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PHYLOGENETIC ANALYSIS OF THE TRIBE PTOMAPHAGINI, WITH DESCRIPTION OF NEW NEOTROPICAL GENERA AND SPECIES (COLEOPTERA, LEIODIDAE, CHOLEVINAE, PTOMAPHAGINI)

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ABSTRACT

A phylogenetic analysis of the tribe Ptomaphagini is given, based on both male and female characters of known and new genera. New genera and species are described: Peckena new genus, type species: Peckena ventralis new species, from Peru; Amplexella new genus, type species: Amplexella dimorpha new species, from Venezuela; Amplexella similis new species, from Venezuela; Parapaulipalpina new genus, type species: Parapaulipalpina dentata new species, from Venezuela. The following nomenclatural changes were established. Because the genus Adelopsis has feminine gender, the names of the species of Adelopsis were corrected to feminine endings, whenever appropriate: A. aspera Jeannel, 1936, A. brunnea brunnea Jeannel, 1936, A. b. orcina Szymczakowski, 1975, A. b. pteromoria Szymczakowski, 1975, A. bellatrix Szymczakowski, 1968, A. heterocera Portevin, 1907 (type species), A. insolita Szymczakowski, 1961, A. luculenta Szymczakowski, 1963, and A. triangulifera Szymczakowski, 1961. Echinocoleus and Synaulus are placed as subgenera of Ptomaphagus (new status). Species transferred from Adelopsis to Ptomaphagus (Appadelopsis) new subgenus (n. comb.): P. (App.) alleghenyensis (Peck, 1978), P. appalachianus (Peck, 1978), P. bedfordensis (Peck, 1978), P. cumberlandus (Peck, 1978), P. fumosus (Peck, 1978), P. joanna (Peck, 1978), P. jonesi (Peck, 1978), P. mitchellensis (Hatch, 1933), P. nashvillensis (Peck, 1978), P. orichalcum (Peck, 1978), P. pecki n.nom. (for P. altus (Peck, 1978), not P.

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(*Adelops*) *altus* Peck, 1973), *P. pisgahensis* (Peck, 1978), *P. richlandensis* (Peck, 1978), *P. scottsboroensis* (Peck, 1978), *P. steevesi* (Peck, 1978), and *P. suteri* (Peck, 1978), from the southern Appalachians (USA). Species transferred from *Adelopsis* to *Ptomaphagus* (n.comb.): *P. bordoni* (Jeannel, 1964), from Venezuela, and *P. sciakyi* (Zoia, 1993), from Ecuador. Species transferred from *Adelopsis* to *Paulipalpina* (n.comb.): *P. simoni* (Portevin, 1903) from Venezuela; *P. dispar* (Portevin, 1903) and *P. exigua* (Kirsch, 1870) from Colombia. The specific status of *P. dispar* is resurrected from synonym with *P. exigua*. Species transferred from *Adelopsis* to *Parapaulipalpina* (n.comb.): *P. filicornis* (Jeannel, 1936) from Colombia. Species transferred from *Ptomaphagus* to *Adelopsis* (n.comb.): *A. picunche* (Gnaspini, 1991), from Argentina. From the phylogenetic analysis, the subtribe *Ptomaphaginina* resulted to be non-monophyletic and, therefore, the use of the subtribes *Ptomaphagina* and *Ptomaphaginina* is abandoned. A checklist of the known genera and species of the tribe *Ptomaphagini* after the nomenclatural changes made herein is given.

Keywords: *Amplexella* gen. n., Cholevinae, Coleoptera, *Parapaulipalpina* gen. n., *Peckena* gen. n., phylogenetic analysis, revision.

INTRODUCTION

Until recently, the tribe *Ptomaphagini* has contained 7 described genera: *Ptomaphaginus* and *Pandania* (Oriental), *Proptomaphaginus* (Neotropical - West Indies and Mexico), *Ptomaphagus* (with four subgenera - *Ptomaphagus*, Palearctic; *Merodiscus*, Palearctic; *Adelops*, Nearctic and Mexico; and *Tupania*, Neotropical), two myrmecophilous genera *Echinocoleus* (Nearctic) and *Synaulus* (Palearctic), and *Adelopsis* (Neotropical and Appalachians of USA). Recently, a new Neotropical genus was added to the list (*Paulipalpina* - Gnaspini & Peck, 1996); and *Echinocoleus* was recognized as a subgenus of *Ptomaphagus* (Peck & Gnaspini, in press).



As stressed by Gnaspini & Peck (1996), *Adelopsis* and *Ptomaphagus* seem to be non-monophyletic genera. Hence, a revision is needed to solve the question. Because of the very large Neotropical collections of Stewart B. Peck, which includes more than 100 new species of "*Adelopsis*", this group was selected as a start of a revision of *Ptomaphagini*. This paper is the second in a proposed series dealing with a revision of "*Adelopsis*" and focuses on the description of new genera and species, based on a phylogenetic study made upon specimens of all recognized genera of *Ptomaphagini*.

Gnaspini, P., 1997. Phylogenetic analysis of the tribe Ptomaphagini, with description of new Neotropical genera and species (Coleoptera, Leiodidae, Cholevinae, Ptomaphagini). *Pap. Avuls. Zool.*, S.Paulo 39(24): 509-556.

ERRATA

Na p. 556 a espécie *Ptomaphagus cibiricus* Jeannel, 1934 aparece pelo formato adotado sob *P. sericatus*, quando no entanto, deveria aparecer como espécie válida.

Na p. 543, Couplet 17 deve ser lido como:

17. Ligula: 0, divided (); 1, undivided (fused) ().

METHODS AND MATERIALS

The specimens used in this study were either preserved in 70% alcohol or as dried specimens mounted on cards fixed on entomological pins. To dissect the genitalia, the specimens were relaxed by being boiled in water. Some structures with much adhered tissue were cleaned for a few minutes in hot 10% KOH. The dissected genitalia were mounted in PVA on a microslide, which was attached to the same pin.

The holotypes or representatives of the species studied herein are deposited in the following collections: Field Museum of Natural History, Chicago (FMNH), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP), Muséum National d'Histoire Naturelle, Paris (MNHN), The Natural History Museum, London (BMNH), Naturhistoriska Riksmuseet, Stockholm (NHRS), Nrodní Muzeum v Praze, Praha (NMPC), Stefano Zoia collection, Milano (SZ), Stewart B. Peck collection, Ottawa (SBP), and Museum für Naturkunde der Humboldt-Universität, Berlin (ZMHB).

The list of types and other specimens of "Adelopsis" borrowed from the collections and seen during this study is given in table 1.

In the list of material for each species, when not otherwise noted, data such as locality, altitude and collector are the same as the immediately previously cited data. When not noted, the specimens are deposited in the SBP collection.

The definition of the new taxonomic groups follows standard phylogenetic methodology (Hennig, 1966; Wiley et al., 1991), using characters of both external features and genitalia, and the methodology of comparison with the outgroup (after Watrous & Wheeler, 1981; Maddison et al., 1984). Species of *Dissochaetus* and *Eucatops* were used as outgroup. For processing the data matrix, I used the option "bb" in program HENNIG86 and, afterwards, the option "nelsen" to obtain the consensus tree.

SYSTEMATICS

I here follow the suprageneric classification proposed by Newton & Thayer (1992).

Family Leiodidae Fleming, 1821
Subfamily Cholevinae Kirby, 1837
Tribe Ptomaphagini Jeannel, 1911

Previous taxonomic definition of genera

The tribe Ptomaphagini is divided into two subtribes: Ptomaphagina and Ptomaphaginina.

The Ptomaphaginina contains three genera:

Proptomaphagus - Neotropical (Mexico and West Indies) - 6 described spp. (Peck, 1983).

Ptomaphagus - Oriental - 84 described spp. (no recent review - Szymczakowski, 1964, 1970a, 1972a, 1972b, 1974, 1975a, 1980; Hayashi 1969; Jarrige, 1969; Peck, 1981; Nakane, 1982; Schilthuizen, 1984; Perreau, 1986, 1988, 1991, 1992a, 1992b, 1995, 1996; Perkovsky, 1992; Zoia, 1994). Some new species have been recently described, mainly by M. Perreau.

Pandania - Oriental - 1 described sp. (Szymczakowski, 1964). Based on the description, it may be synonym of *Ptomaphagus* - it deserves revision. The Ptomaphagina contains the following taxa:

Synaulus - myrmecophilous, Palearctic - 2 described spp. (Jeannel, 1936).

Ptomaphagus (Echinocoleus) - myrmecophilous, Nearctic - 4 described spp. (Peck & Gnaspi, in press).

Ptomaphagus (Ptomaphagus) - Palearctic - 26 described spp. (no recent review - Jeannel, 1936; Nakane, 1963; Szymczakowski, 1964, 1976; Perreau, 1988, 1996; Schilthuizen, 1989; Nishikawa, 1993).

Ptomaphagus (Merodiscus) - Palearctic - 2 described spp. (Ruzicka, 1993).

Ptomaphagus (Tupania) - Neotropical - 6 described spp. (Peck, 1977).

Ptomaphagus (Adelops) - Nearctic and Mexico - 60 described spp. (Peck, 1973a, 1973b, 1977, 1978b, 1984).

Ptomaphagus picunche - recently described from Argentina. It does not fit into present subgenera (Gnaspi, 1991).

Adelopsis - Neotropical and Appalachians of USA. Besides 14 recently described new spp. from Costa Rica and Panama (Gnaspi & Peck, 1996), the genus *Adelopsis* contains 25 described Neotropical species (one of them with 6 subspecies) (Jeannel, 1936, 1964; Szymczakowski, 1961, 1963, 1968, 1970b, 1975b; Blas, 1980; Gnaspi, 1993; Zoia, 1993), and 16 Appalachian species (Peck, 1973a, 1978a).

Paulipalpina - Neotropical, recently described - 4 described species (Gnaspi & Peck, 1996).

Until 1978, *Adelopsis* contained only Neotropical species, characterized by having a short, generally globose, aedeagus, contrary to the remaining species of Ptomaphagini, which have an elongate aedeagus. Peck (1978a) de-

scribed several new species from the Appalachians of USA, widening the generic distribution to include the Nearctic region. Because these species have a somewhat elongate aedeagus, the generic characteristics were redefined to include species with both short and elongate aedeagi. Besides, these species share several characters with the other genera of Ptomaphagina (*Ptomaphagus*, *Echinocoleus* and *Synaulus*), and might be more closely related to them than to *Adelopsis*. Thus, *Adelopsis* seems to be a non-monophyletic taxon, with at least three groups: the Nearctic species (which would belong to *Ptomaphagus* or a closer genus), the species actually belonging to the recently described genus *Paulipalpina*, and the remaining Neotropical species (which may or may not belong to the same monophyletic group). It is clearly apparent that *Adelopsis* needs a taxonomic redefinition, based on phylogenetic systematics.

In turn, *Echinocoleus* and *Synaulus* seem to represent lineages derived from different lineages of *Ptomaphagus*: *Ptomaphagus* shows a Holarctic distribution, and has produced two myrmecophilous lineages, both with a derived morphology (mainly shortening of antennae and appendages and broadening of body). The North American lineage is recognized as *Echinocoleus*, and the North African one as *Synaulus* (after figure 212 from Peck, 1973a). This equally implies the non-monophyly of *Ptomaphagus*.

Therefore, a revision at the subtribe level is needed, aiming at a redefinition of genera and subgenera. The present study is concerned with a revision of the genus *Adelopsis* (and with definition of its intrageneric monophyletic groups) and a redefinition of the genera of Ptomaphagini. It was based on characters taken from specimens of *Adelopsis* and other genera of Ptomaphagini and other tribes of Cholevinae available in the SBP collection; and from specimens of *Adelopsis* (including types) borrowed from several museums.

Description of new genera and species

The new genera described herein are based on the phylogenetic analysis presented later in this paper and summarized in the cladograms shown in figures 1 to 3.

The following species are characterized, except when noted, by the following typical characters of the tribe: Shape oblong. Pubescence golden, with many short recumbent setae, setal sockets forming strigae on the head, pronotum and elytra. Antenna 11-segmented, segment 8 smaller than 7 and 9. Pronotum transverse with transverse strigae. Sutural striae entire. Mesosternum with longitudinal carina. Apex of tibiae armed with a comb of many short and equal fixed spines. Anterior tarsi laterally expanded in males.

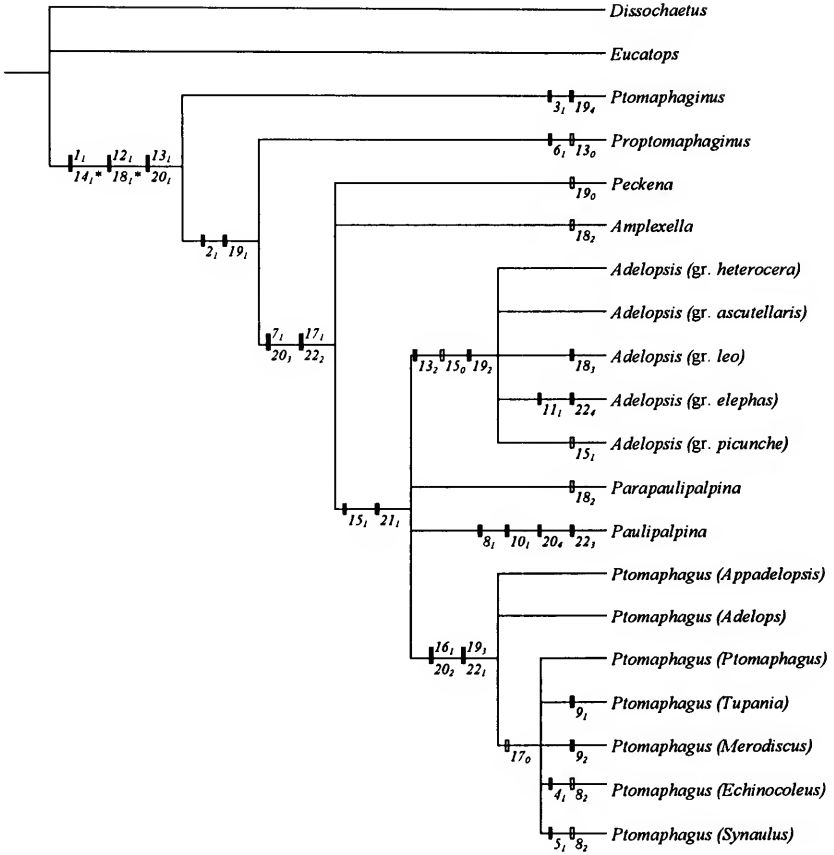


Figure 1. Strict consensus cladogram of supraspecific groups of Ptomaphagini, using proposed changes to nomenclature, and based on the data matrix in table 4. Numbers refer to characters in tables 3 and 4; subscripts refer to state of the characters. Black rectangles indicate synapomorphies; open rectangles indicate homoplasies (convergences or reversions). Apomorphies of outgroups are not shown in figure. * Characters 14 and 18 may be either a synapomorphy or a convergence with *Eucatops*.

