denticles on inner margin of hind tibiae (♂): 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 (♂): 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 (♀): 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. Nodulus 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 90º) (Fig. 23) (0); obtuse (Fig. 25) (1); almost flat (near 180º) (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 *Galapaganus 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 (Bensansson *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 “?”.

						1	*2*	*3*	*4*	*5*	*6*
	0	*1*	*2*	*3*	*4*	*56789*	*0123456789*	*0123456789*	*0123456789*	*0123456789*	*0123456789*	*0*
G. howdenae	1.35	1.46	1.5	3.03	1.6	00111	0010100010	0101012200	0100110001	0010000010	0120011010	0
G. galapagoensis	1.31	1.27	1.35	2.16	1.67	00010	0010010100	0001011202	0?01100011	0010000010	0020001000	0
N. xanthographus	1.33	1.12	1.66	2.63	1.33	00110	0010100010	0000110101	1011000000	0101000111	0000110120	1
N. cinereidorsum	1.33	1.34	1.55	2.91	1.36	00010	0010020110	0000011001	1000000111	0031000201	1000110000	1
N. leucoloma	1.35	1.24	1.46	2.68	1.55	00111	1100010110	0000121000	0011100111	0031000201	1000100200	2
N. laticeps	1.33	1.31	1.51	2.75	1.42	00011	1021020010	0000001001	1010100111	0011013101	0020010101	1
N. virescens	1.36	1.38	1.49	2.7	1.38	00011	1111010020	0000001001	1010100111	0001002111	0020010101	1
N. sulfuratus	1.3	1.3	1.64	2.59	1.4	01011	1010010010	0000011011	1010110121	0012001211	0020110020	0
P. stupidus	1.47	1.24	1.41	2.6	1.33	11010	1010010010	0001221011	1011110121	0011000211	0020110020	0
P. femoratus	1.35	1.23	1.46	2.21	1.3	01010	1010010000	0001111000	0001000100	0002000111	0020010001	0
P. picturatus	1.33	1.26	1.44	2.6	1.41	11010	1010010010	0001220200	1111110111	0011000221	0020110202	2
P. circumcinctus	1.3	1.21	1.75	2.46	1.46	11010	0010010110	0001220200	1111110121	0012000221	0020110202	2
P. salvini	1.33	1.32	1.52	2.6	1.2	11010	0010010110	0001220200	0111120121	0012000221	0020110101	1
P. dorsalis	1.37	1.27	1.47	2.1	1.36	11010	1010010110	0001221200	0111100121	0011000221	0020110202	2
P. salvadorensis	1.35	1.2	1.6	2.12	1.25	11010	1010010010	0001220200	1111100121	0011000221	0020110202	2
P. picipes	1.47	1.25	1.48	2.11	1.23	11000	1010021110	0001221200	0011120121	0012000211	0021010002	1
P. sobrinus	1.34	1.32	1.52	2.27	1.16	11000	1010010110	0001220000	1001100121	0021010211	0020110101	1
P. subcinctus	1.32	1.22	1.56	2.21	1.2	11000	1010010110	0001221200	0001120121	0021010211	0020110001	1
P. longulus	1.36	1.36	1.6	2.71	1.3	11000	1010010110	0001220000	1001120121	0022000311	002111????	?
P. rudis	1.44	1.35	1.28	2.13	1.3	11110	1011020100	0201221200	1001100121	0021000111	0021010000	1
P. horridus	1.43	1.3	1.28	2.22	1.2	11000	1111010100	0201221200	0001000121	0012000111	0021010001	0
P. comes	1.33	1.3	1.4	2.17	1.3	11000	1010120110	0001121100	0001000121	0011000111	0020010000	1
P. parvulus	1.43	1.2	1.37	2.24	1.11	11000	1010021110	0201221100	0021000121	0011000101	0020110000	1
P. albosignatus	1.45	1.31	1.29	2.52	1.1	11000	1010021110	0201221100	0021000121	0011000101	002011????	?
P. globicollis	1.25	1.13	1.36	1.6	1.65	00100	0010100101	1002222001	1021001001	1102200000	0110120000	1
P. brevipes	1.16	1.19	1.43	1.69	1.6	10100	0010100111	1202222001	1021001001	1102200000	0110120000	1
P. albicans	1.29	1.12	1.46	1.76	1.54	10100	0010100111	1002222001	1001001001	1102300000	0110120000	1
P. viridicans	1.35	1.15	1.48	1.75	1.6	10100	0010100101	1002222001	1001001001	1102300000	0110120000	1
P. strabo	1.33	1.21	1.37	1.75	1.44	10100	0200100100	1002222001	1021001001	1102100000	0110120000	1
P. sulfureus	1.45	1.17	1.43	1.7	1.33	10000	1200010100	1002222001	1001001111	0002000110	0110120000	1
Ph. elegans	1.43	1.1	1.47	2.29	1	10000	0010110110	0012221001	1001000001	1002000000	0210120000	1
Ph. candidus	1.49	1.12	1.44	2.23	1.18	10000	0100110110	0011111001	1001000001	1102310000	0210120010	1
Ph. planitiatus	1.49	1.16	1.46	2.26	1.13	10000	0100120110	0011111000	0001000001	1102310000	0210120010	1
Ph. obscurus	1.56	1.17	1.34	2.13	1.14	10000	1010121110	0011221000	0001000001	1002010000	0210120000	1
Ph. viridis	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 *Pantomorus*, *Naupactus* and *Phacepholis* 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).

