

Tackling generic limits for the Neotropical Philonthina with a phylogenetic approach: revision of the genera *Linoderus* Sharp and *Odontolinus* Sharp (Coleoptera: Staphylinidae)

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Abstract

A systematic revision and a phylogenetic analysis of the Neotropical genera *Linoderus* Sharp, 1885 and *Odontolinus* Sharp, 1885 (Staphylininae: Staphylinini: Philonthina) including a broad selection of outgroup taxa is presented. Two valid species are recognized for *Linoderus*: *L. gracilipes* Sharp and one new species, *L. alajuelensis* sp.n. *Linoderus navarretei* López-García & Méndez-Rojas, 2014 is excluded from the genus *Linoderus* and synonymized with *Belonuchus albovariegatus* Bernhauer, 1916. Two valid species are recognized for *Odontolinus*: *O. fasciatus* Sharp and a new species, *O. campanensis* sp.n. Lectotypes are designated for *Linoderus gracilipes* Sharp, *Odontolinus fasciatus* Sharp and *Belonuchus albovariegatus* Bernhauer. The phylogenetic analysis shows both *Odontolinus* and *Linoderus* as monophyletic genera that form together with other Central and South American Philonthina a well-supported clade within the Neotropical lineage of this subtribe. The systematic utility of sexually dimorphic characters within the Neotropical lineage is discussed.

Key words

Staphylininae, Philonthina, systematics, Neotropical, Central America, *Linoderus*, *Odontolinus*.

1. Introduction

Philonthina is the largest and most globally distributed subtribe within the mega-diverse rove beetle tribe Staphylinini, and includes 30 genera with over 520 described species currently known to occur in the Neotropical Region (A.F. Newton, unpublished database). Among them, 17 genera and about 180 species are known exclusively from the Neotropics (CHANI-POSSE 2014a; A.F. Newton, unpublished database). The great majority of these Neotropical genera and species are poorly known taxa that have never been revised after their outdated original descriptions from late 19th or early 20th centu-

ries (CHANI-POSSE 2014a). Recently CHANI-POSSE (2013, 2014a) provided a phylogenetic framework and a regional generic key for the Neotropical Philonthina. In particular, CHANI-POSSE (2013) discovered a species-rich Neotropical clade within the world Philonthina whose further exploration seems very promising for understanding the unique Neotropical biota. Still, species-rich genera like *Philonthus*, *Belonuchus*, or *Paederomimus* are poorly defined and numerous more diagnosable but mainly monotypic genera are likely nested within the former large genera. Their generic limits and sister group relationships

are mostly unknown and remain as big obstacles to the systematic resolution of the Neotropical Philonthina.

The genera *Linoderus* and *Odontolinus*, which are the subjects of this paper, belong to the recently discovered Neotropical philonthine clade and represent some of the mentioned monotypic genera requiring better understanding. SHARP (1885) had erected them for two species from Panama, *Linoderus gracilipes* and *Odontolinus fasciatus*, respectively. As it was assumed by SHARP (1885) and confirmed in recent analyses (CHANI-POSSE 2013, 2014b) both genera are closely related to each other and to the Neotropical genera *Pescolinus* and *Neopescolinus*. Phylogenetic relationships within this group of genera, however, appear controversial: *Linoderus* was sister to the clade *Odontolinus* + *Pescolinus* in CHANI-POSSE (2013), while in CHANI-POSSE (2014b) it was sister to *Pescolinus*, and both together comprised the sister to *Odontolinus*. That entire generic complex seems to be closely related to the species-rich genera *Paederomimus* Sharp and *Belonuchus* Nordmann, whose generic limits, in turn, represent an even bigger problem to solve (CHANI-POSSE 2013). There is broad consensus on the non-monophyly of *Belonuchus* (e.g., LI & ZHOU 2011; CHANI-POSSE 2013; CHANI-POSSE et al. 2017) and at least some suspicion about *Paederomimus* (CHANI-POSSE 2014a). The blurred limits between the Neotropical philonthine genera combined with the lack of detailed descriptions and illustrations make it difficult or impossible to design badly needed broader phylogenetic work, or even to progress with taxonomic studies without making mistakes. For example, a new species of *Linoderus* was recently described from Colombia (LÓPEZ-GARCÍA & MÉNDEZ-ROJAS 2014) whose generic assignment appeared highly doubtful. That doubtful taxon, on the one hand, and new species presumably belonging to *Linoderus* and *Odontolinus* discovered in collections, triggered this paper.