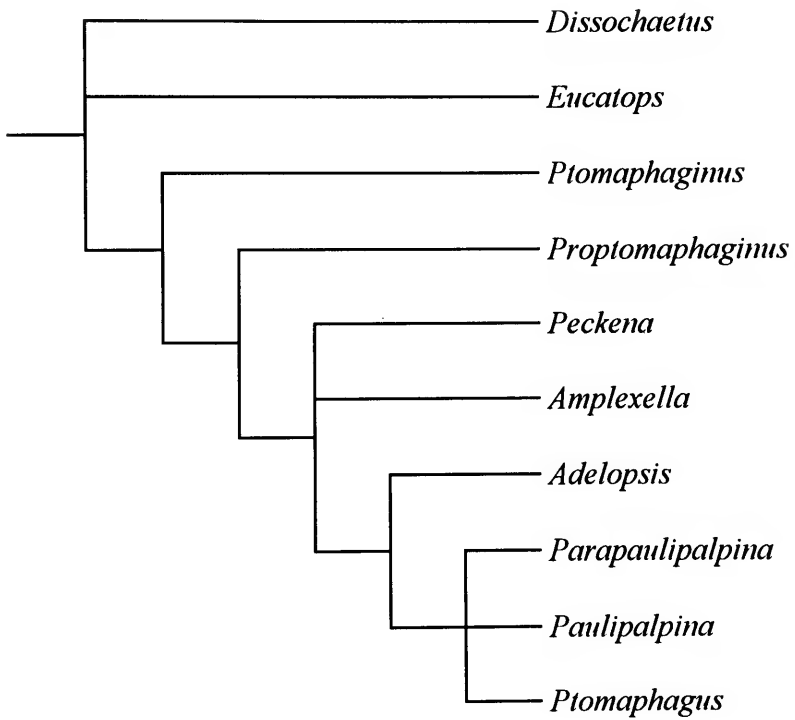
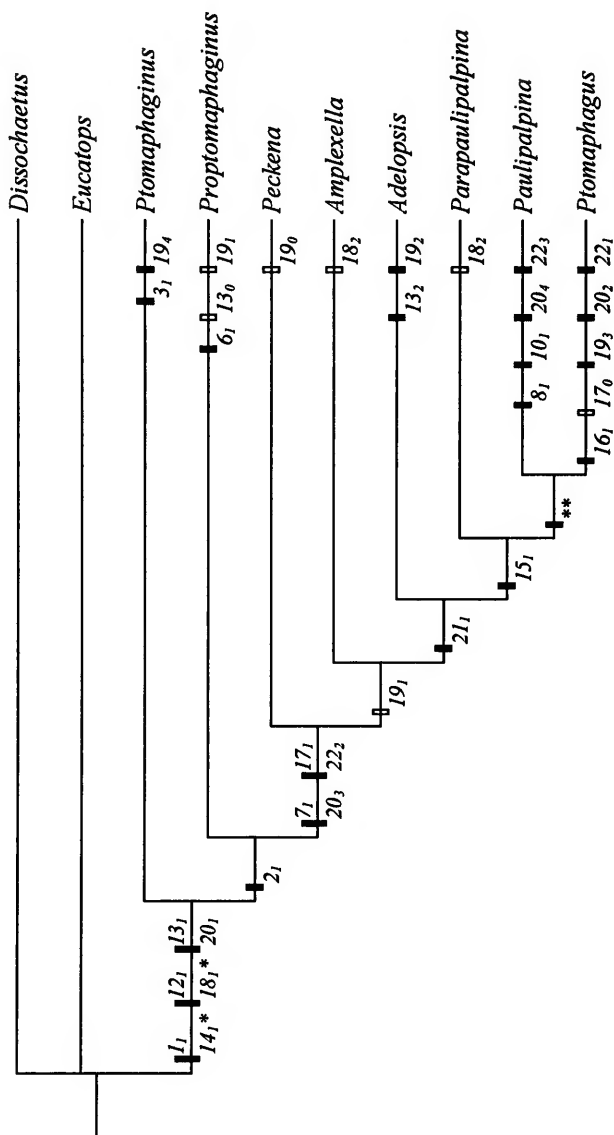


Figure 2. Strict consensus cladogram of generic groups of Ptomaphagini, using proposed changes to nomenclature, and based on the data matrix in table 4, simplified.



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Figure 3. Semi-strict consensus cladogram of generic groups of Ptomaphagini, using proposed changes to nomenclature, and based on the data matrix in table 4, simplified. Numbers refer to characters in tables 3 and 4; subscripts refer to state of the characters. Black rectangles indicate synapomorphies; open rectangles indicate homoplasies (convergences or reversions). Apomorphies of outgroups are not shown in figure. * Characters 14 and 18 may be either a synapomorphy or a convergence with *Eucatops*. ** State of character 20 could be either 2 or 4; and state of character 22 could be either 1 or 3.

Peckena, gen. n.

Diagnosis and Description. Besides the typical characters of the tribe, cited above: Antennal segments 3-6 short, together much shorter than 1st and 2nd together. Posterior angles of pronotum acute. Aedeagus elongate, symmetrical; apical orifice ventral; flagellum somewhat short and broad, armed. Genital segment globular, spiculum gastrale straight and short.

The genus is characterized by the opening of the aedeagus still ventral. In the only known species, the spermatheca has 2-turns, and an elongate apical bulb.

The genus is known so far for only one species, described below.

Etymology. The genus is named for Stewart B. Peck, in recognition of his extensive field work and extensive collections from the Neotropical region, and his large contribution to systematics of Ptomaphagini. The name is derived from "Peck" + "ena" (diminutive feminine); besides, it sounds like "pequena", which means "small" in Portuguese (= "pequeña" in Spanish), referring to the small size of the specimens.

Gender: Feminine.

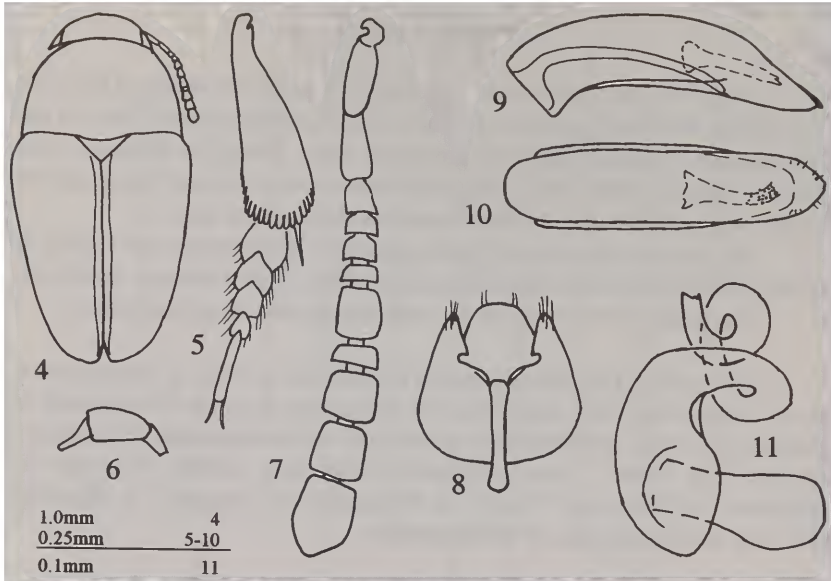
Type Species. *Peckena ventralis* new species, present designation.

Peckena ventralis, sp. n.

(figs. 4 - 11)

Holotype, male (FMNH). Type locality and data: Peru: Huanuco: Cordillera Azul, 39 km NE Tingo Maria, 1700m, 11-14.i.1983, mont. rainfor. windowtr., A. Newton & M. Thayer. 6 male and 1 female paratypes with the same data (FMNH, SBP, MZSP).

Diagnosis and Description. Length: 1.65-1.95 mm; width: 0.8-0.95 mm. Besides characteristics listed above, it is defined by the following characters: Colour light brown. Eyes and wings fully developed. Antenna (fig. 7) 1.35 times as long as pronotum, reaching base of elytra when laid back; tip of last segment pale; proportions of length of each segment and that of the 9th from 1st to 11th: 1.55, 1.45, 0.65, 0.35, 0.5, 0.4, 1.05, 0.5, 1.0, 1.05, 1.6. Proportions of length and width of each segment of the club, from 7th to 11th: 1.15, 0.55, 1.0, 1.0, 1.35. Palp (fig. 6) somewhat short and broad. Elytra (fig. 4) together 1.3 times as long as wide; with dense transversal strigae. First segment of male protarsus (fig. 5) 0.7 times as wide as the maximum width of



Figures 4-11, *Peckena ventralis*, sp. n., 4-10, male. 4, habitus, dorsal view; 5, protarsus and protibia, dorsal view; 6, maxillary palp; 7, antenna; 8, genital segment, ventral view; 9-10, aedeagus, left lateral and dorsal views; 11, female, spermatheca.

tibia. Proportions of length and width of each segment, from 1st to 5th: 1.4, 1.1, 1.25, 1.3, 4.7. Mesotibia curved in both sexes. Metatibia straight in both sexes. Genital segment with short spiculum gastrale (fig. 8). Aedeagus (figs. 9-10) symmetrical with ventral opening, bearing 5 setae at each side of apex; flagellum short and thick, bearing several small teeth over the apical half. Spermatheca (fig. 11) coiled with 2-turns, and bearing a long and broad apical bulb.

Etymology. The name is derived from Latin for "ventral", referring to the opening of the aedeagus, which is ventral in the species, instead of dorsal as in other Ptomaphagini.

Amplexella, gen. n.

Diagnosis and Description. Besides the typical characters of the tribe, cited above: Colour dark brown. Antenna somewhat slim, with first 5 segments elongate, together taking more than half the length of the antenna. Palp somewhat elongate. Male protibia bearing very long setae externally. Mesotibia curved in both sexes. Metatibia straight in both sexes. Posterior angles of

pronotum acute. Aedeagus globose, somewhat short and broad, with short parameres bending ventrally towards apex; apical orifice dorsally subterminal and cutting the apex of the aedeagus slightly left from the median axis; the dorsal opening unnoticeable; flagellum extremely long and coiled, kept very densely coiled inside the aedeagus in rest position. Genital segment globular, spiculum gastrale straight and short, broader posteriorly. Spermatheca with a short coil followed by a long curve ending in a short and broad bulb.

The genus is known so far for only two species, described below.

Etymology. The name is derived from Latin for “Amplexor” (wind, embrace; = “Amplexor”) + “ella” (diminutive feminine), referring to the highly coiled flagellum of the aedeagus.

Gender: Feminine.

Type Species. *Amplexella dimorpha*, sp. n., present designation.

***Amplexella dimorpha*, sp. n.**

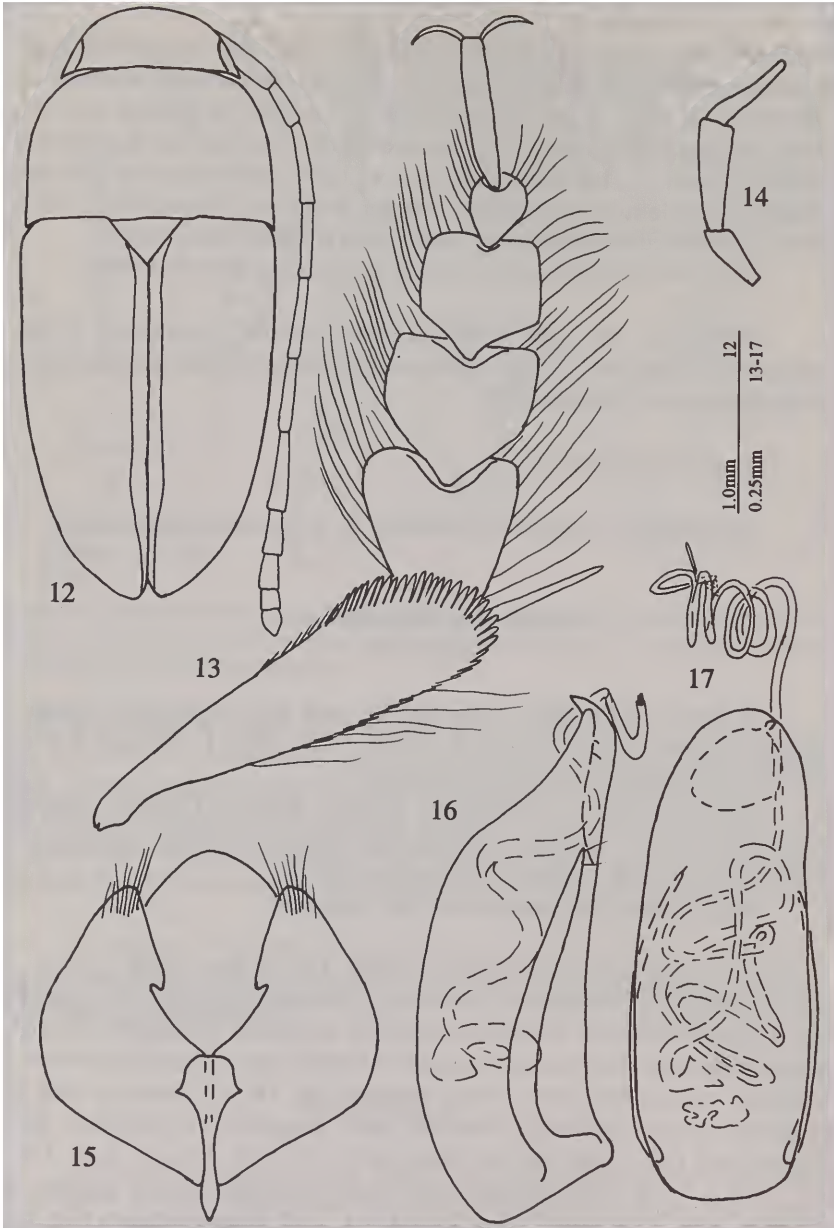
(figs. 12 - 20)

Holotype, male (SBP). *Type locality and data:* Venezuela: Aragua: Rancho Grande, 10°21'N 67°41'W, 1500m, 22.vi.1987, C. Bordón. 4 male and 2 female paratypes with the same data.

