

Phylogeny of the tribe Naupactini (Coleoptera: Curculionidae) based on morphological characters

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Abstract. Naupactini (Curculionidae: Entiminae) is a primarily Neotropical tribe of broad-nosed weevils with its highest genus and species diversity in South America. Despite several taxonomic contributions published during the last decades, the evolutionary history of Naupactini remains poorly understood. We present the first comprehensive phylogenetic analysis for this tribe based on a data matrix of 100 adult morphological characters scored for 70 species, representing 55 genera of Naupactini (ingroup) and four outgroups belonging to the entimine tribes Otiiorhynchini, Entimini, Eustylini and Tanymecini. According to the most parsimonious tree *Artipus* does not belong to Naupactini; the genera with flat and broad antennae, formerly assigned to other entimine tribes, form a monophyletic group (*Saurops* (*Curiades* (*Aptolemus* (*Platyomus*)))) related to the clade (*Megalostylus* (*Megalostylodes* (*Chamaelops* (*Wagneriella*))); and the genera distributed along the high Andes, Paramos and Puna form a natural group (*Asymmathetes* (*Amphideritus* (*Leschenius* (*Amitrus* (*Obrieniolus* (*Melanocyphus* (*Trichocyphus*))))))), nested within a larger clade that includes *Pantomorus*, *Naupactus* and allied genera. *Atrichonotus*, *Hoplopactus*, *Mimographus* and *Naupactus* are not recovered as monophyletic. In order to address the taxonomic implications of our phylogenetic analysis, we propose the following nomenclatural changes: to transfer *Artipus* from Naupactini to Geonemini, to revalidate the genera *Mimographopsis* (type species *M. viridicans*), and to revalidate the genus *Floresianus* (type species *F. sordidus*). The evolution of selected characters is discussed.

Introduction

Naupactini (Curculionidae: Entiminae) are a primarily Neotropical tribe of broad-nosed weevils with about 500 morphologically diverse species distributed mostly in South America (O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986). Species are 3.5–35 mm long and colour patterns vary widely. Some of them are completely covered with colourful iridescent scales (bluish, greenish or golden), others have dull-coloured scales or setae, and some are subglabrous. Flightlessness and parthenogenesis are frequent in species occurring in sparsely vegetated or treeless areas, such as steppes and high-elevation environments (Lanteri & Normark, 1995; Guzmán *et al.*, 2012; Lanteri *et al.*, 2013b).

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Females of Naupactini usually lay their eggs between adjoining surfaces (e.g. in litter between fallen leaves, in cracks in the soil, and in crevices of tree trunks and calices of fruits), in batches covered by an adhesive substance (Marvaldi, 1999). Their ectophytic larvae live in soil where they feed externally on the roots of their host plants (Marvaldi *et al.*, 2002, 2014; Oberprieler *et al.*, 2014). Although naupactine weevils are polyphagous, the majority of them show at least some preference for certain plant families, especially Fabaceae (Lanteri *et al.*, 2002). Several species are considered agricultural pests in both their native ranges and places where they have been introduced due to human activities (Lanteri *et al.*, 2013a).

Naupactini have been classified in different subfamilies, according to historical changes that have occurred in the higher classification of Curculionidae. In the *Biologia Centrali Americana* (Sharp *et al.*, 1889–1911) the known genera were placed in Otiiorhynchinae, and in various later catalogues and checklists they were placed in either Brachyderinae (Dalla Torre *et al.*, 1936; van Emden, 1944; Blackwelder, 1947; O'Brien

& Wibmer, 1982) or in Polydrusinae (Wibmer & O'Brien, 1986). In the most recent generic catalogue (Alonso-Zarazaga & Lyal, 1999) and the most comprehensive treatment of the Curculionoidea (Marvaldi *et al.*, 2014) Naupactini are considered as a separate tribe of Entiminae.

Most genera of Naupactini were described in the work of Schoenherr (1833, 1840). Lacordaire (1863) classified the genera of this tribe into two main groups, 'Cyphides', which included genera morphologically similar to *Cyphus* Germar (current junior synonym of *Cyrtomon* Schoenherr) (Fig. 1A–F), and 'Naupactides', which included *Naupactus* Dejean and its allies (Fig. 2A–F). Within 'Naupactides' he placed some genera that are now classified in other tribes of Entiminae, e.g. *Anypotactus* Schoenherr in Anypotactini, *Polydrusus* Germar in Polydrusini, and *Sitona* Germar in Sitonini. Within 'Cyphides', there were also some genera that are now assigned to Eustyliini and Geonemini, e.g. *Compsus* Schoenherr, *Exophthalmus* Schoenherr, *Lachnopus* Schoenherr and *Oxyderces* Schoenherr.

Naupactini from Central America were classified in two main groups, the 'Otiiorhynchinae apterous', Epicerina group (genus *Pantomorus* Schoenherr) (Sharp, 1891) and the 'Otiiorhynchinae alatae', Cyphina group (all winged Naupactini) (Champion, 1911). *Platyomus* Sahlberg (Fig. 3A) and *Artipus* Sahlberg were included in the Platyomina group of the 'Otiiorhynchinae alatae', along with *Compsus*, *Eustylus* Schoenherr and other genera currently classified in Eustyliini (Champion, 1911).

The taxonomic works of later authors (Kuschel, 1945, 1949, 1950; Hustache, 1947; Voss, 1954; Bordón, 1991, 1997) contributed to knowledge the diversity of the tribe Naupactini in the Neotropics, and the revisions and phylogenetic analyses published by other specialists have shed light on the relationships of several Neotropical genera and species (Lanteri, 1990a, 1990d, 1992, 1995; Lanteri & O'Brien, 1990; Lanteri & Morrone, 1991, 1995; Lanteri & Díaz, 1994; Normark & Lanteri, 1998; Sequeira *et al.*, 2000, 2008a, 2008b; Scatagliini *et al.*, 2005; del Río *et al.*, 2006, 2012; Rosas–Echeverría *et al.*, 2011a; Lanteri & del Río, 2016). Nevertheless, several problems still remain unresolved. For example, *Pantomorus* sensu lato and *Naupactus* are probably not monophyletic (see Scatagliini *et al.*, 2005; Rosas–Echeverría *et al.*, 2011a); the inclusion of *Artipus* within Naupactini is doubtful (Franz, 2012); and *Platyomus*, *Curiades* Pascoe, *Mionarthrus* Kuschel, *Aptolemus* Schoenherr and *Saurops* Kuschel were transferred from Phyllobiini or Eustyliini to Naupactini without an accompanying analysis to support these changes (Kuschel in Wibmer & O'Brien, 1986).

At present, Naupactini include 67 genera (Alonso-Zarazaga & Lyal, 1999; Lanteri & del Río, 2006a; del Río & Lanteri, 2007a, 2011a; del Río *et al.*, 2012), and while most of them occur in the Neotropical region, one extinct fossil genus (*Protonaupactus* Zherikin) from the Oligocene Baltic Amber and 11 extant genera are distributed elsewhere (Holarctic, Nearctic, African, Australian and Subantarctic regions). The most diverse genus of the tribe is *Naupactus* Dejean, with c. 200 described species occurring in South America (Wibmer & O'Brien, 1986) and five Central American species (O'Brien & Wibmer, 1982), although this species number is probably much higher.

Here we present the first comprehensive phylogenetic analysis of the tribe Naupactini to reconstruct a genus-level phylogeny. We will address the following major questions: (i) does the Caribbean genus *Artipus* belong to the tribe Naupactini; (ii) what are the main groups of genera of this tribe; (iii) how do the genera with flat and broad antennae relate to other Naupactini; and (iv) is the so-called *Pantomorus*–*Naupactus* complex monophyletic; and (v) do the genera from the high Andes, Paramos and Puna form a monophyletic group? How do they relate with other Naupactini?

Material and methods

Selection of terminal taxa

The Neotropical genera treated herein are listed in Alonso-Zarazaga & Lyal (1999), except those whose circumscription was modified after 1999, such as *Cyphopsis* Roelofs and *Stenocyphus* Marshall (Lanteri & del Río, 2006a; del Río & Lanteri, 2013), and the genera that were subsequently described, including *Thoraconaupactus* del Río & Lanteri, *Obrieniolus* del Río, and *Leschenius* del Río (del Río & Lanteri, 2007a, 2011a; del Río *et al.*, 2012). The name *Lanterius micaceus* (Hustache) **comb.n.** is used in reference to the nomenclatural actions taken by Alonso-Zarazaga & Lyal (1999) with respect to *Mimographus* Schoenherr and *Lanterius* Alonso-Zarazaga. The Nearctic genus *Glaphyrometopus* Pierce and the South American genera *Mionarthrus* Kuschel (central Chile) and *Parasynonychus* Voss (Ecuador) (O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986) were not included in this study due to insufficient available material. The Holarctic genus *Mesagroicus* Schoenherr (Alonso-Zarazaga & Lyal, 1999), was excluded from the analysis because it does not show the typical larval characters of Naupactini instead suggest a close relationship with the Palaearctic genus *Psallidium* Herbst (Entiminae, Psallidiini) (A.E. Marvaldi, unpublished data). Naupactini occurring outside of the New World were also excluded from our analysis due to the lack of sufficient material.

An exemplar approach (Prendini, 2001) was applied in our cladistic analysis. In most cases we used the type species of each genus, except when material was not available. For genera in which different species groups have been recognized or subjective synonyms have been established, we included more than one species, e.g. *Atrichonotus* Buchanan (Lanteri & O'Brien, 1990), *Cyphopsis* (Lanteri & del Río, 2006a), *Cyrtomon* (Lanteri, 1990c), *Enoplopactus* Heller (Lanteri, 1990d), *Ericydeus* Pascoe (Lanteri, 1995), *Galapaganus* Lanteri (Lanteri, 1992, 2004), *Hoplopactus* Chevrolat, *Mimographus* Schoenherr, *Naupactus* (Lanteri & Marvaldi, 1995), *Platyomus*, *Priocyphus* Hustache (Lanteri, 1990b), *Stenocyphus* (del Río & Lanteri, 2013) and *Thoracocyphus* Emden (Lanteri & del Río, 2004).