Our objectives are to conduct a cladistic analysis defining the limits of both *Linoderus* and *Odontolinus* and to justify generic assignments of their previously described and new species. Also we aim to further assess their sister group relationships and provide a comprehensive taxonomic revision of all species involved.

2. Material and methods

2.1. Examination of material and terminology

The material studied was borrowed from the following collections: **BMNH** – The Natural History Museum, London, UK (Roger Booth); **FMNH** – Field Museum of Natural History, Chicago, USA (Alfred F. Newton, Margaret K. Thayer); **INBio** – Instituto Nacional de Biodiversidad, San José de Costa Rica (Angel Solís); **SEMC** – Snow En-

tomological Collection, Natural History Museum / Biodiversity Research Center, University of Kansas, Lawrence, USA (Zachary H. Falin); **ZMHB** – Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (Johannes Frisch, Joachim Willers); **ZMUC** – University of Copenhagen, Zoological Museum, Copenhagen, Denmark (Alexey Solodovnikov, Sree Selvantharan).

Beetle specimens were examined using a Leica MZ6 dissecting microscope. They were mostly examined as pinned dry specimens, but a few were first relaxed in warm soapy water, rinsed, disarticulated and examined as wet preparations in glycerin. Techniques for the preparation and examination of male and female genitalia follow SMETANA (1982). Photographs were taken using a digital camera attached to the dissecting microscope. Line drawings were traced from digital photographs. Depositories of type material retain the copyright of the photographs. SEM pictures were obtained by using a JSM-6610 system. Measurements (given in millimeters) were made with an ocular micrometer. Overall body length was measured from the apex of the labrum to the apex of the abdomen. Other measurements were taken and abbreviated as follows: **HW** – head capsule maximum width (measured at widest point); **HL** – length of head capsule, from anterior margin of frontoclypeus to neck constriction (along midline); **Lp2L**, **Lp3L** – length of 2nd or 3rd labial palpomere; **PW** – pronotum maximum width; **PL** – pronotum length along midline; **EL** – eye length (seen from above); **TL** – temple length (from the posterior margin of the eye to the nuchal groove; seen from above); **NW** – neck width; **S1** – length of 1st metatarsomere; **S5** – length of 5th metatarsomere (last); **EtL** – elytron length at side (straight line from humerus to apex; seen from above); **EtI** – elytron length along suture.

Terminology follows authors and criteria as stated in CHANI-POSSE (2014b). Biogeographical provinces considered in the geographical distribution of the species follow the most recent regionalization of MORRONE (2014). All records and the general distribution given for each species are based strictly on examined specimens. Handwriting on labels of type specimens was compared to the respective author's handwriting as shown by HORN et al. (1990). All locality data were recorded from specimen labels, georeferenced by Google Earth (Google Inc.) and plotted onto a relief map derived from a digital elevation model using Quantum GIS 2.18.0 (QUANTUM GIS DEVELOPMENT TEAM 2016).

2.2. Phylogenetic analysis

2.2.1. Outgroup and ingroup taxa

The chosen outgroup taxa include 14 species. One species, *Xanthopygus chapareanus* Scheerpeltz, represents Xanthopygina, a subtribe presumably sister to Philonthina (BRUNKE et al. 2016; CHANI-POSSE 2013; CHATZIMANO-