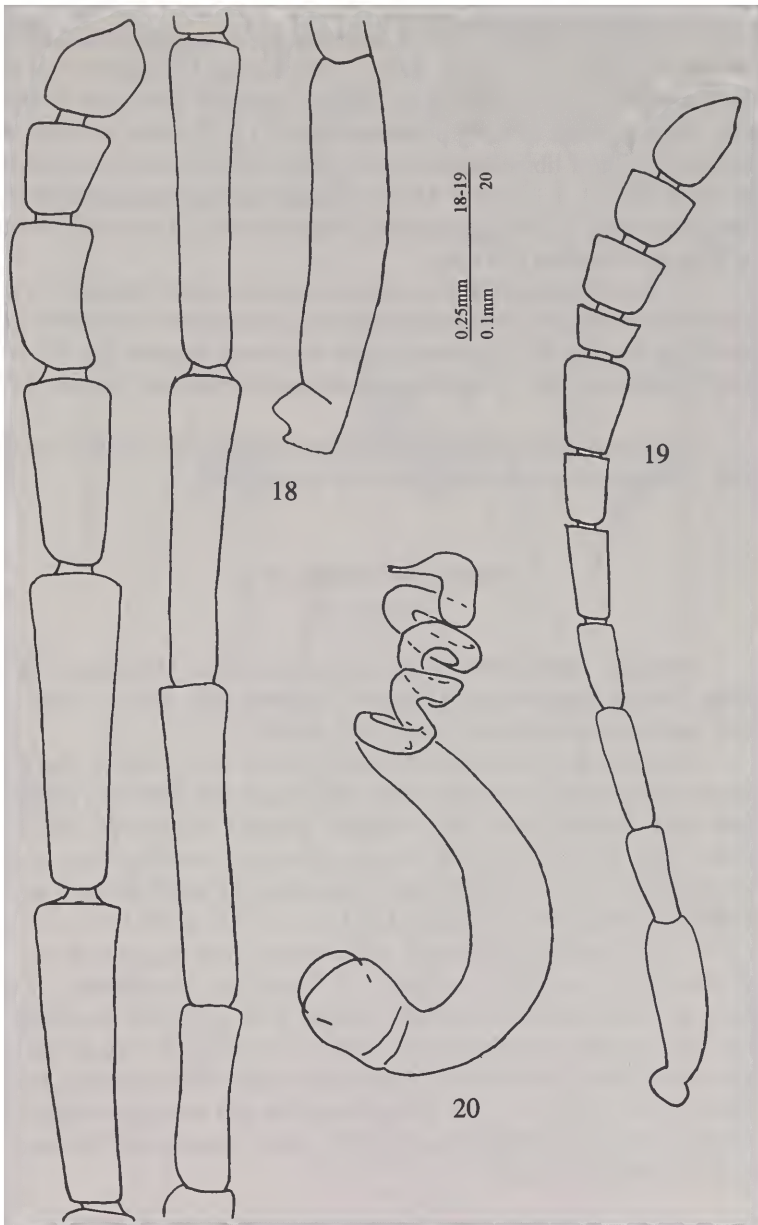
Other paratypes: Venezuela: Aragua: Rancho Grande, 1400m, 04.xi.1986, FIT, C. Bordón, 5 males and 1 female (MZSP); 1200m, 27-30.viii.1983, B. Gill, 1 male and 3 females (SBP).

Several other specimens in the SBP collection.

Diagnosis and Description. Length: 2.8-3.3 mm; width: 1.35-1.45 mm. General characteristics as listed above, differing in the following characters: Colour dark brown. Eyes and wings fully developed. Dimorphic antenna, being much elongate in males; 8th segment slightly pale (yellowish) and last 3 segments pale in both sexes. Male antenna (fig. 18) 4.5 times as long as pronotum, longer than body when laid back; proportions of length of each segment and that of the 9th from 1st to 11th: 2.4, 1.25, 2.2, 2.1, 2.25, 2.05, 2.1, 1.25, 1.0, 0.6, 0.75; proportions of length and width of each segment of the club, from 7th to 11th: 3.35, 2.15, 1.8, 1.1, 1.35. Female antenna (fig. 19) reaches base of elytra when laid back; proportions of length of each segment and that of the 9th from 1st to 11th: 2.3, 1.55, 1.95, 1.35, 1.45, 1.1, 1.45, 0.6,



Figures 12-17. *Amplexella dimorpha*, sp. n., male. 12, habitus, dorsal view; 13, protarsus and protibia, dorsal view; 14, maxillary palp; 15, genital segment, ventral view; 16-17, aedeagus, left lateral and dorsal views.



Figures 18-20. *Amplexella dimorpha*, sp. n., 18, male, antenna; 19-20. female, 19, antenna; 20, spermatheca.

1.0, 1.0, 1.6; proportions of length and width of each segment of the club, from 7th to 11th: 1.35, 0.6, 0.85, 0.85, 1.7. Elytra (fig. 12) together 1.45 times as long as wide; with dense strigae, oblique from one fourth the length onwards. First segment of male protarsus (fig. 13) 1.35 times as wide as the maximum width of tibia. Proportions of length and width of each segment, from 1st to 5th: 1.1, 1.1, 1.15, 1.45, 6.3. Genital segment and aedeagus typical of the genus (figs. 15-17). Spermatheca (fig. 20) with a 4-turns coil followed by a long curve ending in a bulb.

It is noteworthy that the antennal segments which elongate in males are only those from 1st to 8th, which makes the 8th segment to become longer than the 9th (figures 12, 18 - compare with the female antenna, fig. 19), masking the "cholevine rule" of the 8th segment smaller than the 7th and the 9th.

Etymology. The name is derived from Greek for "di" (two) + "morphe" (form), referring to sexual dimorphism in the antennae.

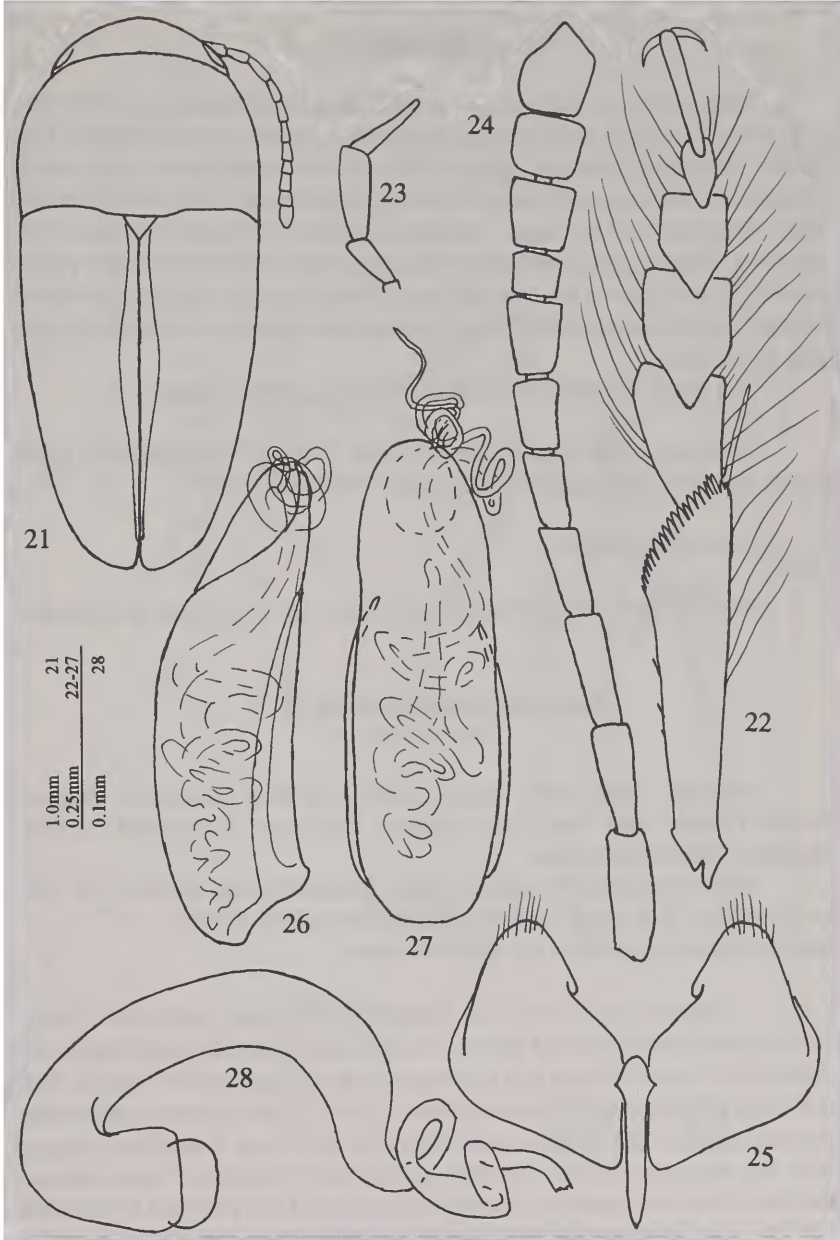
Amplexella similis, sp. n.

(figs. 21 - 28)

Holotype, male (SBP). Type locality and data: Venezuela: Aragua: Rancho Grande, Berlese 194, 51kg litter, undated, S.B. Peck. 7 male and 5 female paratypes with the same data (SBP, MZSP).

Diagnosis and Description. Length: 2.7-3.2 mm; width: 1.25-1.4 mm. General characteristics as listed above, differing in the following characters: Colour dark reddish brown. Eyes slightly reduced; wings fully developed. Antenna (fig. 24) 1.45 times as long as pronotum, reaching base of elytra when laid back; last 3 segments pale; proportions of length of each segment and that of the 9th from 1st to 11th: 1.9, 1.6, 1.55, 1.2, 1.15, 1.05, 1.15, 0.65, 1.0, 0.9, 1.4. Proportions of length and width of each segment of the club, from 7th to 11th: 1.45, 0.85, 1.05, 0.9, 1.5. Elytra (fig. 21) together 1.5 times as long as wide; with dense strigae, oblique from one third the length onwards. First segment of male protarsus (fig. 22) 1.1 times as wide as the maximum width of tibia. Proportions of length and width of each segment, from 1st to 5th: 1.45, 1.5, 1.55, 1.9, 5.7. Genital segment and aedeagus typical of the genus (figs. 25-27). Spermatheca (fig. 28) with a 2-turns coil followed by a long curve ending in a bulb.

Etymology. The name is derived from Latin for "equal", referring to the same antenna in male and female, in contrast with the other named species of the genus.



Figures 21-28. *Amplexella similis*, sp. n., 21-27, male. 21, habitus, dorsal view; 22, protarsus and protibia, dorsal view; 23, maxillary palp; 24, antenna; 25, genital segment, ventral view; 26-27, aedeagus, left lateral and dorsal views; 28, female, spermatheca.

Parapaulipalpa, gen. n.

Diagnosis and Description. Besides the typical characters of the tribe, cited above: Generally small bodied cholevines. Antenna somewhat short. Palp normal. Aedeagus elongate, apical orifice dorsally subterminal and cutting the apex of the aedeagus slightly left from the median axis; the dorsal opening being somewhat oval in shape; aedeagus somewhat S-shaped in dorsal view; flagellum elongate, longer than the aedeagus; basal bulb of the flagellum placed outside the aedeagus in the rest position. Genital segment globular, spiculum gastrale straight and somewhat long. Spermatheca bearing a 2-turns coil and a long apical bulb.

The genus is known for several still undescribed species.

Etymology. The name is derived from “Para” + “Paulipalpa”, referring to the sister relationship of this genus with *Paulipalpa*.

Gender: Feminine.

Type Species. *Parapaulipalpa dentata*, sp. n., present designation.