The ingroup comprises 70 species representing 55 genera of Naupactini and the outgroup comprises four other entimine species: *Otiiorhynchus sulcatus* (Fabricius) (Otiiorhynchini) (Fig. 3C), *Polyteles stevenii* (Schoenherr) (Entimini) (Fig. 3E), *Compsus argyreus* (Linnaeus) (Eustyliini) and *Hadromeropsis*

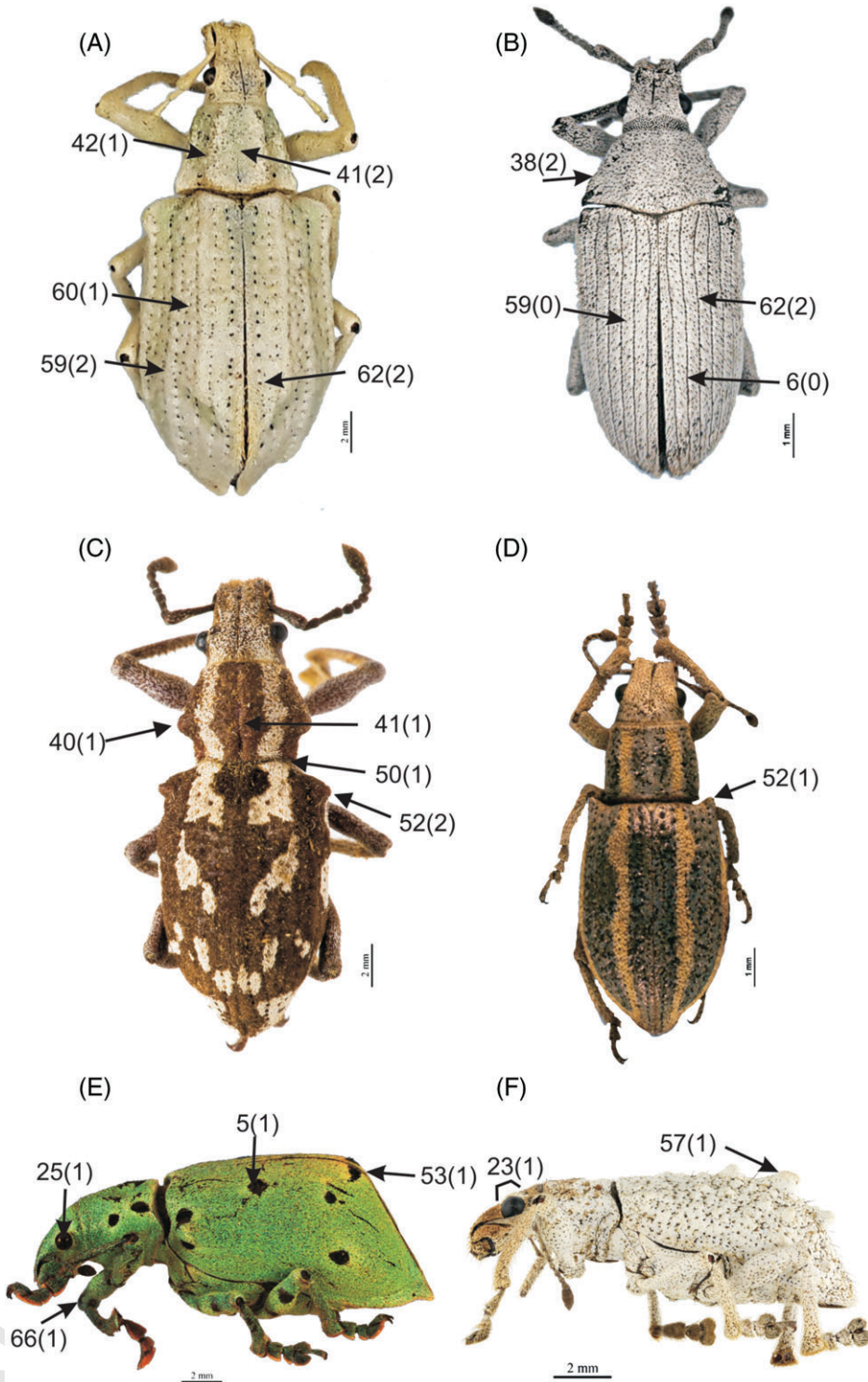


Fig. 1. Representative species of genera of Naupactini. Habitus, dorsal and lateral views. (A) *Cyrtomon gibber*; (B) *Megalostylus albicans*; (C) *Thoracocyphus denticollis*; (D) *Enoplopactus lizeri*; (E) *Ericydeus sedecimpunctatus*; (F) *Stenocyphus tuberculatus*. Numbers and numbers between parentheses refer to phylogenetic characters and their states, respectively (see Table S2).

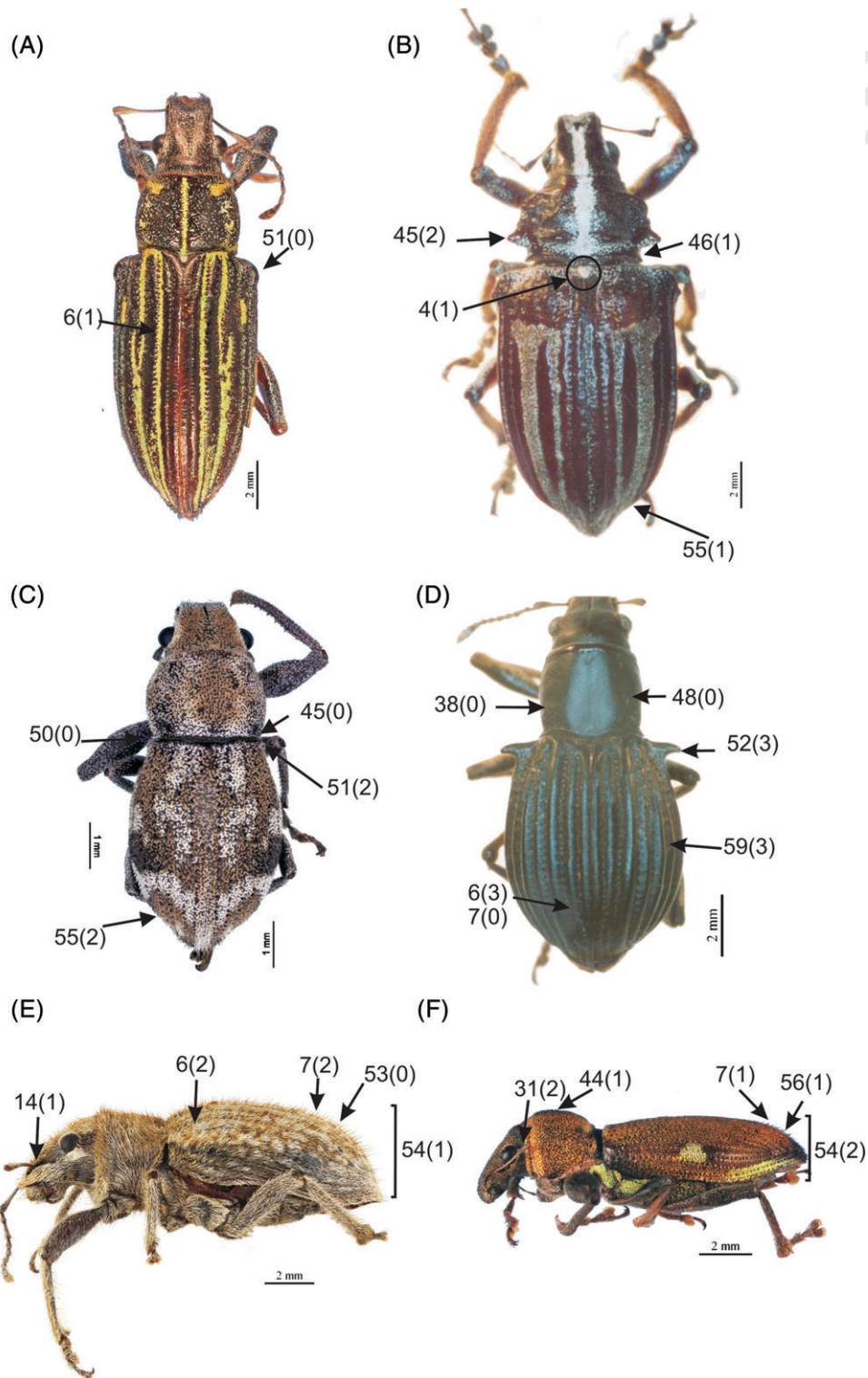


Fig. 2. Representative species of genera of Naupactini. Habitus, dorsal and lateral views. (A) *Naupactus rivulosus*; (B) *Thoraconaupactus vaninii*; (C) *Parapantomorus fluctuosus*; (D) *Melanocyphus bispinus*; (E) *Trichonaupactus densius*; (F) *Alceis longimanus*. Numbers and numbers between parentheses refer to phylogenetic characters and their states, respectively (see Table S2).