LIS 2014) and used here to root the tree. Other species come from eight genera of the subtribe Philonthina as follows: *Philonthus* Stephens, 1829 [*P. splendens* (Gravenhorst)], *Belonuchus* Nordmann, 1837 [*B. haemorrhoidalis* (Fabricius), *B. rufipennis* (Gravenhorst) and *B. subaeneus* Bernhauer], *Bisnius* Stephens, 1829 [*B. sordidus* (Gravenhorst)], *Chroaptomus* Sharp [*C. flagrans* (Erichson)], *Gabrius* Stephens, 1829 [*G. picipennis* (Mäklin)], *Paederomimus* Sharp, 1885 [*P. difformiceps* Sharp, *P. pectoralis* Sharp and *P. nobilis* Sharp], *Pescolinus* Sharp, 1885 [*Pescolinus palmatus* Sharp and *P. schmidtii* Bierig] and *Neopescolinus* Chani-Posse, 2014 [*N. nevermanni* Chani-Posse].

Both species of *Linoderus* (the type and the new species), *Belonuchus albovariegatus* (previously classified as *Linoderus navarretei* in LÓPEZ-GARCÍA & MÉNDEZ-ROJAS 2014), and both species of *Odontolinus* (the type and the new species) form our ingroup.

2.2.2. Characters

Fifty-two morphological characters were coded and scored for the 19 terminal units, their selection and definition mainly following the character system developed by SMETANA & DAVIES (2000) and SOLODOVNIKOV & NEWTON (2005) with further modifications by BRUNKE & SOLODOVNIKOV (2013) and CHANI-POSSE (2013, 2014a). Forty-two characters were derived from external morphology, nine from male genitalia, and one from female genitalia. Among these, eight characters (in parentheses) are uninformative with regard to phylogenetic relationships. They were excluded from the analysis for the calculation of tree statistics but retained in the matrix to make them traceable in the tree as potential autapomorphies. All characters were treated as unordered (non-additive) and given equal weight. Following SERENO (2007, 2009), neomorphic (presence / absence) and transformational (transformation from one state to another) characters referring to the same structure were coded separately. Four characters from this list marked with the asterisk (*) are novel, the remaining characters were already used and most of them illustrated in previous studies (SMETANA & DAVIES 2000; LI & ZHOU 2011; CHANI-POSSE & ASENJO 2013; CHANI-POSSE 2013, 2014a,b).