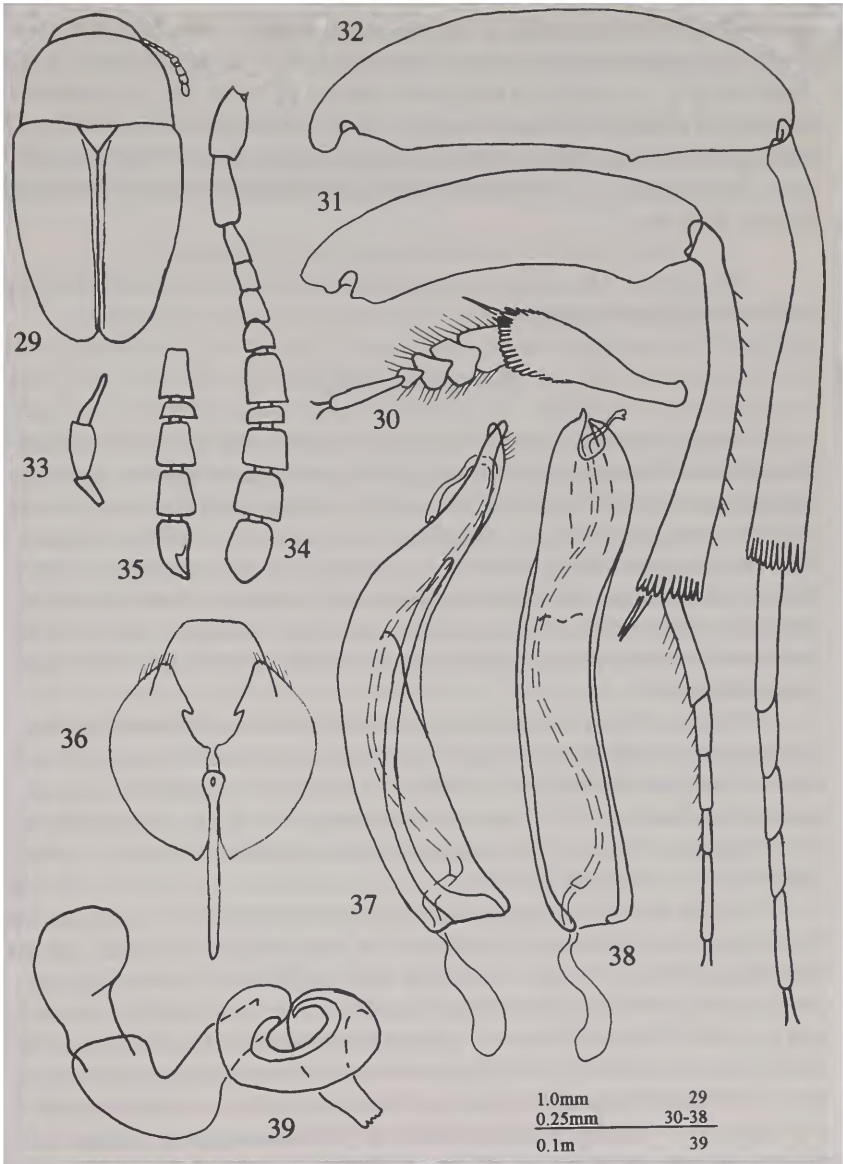
Parapaulipalpa dentata, sp. n.

(figs. 29 - 39)

Holotype, male (SBP). Type locality and data: Venezuela: Aragua: Rancho Grande, Port. Pass, H.D., undated, S.B. Peck. 2 male and 1 female paratypes with the same data.

Other paratypes: Venezuela: Aragua: Rancho Grande, Berlese 194, 51kg litter, undated, S.B. Peck, 4 males and 6 females (SBP, MZSP). Several other specimens in the SBP collection.

Diagnosis and Description. Length: 1.7-1.85 mm; width: 0.8-0.9 mm. Besides characteristics listed above, it is defined by the following characters: Colour dark brown in head and pronotum, and reddish brown in elytra. Eyes and wings fully developed. Antenna (figs. 34-35) 1.3 times as long as pronotum, almost reaching base of pronotum when laid back; last 2 segments slightly pale; last segment concave ventrally; proportions of length of each segment and that of the 9th from 1st to 11th: 1.65, 1.55, 0.95, 0.7, 0.7, 0.55, 1.15, 0.4, 1.0, 1.0, 1.45. Proportions of length and width of each segment of the club, from 7th to 11th: 1.3, 0.45, 1.0, 0.9, 1.35. Elytra (fig. 29) together 1.25 times as long as wide; with dense oblique strigae. First segment of male protarsus



Figures 29-39. *Parapaulipina dentata* sp. n., 29-38, male. 29, habitus, dorsal view; 30, protarsus and protibia, dorsal view; 31, mesotarsus, mesotibia and mesofemur, ventral view; 32, metatarsus, metatibia and metafemur, ventral view; 33, maxillary palp; 34-35, antenna; 36, genital segment, ventral view; 37-38, aedeagus, left lateral and dorsal views; 39, female, spermatheca.

(fig. 30) 0.75 times as wide as the maximum width of tibia. Proportions of length and width of each segment, from 1st to 5th: 1.15, 0.85, 0.8, 1.0, 5.0. Mesotibia (fig. 31) curved in both sexes. Male mesofemur (fig. 31) somewhat narrow and curved. Male metatibia (fig. 32) curved. Male metafemur (fig. 32) bearing a tubercle at the posterior margin. Aedeagus (figs. 37-38) pointed at apex. Spermatheca (fig. 39) with a 2-turns coil followed by a short curve ending in a long bulb.

Etymology. The name is derived from Latin for “with tooth”, referring to the toothed male metatibiae.

Phylogenetic analysis

During this study, several characters important for the characterization of specific and supraspecific taxa were recognized. They have been polarized, and grouped into a data matrix. This analysis resulted in a recharacterization of some supraspecific groups, based on synapomorphies. Thus, new combinations are proposed herein. However, one should note the preliminary scope of this analysis, because the data were taken mostly from *Adelopsis* species and only few species of the other genera in the tribe. Therefore, with the later inclusion of new characters and taxa, a new analysis could improve the resulting cladogram.

The list of taxa examined, the list of characters with the interpretation of their states, and the data matrix are given respectively in tables 2 to 4. Option “bb*” of HENNIG86 resulted in 25 trees with a length of 42 steps, a consistency index $ci = 0.90$ and a retention index $ri = 0.93$. Afterwards, running the option “nelsen”, a consensus tree was obtained (figure 1), having length 43, $ci = 0.88$ and $ri = 0.91$.

Based on this consensus tree, the monophyletic taxa *Adelopsis* and *Ptomaphagus* were treated as single taxa. A new analysis was made, excluding characters 4, 5, 9 and 11 (because they characterize internal groups of *Adelopsis* or *Ptomaphagus*) and resulted in four trees with length 33, $ci = 0.90$ and $ri = 0.85$. The resulting strict consensus tree also has length 33, $ci = 0.90$ and $ri = 0.85$ (figure 2). This cladogram resulted in a further resolved tree, with *Adelopsis* being sister group of *Parapaulipalpina* + *Paulipalpina* + *Ptomaphagus*. Actually, when the “semi-strict” consensus rule is used (combinable component consensus - Bremer, 1990), the resulting tree is completely resolved, with same length and indexes (figure 3).

Herein I used informal *Adelopsis* species-group names in order to facilitate recognition of and reference to such groups. However, their monophyletic status and their phylogenetic relationships are not yet completely established.

The Oriental genus *Pandania* was not included in the analysis because it was described based on only one female and, therefore, information for the matrix lacks.

Below, I discuss some of the characters used in the analysis, and the former and new supraspecific taxa, and propose some taxonomic changes, based on the phylogenetic analysis presented herein.

Discussion of some characters used in the analysis

Presence of carina in sternum (character 1). Jeannel (1936) characterized Ptomaphagini by having a large triangular metepisternum with the base facing the posterior region of body, contrary to the usual condition of this structure in the subfamily (triangular and narrow, with base facing anteriorly) (see figure 40, *Jm*). All authors afterwards followed Jeannel's characterization, even to the present. When making a comparative analysis among specimens of Ptomaphagini and other Cholevinae, I noticed indeed the presence of a large triangular "plate" on the metasternum, which should be considered apomorphic at the tribal level. However, Jeannel and following authors were equivocal in identifying it as the metepisternum. The metepisternum is easily recognized as lying laterally to the anapleural suture. While analysing specimens of the tribe, I noticed that the metepisternum and metepimeron are similar in the remaining Cholevinae, and that this "triangular plate" is located in the metasternum (figures 41 to 50 show sternal plates in several cholevines). Therefore, the carina is a new feature and should be considered as an apomorphy (see figure 40, *mc*). In addition, the carina is usually not complete, hence a complete plate is not present. Moreover, the same metasternal carina was noticed in some Oriental Nemadini (*Nemadus*, *Micronemadus* - figure 47), whereas it is absent in Neotropical and Transantarctic Nemadini (*Dissochaetus*, *Pseudonemadus* - figure 48), and other cholevines (figures 49 and 50), including the Eucatopini (*Eucatops*), which has been considered to be the sister group of Ptomaphagini. Taking into account that the Nemadini are generally characterized to be the most primitive group among Cholevinae (i.e., they are not characterized by apomorphies, but by the lack of such), there are two phylogenetic possibilities to be considered: (1) the Nemadini are monophyletic and the metasternal carina is a convergence among Ptomaphagini and Oriental Nemadini, being an apomorphy for each group; or (2) the Nemadini are non-monophyletic and the Oriental Nemadini and the Ptomaphagini together are a monophyletic group, and the metasternal carina is a synapomorphy for the group. This second hypothesis might be supported by the fact that in the present phylogenetic analysis the only Oriental genus *Ptomaphaginus* resulted

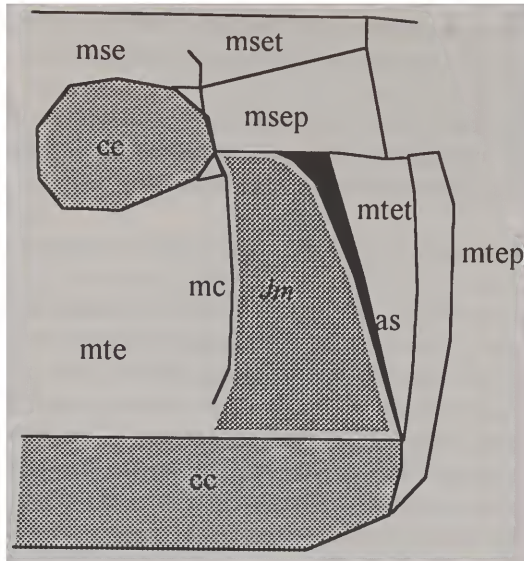


Figure 40. Schematic drawing of sternal plates in Ptomaphagini. cc = coxal cavity; mse = mesosternum; msep = mesepimeron; mset = mesepisternum; mte = metesternum; mtep = metepimeron; mtet = metepisternum; as = anapleural suture; mc = metesternal carina. *Jm* = Jeannel's metepisternum.

to have a basal position in the tribe. This should be further tested and may bring a complete redefinition of the phylogenetic relationships for both Cholevinae tribes and within the Ptomaphagini.

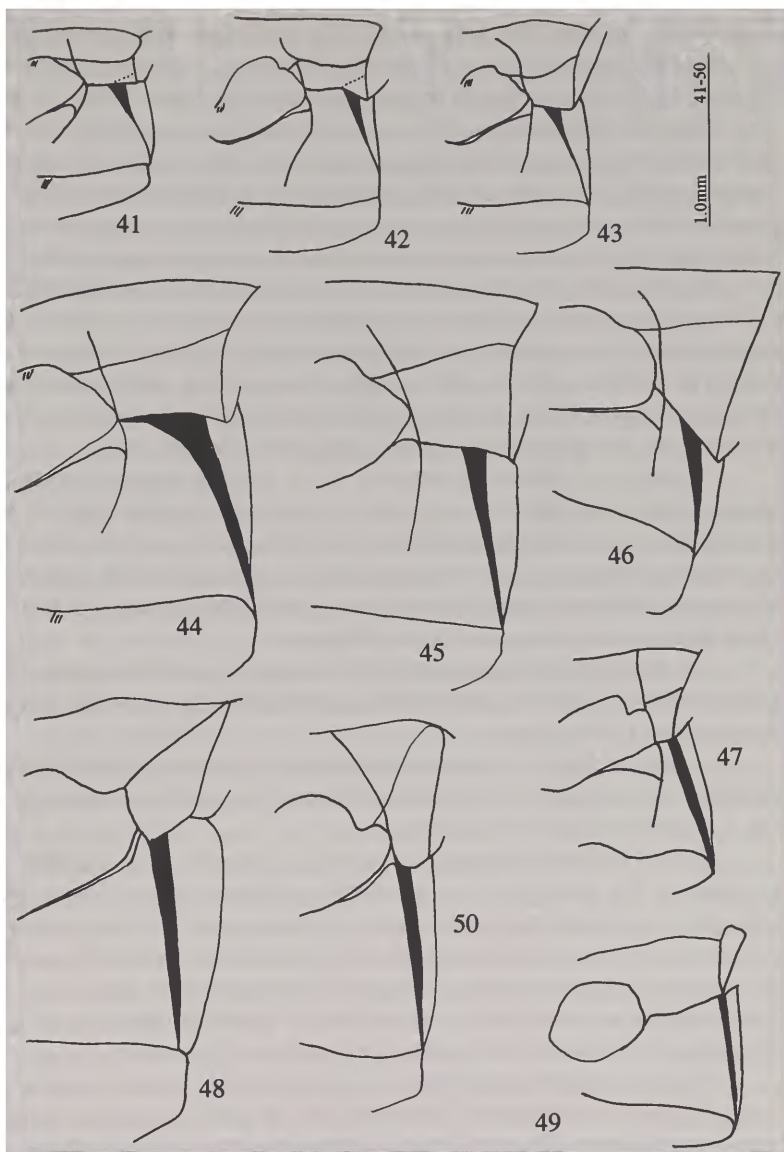
Margins of mesepimeron (characters 2 and 3). The mesepimeron is characterized as being trapezoidal in most Ptomaphagini (Jeannel, 1936). However, when analysing this structure I noticed that the posterior suture is in reality transverse. Additionally, the mesepimeron projects to partly lie over the metepisternum. This projection gives the trapezoidal shape to the structure. This occurs even in genera which have a transverse mesepimeron (*Ptomaphaginus* and *Proptomaphaginus* - figures 41 and 42).

Dorsal setae both long and short (character 4, state 1) is autapomorphic in *Echinocoleus*.

Very short legs (character 5, state 1) is autapomorphic in *Synaulus*.

Protarsi not-expanded in males (character 6, state 1) is autapomorphic in *Proptomaphaginus*.