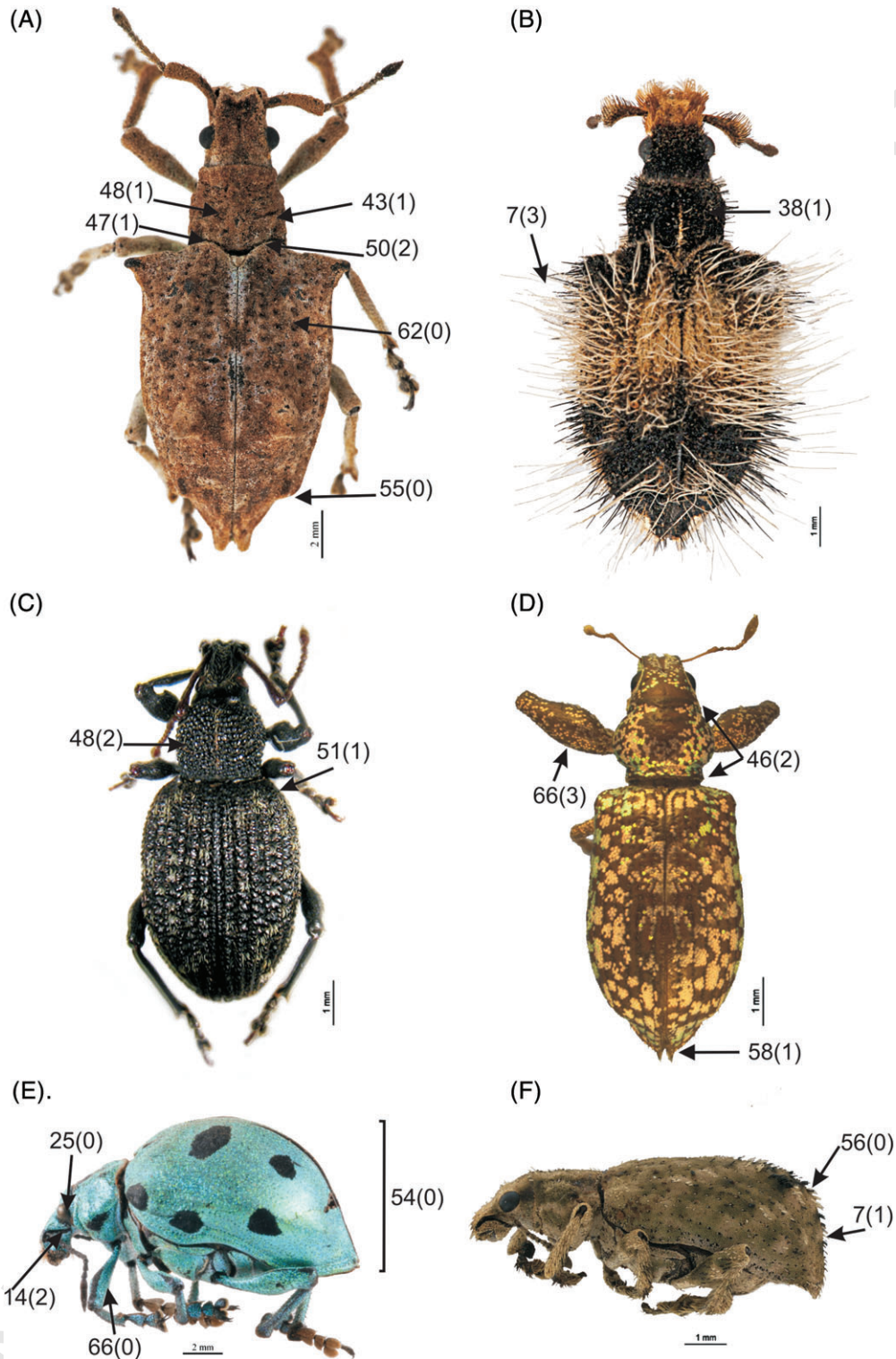


Fig. 3. Representative species of genera of Naupactini and of Entiminae used as outgroups. Habitus, dorsal and lateral views. (A) *Platylomus nodipennis* (Naupactini); (B) *Curiades boisduvali* (Naupactini); (C) *Otiorynchus sulcatus* (Otiorynchini); (D) *Hadromeropsis superbus* (Tanymecini); (E) *Polyteles stevenii* (Entimini); (F) *Hadropus albiceris* (Naupactini). Numbers and numbers between parentheses refer to phylogenetic characters and their states, respectively (see Table S2).

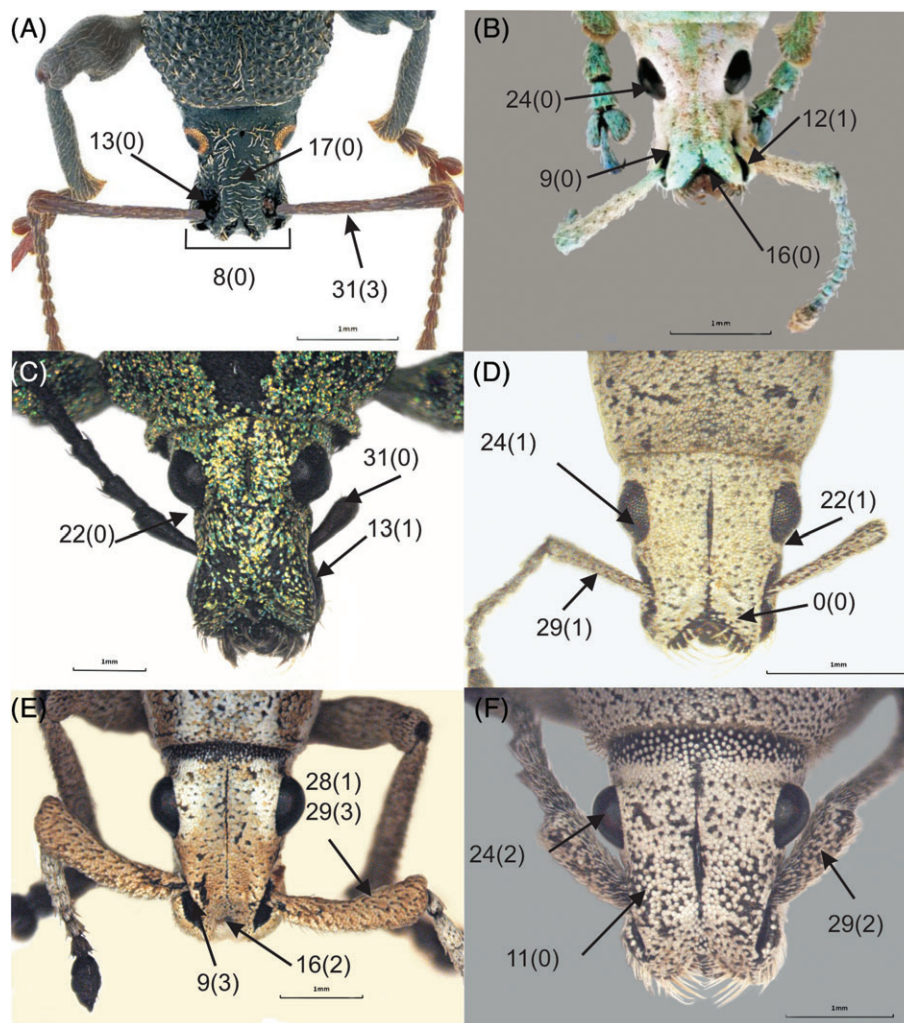


Fig. 4. Representative species of genera of Naupactini and of Entiminae used as outgroups. Heads, frontal views. (A) *Otiorhynchus sulcatus*; (B) *Compsus argyreus*; (C) *Polyteles stevenii*; (D) *Artipus floridanus*; (E) *Platymus elegantulus*; (F) *Megalostyloides hirsutus*. Numbers and numbers between parentheses refer to phylogenetic characters and their states, respectively (see Table S2).

superbus (Heller) (Tanymecini) (Fig. 3D). All of them occur in the Neotropics except for *Otiorhynchus*, which is Palearctic but includes some species introduced to North and South America probably in as ballast on trading ships which was dumped in harbours (del Río *et al.*, 2010).

A synoptic set of all the taxa studied herein is deposited at the Museo de la Plata. A list of ingroup taxa, with complete species names (including authors), geographic distributions (including countries and provinces or states) and biogeographic areas is given in Table S1.

Selection of morphological characters

This study was based on 100 discrete characters from the morphology of the adults (Table S2), including 78 from external

morphology (Figs 1–5), 17 from female genitalia (Figs 6–8) and five from male genitalia (Fig. 9). Characters of female and male genitalia were analysed using standard entomological techniques (see Lanteri & O'Brien, 1990). Characters of larvae proved to be valuable to resolve phylogenetic relationships of Entiminae at the tribal level (Marvaldi, 1998), but they were not used in this analysis because information on larval morphology is unavailable for many genera of Naupactini (Marvaldi & Loiacono, 1994). Observations of externally visible and dissected structures were made with a Nikon SMZ100 stereomicroscope; line drawings were done with a camera lucida attached to this scope, and photographs were taken with a Micrometrics 391CU 3.2m digital camera attached to a stereomicroscope with the same characteristics as the Nikon. The morphological terminology used is in accordance with that of Marvaldi *et al.* (2014) and Vaurie (1963) for the nasal plate.

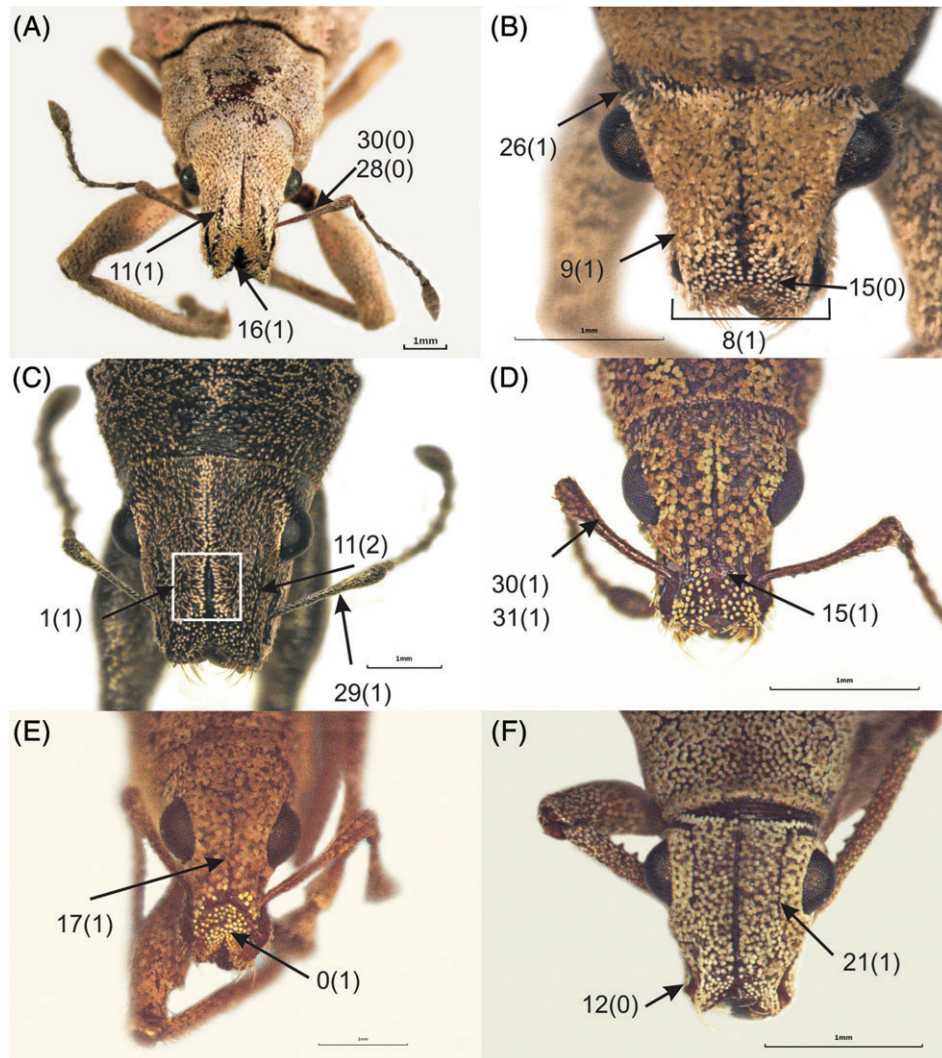


Fig. 5. Representative species of genera of Naupactini. Heads, frontal views. (A) *Stenocyphus bituberosus*; (B) *Litostylus diadema*; (C) *Teratopactus nodicollis*; (D) *Brachystylodes pilosus*; (E) *Hoplopactus pavidus*; (F) *Plectrophoroides lutra*. Numbers and numbers between parentheses refer to phylogenetic characters and their states, respectively (see Table S2).

Most critical characters have been illustrated with photographs and line drawings in order to facilitate identification of different character states and the discussion of their evolution (Figs 1–9). Several illustrations exemplify multiple character states, which are highlighted with an arrow, with an indication of character numbers and applicable states given in parentheses. Only one example of each character state is highlighted.

The biogeographical schemes used for describing the distributions of Naupactini genera agree with those of previous biogeographical analyses by Rosas–Echeverría *et al.* (2011b) and del Río *et al.* (2015), except that we consider the Espinal (*sensu* Cabrera & Willink, 1973) as separate from Chacoan and Pampean biogeographic provinces. The Espinal is a xerophyllous forest dominated by *Prosopis* that forms an arch between the two latter biogeographic provinces, in Argentina.