1. Antennal insertions (ai), position in relation to frontoclypeus and eye: [0] closer to frontoclypeus (CHANI-POSSE 2013: fig. 1A); [1] at equal distance or closer to eye (CHANI-POSSE 2014a: fig. 11D).
- 2*. Antennal insertions, distance between left and right one relative to distance to eye (aa/ae), male: [0] << 2.0; [1] 2.0–2.5; [2] >> 2.5.
- 3*. Antennae, antennomere 1, apical macroseta (aS), shape: [0] not spine-like; [1] spine-like (Fig. 10).
4. Antennae, antennomere 1, length relative to length of head (a1/HL): [0] ≤ 0.5; [1] >> 0.5 but < 1.0; [2] 1.0.
5. Antennae, length ratio of antennomeres 3 and 2 (a3/a2): [0] 1.2–1.5; [1] >> 1.5.
6. Antennae, antennomere 6, apical long setae (see CHANI-POSSE 2014b): [0] absent (fig. 10); [1] present (fig. 11).
7. Antennae, antennomere 9 (proportions): [0] elongate; [1] quadrate; [2] transverse.
8. Antennae, antennomere 10 (proportions): [0] elongate; [1] quadrate; [2] transverse.
- 9*. Head, dorsal surface punctuation: [0] not sexually dimorphic (i.e., both male and female with same punctuation); [1] sexually dimorphic (i.e., with dense punctuation in males, scarcely punctuated to almost glabrous in females) (CHANI-POSSE 2014b: fig. 12E) (Figs. 6, 7).
10. Head, infraorbital ridge (see CHANI-POSSE 2014a): [0] absent (fig. 2B,D,I); [1] present (fig. 2A,F–H,J,K).
- (11). Head, ligula, size and shape (see LI & ZHOU 2011): [0] large and more or less bilobed, with variously developed rounded lobes (fig. 7C); [1] small but distinct, entire (or at most slightly notched medially) (fig. 7A,B).
12. Labial palpus, palpomere 3 (apical), shape: [0] subacute, i.e., narrowed at base and evenly converging towards apex (LI & ZHOU 2011: fig. 8B–D); [1] fusiform to apically expanded, i.e., narrowed at base but not converging towards apex (LI & ZHOU 2011: fig. 8A,E,F); [2] subcylindrical “rod-like”, i.e., parallel-sided at most of its length, apex subtruncate (CHANI-POSSE 2013: fig. 1H).
13. Labial palpus, relative length of palpomeres 3 (Lp3, apical) and 2 (Lp2, preapical) (Lp3/Lp2): [0] << 1.0; [1] ~ 1.0; [2] >> 1.0.
14. Maxillary palpus, palpomere 4 (apical), shape: [0] subacute, i.e., narrowed at base and evenly converging towards apex (LI & ZHOU 2011: fig. 6A,C); [1] fusiform to expanded apically, i.e., narrowed at base but not converging towards apex (LI & ZHOU 2011: fig. 6D,F); [2] subcylindrical “rod-like”, i.e., parallel-sided at most of its length, apex subtruncate (CHANI-POSSE 2013: fig. 1A).
15. Maxillary palpus, relative length of palpomeres 4 (Mp4, apical) and 3 (Mp3, preapical) (Mp4/Mp3): [0] > 2.0; [1] ≤ 1.0.
16. Gular sutures (gs), extent of median connection (see CHANI-POSSE 2013): [0] gs joined before neck (fig. 3A,D,E); [1] gs not joined before neck, extended close to each other at base of head capsule (fig. 3B,C,F).
17. Neck, transverse carina: [0] absent; [1] present (CHANI-POSSE 2013: fig. 1A) (Fig. 11).
18. Prothorax, hypomeron, degree of inflexion: [0] not inflexed (most of its surface visible in lateral view); [1] slightly inflexed (most of its surface hidden in lateral view); [2] strongly inflexed (not visible in lateral view).