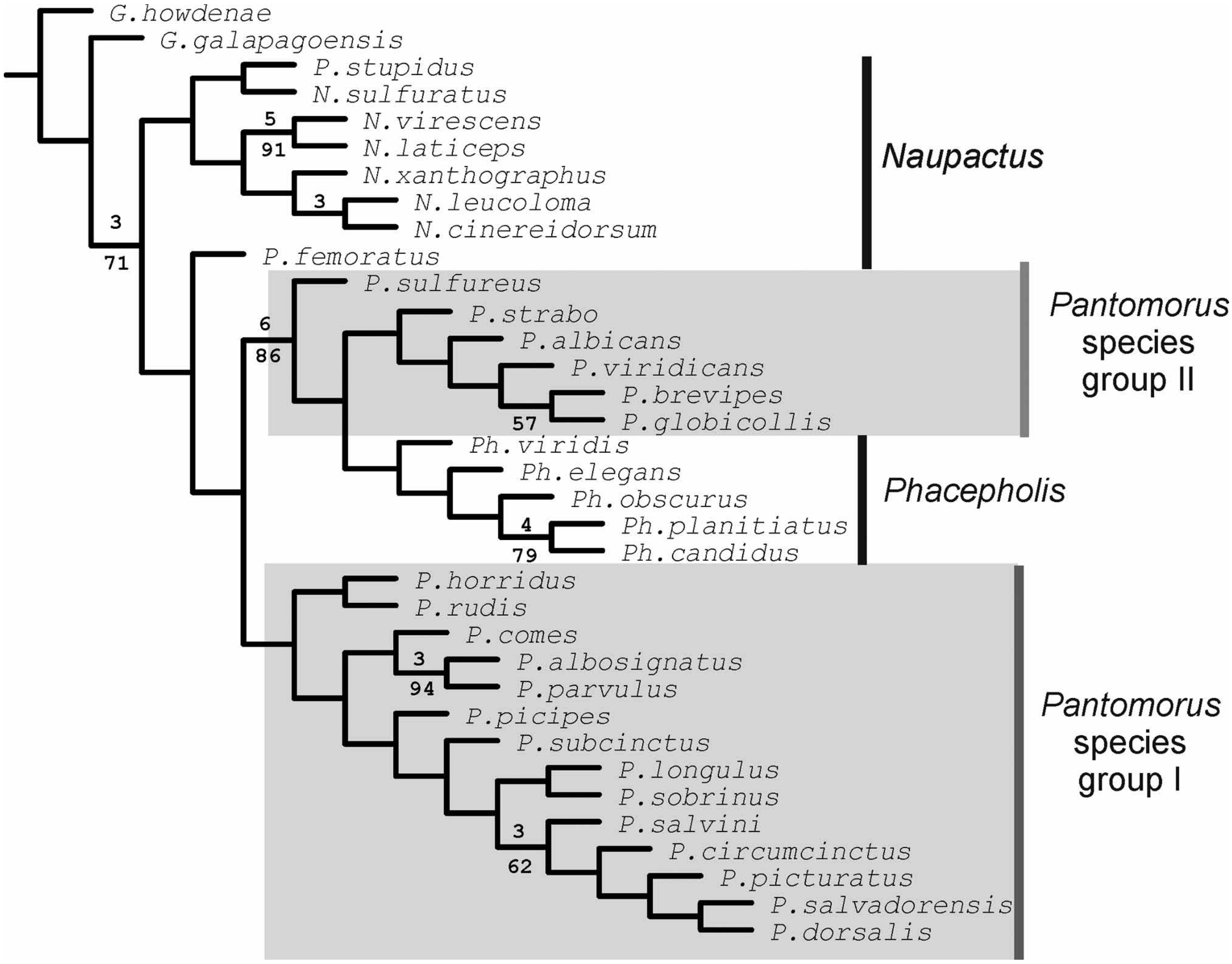


FIGURE 1. Most parsimonious morphological tree under equal weights, with 17 morphological characters coded as additive. Bremer support values over 3 are given above each corresponding branch and bootstrap values over 50% are below the branches.

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. cinereidorum* (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.