Phylogenetic analysis

A data matrix of 74 terminal taxa (70 for the ingroup plus four outgroups) and 100 morphological characters was compiled for this cladistic analysis (Table S3). Character states of species for which male genitalia could not be examined (because of insufficient material or because males are unknown for these species) were scored with ‘?’ and treated as missing data (Maddison, 1993).

All characters (either binary or multistate) were treated as nonadditive and were primarily analysed under equal weights. As more than one most parsimonious tree was obtained, we calculated a strict consensus tree among them (Goloboff & Farris, 2001). Moreover, the matrix was analysed under the implied weighting procedure (Goloboff, 1993) implemented

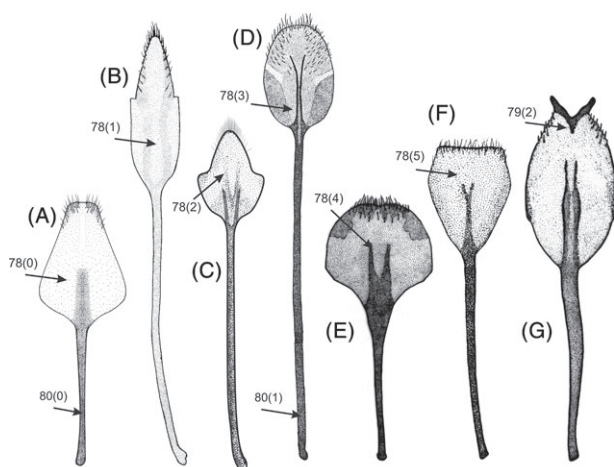


Fig. 6. Female terminalia, sternite VIII. (A) *Cyphopsis laticeps*; (B) *Phacepholis elegans*; (C) *Stenocyphus tuberculatus*; (D) *Naupactus rivulosus*; (E) *Lamprocypophopsis viridinitens*; (F) *Eurymetopus fallax*; (G) *Trichonaupactus densius*. Numbers and numbers between parentheses refer to phylogenetic characters and their states, respectively (see Table S2).

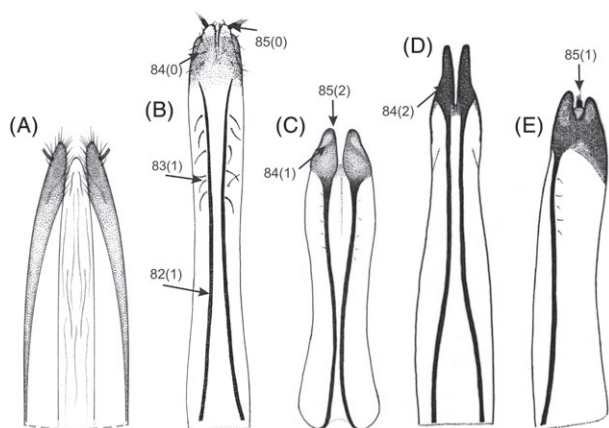


Fig. 7. Female terminalia, ovipositors of Naupactini, ventral and lateral views. (A) *Cyphopsis clathrata*; (B) *Acyphus funicularis*; (C) *Eurymetopus fallax*; (D) *Teratopactus nodicollis*; (E) *Priocyphus bosqi*. Numbers and numbers between parentheses refer to phylogenetic characters and their states, respectively (see Table S2).

in TNT v1.5 (Goloboff & Catalano, 2016), applying different values of the concavity constant (k) (Goloboff *et al.*, 2008a). Weighting against homoplasy improves phylogenetic analysis of morphological datasets (Goloboff *et al.*, 2008b). In this method, characters are weighted during tree searches and the weights applied to each character are summed to determine the fit, such that the cladogram with maximum total character fit is chosen as the most parsimonious cladogram (MPC) (da Silva *et al.*, 2015).

Searches for the most parsimonious trees (MPTs) were conducted using the heuristic 'traditional search' algorithm of TNT (Goloboff *et al.*, 2008a), with 700 random addition sequences, tree bisection and reconnection (TBR) branch swapping,

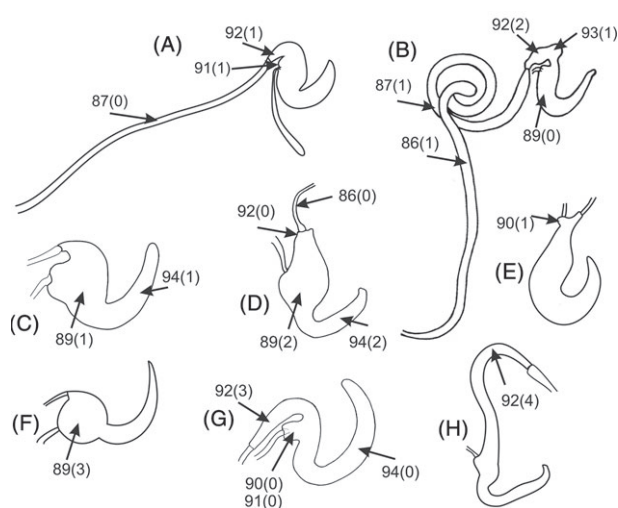


Fig. 8. Spermathecae of Naupactini. (A) *Obrieniolus robustus*; (B) *Aramigus tessellatus*; (C) *Briarius augustus*; (D) *Enoplopactus brunneomaculatus*; (E) *Artipus floridanus*; (F) *Megalostylodes hirsutus*; (G) *Acyphus renggeri*; (H) *Cyphopsis laticeps*. Numbers and numbers between parentheses refer to phylogenetic characters and their states, respectively (see Table S2).

holding 30 trees during each replication. To evaluate branch support we applied symmetric resampling (SR) (Goloboff *et al.*, 2003) and relative Bremer support (BS) (Goloboff & Farris, 2001). Support values over 50% were mapped onto (BS) and below (SR) the internal nodes of the tree. For the MP trees under equal weights we provide the total length (L), the consistency index (CI) (Kluge & Farris, 1969) and the retention index (RI) (Farris, 1989), calculated excluding the uninformative characters. For the selected tree under implied weights we give the FIT value. Characters were optimized under different optimization schemes (Agnarsson & Miller, 2008) using WINCLADA version 1.00.08 (Nixon, 2002).

Results and discussion

The heuristic search for MP trees analysed under equal weights yielded seven equally parsimonious trees ($L=800$ steps, $CI=0.21$, $RI=0.54$). The strict consensus of the seven trees (Figure S1) and the tree obtained under implied weights with K45 (Fig. 10) shows the following phylogenetic sequence: *Polyteles stevenii* (*Otiorynchus sulcatus* (*Compsus argyreus* (*Hadromeropsis superbus* (*Artipus floridanus*, Naupactini)))). Within Naupactini we recovered three main clades: *Neoericydeus graciosus* to *Platyomus nodipennis* (clade I), *Acyphus renggeri* to *Priocyphus kuscheli* (clade II), and *Litostylus diadema* to *Trichocyphus formosus* (clade III). Within clade III, *L. diadema* is the sister taxon of the remaining species, which are grouped in three main subclades, subclade A (*Plectrophoroides lutra* to *Moropactus perfidus*), subclade B (*Lanterius micaceus* to *Thoraconaupactus vaninii*) and subclade C (*Hoplopactus lateralis* to *Trichocyphus formosus*) (Fig. 10). In the consensus tree, subclades B and C form a large polytomy, because

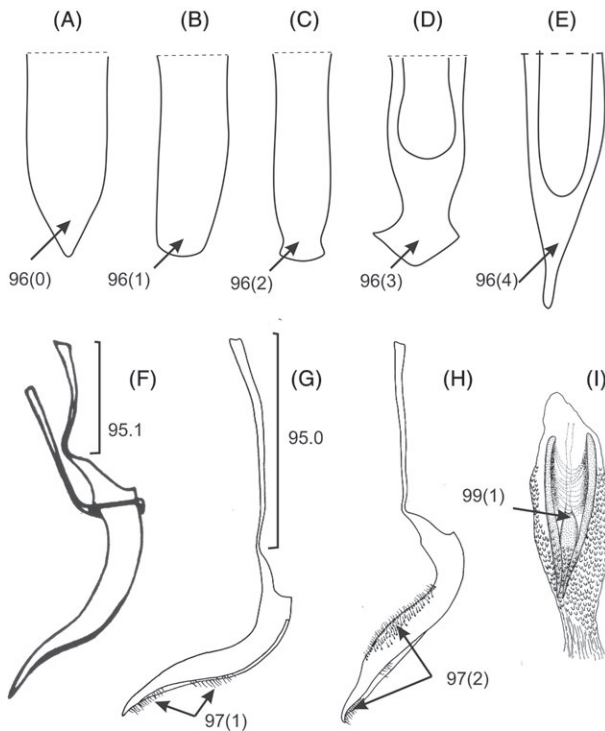


Fig. 9. Male genitalia of Naupactini. Apex of median lobe, ventral views. (A) *Acyphus renggeri*; (B) *Galapaganus howdenae*; (C) *Eriocydeus hancocki*; (D) *Cyrtomon gibber*; (E) *Polyteles stevenii*. Median lobe, lateral views. (F) *Eriocydeus hancocki*; (G) *Galapaganus galapagoensis*; (H) *Galapaganus howdenae*. Endophallus and internal pieces. (I) *Cyrtomon* type. Numbers and numbers between parentheses refer to phylogenetic characters and their states, respectively (see Table S2).

the relationships among some of their members are not fully resolved (Figure S1).

Platyomus and allied genera with flat and broad antennae (*Platyomus* group) are nested within clade I and the genera from the high Andes, Paramos and Puna (*Asymmathetes pascoei* to *Trichocyphus formosus*), herein referred to as the Andean group, are nested within clade III (Fig. 10).

Support values are high for the clade *Hadromeropsis* (*Artipus* + *Naupactini*) but low and particularly wanting for the deeper divergences of the tribe Naupactini. The genera and groups of genera supported by the highest support values (SR and BS) are as follows (Fig. 10): *Stenocyphus*, *Eriocydeus*, *Trichaptus* + *Thoracocyphus*, *Enoplopactus*, clade *Megalostylus* to *Platyomus*, clade *Saurops* to *Platyomus*, *Acyphus* + *Cyphopsis*, *Cyphopsis*, clade *Lamprocyphopsis* to *Priocyphus*, *Mimographus* + *Tetragonimus*, *Galapaganus*, *Naupactus* + *Thoraconaupactus*, *Aramigus* + *Naupactus cervinus* and *Atrichonotus taeniatus* + *Eurymetopus*.

The genera *Mimographus*, *Hoplopactus* and *Naupactus* are not recovered as monophyletic, and *Atrichonotus* is paraphyletic with respect to *Eurymetopus*.