19. Prothorax, anterior angles of pronotum (aap) relative to anterior margin of prosternum (amp) (see CHANI-POSSE 2013): [0] aap not strongly produced beyond amp (fig. 2C); [1] aap strongly produced beyond amp (fig. 1N).
20. Prothorax, large lateral setiferous puncture (llsp), position in relation to superior marginal line of pronotum (smlp) (see CHANI-POSSE 2014a): [0] llsp situated very close to smlp or at a distance no more than $3 \times$ its diameter (fig. 4F); [1] llsp remote from smlp at a distance at least $3 \times$ its diameter (fig. 4G–I) (Fig. 12).
21. Prothorax, basisternum (bs), length relative to length of furcasternum (fs) (bs/fs, measured laterally): [0] 1.1–1.5; [1] $\gg 1.5$.
22. Prothorax, prosternum, transverse carina on basisternum (see CHANI-POSSE 2014a): [0] absent (fig. 2B); [1] present (figs. 2A, 4B).
23. Prothorax, prosternum, transverse carina on basisternum (tc), development (when present) (see CHANI-POSSE 2014a): [0] tc not distinct medially (if so, very shallow) (fig. 2A); [1] tc distinct medially (fig. 4B).
- (24). Prothorax, hypomeron, inferior marginal line (iml), development (see SMETANA & DAVIES 2000): [0] iml not continued as a separate entity beyond anterior pronotal angles (figs. 42–44); [1] iml continued as a separate entity beyond anterior pronotal angles and curving around them (fig. 53); [2] iml continued as a separate entity beyond anterior pronotal angles and continuous with them (fig. 49).
- (25). Prothorax, postcoxal process (see LI & ZHOU 2011): [0] absent (fig. 10A,D); [1] present (fig. 10B,C).
26. Prothorax, prosternum, basisternum, pair of macrosetae: [0] absent; [1] present (SMETANA & DAVIES 2000: fig. 86) (Fig. 12).
27. Mesothorax, sternopleural (anapleural) suture (see CHANI-POSSE 2014a): [0] transverse, or nearly transverse (very slightly oblique) (fig. 8B); [1] distinctly oblique (medial end of suture anterior to its lateral end) (fig. 8C); [2] sinuate (fig. 8A).
28. Mesothorax, intercoxal process, apex: [0] rounded or broadly pointed, forming obtuse angle (CHANI-POSSE 2014a: fig. 2B); [1] narrowly pointed forming sharp (acute) angle (LI & ZHOU 2011: fig. 12B–F).
29. Protibiae, shape (see CHANI-POSSE 2014a): [0] cylindrical to slightly broadened apically (fig. 6B–D); [1] subconical, moderately broadened apically (fig. 7F,G).
30. Protarsi, shape of tarsomeres 1–4 (see CHANI-POSSE 2014a): [0] more or less cylindrical, not transversely widened and not flattened dorso-ventrally (fig. 6C); [1] more or less flattened dorso-ventrally and widened (fig. 7F,G).
31. Protarsi, ventral setation, modified pale (adhesive) setae: [0] absent; [1] present (LI & ZHOU 2011: fig. 16A,B).
32. Male metatrochanters, dorsal spines: [0] absent; [1] present.
33. Male metafemora, ventrolateral spines: [0] absent; [1] present.
- (34). Metarsomere 1, setal comb: [0] absent; [1] present.
35. Metarsomere 1 (S1), length: [0] not sexually dimorphic (i.e., male and female with same S1 length); [1] sexually dimorphic (i.e., S1 in male distinctly longer than in female).
- (36). Pretarsus, empodial setae (see SMETANA & DAVIES 2000): [0] absent (figs. 70, 71); [1] present (figs. 67–69).
- (37). Pretarsal claws (as “tarsal claws” in CHANI-POSSE 2014a), medial tooth (mt): [0] absent; [1] present (Fig. 13).
- (38). Abdomen, protergal glands, cuticular manifestation (see LI & ZHOU 2011): [0] well-developed acetabula (i.e., distinct cavities without openings) (fig. 17C); [1] more or less invaginated capsules with smaller openings (fig. 17A,B).
- (39). Abdomen, sternum 3, basal transverse carina, medial area (see LI & ZHOU 2011): [0] straight to arcuate (fig. 18C); [1] angulate (fig. 18B).
40. Male sternum 8, posterior margin, medial projection: [0] absent; [1] present (CHANI-POSSE 2014b: figs. 21, 30, 47, 51, 59).
41. Female sternum 8, posterior margin, medial projection: [0] absent; [1] present (CHANI-POSSE 2014b: figs. 26, 35, 56) (Fig. 25).
42. Male sternum 9, relative length of basal (bp) and distal (dp) portions (bp/dp): [0] ≤ 1.0 (Figs. 29, 34); [1] ≥ 1.6 (Figs. 17, 22).
43. Male sternum 9, basal portion: [0] more or less symmetrical (i.e., both lateral ends similarly produced, not extending far from each other); [1] asymmetrical (i.e., one lateral end distinctly produced, extending far from the other).
44. Male sternum 9, basal portion, asymmetry: [0] strong (CHANI-POSSE 2014b: figs. 22, 31, 39, 48, 52, 60); [1] moderate; [2] slight.
45. Male sternum 9, distal portion, median emargination: [0] distinct (Figs. 17, 22, 29, 34); [1] not distinct.
46. Male sternum 9, distal portion, shape of median emargination (if distinct): [0] acute (CHANI-POSSE & ASEÑO 2013: e.g., fig. 3B,F,L,R); [1] subangulate to concave (CHANI-POSSE 2014b: figs. 22, 31, 39, 48, 52, 60) (Figs. 17, 22, 29, 34).
47. Lateral tergal sclerites 9 (styli), shape: [0] dorso-ventrally flattened (CHANI-POSSE 2014b: figs. 19, 20) (Figs. 8, 15); [1] not dorsoventrally or laterally flattened; [2] laterally flattened.
48. Lateral tergal sclerites 9 (styli) (if dorsoventrally flattened): [0] not sexually dimorphic (i.e., equally wide in both male and female); [1] sexually dimorphic (i.e., distinctly wider in males than in females) (CHANI-POSSE 2014b: figs. 19, 20).
- 49*. Lateral tergal sclerites 9 (styli) (if dorsoventrally flattened), shape of apex, male: [0] rounded; [1] laterally emarginate (Fig. 8).
50. Male: aedeagus, paramere(s), sensory peg setae: [0] absent; [1] present.