Armature of protibia (character 7): only at apex or also along external margin. The latter has been considered to be the apomorphic state, and, thus *Ptomaphaginus* and *Proptomaphaginus* have been grouped in the same subtribe (*Ptomaphaginina*), based mainly on this character. However, because *Eucatops*



Figures 41-50. Sternal plates in Cholevinae: 41, *Ptomaphaginus chapmani* Peck, 1981; 42, *Proptomaphaginus puertoricensis* Peck, 1970; 43, *Peckena ventralis* n.sp.; 44, *Amplexella dimorpha* sp. n.; 45, *Ptomaphagus (Adelops) bordoni* (Jeannel, 1964); 46, *Ptomaphagus (Synaulus) agilis* (Lucas, 1849); 47, *Micronemadus pusillimus*; 48, *Dissochaetus* sp. (Venezuela); 49, *Eucatops* sp. (Panama); 50, *Catops* sp. (Canada).

also shows this feature, Jeannel (1936) and later authors recognized Eucatopini+Ptomaphagini as a single tribe (Eucatopini). Hence, based on this relationship, this feature should be considered plesiomorphic. However, as discussed elsewhere (Gnaspini, 1994), it is still premature to suggest a phylogenetic relationship between Eucatopini and any other tribe, because *Eucatops* has non-comparable and strikingly derived features. It should be noted that several species in different Leiodidae groups have a protibial armature only at the apex, and several other taxa have an armature along the external margin too. Therefore, to determine which is the plesiomorphic and which is the apomorphic state is presently not possible. Herein, I considered the marginal armature to be plesiomorphic. A new analysis was made considering the feature to be apomorphic (treated as state 1), and this did not affect the resulting cladogram - state 1 resulted plesiomorphic in relation to state 0. Hence, after the present phylogenetic analysis, the marginal armature resulted to be plesiomorphic.

Length of antenna (character 8). A slender antenna (state 1) is autapomorphic in *Paulipalpina*. In turn, a very short antenna (state 2) could be considered to be synapomorphic between *Echinocoleus* and *Synaulus*; however, because both taxa are myrmecophilous, it is likely that the reduction of the antenna is a convergence. Furthermore, although antenna in both are reduced, their general shapes are quite different.

Antennal club (character 9) with 7 segments (state 1) is autapomorphic in *Ptomaphagus (Tupania)*; and with 8 segments (state 2) is autapomorphic in *Ptomaphagus (Merodiscus)*.

Ratio of length of last and penultimate segment of maxillary palp (character 10) smaller than 1 is autapomorphic in *Paulipalpina*; whereas greater than 1 is autapomorphic in *Eucatops*.

Ventral abdominal projection in males (character 11). Together with the shape of the aedeagus, this characterizes species in the *elephas* group, although it is polymorphic (some species of the group do not have abdominal projections) and some other species of *Adelopsis* also show sternal projections. For instance, it is polymorphic in the two known species in *picunche* group. This character will be closely analysed in the future to determine if it is a convergence or synapomorphy among such groups of species.

Genital segment (characters 12 and 13). The genital segment in Ptomaphagini is considered to be reduced to the spiculum gastrale and two latero-ventral plates. However, *Proptomaphaginus* has an intermediate stage, where a slight connection between the plates still occurs. This was considered to be the plesiomorphic state in the tribe. From state 1 of character 13, first figure, which is closest to what is considered to be the "typical" state of the tribe, the spiculum gastrale has become modified, possibly independently, re-

sulting in three different states: spiculum largely elongate (also considered in state 1), generally associated with an elongate aedeagus; spiculum broad, taking a shape of a rectangular or trapezoidal plate; and spiculum divided at apex, taking a saddle shape. The last two (considered together as state 2) are generally associated with short and straight or globose aedeagus. Previously, all four forms were treated as different states. However, this did not help solving some groups. In addition, the character is polymorphic in some taxa (e.g., *Ptomaphagus* species have either first or second form of state 1). Because considering them together two by two did not affect the final result, it was preferred in the final analysis herein presented in order to simplify it.

Ligula (character 17) is polymorphic in *Ptomaphagus* as can be seen from table 4. When running the simplified second analysis (shown in figures 2 and 3) either considering it plesiomorphic (state 0) or apomorphic (state 1) in the genus resulted the same topology. When considering it as state 0, it resulted to be a reversion.

Apical opening of aedeagus (character 19). Jeannel (1936) and later authors characterized *Ptomaphagus*, *Adelopsis*, *Echinocoleus* and *Synaulus* as having a dorsal opening; and the passage of the opening from the ventral region to the dorsal surface forms a narrow slit, always on the left side of the aedeagus. In turn in *Proptomaphagus* and *Ptomaphagus*, the opening is either ventral or dorsal, and in this last case then cuts the right side of the aedeagus tip. Analysing a large number of specimens in the tribe, I noticed a large number of types of cuts to achieve the dorsal region. The plesiomorphic state is the maintenance of the opening in a ventral position. In some species, the migration to the dorsal region occurs by cutting the sagittal plane, resulting in two apical lobes equal or subequal (state 1), which is the case of *Proptomaphagus*, *Paulipalpina* and *Parapaulipalpina*. In *Ptomaphagus*, some species have a ventral opening, whereas in others the cut occurs on the right side (state 4). The latest was the one considered in the analysis herein presented; however, considering state 0 for the genus did not affect the final cladogram. Due to a lack of material and because it was not the primary target of this study, I did not check if there could be two different Oriental lineages and thus two different genera. Among those species in which the opening cuts the left side, this cut may be placed medially, and the apical setae are placed opposite in relation to the slit (state 2), as is the case of *Adelopsis*; or more laterally, and the apical setae are placed at the same side of the slit (state 3), which is the case of *Ptomaphagus*. This character was treated as unordered, because it is not possible to establish a transformation series.

Spermatheca (characters 20 to 22). The simple curved sac (character 20, state 1; character 22, state 0) was considered to be the plesiomorphic state

in the tribe. From the plesiomorphic state of the apex of the spermatheca (simple sac), three derived states possibly developed independently - in all three of them there is a bulbous widening of the tip, which could be related to capture and/or expulsion of the sperm. Another transformation is the progressive coiling of the spermatheca (character 22). State 4 is associated with a second widening of the spermatheca, which occurs in the duct before the coil. Technically, this widening should be considered a separate character; however, because it is autapomorphic in the *elephas* group (although polymorphic - some species show type 2), as is state 4 itself, it was not helpful in establishing a phylogenetic relationship among groups. It should be also noted that there is an apparent relationship between the states of character 20 and states of character 22. Because of that, different morphologies were considered in the same state because they appeared in the same taxonomic unit. Previously, they were considered to be independent states; however, because they did not affect the final result, they were grouped to simplify the final analysis herein presented.

Supraspecific taxa

Ptomaphaginus and *Proptomaphaginus*: from the literature, they constitute the subtribe Ptomaphaginina, characterized by having the protibia provided with a comb of equal spines both at the apex and along the external margin, contrary to the remaining genera (which constitute the Ptomaphagina), which show only a comb of spines at the tibial apex. This first character also characterizes *Eucatops* and Eucatopini, considered by Jeannel (1936) and later authors to be the sistergroup of Ptomaphagini, based partly on the presence of this marginal tibial comb. Following this definition, the protibial marginal comb should be considered to be plesiomorphic inside Ptomaphagini. In turn, it could be considered synapomorphic for Ptomaphaginina, and a convergence with *Eucatops*. However, the present phylogenetic analysis resulted in the marginal comb to be plesiomorphic. Therefore, I suggest here that the use of the subtribes Ptomaphagina and Ptomaphaginina is abandoned.

Ptomaphaginus is characterized by having the following synapomorphies: anterior lateral margin of mesepimeron transverse, and apical opening of aedeagus cutting the right side (although this character is polymorphic, and some species show the plesiotypic condition). And *Proptomaphaginus* is characterized by the non-expanded male protarsus, and a simple genital segment with lateral plates not totally distinct from the spiculum gastrale (which resulted to be apomorphic after the phylogenetic analysis, and not plesiomorphic as previously treated).

Peckena (figures 4-11, 43): this so far monotypic new genus shows the plesiomorphic state in the opening of the aedeagus, which is still ventral. Be-

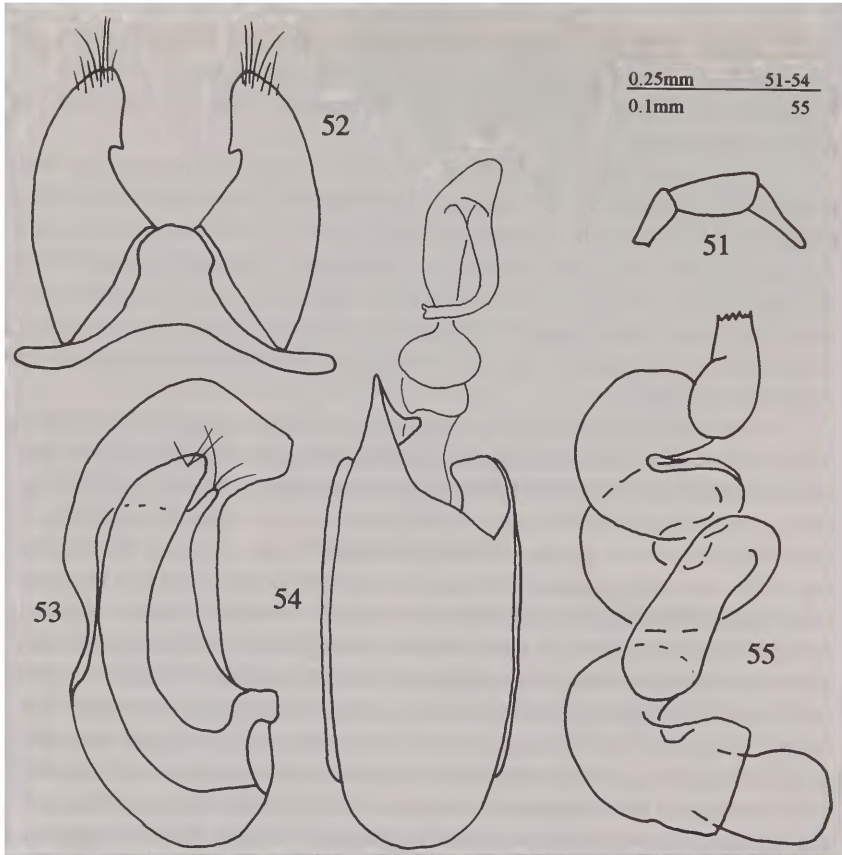
cause it is monotypic, it is premature to define autapomorphies for the genus (because they could actually be specific autapomorphies). Anyway, as far as I know, an armed flagellum is unique in the subfamily, and may constitute the generic apomorphy.

Amplexella (figures 12-28, 44): this new genus contains only two new species from Venezuela so far, and is characterized by a very short and globose aedeagus, provided with an extremely long flagellum, which rests completely coiled inside the aedeagus. Besides, the migration of the opening cuts along the sagittal plane, without a well defined slit. Moreover, one of the species (*A. dimorpha*) shows what seems to be the first case of extreme antennal sexual dimorphism in the family: the 1st to 8th segment of the male antenna are extremely elongate.

Adelopsis (figure 51-55): the genus as has been used in the literature was previously non-monophyletic, as already discussed. After the present analysis, it is redefined to have the following synapomorphies: opening of aedeagus cutting the left side, to the right of the apical setae, so that the resulting slit stays between the two groups of setae (character 19, state 2); and the broadening of the spiculum gastrale of the genital segment which result in a rectangular or saddle-shaped plate (character 13, state 2). However, because there are sometimes big variations in some character complexes, it is still premature to attempt to analyse intrageneric phylogenetic relationships. Further analysis may even define generic status for some groups. Some groups, however, show typical morphologies. The species in *elephas* group show a ventral projection at the aedeagus tip, which resembles a beak or snout in lateral view. The Brazilian species in the subgenus *Iutururuca* (here referred as the *Adelopsis leo* group) have a coiled ribbon-shaped flagellum. Although the etymology and description of *Iutururuca* (Gnaspini, 1993) defined it to have the spiculum gastrale of the genital segment divided at the apex, this character also appears in other groups of species (e.g., in the *elephas* group). If it is synapomorphic or symplesiomorphic remains to be determined.

Parapalpalpina (figures 29-39): the species of this new genus show an aedeagus similar to that of *Palpalpina* (character 19, state 1). However, the aedeagus seems somewhat medially "bent" in lateral view and "twisted" in dorsal view; and the bulb of the long flagellum lies outside the aedeagus base.

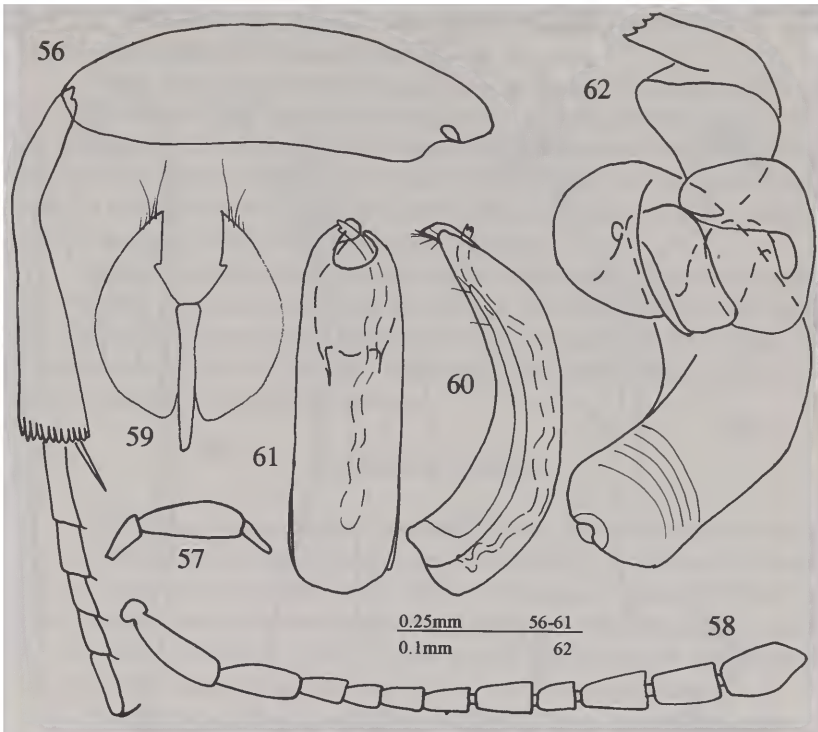
Palpalpina (figures 56-62): previously included in *Adelopsis*, this recently described genus (Gnaspini & Peck, 1996) show synapomorphies such as (1) the last segment of the maxillary palp shorter than the penultimate (approximate ratio 1:2); (2) a slender antenna; and (3) spermatheca of type 3 (character 22) with apex of type 4 (character 20). Although the slender antenna gives an impression of being elongate, the ratio between its length and



Figures 51-55. *Adelopsis leo* Gnaspini, 1993, 51-54, male. 51. maxillary palp; 52. genital segment, ventral view; 53-54. aedeagus, left lateral and dorsal views; 55. female, spermatheca.