The single tree obtained under implied weighting with concavity constant K45 scores FIT value of 11.32, and was chosen to illustrate the character state optimizations (Figs 11, 12).

Phylogenetic position of Naupactini

Naupactini are recognized by a particular combination of characters including: (i) the presence of a mandibular scar; (ii) adelognathous mouthparts (prementum completely covering maxillae); (iii) median longitudinal groove along dorsal side of rostrum and frons; (iv) rostrum not expanded at apex (frons usually wider than rostrum); (v) scrobes incompletely visible from above, descending and usually passing below eyes; (vi) eyes usually laterally placed; (vii) pronotum without postocular lobes and lacking vibrissae; and (viii) tarsi with free claws and lacking auxiliary claws (van Emden, 1944). When analysed in a phylogenetic context, none of these characters constitute a synapomorphy of Naupactini, e.g. mandibular scar and adelognathous mouthparts are shared with most Entiminae and several tribes outside Naupactini lack postocular lobes and vibrissae (Marvaldi *et al.*, 2014). According to our tree, the median groove along the rostrum (17–1) and rounded and antero-posteriorly oriented eyes (25–1) are putative synapomorphies for the clade comprising Eustylini (Tanymecini (*Artipus*, Naupactini)), and the rostrum not expanded at the apex and equally wide to narrower than the frons (8–1), scrobes variously curved downwards towards ventral margin of the eye (14–1), and the eyes entirely lateral (24–2) are probably synapomorphies for the clade that includes Tanymecini, *Artipus* and Naupactini.

The definition of Naupactini by van Emden (1944) is herein complemented with the following apparent synapomorphies resulting from our cladistic analysis: (i) nasal plate narrow, V-shaped, descending and not separated from epistome by a carina or elevation (16–1); (ii) prementum without setae (20–0); (iii) funicular article 2 more than 2× longer than article 1 (33–1); funicular article 7 longer than wide (35–1); sternite VIII of females subrhomboidal (78–2); and temons about as long as median lobe (95–0). Moreover, within Naupactini the occipital sutures are usually reduced to indistinct (18–2), the distal comb of the hind tibiae is extended in a dorsal comb (except in *Eurymetopus*) and the ovipositor is a membranous tube with baculi (82–1), usually longer than half the abdomen (81–1).

Additional information suggests that Naupactini are monophyletic: (i) a molecular analysis including more than 100 species representing ten tribes of Entiminae, based on five molecular markers (mitochondrial and nuclear) recovers Naupactini as a monophyletic group with strong support values (Pereyra *et al.*, in prep.); and (ii) the evidence of larval characters compared with those of other tribes of Entiminae, e.g. head retracted into the thorax, bifurcated labral rods, mandibular setae transverse with respect to the scrobe, abdominal segment VII with a postdorsal setae, and abdominal segment IX with one additional dorsal seta (A.E. Marvaldi, unpublished data).

Phylogenetic position of Artipus

The Nearctic genus *Artipus*, currently classified in Naupactini (O'Brien & Wibmer, 1982; Alonso-Zarazaga & Lyal, 1999) shows several characters that are not recorded for any other genus of this tribe, e.g. nasal plate large, triangular and not

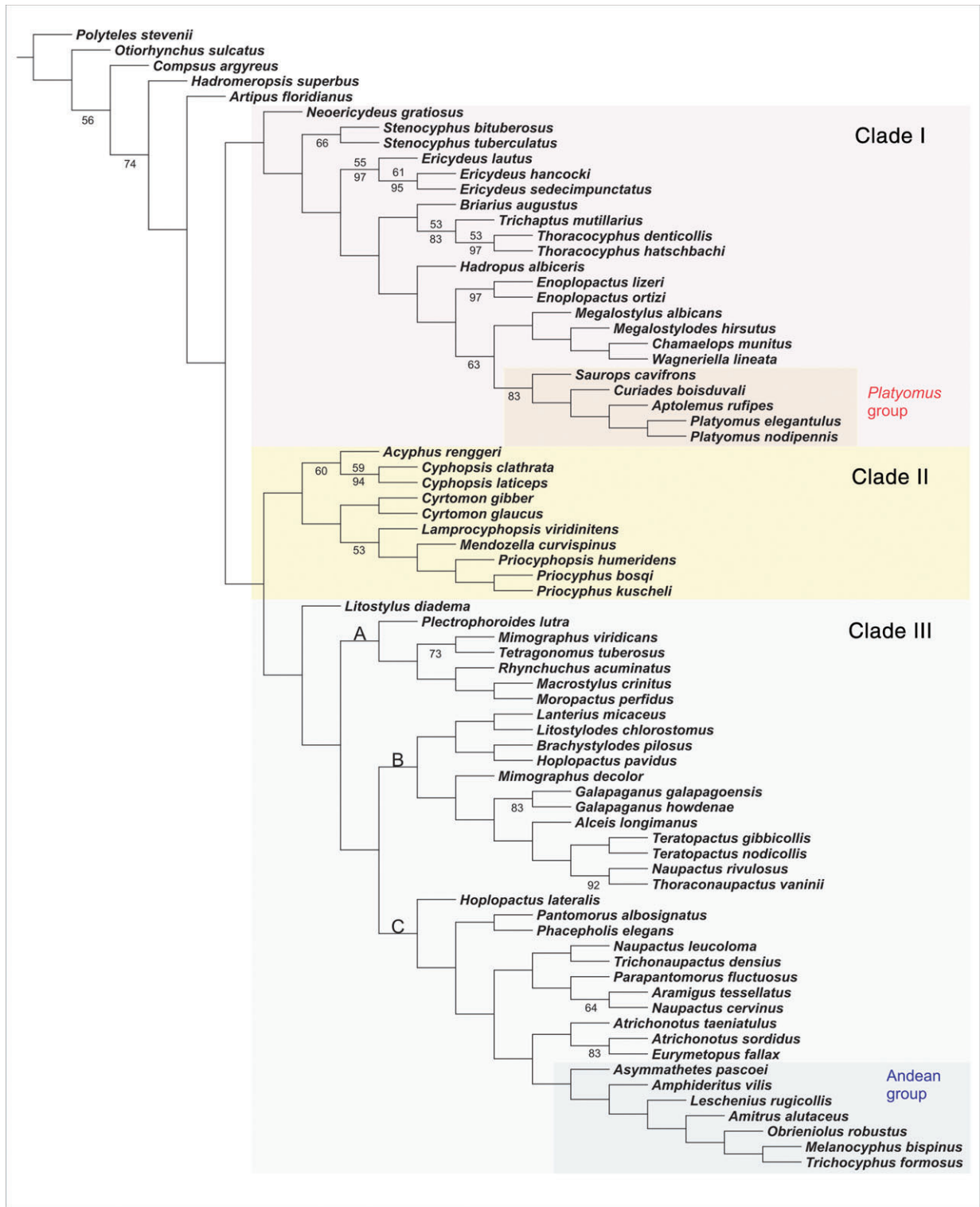
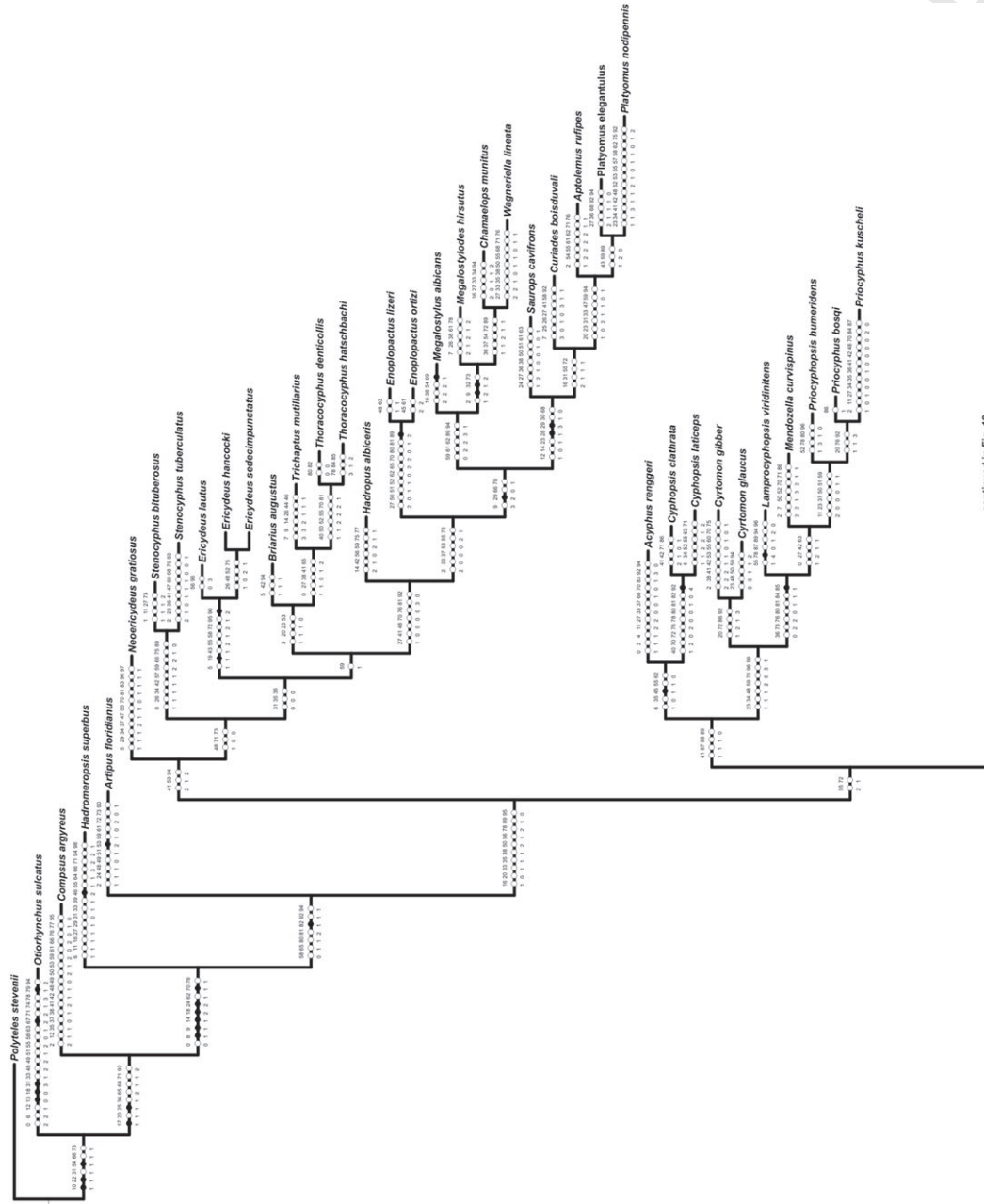


Fig. 10. Most parsimonious tree for 70 taxa of Naupactini and four outgroups, obtained with implied weights ($K = 45$). Values of relative Bremer support (BS) and symmetric resampling (SR) are indicated on and below branches, respectively. The main clades (I, II and III) and the Platyomus and Andean groups are highlighted. Subclades of clade III are indicated with capital letters (A–C) on branches.



continued in Fig. 12

Fig. 11. Partial tree from Fig. 10 (Clades I and II), showing character optimization. Black circles indicate nonhomoplasious character state transformations, whereas the white circles indicate homoplasious character state transformations. The numbers on and below each circle correspond to character and state codes, respectively. Preferred state optimizations are as follows: ACCTAN optimization, characters 11, 23, 29, 31, 48, 52, 55, 59, 61, 72, 73, 89, 96 and 97; DELTRAN optimization, characters 2, 4, 6, 7, 12, 16, 27, 33, 34, 36, 37, 38, 44, 50, 53, 54, 66, 70, 71, 76, 81, 92 and 94. The tree continues in Fig. 12.