Redescription. Length 7.0–10.0 mm. **Colouration:** Head and thorax reddish brown or metallic blue to greenish blue or green; elytra metallic blue or green; abdomen entirely reddish brown or first four abdominal segments reddish brown with apical segments distinctly darker, dark brown to black; antennae with both first and apical segments distinctly lighter than inner segments, palpi and legs reddish brown to dark brown or black.

Head of rounded-quadrangular shape with distinctly rounded hind angles (Figs. 6, 7), at one third from posterior end slightly narrower than in anterior third in both sexes; about as long as wide, slightly to moderately wider than pronotum at widest point. Punctuation sexually dimorphic, dense in males, scarce in females. Eyes moderately convex, moderately to distinctly shorter than temples seen from above (Figs. 6, 7). Antennae inserted at about equal distance to both the anterior margin of frontoclypeus and eyes, separated from each other by no more than $2.5 \times$ the distance to eye, 1st antennomere not longer than half of head length, 3rd moderately longer than 2nd, 1st–5th with distinct long setae. Labrum subrectangular, distinctly transverse. Mentum with anterior margin straight to slightly emarginated and about as long as to distinctly longer than submentum. Labial palpus moderately long, 2nd palpomere with 3–4 setae at medial basal half and about $2 \times$ as long as 1st, 3rd medially inflated and moderately shorter than 2nd (Lp3L/Lp2L = 0.8).

Prothorax: Pronotum slightly to moderately longer than wide, slightly broadened anteriorly; front margin subtruncate, hind margin arcuate, anterior and posterior angles rounded (Figs. 1, 2); disc with dorsal rows of punctures sub-parallel to each other, each with 4–5 punctures. Prosternum without distinct mid-longitudinal carina. **Legs:** Profemora cylindrical in shape, with scarce setae; protarsi with first four segments more or less cylindrical, not flattened dorsoventrally and not sexually dimorphic (Figs. 1, 2); 1st metatarsomere sexually dimorphic in length, distinctly longer in males (S1/S5 = 1.8) than in females (S1/S5 = 1.3). **Elytra** at suture distinctly shorter than pronotum at midline (Figs. 1, 2); punctuation fine and sparse.

Abdomen: Abdominal terga 3–5 with posterior basal transverse carina complete and straight, punctuated. Hind margin of tergum 8 (sixth visible) arcuate in both sexes.

Male sexual characters: Sternum 8 with a medially produced projection (Figs. 16, 21). Genital segment with lateral tergal sclerites 9 (styli) dorsoventrally flattened and distinctly dilated, with latero-apical emargination (Fig. 8); tergum 10 subtruncate at apex with two apical setae and two subapical setae (Fig. 18); sternum 9 with basal portion distinctly asymmetrical, 1.8 – $2.0 \times$ as long as distal portion and deeply emarginate apically, with three to four apical setae at each side of emargination (Figs. 17, 22). Aedeagus with parameres fused to one short sclerite, completely fused to median lobe and without sensory peg setae; median lobe elongate, with apical part narrowed into rather acute apex (Figs. 19–20, 23–24). **Female sexual characters:** Sternum 8 with hind margin projected

medially (Fig. 25). Genital segment with lateral tergal sclerites 9 (styli) dorsoventrally flattened and slightly dilated, without a latero-apical emargination; tergum 10 subangulate to subacute apically; second gonocoxites each with a long macroseta distally, with minute stylus (Fig. 27) bearing one long apical macroseta.