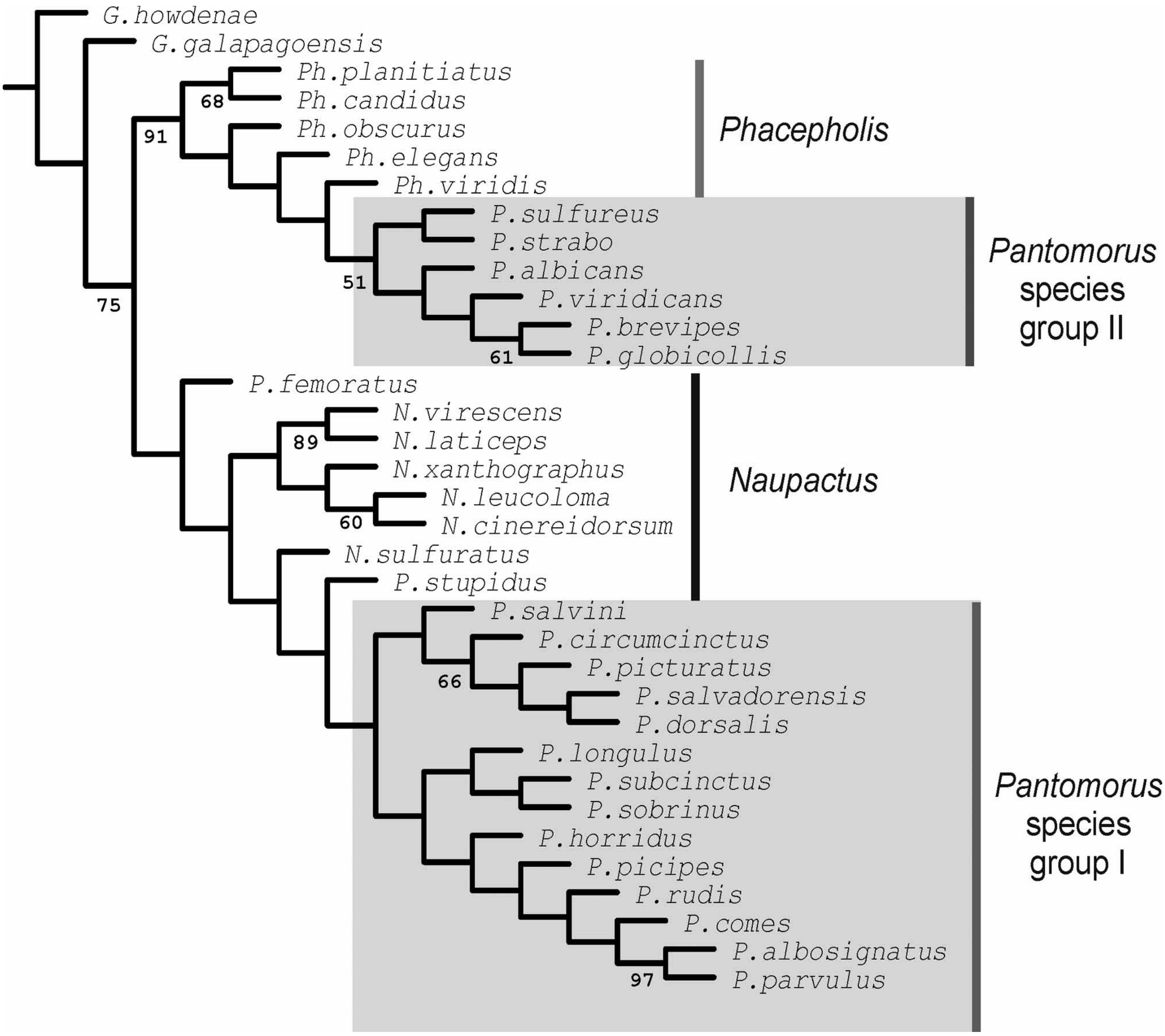


FIGURE 2. Most parsimonious combined tree under equal weights, with 17 morphological characters coded as additive. Bootstrap values over 50% below the corresponding branches.

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. sulfureus* 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. brevipes* 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).