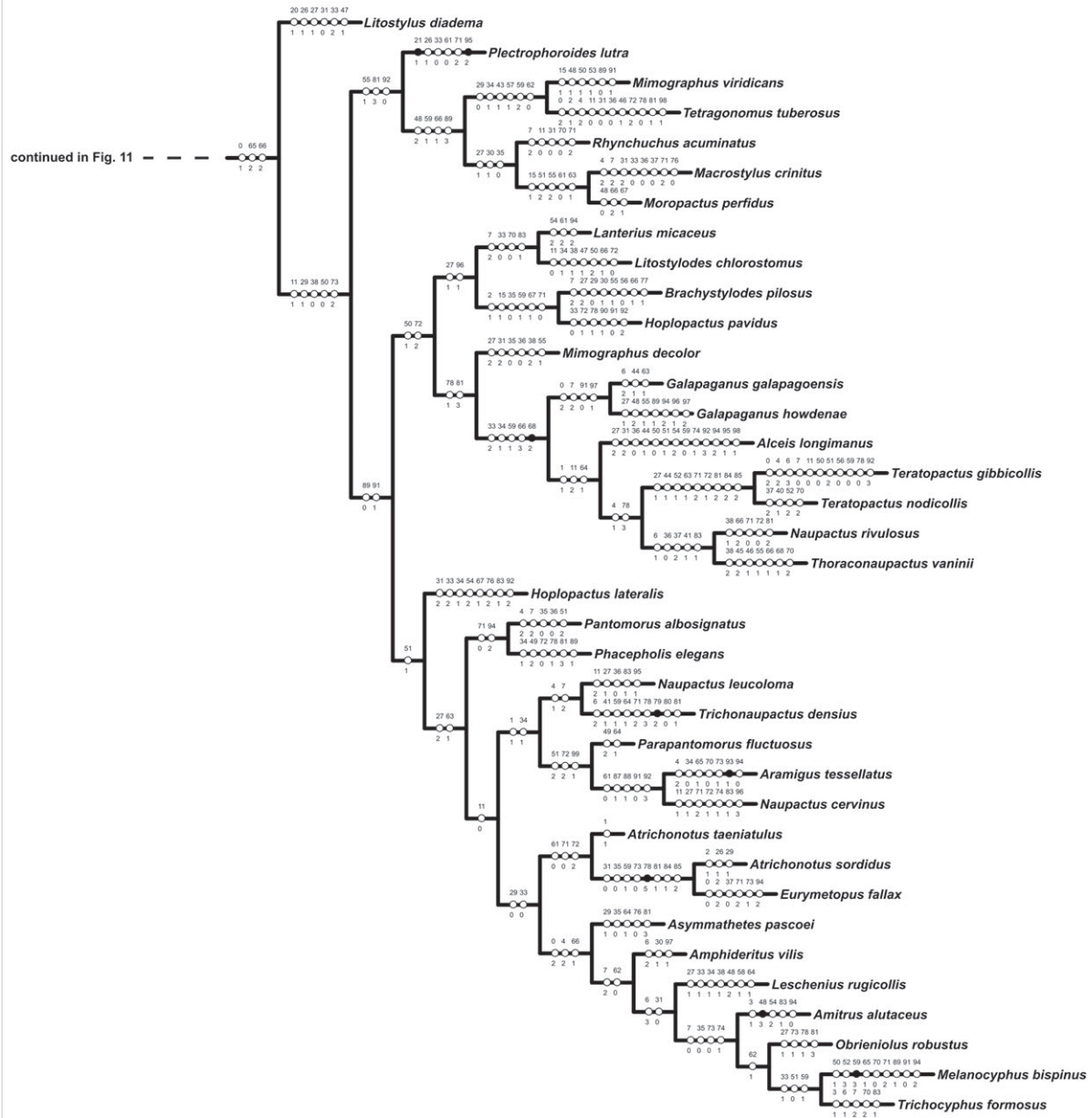


Fig. 12. Partial tree from Fig. 10 (clade III), showing character optimization. Black circles indicate nonhomoplasious character state transformations, whereas the white circles indicate homoplasious character state transformations. The numbers on and below each circle correspond to character and state codes, respectively. Preferred state optimizations are as follows: ACCTRAN optimization, characters 11, 23, 29, 31, 48, 52, 55, 59, 61, 72, 73, 89, 96 and 97; DELTRAN optimization, characters 2, 4, 6, 7, 12, 16, 27, 33, 34, 36, 37, 38, 44, 50, 53, 54, 66, 70, 71, 76, 81, 92 and 94.

descending (16–0) and scutellum quadrate to rounded (49–2). Moreover, the rostrum of *Artipus* is more quadrate (less divergent towards apex) than in most genera of Naupactini, and the spermatheca, with the ramus emerging at the proximal extreme of the corpus, close to the collum (90–1) (Fig. 8E), is a character uncommon in the tribe (it was only seen in *Plectrophoroides* and *Hoplopactus pavidus*).

Franz & Girón (2009) suggested that *Artipus* is probably close to the genus *Scelianoma* (Geonemini), and Franz (2012) published a phylogenetic analysis of some genera of the Eustylini + Geonemini clade, based on morphological characters, in which he recovered *Artipus* within the tribe Geonemini. However, no decision on the tribal placement of *Artipus* has been taken yet.

The results of our cladistic analysis demonstrate that *Artipus* is not nested within Naupactini, but it was recovered as the sister taxon of the remaining members of the tribe. Moreover, a molecular analysis that includes genera of several tribes of Entiminae suggests that *Artipus* is part of the Eustylini + Geonemini clade, and it is close to the genus *Apotomoderes* (Pereyra *et al.*, in prep.).

Main groups of Naupactini and generic relationships

The main groups of genera of Naupactini are weakly supported, because characters whose transformations are fully consistent with each other (i.e. objective unique synapomorphies) are very rare, and there is a high number of homoplasies in the postulated phylogeny. This result is typical of groups of recent radiation, such as Naupactini, the phylogenies of which used to lead to a Hennigian bush-type topology (=with several polytomies) (Silva *et al.*, 2016). Under these circumstances we do not consider it appropriate to propose a subtribal classification. The only attempt to classify Naupactini in subtribes was done by Voss (1954) who recognized four subtribes – Naupactina, Canephorotomina, Pantomorina and Plectrophorina – all of them probably artificial and only based on fauna from Peru.

Despite the limitations mentioned above, our results allow us to draw some conclusions about the relationships of certain genera and groups or genera:

Clade I includes 16 genera and it is mainly supported by the following characters (Fig. 11): 41–2 (median impression and groove along the disc of the pronotum) (Fig. 1A) and 53–1 (elytra ascending towards declivity = humped) (Fig. 1E). *Neoericydeus* is the genus closest to the root and differentiates by a particular combination of characters, some of them infrequent within the tribe, e.g., rows of setae along the ovipositor (83–1) (Fig. 7B) and setae around the apex of the aedeagus (97–1) (Fig. 9G). Even though the genus name *Neoericydeus* suggests a possible relationship with *Ericydeus*, this hypothesis was not confirmed by our results.

Stenocyphus is recovered as monophyletic, based on several characters, e.g. pair of longitudinal impressions on sides of the pronotum (42–1) (Fig. 1A), elytra with tubercles on disc and declivity (57–1) (Fig. 1F), and uneven intervals (except suture) of elytra strongly convex (59–2) (Fig. 1A). The taxonomic decision taken by del Río & Lanteri (2013), who transferred *Stenocyphus tuberculatus* (originally described in *Compsus*) from *Neoericydeus* to *Stenocyphus*, is supported by the results of our analysis.

Ericydeus (Fig. 1E) is a monophyletic genus mainly justified by two synapomorphies, ventral side of rostrum with one elongate triangular impression flanked by long, nonfoveate hypostomal-labial sutures (19–1), and aedeagal apex with a typical rounded shape (96–2) (Fig. 9C). Within *Ericydeus* there are two main species groups, one from North and Central America (herein represented by *E. lautus*) and the other from South America, herein represented by *E. hancocki* + *E. sedecimpunctatus* (Lanteri, 1995).

Briarius, *Trichaptus* and *Thoracocyphus* (Fig. 1C) are closely related genera, as was suggested in previous taxonomic revisions (Lanteri & del Río, 2003, 2004, 2005). The relationship among them is mainly justified by the setae on the external face of the prementum (20–1), which have evolved also in *Compsus*, *Hadromeropsis*, *Cyrtomon* and *Priocyphus*. The monophyly of *Thoracocyphus* is mainly supported by the characters 40–1 (lateral tubercles on sides of the pronotum) (Fig. 1C) and 70–2 (rows of denticles on the inner margin of all tibiae). Both characters show parallel evolution in other genera, e.g. *Cyphopsis* and *Teratopactus nodicollis*.

Hadropus, with a single and highly variable species (del Río & Lanteri, 2011b), does not show clear relationships with other members of clade I. The rostrum is less convergent towards the apex and the elytral declivity is more abrupt than in most Naupactini (56–0) (Fig. 3F); ventrite 1 is about as long as ventrite 2 (77–1) and these ventrites show a median impression (75–1). The characters of the ventrites are not unique for *Hadropus* but they are uncommon in Naupactini.

The monophyly of *Enoplopactus* is mainly supported by the synapomorphy 89–2, anphora-shaped spermatheca (Fig. 8D) (Lanteri, 1990d) and the apparent synapomorphies 52–1 (humeri with small anteriorly directed tubercle) (Fig. 1D), 62–0 (elytral striae with large punctures) and 70–2 (all tibiae with rows of denticles on inner margin).