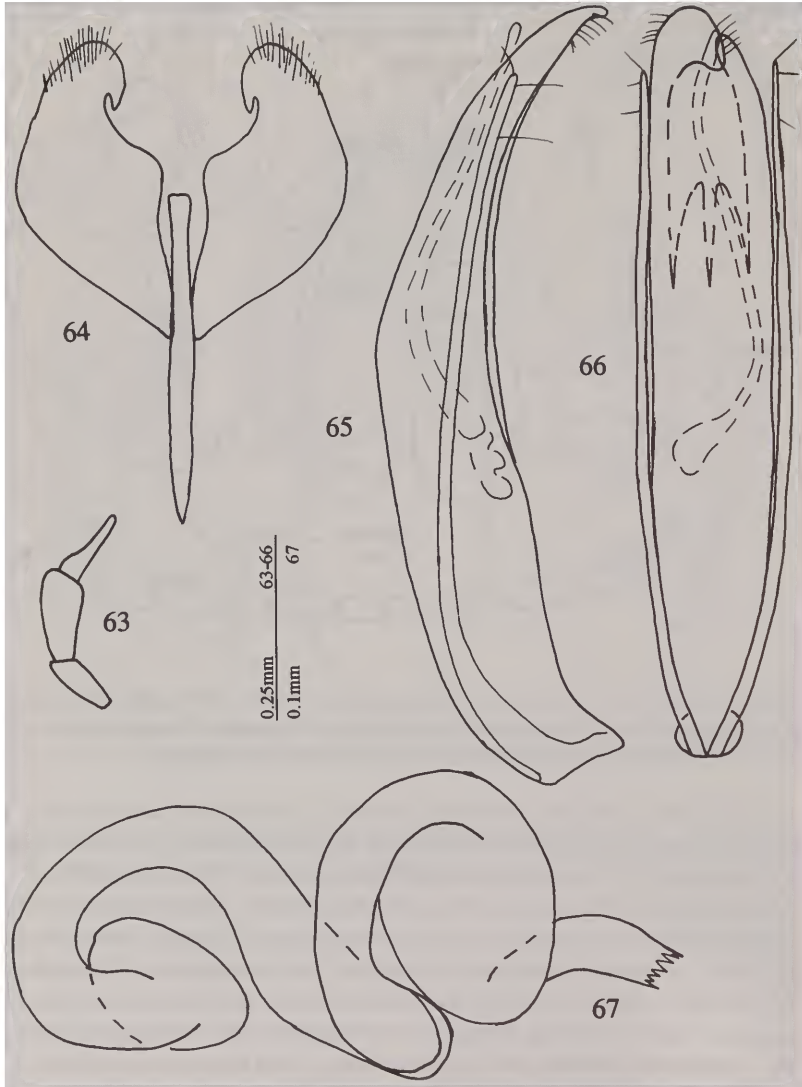
that of the pronotum fits in the range of other *Ptomaphagini*. Thus, a reduction in the thickness of each segment probably occurred. It should be noted that, despite being previously included in *Adelopsis*, it is one of the few groups in the tribe which is easily recognized by external characters. Because of this easy external identification and due to the general homogeneity of specific external characters, several species of *Paulipalpina* were previously recognized as belonging to the same species of *Adelopsis* (*simoni*).

Ptomaphagus (figures 45, 46, 63-67): the species of the former four subgenera of *Ptomaphagus*, *Echinocoleus*, *Synaulus* and the "*Adelopsis*" from the Appalachians (USA) share a series of apomorphies, such as (1) base of the elongate aedeagus laterally compressed, forming a ventral keel, resulting in



Figures 56-62. *Paulipalpina claudicans* (Szymczakowski, 1980), 56-61, male. 56, mesotarsus, mesotibia and mesofemur, ventral view; 57, maxillary palp; 58, antenna; 59, genital segment, ventral view; 60-61, aedeagus, right lateral and dorsal views; 62, female, spermatheca.

an upside-down piriform transverse section; (2) aedeagus opening cutting the left side left of the apical setae (character 19, state 3); and (3) spermatheca of type 1 (character 22) with apex of type 2 (character 20). The taxa *Echinocoleus*, *Synaulus*, *Merodiscus* and *Tupania* have easily recognisable external autapomorphies and probably represent monophyletic groups. However, there are, so far, no striking apomorphies defined for the subgenera *Ptomaphagus* and *Adelops* - they are defined by the lack of the apomorphies of the other subgenera and by having, respectively, a Nearctic and a Palearctic distribution. Because they form a monophyletic group and because the relationships among the subgenera of *Ptomaphagus* and with related genera are yet precisely definable, I prefer to consider the whole group under the genus *Ptomaphagus*. Due to the doubt about the monophyly of *Ptomaphagus* (*s. str.*)



Figures 63-67. *Ptomaphagus bordoni* (Jeannel, 1964) comb.n., 63-66, male. 63, maxillary palp; 64, genital segment, ventral view; 65-66, aedeagus, left lateral and dorsal views; 67, female, spermatheca.

and *Adelops*, I now prefer not to split all groups into genera. However, a future and more complete phylogenetic analysis of this group may better define the generic and subgeneric status of each group.

Thus, while this further analysis is lacking, I prefer to define the genera *Echinocoleus* and *Synaulus* as subgenera of *Ptomaphagus*, and to create the new subgenus *Appadelopsis* to group the species from the Appalachians previously placed in *Adelopsis* by Peck (1978a). Moreover, the recent description of a new species of *Echinocoleus* also helps considering it to be a subgenus of *Ptomaphagus* (see Peck & Gnaspini, in press).

Moreover, although the southern limit of the distribution of the subgenus *Adelops* was previously defined to be Mexico, the SBP collection has several new species of *Ptomaphagus* distributed more to the south, into Costa Rica, Panama, Venezuela and Ecuador. These species do not belong in *Tupania* and should probably be placed in *Adelops*.

Nomenclatural changes

The genus *Adelopsis* has a feminine gender, but several described species have been given masculine gender endings (c.g., *A. brunneus* Jeannel, 1936, *A. insolitus* Szymczakowski, 1961). Furthermore, Jeannel (1936) "corrected" some feminine names to masculine endings, including the type species (*A. heterocera* Portevin, 1907). Thus, herein the names of the species of *Adelopsis* are corrected to feminine gender, whenever appropriate.

The analysis of types and other specimens from several collections allowed the more appropriate characterization of the species with available genitalia. The analysis of the genitalia and the phylogenetic analysis led to new combinations of taxa. Moreover, the labelled specimens were checked, and several wrong identifications were detected, including specimens belonging to the type series.

The complete list of all described species of *Ptomaphagini*, as far as I know from the literature, after all nomenclatural changes proposed herein is given in the Appendix.

Herein, I propose several taxonomic changes. However, the redefinition of types and the redescription and illustration of the species, when appropriate, will be given in future papers of the series dealing with the revision of "*Adelopsis*".

The genus *Echinocoleus* is defined to be a subgenus of *Ptomaphagus*:
Echinocoleus Horn, 1885; Jeannel, 1936; Peck, 1976.
Ptomaphagus (*Echinocoleus*); Peck & Gnaspini, in press.

The genus *Synaulus* is defined to be a subgenus of *Ptomaphagus*:
Synaulus Portevin, 1903; Jeannel, 1936.
Ptomaphagus (*Synaulus*), st. n.

The species of “*Adelopsis*” from the Appalachians are transferred to the following new subgenus of *Ptomaphagus*.

***Ptomaphagus* (*Appadelopsis*), subg. n.**

Diagnosis and Description are thoroughly given by Peck (1978a).

Etymology. The name refers to the “*Adelopsis*” from the “Appalachians”.

Gender: Feminine.

Type Species. *Adelops mitchellensis* Hatch, 1933, present designation.
List of species transferred from *Adelopsis*: *P. (App.) alleghenyensis* (Peck, 1978), *P. appalachianus* (Peck, 1978), *P. bedfordensis* (Peck, 1978), *P. cumberlandus* (Peck, 1978), *P. fumosus* (Peck, 1978), *P. joanna* (Peck, 1978), *P. jonesi* (Peck, 1978), *P. mitchellensis* (Hatch, 1933) (described under *Adelops*, genus posteriorly defined as a subgenus of *Ptomaphagus*, and transferred to *Adelopsis* by Peck, 1973), *P. nashvillensis* (Peck, 1978), *P. orichalcum* (Peck, 1978), *P. pecki*, nom. n. (for *Ptomaphagus (Appadelopsis) altus* (Peck, 1978) comb. n., not *Ptomaphagus (Adelops) altus* Peck, 1973), *P. pisgahensis* (Peck, 1978), *P. richlandensis* (Peck, 1978), *P. scottsboroensis* (Peck, 1978), *P. steevesi* (Peck, 1978), and *P. suteri* (Peck, 1978).

Species transferred from *Adelopsis* to *Ptomaphagus*: *P. bordoni* (Jeannel, 1964), from Venezuela; and *P. sciakyi* (Zoja, 1993), from Ecuador. As previously discussed, these species probably belong in the present subgenus *Adelops*.

Species transferred from *Adelopsis* to *Paulipalpina*, in addition to *P. claudicans* (Szymczakowski, 1980), from Brazil (type species of *Paulipalpina*, Gnaspini & Peck, 1996): *P. simoni* (Portevin, 1903) (described under *Catops*, transferred to *Pseudonemadus* by Portevin, 1914, and to *Adelopsis* by Jeannel, 1936), from Venezuela; *P. dispar* (Portevin, 1903) (described under *Catops*, transferred to *Pseudonemadus* by Portevin, 1914, and to *Adelopsis* by Jeannel, 1936) and *P. exigua* (Kirsch, 1870) (described under *Choleva* and transferred to *Adelopsis* by Jeannel, 1936), from Colombia.

P. dispar was treated as a synonym of *P. exigua* by Jeannel, 1936, based

only on the descriptions. Because apparently the type of *P. exigua* is not available, because the difference in size is big - 1,0 and 1,5 mm -, and because the species of this genus are mostly externally similar to each other (leading to misidentification without dissection of genitalia), I found it better to resurrect *P. dispar* and maintain *P. exigua* as a nominal species, probably transferred to *Paulipalpina*.

Species transferred from *Adelopsis* to *Parapaulipalpina*, gen. n.: *P. filicornis* (Jeannel, 1936), from Colombia. The male type seen was previously dissected (probably by Jeannel) but genitalia was not available. Therefore I could not check the characters. However, based on the drawings from Jeannel (1936) and the characters of the new genus, it is here transferred to *Parapaulipalpina*.

Species kept in *Adelopsis*: *A. ascutellaris* (Murray, 1856) (described under *Catops*), and *A. ovalis* Jeannel, 1936, from Venezuela; *A. brunnea* Jeannel, 1936 ["*brunneus*"], from Venezuela, Colombia and Trinidad (this species has six described subspecies, which will probably receive status of species after further study of all types: *A. b. azzalii* Szymczakowski, 1975, *A. b. linarezi* Szymczakowski, 1969 (not examined), *A. b. orcina* Szymczakowski, 1975 ["*orcinus*"], and *A. b. pteromorioria* Szymczakowski, 1975 ["*pteromorius*"], from Venezuela, *A. b. brevicollis* Szymczakowski, 1975 (not examined), from Trinidad, and *A. b. brunnea* Jeannel, 1936 ["*brunneus*"] (not examined), from Colombia); *A. asperoides* Szymczakowski, 1963, *A. benardi* Portevin, 1923, *A. brasiliensis* Jeannel, 1936, *A. grouvellei* Jeannel, 1936, *A. insolita* Szymczakowski, 1961 ["*insolitus*"], *A. leo* Gnaspini, 1993, *A. luculenta* Szymczakowski, 1963 ["*luculentus*"], *A. piruapuera* Gnaspini, 1993, and *A. triangulifera* Szymczakowski, 1961 ["*triangulifer*"], from Brazil; *A. aspera* Jeannel, 1936 ["*asper*"], from Brazil and Paraguay; *A. bellatrix* Szymczakowski, 1968 ["*bellator*"], and *A. peruviansis* Blas, 1980 (not examined), from Peru; *A. bruchi* (Pic, 1926) (described under *Ptomaphagus*), from Argentina; *A. darwini* Jeannel, 1936, from Uruguay; and *A. heterocera* Portevin, 1907 (type species), and *A. ruficollis* (Portevin, 1903) (described under *Catops*), from Bolivia.

Species transferred from *Ptomaphagus* to *Adelopsis*: *A. picunche* (Gnaspini, 1991), from Argentina. Because it lacks apomorphies of *Ptomaphagus* and because it shows some characters of *Adelopsis*, this species is here transferred. However, together with some undescribed species, it might constitute a separate group, which will be tested with the improvement of the phylogenetic study.

Finally, among the labelled material from other collections, some specimens were misidentified, as follows. The proper corrections and descriptions will be made in future papers.