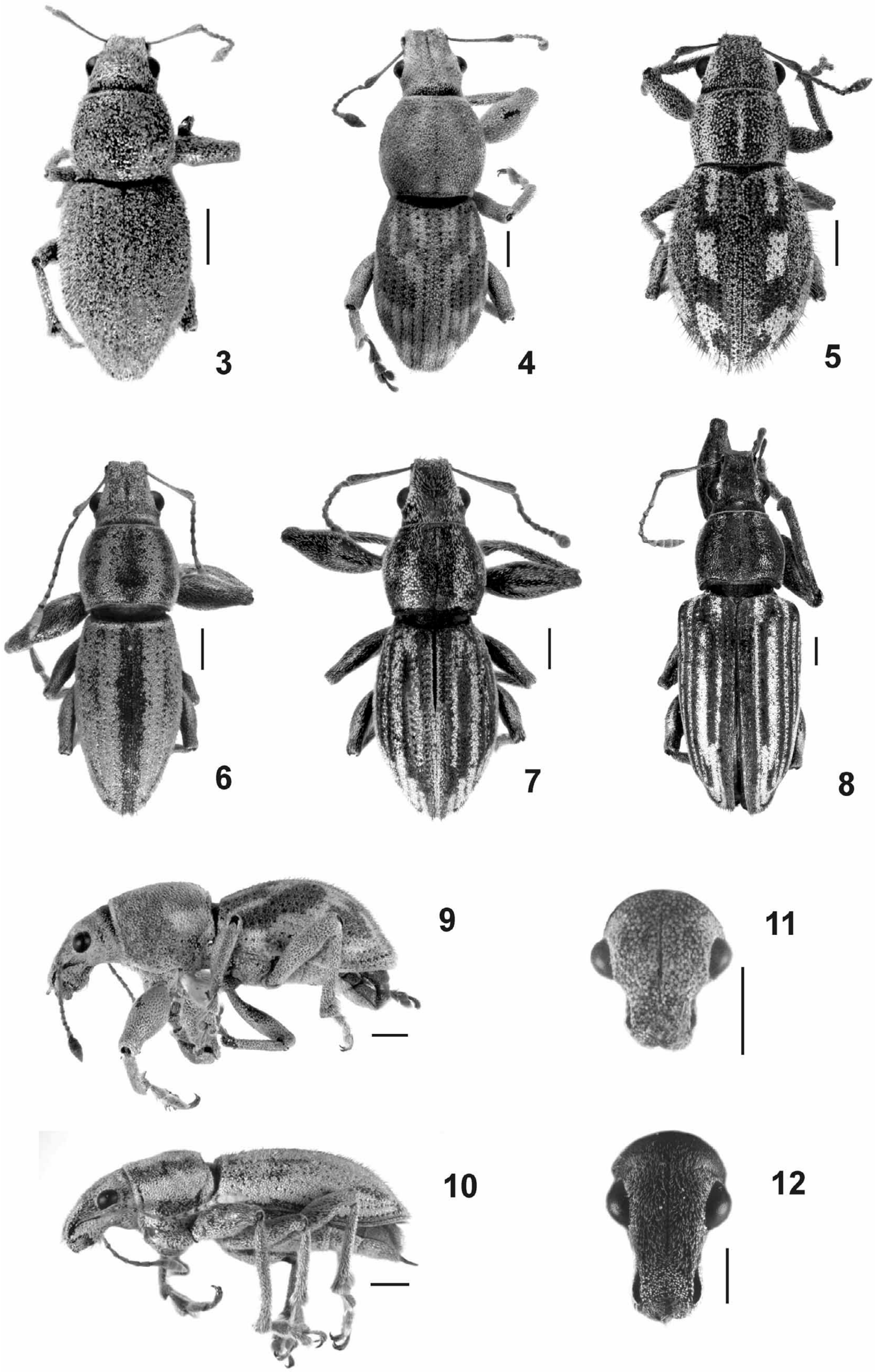
2. Non-additive coding scheme

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 *Phacepholis* 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).