The genera transferred to Naupactini from Phyllobiini and Eustylini by G. Kuschel (Wibmer & O'Brien, 1986) are recovered as a monophyletic group with the following phylogenetic sequence: *Saurops* (*Curiades* (*Aptolemus* (*Platyomus*))). This group, herein called *Platyomus* group, is justified by the presence of antennal scape flat in cross section (28–1), spatulate (29–3) and curved (30–1) (Fig. 4E) and it is probably related to another group of genera with broad but not flat and spatulate antennae: *Megalostylus* (*Megalostylodes* (*Chamaelops* (*Wagneriella*))). The close relationship of both groups is mainly supported by characters 9–3 (dorsolateral margins of rostrum curved and convergent towards apex in both sexes) (Fig. 4E) and 29.2 (antennal scape clavate) (Fig. 4F). The characters of the scape and the rostrum show sexual dimorphism in the clade *Megalostylodes* (*Chamaelops* (*Wagneriella*))). The sister relationship of *Chamaelops* and *Wagneriella* confirms the previous hypothesis by van Emden (1944) and Lanteri (1982).

Clade II includes seven genera and it is mainly justified by the following characters (Fig. 11): 41–1 (disc of pronotum with broad median groove), 87–1 (spermathecal duct curled) and 88–1 (spermathecal duct strongly sclerotized). We recovered two main subclades, one including *Acyphus* plus *Cyphopsis*, and the other including *Cyrtomon* (*Lamprocyphopsis* (*Mendozella* (*Priocyphopsis* (*Priocyphus*))).

Cyphopsis (type species *C. clathrata*) was synonymized with *Miocyphus* Hustache (type species *M. laticeps*) by Lanteri & del Río (2006a). Our results supports this decision, as the two species of *Cyphopsis* form a monophyletic group, mainly justified by synapomorphy 92–4 (spermatheca with long sub-cylindrical collum extended in the same direction of corpus) (Fig. 8H). We also confirm the hypothesis that *Cyphopsis* is probably related to *Acyphus* (Lanteri & del Río, 2006b) and

to *Cyrtomon* and allied genera (Lanteri & del Río, 2016). The relationship of *Acyphus* and *Cyphopsis* is mainly supported by synapomorphy 45–1 (posterolateral angles of the pronotum projected). The clade *Cyrtomon* to *Priocyphus* is mainly justified by two characters of the aedeagus, apex arrow-shaped (96–3) (Fig. 9D) and internal sclerites consisting of a pyriform piece and a pair of lateral struts (99–1) (Fig. 9I). Within this clade, *Cyrtomon* is separated from the group *Lamprocyphopsis* (*Mendozaella* (*Priocyphopsis* (*Priocyphus*))), mainly justified by the synapomorphy 85–1 (styli of the ovipositor present but hidden by distal coxites) (Fig. 7E).

Clade III is the most species diverse group of Naupactini. It includes 30 genera mainly united by the following apparent synapomorphies (Fig. 12): 0–1 (epistome covered with scales smaller, sparser and usually of different colour to those of post-rostrum) (Fig. 5E), 65–2 (anterior coxae twice as close to anterior margin as to posterior margin of prosternum), and 66–2 (front femora distinctly wider than hind femora). *Litostylus* is the sister taxon of the remaining genera of this clade. All of them share characters 11–1 (rostral carinae subparallel to convergent towards frons) (Fig. 5A), 29–1 (antennal scape capitate) (Fig. 5C), 38–0 (pronotum subcylindrical) and 73.2 (tarsite 2 longer than wide).

Within clade III we recognize three subclades (Fig. 10): subclade A includes *Plectrophoroides* to *Moropactus*, subclade B includes *Lanterius* to *Thoraconaupactus*, and subclade C includes *Hoplopactus lateralis* to *Trichocyphus formosus*. *Plectrophoroides* is the sister species of the rest of the species of subclade A. It is distinguished by the autapomorphy of the arched grooves on the frons (21–1) (Fig. 5F).

Mimographus sensu Alonso-Zarazaga & Lyal (1999) (senior synonym of *Steirarrhinus* Champion and *Mimographopsis* Champion) is herein represented by two species that do not form a monophyletic group. The type species *M. decolor* was recovered within subclade B, close to *Naupactus* and allied genera, and the type of *Mimographopsis*, *M. viridicans*, is nested within subclade A, as a sister species of *Tetragononmus tuberosus*. The main characters that justify the relationship between *M. viridicans* and *T. tuberosus* are the elytra with tubercles on disc and declivity (57–1) and the uneven intervals (except suture) of the elytra strongly convex (59–2). Both species inhabit parts of northern South America and southern Central America (Panama, Costa Rica, Colombia and Ecuador).

Hoplopactus (type species *H. injucundus*), a genus mainly diagnosed by the presence of one to three small denticles in the internal side of the front femora is not monophyletic. *Hoplopactus lateralis* is recovered near the root of subclade C, whereas *H. pavidus* is nested within subclade B, as a sister species of *Brachystylodes pilosus*. The most important character that supports the relationship between *H. pavidus* and *B. pilosus* is the epistome elevated relative to the post-rostrum (15–1) (Fig. 5D).

The *Pantomorus*–*Naupactus* complex sensu Buchanan (1939), including *Alceis*, *Naupactus* and *Pantomorus sensu lato* (see Dalla Torre *et al.*, 1936; O'Brien & Wibmer, 1982), is not recovered as monophyletic, because their species are spread

across subclades B and C, and within these subclades there are other genera never assigned to this complex, e.g. those of the Andean group.

Subclades B and C are weakly supported by apparent synapomorphies. The former includes most genera often related to *Naupactus* (e.g. *Alceis*, *Teratopactus*, *Mimographus*, *Thoraconaupactus*) and the latter includes most genera often related to *Pantomorus sensu lato* (e.g. *Atrichonotus*, *Aramigus*, *Phacepholis*, *Parapantomorus*) plus the Andean group (*Asymmathetes* to *Trichocyphus*).

Subclade C is only supported by the reduction of the elytral humeri (51–1) and the remaining species within this subclade (all except *H. lateralis*) are nested in a group justified by the character 63–1 (lack of metathoracic wings). Both characters used to evolve convergently, and if not accompanied by other synapomorphies they should be not taken into account as evidence of a close phylogenetic relationship.

In the consensus tree (Figure S1), most genera of subclades B and C collapse in a polytomy, although some relationships are consistently recovered, e.g. *Naupactus rivulosus*–*Thoraconaupactus*, *Teratopactus nodicollis*–*T. gibbicollis*, *Phacepholis elegans*–*Pantomorus albosignatus*, *Naupactus cervinus*–*Aramigus tessellatus*, *Galapaganus galapagoensis*–*G. howdenae*, *Atrichonotus taeniatus* (*A. sordidus* *Eurymetopus*), and the genera of the Andean group (*Asymmathetes* to *Trichocyphus*).

The highly diverse genus *Naupactus* is not recovered as monophyletic, in agreement with the results of Scatagliani *et al.* (2005) and Rosas–Echeverría *et al.* (2011a). *Naupactus rivulosus* (type species of *Naupactus*) does not form a clade neither with *N. leucoloma* (type species of the junior synonym *Graphognathus*) (Lanteri & Marvaldi, 1995) or with *N. cervinus* (type species of *Asynonychus* Crotch, junior synonym of *Naupactus* according to Alonso-Zarazaga & Lyal, 1999). It is nested within a monophyletic group that includes *Galapaganus* (*Alceis* (*Teratopactus* (*Naupactus*, *Thoraconaupactus*))), mainly supported by synapomorphy 68–2 (mucro large).

The monophyly of *Galapaganus* is mainly justified by character 97–1 (aedeagus with setae around ostium) (Fig. 9G) with further evolution in *G. howdenae*, 97–2 (aedeagus with setae around ostium and on ventral surface) (Fig. 9H). The monophyly of *Teratopactus* is justified by characters 44–1 (pronotum strongly convex), 71–2 (metatibial apex simple), 72–1 (dorsal comb of hind tibiae about as long as distal comb), and 84–2 (distal coxites strongly sclerotized and strongly projected in a long nail-shaped piece) (Fig. 7D). The sister relationship of *Naupactus* and *Thoraconaupactus* is mainly justified by characters 37–2 (fusiform antennal club) and 83–1 (ovipositor with rows on setae) (Fig. 7B).

Due to the insufficient taxon sampling of *Naupactus* (about 75% of Naupactini are attributed to this genus), it is not possible to draw a conclusion relative to the phylogenetic position of *N. cervinus* and *N. leucoloma*. *Naupactus cervinus* was recovered as sister species of *A. tessellatus* based on some characters of the spermatheca and the spermathecal duct (87–0, 88–1, 91–0, 92–3) and *Naupactus leucoloma*, as a sister species of *Thoraconaupactus densius*, based on characters of the vestiture (4–1,

7–2). However, additional morphological evidence for other species of *Naupactus*, and preliminar molecular analyses based on a large taxon sampling suggest that *N. cervinus* and *N. leucoloma* belong to different species groups of this genus (Lanteri & Marvaldi, 1995; Scataglini *et al.*, 2005; M. Rodriguez *et al.*, unpublished data). *Aramigus tessellatus*, *N. cervinus* and *N. leucoloma* are derived lineages of the *Pantomorus*–*Naupactus* complex sensu Buchanan (1939) which have accumulated several apomorphic characters, among them reduction of humeri and hindwings and parthenogenetic reproduction (Normark & Lanteri, 1998; Guzmán *et al.*, 2012; Rodriguez *et al.*, 2013, 2016).

Pantomorus sensu lato (Dalla Torre *et al.*, 1936; O'Brien & Wibmer, 1982) is not monophyletic, because the species traditionally classified in this genus, e.g. *A. tessellatus*, *A. taeniatulus*, *P. elegans*, *N. leucoloma* and *N. cervinus*, do not all group together. Based on the hypothesis of nonmonophyly of *Pantomorus* sensu lato, some generic names considered as junior synonyms of *Pantomorus* in the old catalogues, e.g. *Atrichonotus*, *Aramigus* and *Phacepholis*, have been revalidated and treated as independent (Lanteri, 1990; Lanteri & O'Brien, 1990; Lanteri & Díaz, 1994).

Pantomorus albosignatus (type species of *Pantomorus*, from Mexico) was recovered as sister species of *P. elegans* (type species of *Phacepholis* from USA), mainly based on the broad and squamose corbels of the hind tibiae (71–0). This result is in agreement with the cladistic analysis of the *Pantomorus*–*Naupactus* complex in Mexico and North America (Rosas–Echeverría *et al.*, 2011a), and with a preliminary molecular analysis of the *Pantomorus*–*Naupactus* complex, including species from the whole of America (Lanteri *et al.*, 2010).

The two species of *Atrichonotus*, *A. taeniatulus* and *A. sordidus*, are recovered as paraphyletic with respect to *Eurymetopus*. The relationship of *A. sordidus* and *Eurymetopus* is supported by the synapomorphy of the sternite VIII subpentagonal (78–5) (Fig. 6F), and by other characters with parallel evolution in unrelated genera inhabiting a similarly dry environment to South America. The characters of the antennae reverse to their primitive states in both genera, e.g. scape not reaching hind margin of eye (31–0) and funicular article 7 wider than long at apex (35–0). Preliminary molecular analyses also support the sister relationship of *A. sordidus* and *Eurymetopus* and their separation from *A. taeniatulus* (Pereyra *et al.*, in prep.).