- Adelopsis ascutellaris*: the series from MNHN identified by Portevin, 1902 includes specimens of the species and of different species.
- A. asperoides*: the five males from MZSP identified and illustrated by Gnaspini (1993) do not belong in that species.
- A. benardi*: the male from NMPC identified by Szymczakowski (1963) as *?benardi* (sic) does not belong in that species.
- A. grouvellei*: the three males from NMPC identified by Szymczakowski (1963) belong in two different undescribed species.
- Paulipalpina simoni*: the male from BMNH, from Brazil, identified and illustrated by Jeannel (1936) belongs in an undescribed species; the male from NMPC, from Brazil, identified by Szymczakowski (1963) belongs in *P. claudicans*; the specimens from MNHN, from Venezuela, identified by Szymczakowski (1968) belong in a second undescribed species; and the male from ZMHB, from Mexico, identified by Szymczakowski (1968) belongs in a third undescribed species.
- Parapaulipalpina filicornis*: the female cotype from MNHN belongs in the genus *Paulipalpina*.

Conclusions and perspectives

Because of the large number of new species of "*Adelopsis*" to be described and because of the large number of already described species of the other genera, this phylogenetic study should be considered preliminary. However, several monophyletic groups have been recognized in this analysis, leading to a redefinition of some taxa. Still some taxa deserve further study for proper definition. In turn, the availability of a large number of specimens has offered the opportunity to identify structures not used before in Cholevinac taxonomy, and which have been shown to be important to characterize specific and supraspecific taxa. Therefore, future phylogenetic studies are needed to help understand taxonomic relationships among the Cholevinac, and especially the Ptomaphagini and related taxa.





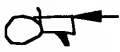
Table 1. Specimens (including types) of *Adelopsis* borrowed from collections (except MZSP and SBP) and seen during the study to allow better definition of taxa and definition of nomenclatural changes. The listed taxa follow the taxonomy used previous to the present paper

- A. ascutellaris* (Murray, 1856) - 2 male (Portevin det. 1902) (MNHN); 1 type male, 1 type female (BMNH).
- A. asper* Jeannel, 1936 - 1 type male, 1 type female (MNHN); 1 type male (BMNH); 4 female (Szymczakowski det., 1963) (NMPC).
- A. asperoides* Szymczakowski, 1961 - 1 holotype male, 1 paratype male (NMPC).
- A. bellator* Szymczakowski, 1968 - 1 holotype male, 13 paratypes (ZMHB).
- A. benardi* Portevin, 1923 - 1 type male, 1 type female (MNHN); 1 male (Szymczakowski det., 1963) (NMPC).
- A. bordoni* Jeannel, 1964 - 1 holotype male, 1 allotype (MNHN).
- A. brasiliensis* Jeannel, 1936 - 1 type male (MNHN).
- A. bruchi* (Pic, 1926) - 2 types male, 1 type female (MNHN); 3 types, 24 individuals (MACN).
- A. claudicans* Szymczakowski, 1980 - 1 female (Gnaspini det., 1994) (NHRS).
- A. darwini* Jeannel, 1936 - 1 holotype female (BMNH).
- A. exiguus* (Kirsch, 1870) - 1 type male, 1 type female, of *A. dispar* (Portevin, 1903) (MNHN).
- A. filicornis* Jeannel, 1936 - 1 type male, 1 type female (MNHN).
- A. grouvellei* Jeannel, 1936 - 1 type male (MNHN); 1 type female (BMNH); 3 male (Szymczakowski det., 1963) (NMPC).
- A. heterocerus* Portevin, 1907 - 2 types male (MNHN).
- A. insolitus* Szymczakowski, 1961 - 1 holotype male (NHRS).
- A. luculentus* Szymczakowski, 1963 - 1 holotype male (NMPC).
- A. ovalis* Jeannel, 1936 - 1 type male (MNHN).
- A. ruficollis* (Portevin, 1903) - 2 types male (MNHN).
- A. sciakyi* Zoia, 1993 - 1 holotype male (SZ).
- A. simoni* (Portevin, 1903) - 1 holotype female; 2 male (no det. label, probably Szymczakowski det., 1968) (MNHN); 1 male (Jeannel det., 1936) (BMNH); 1 male (Szymczakowski det., 1963) (NMPC); 1 male (Szymczakowski det., 1967) (ZMHB).
- A. triangulifer* Szymczakowski, 1961 - 1 holotype male (NHRS); 1 male (Szymczakowski det., 1963) (NMPC).






Table 2. Taxa used in the cladistic analysis of supraspecific groups of Ptomaphagini, for constructing the matrix in table 4.

- Dissochaetus: vanini* (Brazil), sp. (Venezuela).
Eucatops: sp. (Panama).
Ptomaphagus: chapmani (Borneo).
Proptomaphagus: puertoricensis (Puerto Rico).
Peckena: ventralis (Peru).
Amplexella: dimorpha (Venezuela).
Adelopsis (gr. heterocera): sp. (Peru).
Adelopsis (gr. ascutellaris): coronaria (Costa Rica/Panama).
Adelopsis (gr. leo): leo, sp. (Brazil).
Adelopsis (gr. elephas): pileata (Costa Rica), *rostrata* (Costa Rica/ Panama).
Adelopsis (gr. picunche): picunche (Argentina), sp. (Ecuador).
Parapaulipalpina: dentata (Venezuela), sp. (Colombia).
Paulipalpina: clavigera (Costa Rica/Panama), *claudicans* (Brazil).
Ptomaphagus (Appadelopsis): cumberlanda (USA).
Ptomaphagus (Adelops): barri, nevadicus, texanus (USA), *bordoni* (Venezuela).
Ptomaphagus (Ptomaphagus): subvillosus sericatus (Europe).
Ptomaphagus (Tupania): yuvila (Mexico).
Ptomaphagus (Merodiscus): validus (Europe).
Ptomaphagus (Echinocoleus): setiger (USA).
Ptomaphagus (Synaulus): agilis (Northern Africa).



Table 3. Characters used in the cladistic analysis of supraspecific groups of Ptomaphagini, relative to the matrix in table 4, with definition of states. 0 = plesiomorphic; 1-4 = apomorphic. Multiple states are treated as unordered.

1. Presence of carina in metasternum: 0, absent; 1, present (arrow) 
2. Posterior lateral corner of mesepimeron:
 0, pointing anteriorly;  1, pointing posteriorly. 
3. Anterior lateral margin of mesepimeron: 0, inclined anteriorly;
 1, transverse 
4. Dorsal setae: 0, short; 1, long and short.






- 5. Legs: 0, normal; 1, very short.
- 6. Male protarsus: 0, expanded; 1, not-expanded.
- 7. Armature of protibia: 0, at apex and along external margin; 1, only at apex.
- 8. Antenna: 0, normal; 1, slender (with normal length); 2, very short.
- 9. Antennal club: 0, with 4 segments; 1, with 7 segments; 2, with 8 segments.
- 10. Ratio between length of last and penultimate segment of maxillary palp: 0, almost equal; 1, << 1; 2 >> 1.
- 11. Ventral projection on third ventrites of males: 0, absent; 1, present.
- 12. Genital segment: 0, tubular; 1, reduced to the spiculum gastrale and lateral plates.




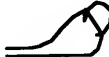

- 13. Shape of genital segment: 0,  ; 1  or;  2,  or 

- 14. Tegmen: 0, complete; 1, absent, parameres inserted onto aedeagus.
- 15. Relation length/width of aedeagus: 0, 2.5-3.5; 1, >4.0; 2, <2.0.
- 16. Cross section of base of aedeagus: 0, cylindrical; 1, upside down piriform (aedeagus with single ventral keel).

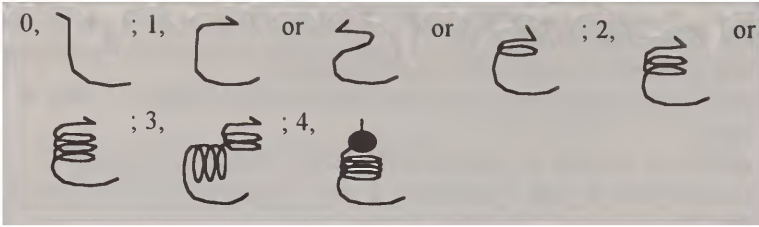
- 17. Ligula: 0, divided (); 1, undivided (fused) ().

- 18. Flagellum of internal sac: 0, short and thin; 1, short and thick; 2, elongate; 3, ribbon (helicoid).

- 19. Apical opening of aedeagus: 0, ventral medial  ; 1, dorsal medial  ; 2, dorsal, slightly to left  ; 3, dorsal, to left  ; 4, dorsal, to right  .

- 20. Spermatheca type (apex): 0,  ; 1,  ; 2,  3,  ; 4,  .

- 21. Spermatheca duct: 0, long; 1, short.
- 22. Spermatheca type (number of turns):



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Appendix. Checklist of genera and species of Ptomaphagini, after the nomenclatural changes made herein. References are indicated after each genus/subgenus - only the last broad review was used, in this case it is cited between brackets after the species name.

Proptomaphagus Szymczakowski, 1969 - 6 spp. [Peck, 1970, 1983]

P. apodemus Szymczakowski, 1969 (type) [Peck, 1983]

P. darlingtoni (Jeannel, 1936) (*Ptomaphagus (Adelops)*) [by Peck, 1970]

P. hispanoliensis Peck, 1983

P. microps Peck, 1973 [Peck, 1983]

P. puertoricensis Peck, 1970

P. reddelli Peck, 1983

Ptomaphagus Portevin, 1914 - 84 spp. [Szymczakowski, 1964, 1970a, 1972a, 1972b, 1974, 1975a, 1980; Hayashi, 1969; Jarrige, 1969; Peck, 1981; Nakane, 1982; Schilthuizen, 1984; Perreau, 1986, 1988, 1991, 1992a, 1992b; 1995, 1996; Perkovsky, 1992; Zoia, 1994]

P. angusticornis (Portevin, 1921) (*Ptomaphagus*) (by Jeannel, 1936) [Szymczakowski, 1964]

P. apiculatus Szymczakowski, 1975

P. assimilis Szymczakowski, 1972

- P. balazuci* Perreau, 1995
P. baliensis Perreau, 1995
P. bengalicola Perreau, 1991
P. bengalominus Perreau, 1991
P. besucheti Szymczakowski, 1972
P. bihamatus Szymczakowski, 1972
P. boutini Jarrige, 1969
P. bucculentus Szymczakowski, 1974
P. bryanti Jeannel, 1936 [Szymczakowski, 1964]
P. chapmani Peck, 1981
P. cherrapunjeensis Perreau, 1991
P. cilipes (Portevin, 1907) (*Ptomaphagus*; to *Euptomaphagus* by Hatch, 1928; to *Ptomaphaginus* by Jeannel, 1936) [Szymczakowski, 1964]
P. clibanarius Szymczakowski, 1970
P. coronatus Szymczakowski, 1974
P. depequkri Perreau, 1986
P. flavicornis (Motschoulsky, 1863) (*Catopsimorphus*; to *Ptomaphagus* by Portevin, 1914; to *Anemadus* by Hatch, 1928; to *Ptomaphaginus* by Jeannel, 1936) [Szymczakowski, 1964; Perkovsky, 1992]
P. fornicatus Szymczakowski, 1972
P. franki Perreau, 1992
P. gegenmuelleriae Perreau, 1992
P. gibberosus Szymczakowski, 1972
P. giganteus Szymczakowski, 1980
P. gracilis Schweiger, 1956 [Szymczakowski, 1964]
P. hamatus Szymczakowski, 1975
P. heterotrichus Szymczakowski, 1975
P. honestus Szymczakowski, 1964
P. ishizuchiensis Perreau, 1996
P. jacobsoni Szymczakowski, 1964
P. kosiensis Perreau, 1988
P. kumaominus Perreau, 1991
P. latescens Szymczakowski, 1964
P. lacertosus Szymczakowski, 1970
P. laticornis Jeannel, 1936 [Szymczakowski, 1964]
P. latipes (Pic, 1929) (*Ptomaphagus*) (by Jeannel, 1936) [Szymczakowski, 1964]
P. leclerci Perreau, 1992

- P. leucodon* Szymczakowski, 1975
P. loebli Szymczakowski, 1972
P. longitarsis Portevin, 1914 (type) [Szymczakowski, 1964]
P. major Szymczakowski, 1972
P. megalayanus Perreau, 1991
P. minimus Perreau, 1988
P. minor Szymczakowski, 1975
P. mirabilis Szymczakowski, 1972
P. murphyi Szymczakowski, 1970
P. mussardi Szymczakowski, 1975
P. nitens Jeannel, 1936 [Szymczakowski, 1964]
P. nepalominus Perreau, 1992
P. nipponensis Perreau, 1996
P. obtusus Szymczakowski, 1959 [Szymczakowski, 1964]
P. oribates Szymczakowski, 1965 [Perreau, 1988]
P. pallidicornis (Portevin, 1907) (*Ptomaphagus*; to *Euptomaphagus* by Hatch, 1928) [Szymczakowski, 1972a]
P. palpalis Szymczakowski, 1974
P. palpaloides Perreau, 1988
P. parvulus Henrot & Szymczakowski, 1971 [Szymczakowski, 1972a]
P. pilipennis Perreau, 1991
P. pilipennoides Perreau, 1991
P. pingtungensis Perreau, 1996
P. piraster Szymczakowski, 1975
P. portevini Szymczakowski, 1964
P. pygmaeus Zoia, 1994
P. riedeli Perreau, 1995
P. rubidus (Champion, 1927) (*Ptomaphagus*) (by Jeannel, 1936) [Szymczakowski, 1964]
P. rugosus Perreau, 1991
P. rufus Jeannel, 1936 [Szymczakowski, 1964]
P. sauteri (Portevin, 1914) (*Ptomaphagus*) (by Jeannel, 1936) [Szymczakowski, 1964]
P. scaber Szymczakowski, 1964
P. scaphaner Szymczakowski, 1972
P. schawalleri Perreau, 1992
P. securillus Szymczakowski, 1975
P. shibatai Hayashi, 1969
P. similis Schweiger, 1956 [Szymczakowski, 1964]
P. sinuatus Schilthuizen, 1984