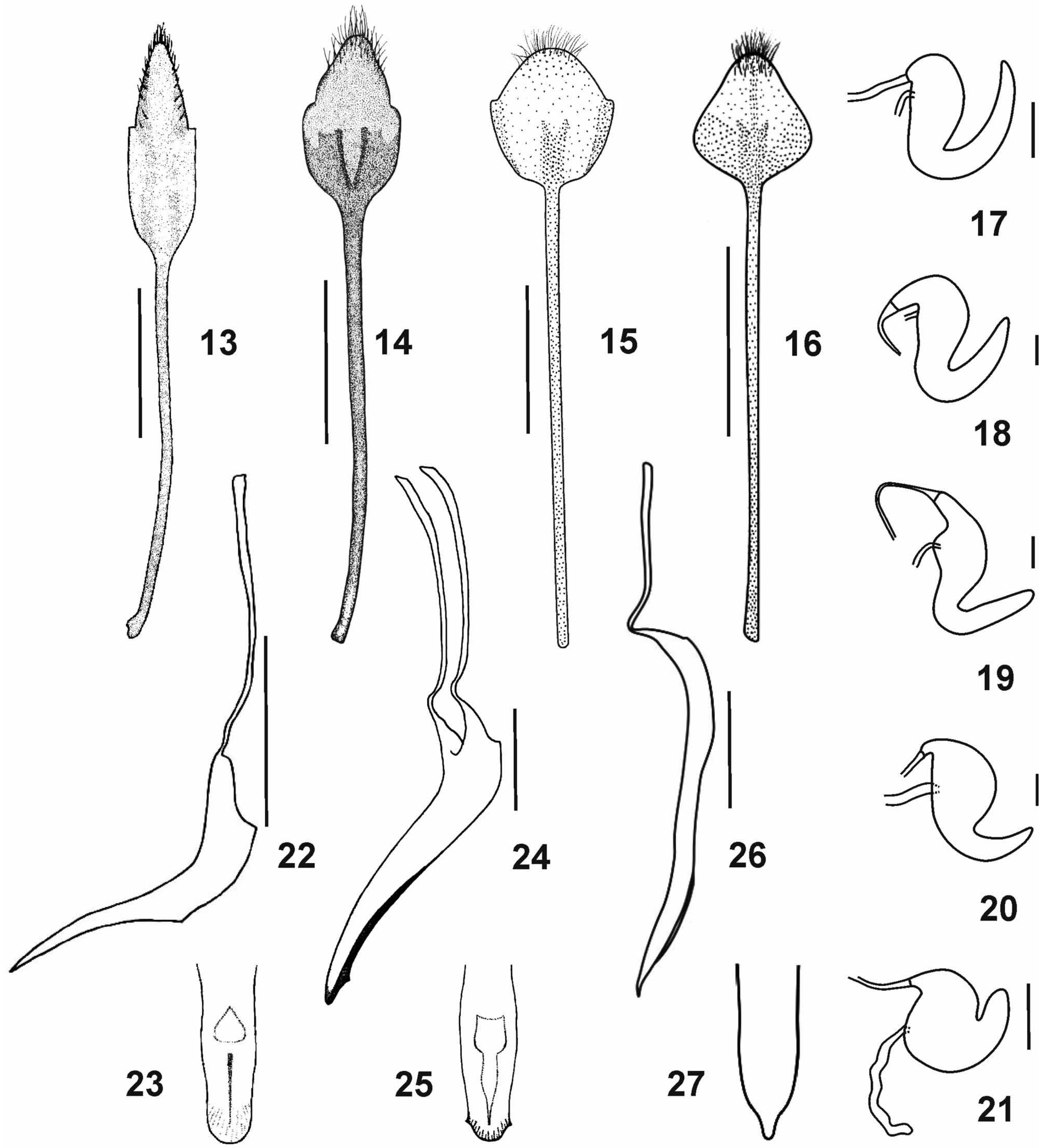
Combined phylogenetic analyses

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 *Phacepholis* 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%), *Phacepholis* 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 *Phacepholis 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-Naupactus* complex in North and Central America. 3–8, Habitus, dorsal views: 3, *Phacepholis elegans* Horn; 4, *Pantomorus globicollis* (Pascoe); 5, *P. albosignatus* Boheman; 6, *P. picturatus* Sharp; 7, *P. stupidus* (Boheman); 8, *Naupactus 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, *Phacepholis elegans* Horn; 14, *Naupactus xanthographus* (Germar); 15, *N. sulfuratus* Champion; 16, *Pantomorus longulus* Sharp. 17–21, Spermathecae: 17, *N. leucoloma* Boheman; 18, *N. sulfuratus* Champion; 19, *P. picipes* Sharp; 20, *P. globicollis* (Pascoe); 21, *Phacepholis elegans* Horn. 22–27, Male genitalia, medial lobe (lateral view and apex). 22–23, *Ph. candidus* Horn; 24–25, *N. xanthographus* (Germar); 26–27, *P. circumcinctus* Sharp. Scales: 1 mm.

Discussion

Phylogenetics. The results of our phylogenetic analyses demonstrate that *Galapaganus galapagoensis*, a species originally described in *Pantomorus* (see Lanteri, 1992), is consistently placed outside this genus as it does not share the synapomorphies of the group including *Pantomorus*, *Naupactus* and *Phacepholis*. *Galapaganus* 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 *Phacepholis* (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. uniformis*", 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. uniformis*. Detailed studies of population-level and geographic variation of *N. sulfuratus*-*P. stupidus* and *N.virescens*-*P. uniformis*, 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 *Galapaganus galapagoensis*, but when some multistate characters are treated as additive it is either the sister taxon of *Phacepholis* 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 *Phacepholis* and those of the *Pantomorus* group II is recovered in all the cladograms (Figs. 1–2). The similarity between *Phacepholis* and *Pantomorus* group II was noticed by Champion (1911, page 333) who stated that "*P. globicollis*, type of *Athetetes* Pascoe, has the tips of the hind tibiae squamose as in *Phacepholis*, 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 *Phace-*

pholis. Both *Phacepholis* 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.

Phacepholis 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 *Phacepholis*, 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 *Phacepholis* 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. A*ll 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; Scataglini *et al.*, 2005; Rodriguero *et al.*, 2010).

Another stable clade within *Pantomorus* group I includes *P. cincumcinctus*, *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 180º 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. rivulosus*. 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 *Phacepholis 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 *Phacepholis* 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 *Phacepholis* 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 *Phacepholis* are: *P. annectens* Sharp and *P. trituberculatus* Champion. *Pantomorus distans* Sharp, placed by its author in *Pantomorus* group II, is probably not a *Phacepholis,* 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).

Phacepholis 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 *Phacepholis* are apterous, steppe or prairie-adapted, showing subtle sexual dimorphism. *Phacepholis 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 *Phacepholis 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, *Phacepholis* 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 *Phacepholis*, 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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