The monophyly of the Andean group is mainly supported by the character 66–1 (the front femora about as wide as hind femora) and some features of the vestiture. In most of the genera, the scaly vestiture is lacking (6–3) and the elytral setae are either erect and long (7.2) or absent (7.0). *Galapaganus* was considered as part of the Andean group (del Río & Lanteri, 2011a); however, the results of the current cladistic analysis does not agree with this hypothesis. The similarity of *G. galapagoensis* and *Amphideritus* in some characters, e.g. elytra covered with seta-like scales (6–2) and setae around ostium of the aedeagus (97–1), would be a consequence of parallel evolution.

Evolution of selected characters

One of the major difficulties in the recognition of morphological homologies in Naupactini is that several characters have probably evolved in adaptation to similar environments several times in the history of this tribe. For example, various groups that inhabit rainforests (*Neoericydeus graciosus*, *Briarius augustus*, most species of *Ericydeus*) have a colour pattern of dark maculae on a usually iridescent green-blue background (5–1); in most genera that occur in deserts and other xeric environments the scales evolved into seta-like scales (6–2) and the short recumbent setae become long and erect (7–2) (e.g. *Amphideritus vilis* and *Trichonaupactus densius*), or else the integument lacks scales and setae (6.3, 7–0) (e.g. *Amitrus*, *Melanocyphus*, *Obrieniolus*), and the two genera that mimic mutillid wasps (*Trichaptus mutillarius* and *Curiades boisduvali*) show similar colour patterns and setosity (7–3).

Other homoplastic characters are the reduction or absence of humeri (51–1, 51–2), the usually correlated reduction or absence of hindwings (63–1), and the presence of straight to slightly bisinuate bases of pronotum and elytra (47–1, 50–1, 50–2). Naupactines with these combinations of characters are usually widespread in treeless or almost treeless environments, e.g. *P. elegans* in the Great Plains of North America (Lanteri, 1990); *P. albosignatus* in the Mexican Plateau (Rosas–Echeverría *et al.*, 2011b); and the species of *Aramigus*, *Atrichonotus*, *Eurymetopus*, *Parapantomus*, *N. cervinus* and *N. leucoloma* in the steppes and prairies of South America (and in similar environments of other continents where they have been introduced).

Most taxa that inhabit xeric woodlands, savannas and shrublands are also flightless but they usually have well-developed humeri bearing tubercles (52–1, 52–3), e.g. *Mendozella* and *Enoplopactus lizeri* (Monte), *Priocypopsis* (Espinal), *Melanocyphus* (Paramos), *Teratopactus nodicollis* (Cerrado); and/or all tibiae have large denticles on the inner side (70–2), e.g. *Mendozella*, *Enoplopactus*, *Melanocyphus*, *Trichocypus* (Puna); and the pronotum is tuberculate (40–1), e.g. *Cypopsis* (Caatinga), *Thoracocypus*, *Teratopactus* and *Thoraconaupactus* (Cerrado).

Naupactines adapted to arboreal life show another combination of characters. They do not have tubercles on pronotum and elytra, their integument is less sclerotized than in weevils from xeric woodlands and shrublands, legs and antennae are usually long, the front femora are often much wider than the hind femora, and the front tibiae usually have a large hook-like micro. All these characters may have evolved independently in different groups, obscuring phylogenetic signal and producing high degrees of homoplasy. Conversely, characters of the rostrum and head are usually less homoplastic than those involved in mobility, e.g. the pair of arched lateral grooves on each side of the frons (21–1) is an autapomorphy of *Plectrophoroides*; the epistome elevated characterizes the relationship of *Brachystylodes* and *Hoplopactus pavidus* (15–1) (5D); and the dorsolateral margins of the rostrum curved and convergent towards the apex (9–3) is synapomorphic for the group of genera with broad antennae.

Characters of the antennae, particularly width, length and curvature of the scape, and length of funicular article 2 relative to length of funicular article 1, are relevant for the systematics of Naupactini. In some genera, e.g. *Megalostylodes*, *Chamaelops* and *Wagneriella*, the width of the scape shows sexual dimorphism (32–1), being wider in males than in females. Other characters traditionally used by authors to diagnose naupactine genera are the presence of long setae on the external face of the prementum (20–1) and the presence or absence of a well-developed corbel at the tip of the hind tibiae (van Emden, 1944; Hustache, 1947). The broad and squamose corbel (71.0) is an apparent synapomorphy of clade I (excluding *Neoericydeus*), with independent evolution in some genera outside this clade. On the contrary, within clade III, subclade C, corbels are often narrow to simple (=corbel plates open) (73.2), and in *Eurymetopus*, a genus that has accumulated several apomorphic characters, corbels are open, and the distal comb of the hind tibiae is not prolonged in a dorsal comb, as in remaining Naupactini.

Characters of the female genitalia highlight some generic relationships, and those of sternite VIII and ovipositor contribute to a better understanding of the evolution of the oviposition habits within the tribe (Guedes & Parra, 2004; Lanteri & del Río, 2008). Subrhomboidal and slightly elongate sternite VIII (78–2) is probably synapomorphic for Naupactini, and evolves in different shapes, e.g. subpentagonal in *Eurymetopus* and *Atrichonotus sordidus* (78–5); suboval and with a pair of sclerotized denticles in *Trichonaupactus* (79–2); and subtriangular in *Cyphopsis* (78–0). The latter shape is considered a reversal to the primitive condition present in most tribes of the outgroup, in which the apodeme of sternite VIII is usually shorter than the plate (80–0) and the ovipositor is about as long as one-third of the abdomen. Conversely, in Naupactini, the apodeme of sternite VIII is usually more than twice as long as the plate (80–1), the ovipositor reaches or exceeds half the length of the abdomen (81–1, 81–2) or the total length of the abdomen (81–3), and the baculi, the pair of struts that give strength to the long membranous ovipositors, are always present (82–1) (except in *Cyphopsis* and *Thoracocyphus denticollis*). In other entimines, ovipositors are usually short and lacking baculi.

In Tanymecini there are two types of ovipositors, long with baculi, e.g. *Pandeleiteius* (Howden, 1982), and short without baculi, e.g. *Pandeleiteius* (Howden, 1996). Moreover, according to Howden (1996), the presence of styli is a primitive character state for the Tanymecini, whereas the loss of styli and the presence of strongly sclerotized distal coxites modified into digging tools are both derived characters associated with a particular type of oviposition in soil (Howden, 1995). Similarly, within Naupactini we recognize two main oviposition habits: (i) species with long ovipositors and slightly sclerotized distal coxites lay eggs in clusters, glued by an adhesive substance between surfaces, usually crevices in the plants, leaves, litter or calices of fruits (behaviour category 9 sensu Howden, 1995); and (ii) species with short ovipositors and strongly sclerotized distal coxites oviposit isolate eggs (not in clusters) in the soil (behaviour category 10 sensu Howden, 1995), e.g. *Atrichonotus sordidus* and species of *Eurymetopus*, *Teratopactus*, *Priocyphus*, *Priocyphopsis*, *Lamprocyphopsis* and *Mendozella*. In

Eurymetopus, not only the ovipositor but also the sternite VIII plays the role of a digging tool; and some *Naupactus* from the xeric environment, the genitalia of which is not adapted to the oviposition in soil, protect the egg postures with their faeces (Marvaldi, 1999). The results of our cladistic analysis allow us to test the hypothesis that soil oviposition is a derived condition for the Naupactini.

The characters of the spermatheca serve to support the monophyly of some genera, e.g. *Enoplopactus* (89–2), *Cyphopsis* (92–4) and *Priocyphus* (92–3), although in some instances similar shapes of spermatheca evolve in parallel in different groups. The presence of long, usually wide and often curled spermathecal ducts is associated with spermathecae having a long tubular collum.

The male genitalia do not provide as many characters as female genitalia. The apodemes of the aedeagus of naupactines are long relative to those of other tribes, and become shorter than the median lobe (95–1) only in a few genera and species, e.g. *Alceis*, *Ericydeus* and *N. leucoloma*. The apex of the aedeagus show great variation, which makes it difficult to code several character states separated by a slight difference, and in some genera, e.g. *Amphideritus*, *Galapaganus* and *Neoericydeus*, it bears setae around the ostium (97–1). Male genitalia could not be analysed for several species, particularly those of clade III, in which males are unknown due to parthenogenetic reproduction or frequent sex bias in their populations.

Taxonomic amendments

In order to address the taxonomic implications of our phylogenetic results, we propose the following nomenclatural changes, relative to Alonso-Zarazaga & Lyal (1999): (i) to transfer the genus *Artipus* to the tribe Geonemini; (ii) to revalidate the genus *Mimographopsis* Champion, considered junior synonym of *Mimographus* Schoenherr, to accommodate *M. viridicans* and *M. pustulatus*; and (iii) to revalidate the genus *Floresianus* Hustache, synonymized with *Atrichonotus* Buchanan by Lanteri & O'Brien (1990) for the single type species *Floresianus sordidus*.

No nomenclatural changes are proposed for the genera *Hoplopactus* and *Naupactus*, despite their condition of being nonmonophyletic, because these changes should be done in the context of a taxonomic revision that includes a larger taxon sampling. Moreover, in the case of *Hoplopactus* we did not include the type species *H. injucundus* (Boheman) in our cladistic analysis, because of the scarce material available. Our preliminary conclusion is that *H. pavidus* and *H. lateralis* belong to two different species groups of *Hoplopactus*, the former closer to *Brachystylodes*. In the future it is possible that some species of *Hoplopactus*, such as *H. pavidus*, should be transferred to the latter genus.

Nomenclatural changes:

Artipus Sahlberg, new placement in the tribe Geonemini.
Mimographopsis Champion, 1911: 229, resurrected genus.
Mimographopsis viridicans Champion, 1911: 229 and *M. pustulatus* Champion, 1922: 230, resurrected species names.

Floresianus Hustache, 1939: 39, resurrected genus.
Floresianus sordidus Hustache, 1939: 40, resurrected species name.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12223

Table S1. List of 70 terminal taxa included in the cladistic analysis of the tribe Naupactini, their geographic distributions (countries and states/provinces) and biogeographic areas.

Table S2. List of 100 morphological characters, character states and codes.

Table S3. Data matrix of 74 taxa and 100 morphological characters of Naupactini and outgroups, used for the cladistic analysis. Inapplicable and missing character states are indicated with a question mark?

Figure S1. Strict consensus tree from the seven most parsimonious trees obtained under equal weights, based on a data matrix of 70 taxa of Naupactini and four outgroups.

File S1. Data matrix of 74 taxa and 100 morphological characters of Naupactini, in WINCLADA format.

File S2. Phylogenetic tree in .tre file format, corresponding to Fig. 10.

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