- P. smetanai* Perreau, 1988
- P. takaosanus* Nakane, 1982
- P. tantillus* Szymczakowski, 1964
- P. tarsalis* Szymczakowski, 1964
- P. thieleni* Perreau, 1992
- P. trautneri* Perreau, 1992
- P. truncatus* Perreau, 1988
- P. turensis* Perreau, 1991

Pandania Szymczakowski, 1964 - 1 sp. [Szymczakowski, 1964]
P. oxytropis Szymczakowski, 1964 (type)

Peckena new genus - 1 sp. [herein]
P. ventralis new species (type)

Amplexella new genus - 2 spp. [herein]
A. dimorpha new species (type)
A. similis new species

Adelopsis Portevin, 1907 - 34 spp. [Jeannel, 1936; Szymczakowski, 1961, 1963, 1968, 1975b; Blas, 1980; Gnaspini, 1993; Gnaspini & Peck, 1996; herein]

- A. albipinna* Gnaspini & Peck, 1996
- A. ascutellaris* (Murray, 1856) (*Catops*) [Jeannel, 1936]
- A. aspera* Jeannel, 1936
- A. asperoides* Szymczakowski, 1963
- A. bellatrix* Szymczakowski, 1968
- A. benardi* Portevin, 1923 [Jeannel, 1936]
- A. brasiliensis* Jeannel, 1936
- A. bruchi* (Pic, 1926) (*Ptomaphagus*) [Jeannel, 1936]
- A. brunnea* Jeannel, 1936 [Szymczakowski, 1975b]
 - A. b. azzalii* Szymczakowski, 1975
 - A. b. brevicollis* Szymczakowski, 1975
 - A. b. brunnea* Jeannel, 1936
 - A. b. linaresi* Szymczakowski, 1969
 - A. b. orcina* Szymczakowski, 1975
 - A. b. pteromorpha* Szymczakowski, 1975
- A. confluens* Gnaspini & Peck, 1996
- A. coronaria* Gnaspini & Peck, 1996
- A. dybasi* Gnaspini & Peck, 1996

- A. darwini* Jeannel, 1936
A. elephas Gnaspini & Peck, 1996
A. galea Gnaspini & Peck, 1996
A. gilli Gnaspini & Peck, 1996
A. grouvellei Jeannel, 1936
A. heterocera Portevin, 1907 (type) [Jeannel, 1936]
A. howdenorum Gnaspini & Peck, 1996
A. insolita Szymczakowski, 1961
A. leo Gnaspini, 1993
A. luculenta Szymczakowski, 1963
A. ovalis Jeannel, 1936
A. perimeces Gnaspini & Peck, 1996
A. peruviansis Blas, 1980
A. picunche (Gnaspini, 1991) (*Ptomaphagus*), comb. n.
A. pileata Gnaspini & Peck, 1996
A. piruapuera Gnaspini, 1993
A. rostrata Gnaspini & Peck, 1996
A. ruficollis (Portevin, 1903) (*Catops*) (by Jeannel, 1922) [Jeannel, 1936]
A. sinuosa Gnaspini & Peck, 1996
A. stella Gnaspini & Peck, 1996
A. triangulifera Szymczakowski, 1961
A. vallicola Gnaspini & Peck, 1996

Parapaulipalпина new genus - 2 spp. [herein]

- P. dentata* new species (type)
P. filicornis (Jeannel, 1936) (*Adelopsis*) n.comb.

Paulipalпина Gnaspini & Peck, 1996 - 7 spp. [Gnaspini & Peck, 1996; herein]

- P. claudicans* (Szymczakowski, 1980) (type) (*Adelopsis*) [by Gnaspini & Peck, 1996]
P. clavigera Gnaspini & Peck, 1996
P. devexa Gnaspini & Peck, 1996
P. dispar (Portevin, 1903) (*Catops*, to *Pseudonemadus* by Portevin, 1914, to *Adelopsis* by Jeannel, 1936), comb. n.
P. exigua (Kirsch, 1870) (*Choleva*, to *Adelopsis* by Jeannel, 1936), comb. n.
P. parvicuspis Gnaspini & Peck, 1996
P. simoni (Portevin, 1903) (*Catops*, to *Pseudonemadus* by Portevin, 1914, to *Adelopsis* by Jeannel, 1936), comb. n.

- Ptomaphagus (Adelops)* Tellkampff, 1844 - 62 spp. [Peck, 1973a, 1973b, 1977, 1978b, 1984; herein]
- P. altus* Peck, 1973
- P. barbarae* Peck, 1973
- P. barri* Peck, 1973
- P. bordoni* (Jeannel, 1964) (*Adelopsis*), comb. n.
- P. brevior* Jeannel, 1949 [Peck, 1973a]
- P. californicus* (LeConte, 1854) (*Catops*, to *Ptomaphagus* by Horn, 1880) [Peck, 1973a]
- P. cavernicola* Schwarz, 1898 [Peck, 1973a]
- P. c. aditus* Peck, 1973
- P. c. cavernicola* Schwarz, 1898
- P. championi* Jeannel, 1936 [Peck, 1973a]
- P. chromolithus* Peck, 1984
- P. colima* Peck, 1977
- P. cocytus* Peck, 1973
- P. conejera* Peck, 1977
- P. consobrinus* (LeConte, 1854) (*Catops*, to *Ptomaphagus* by Horn, 1880) [Peck, 1973a]
- P. distinctus* Peck, 1977
- P. elabra* Peck, 1971 [Peck, 1973a]
- P. episcopus* Peck, 1973
- P. fecundus* Barr, 1963 [Peck, 1984]
- P. fiskei* Peck, 1973
- P. fisus* Horn, 1885 [Peck, 1973a]
- P. giaquintoii* Jeannel, 1936 [Peck, 1973a]
- P. gypsum* Peck, 1973
- P. hatchi* Jeannel, 1933 [Peck, 1984]
- P. hazelae* Peck, 1973
- P. hirtus* (Tellkampff, 1884) (type) (*Adelops*, to *Ptomaphagus (Adelops)* by Jeannel, 1936) [Peck, 1973a]
- P. hubrichti* Barr, 1958 [Peck, 1973a]
- P. jalisco* Peck, 1977
- P. jamesi* Peck, 1973
- P. julius* Peck, 1973 [Peck, 1984]
- P. laselva* Peck, 1977
- P. laticornis* Jeannel, 1949 [Peck, 1984]
- P. leo* Peck, 1973
- P. lincolnensis* Peck, 1978
- P. liquidambar* Peck, 1977

- P. loedingi* Hatch, 1933 [Peck, 1984]
P. longicornis Jeannel, 1949 [Peck, 1984]
P. manzano Peck, 1978
P. mckenziei Peck, 1977
P. meximontanus Peck, 1973
P. nevadicus Horn, 1880 [Peck, 1973a]
P. newtoni Peck, 1973
P. oaxaca Peck, 1973
P. pruina Peck, 1977
P. quercus Peck, 1977
P. reddelli Peck, 1973
P. schwarzi Hatch, 1933 [Peck, 1973a]
P. sciakyi (Zoia, 1992) (*Adelopsis*), comb. n.
P. shapardi Sanderson, 1939 [Peck, 1973a]
P. solanum Peck, 1973 [Peck, 1984]
P. spelaesus (Bilimek, 1867) (*Choleva*, to *Dissochaetus* by Jeannel, 1922,
to *Ptomaphagus* (*Adelops*) by Jeannel, 1936) [Peck, 1973a]
P. szymczakowskii Peck, 1977
P. tabascensis Sbordoni, 1973 [Peck, 1977]
P. talamanca Peck, 1973
P. texanus Melander, 1902 [Peck, 1973a]
P. tierrabaja Peck, 1977
P. torodei Peck, 1984
P. troglomexicanus Peck, 1968 [Peck, 1973a]
P. tuza Peck, 1977
P. ulkei Horn, 1885 [Peck, 1973a]
P. valentinei Jeannel, 1933 [Peck, 1973a]
P. volcanica Peck, 1977
P. walteri Peck, 1973
P. whiteselli Barr, 1963 [Peck, 1973a]

Ptomaphagus (*Appadelopsis*), subg. n. - 16 spp. [Peck, 1978a; herein]

- P. alleghenyensis* (Peck, 1978) (*Adelopsis*), comb. n.
P. appalachianus (Peck, 1978) (*Adelopsis*), comb. n.
P. bedfordensis (Peck, 1978) (*Adelopsis*), comb. n.
P. cumberlandus (Peck, 1978) (*Adelopsis*), comb. n.
P. fumosus (Peck, 1978) (*Adelopsis*), comb. n.
P. joanna (Peck, 1978) (*Adelopsis*), comb. n.
P. jonesi (Peck, 1978) (*Adelopsis*), comb. n.

- P. mitchellensis* (Hatch, 1933) (*Adelops*, to *Adelopsis* by Peck, 1973)
(type), comb. n.
P. nashvillensis (Peck, 1978) (*Adelopsis*), comb. n.
P. orichalcum (Peck, 1978) (*Adelopsis*), comb. n.
P. pecki n.nom. (for *Ptomaphagus (Appadelopsis) altus* (Peck, 1978)
n.comb., not *Ptomaphagus (Adelops) altus* Peck, 1973)
P. pisgahensis (Peck, 1978) (*Adelopsis*), comb. n.
P. richlandensis (Peck, 1978) (*Adelopsis*), comb. n.
P. scottsboroensis (Peck, 1978) (*Adelopsis*), comb. n.
P. steevesi (Peck, 1978) (*Adelopsis*), comb. n.
P. suteri (Peck, 1978) (*Adelopsis*), comb. n.

Ptomaphagus (Echinocoleus) Horn, 1885 - 4 spp. [Peck & Gnaspini, in press]

- P. acutus* Peck & Gnaspini, in press
P. chihuahuensis (Peck, 1976) [by Peck & Gnaspini, in press]
P. setiger (Horn, 1885) (type) [by Peck & Gnaspini, in press]
P. sonorensis (Peck, 1976) [by Peck & Gnaspini, in press]

Ptomaphagus (Merodiscus) Jeannel, 1934 - 2 spp. [Ruzicka, 1993]

- P. biharicus* Jeannel, 1934 [Ruzicka, 1993]
P. validus (Kraatz, 1852) (type) (*Catops*) (by Jeannel, 1934) [Ruzicka, 1993]

Ptomaphagus (Ptomaphagus) Illiger, 1798 - 26 spp. [Jeannel, 1936; Nakane, 1963; Szymczakowski, 1964, 1976; Perreau, 1988, 1996; Schilthuizen, 1989; Nishikawa, 1993]

- P. amamianus* Nakane, 1963
P. aritzensis Jeannel, 1934 [Jeannel, 1936]
P. caucasicus Jeannel, 1934 [Jeannel, 1936]
P. chendai J.Müller, 1921 [Jeannel, 1936]
P. circassicus (Reitter, 1888) (*Catops*) [Jeannel, 1936]
P. clavalis Reitter, 1884 [Jeannel, 1936]
P. dacicus Jeannel, 1934 [Jeannel, 1936]
P. divaricatus Jeannel, 1934 [Jeannel, 1936]
P. hastatellus Szymczakowski, 1976
P. kuntzeni Sokolowski, 1957 [Szymczakowski, 1964]
P. medius Rey, 1889 [Schilthuizen, 1989]
P. nepalensis Perreau, 1988
P. pius Seidlitz, 1887 [Jeannel, 1936]
P. p. fulvus Reitter, 1889

- P. p. pius* Seidlitz, 1887
P. pyrenaicus Jeannel, 1934 [Jeannel, 1936]
P. rhagianicus Sbordoni, 1967 [Szymczakowski, 1976]
P. sardus Seidlitz, 1887 [Jeannel, 1936]
P. sericatus Chaudoir, 1845 [Jeannel, 1936]
 P. s. miser Rey, 1889
 P. s. sericatus Chaudoir, 1845
 P. s. septentrionalis Jeannel, 1934
 P. sibiricus Jeannel, 1934 [Jeannel, 1936]
P. smetanai Perreau, 1996
P. subtruncatus Mäklin, 1881 [Jeannel, 1936]
P. subvillosus Goeze, 1777 (type = *Helops sericeus* Panzer, 1801, synonym) [Jeannel, 1936]
 P. s. chobauti Jeannel, 1934
 P. s. subvillosus Goeze, 1777
P. tauricus Jeannel, 1934 [Jeannel, 1936]
P. tenuicornis (Rosenhauer, 1856) (*Choleva*) [Jeannel, 1936]
 P. t. mauritanicus Jeannel, 1934
 P. t. rosenhaueri Uhagon, 1890
 P. t. tenuicornis (Rosenhauer, 1856)
P. vallombrosae Seidlitz, 1887 [Jeannel, 1936]
P. variicornis (Rosenhauer, 1847) (*Catops*) [Jeannel, 1936]
 P. v. rectipes Jeannel, 1934
 P. v. variicornis (Rosenhauer, 1847)
P. yasutoshii Nishikawa, 1993
- Ptomaphagus* (*Synaulus*) Portevin, 1903 - 2 spp. [Jeannel, 1936; herein]
 P. agilis (Lucas, 1849) (type) (*Myrmecobius*, non *Myrmecobius* Waterhouse) [Jeannel, 1936] comb. n.
 P. pruinosis (Reitter, 1881) [Jeannel, 1936] comb. n.
- Ptomaphagus* (*Tupania*) Szymczakowski, 1961 - 6 spp. [Peck, 1977]
 P. argenticornis Peck, 1977
 P. delsur Peck, 1977
 P. flabellatus Szymczakowski, 1961 [Peck, 1977]
 P. forticornis Matthews, 1888 (type) (by Szymczakowski, 1961) [Peck, 1977]
 P. orientalis Peck, 1977
 P. yuvila Peck, 1977