Comparison and recognition. While the recognition of males of *Linoderus* is straightforward due to the dorsal surface of head being distinctly punctuated, females of *Linoderus* may superficially resemble those of *Chroaptomus* Sharp or *Neopescolinus* given the situation of the antennal insertions which are rather distant from the frontoclypeus. Females of *Linoderus* differ from those of *Chroaptomus* by their elongate habitus (antennomeres 9 and 10 elongate, anterior angles of pronotum distinctly produced beyond the anterior margin of prosternum, mesoventrite with sternopleural suture distinctly oblique) as opposed to that of *Chroaptomus* Sharp (antennomeres 9 and 10 slightly transverse, anterior angles of pronotum slightly produced beyond the anterior margin of prosternum, mesoventrite with sternopleural suture nearly transverse). Females of *Linoderus* and *Neopescolinus* can be distinguished by the shape of their protarsomeres 1–4: more or less cylindrical, not widened in the former and more or less flattened dorsoventrally and widened in the latter.

Immature stages. Unknown.

Bionomics. Specimens have been collected from “moss and fungi on trees” (SHARP 1885), rotting palm trunks and with flight intercept traps.

Distribution and remarks. With its two species known at present *Linoderus* is distributed in the Western Panamanian Isthmus province of the Neotropical region (MORRONE 2014) at elevations of 800–1660 m as indicated by trapping data (Fig. 41).

3.1.1. *Linoderus gracilipes* Sharp, 1885 (Figs. 1, 6, 7, 21–27, 40, 41)

Linoderus gracilipes Sharp, 1885: 452; BERNHAUER & SCHUBERT 1914: 367 (catalog); HERMAN 2001: 2698 (catalog); CHANI-POSSE 2013: 8, 10, 14 (phylogenetic placement); CHANI-POSSE 2014a: 3, 7, 10, 13, 14, 16, 17, 20 (key); CHANI-POSSE 2014b: 239, 242, 250, 252, 254 (characters, phylogenetic affinities).

Diagnosis. *Linoderus gracilipes* differs from *Linoderus alajuelensis* in the distinct colour pattern: head and elytra metallic blue, thorax and abdomen with first four visible abdominal segments reddish brown and apical abdominal segments dark brown to black; antennae, palpi and legs mostly light brown, with antennomeres 4–9, apex of femora and styli and entire tibia dark brown to black.

Redescription. Body length 7.0–8.5 mm. **Colouration:** as in diagnosis. **Head** about as wide as long (HW/HL =



Figs. 1–5. Type specimens of *Linoderus*, *Odontolinus* and *Belonuchus albovariegatus*. (1) *L. gracilipes*, lectotype [BMNH ©]. (2) *L. alajuelensis*, paratype [SEMC ©]. (3) *Belonuchus albovariegatus*, lectotype [FMNH ©]. (4) *O. fasciatus*, lectotype [BMNH ©]. (5) *O. campanensis*, holotype [SEMC ©]. (Scale bar = 1.0 mm)

1.0), slightly to moderately wider than pronotum (HW/PW = 1.1–1.2). Eyes moderately to distinctly shorter than temples (EL/TL = 0.7–0.8) seen from above. Antennae with 1st antennomere distinctly shorter than 2nd and 3rd combined, 3rd about 1.5 × as long as 2nd. Labial

palpus with 2nd palpomere about twice as long as 1st. Maxillary palpus with 4th palpomere (apical) 1.5 × as long as 3rd. Neck about 0.4 × as wide as head at widest point. **Pronotum** slightly to moderately longer than wide (PW/PL = 0.8–0.9), dorsal rows of punctures each

with 4 to 5 punctures. Prosternum without distinct mid-longitudinal carina. *Elytra* at sides about $1.5 \times$ as long as elytra along suture (EtL/Etl = 1.5–1.7). **Male sexual characters:** Sternum 8 with medially produced and sub-angulately emarginate projection (Fig. 21). Aedeagus with median lobe gradually narrowed from apical third and with acute apex; apex of paramere slightly notched at middle (Figs. 23, 24). **Female sexual characters:** As described for genus.

Geographical distribution. *Linoderus gracilipes* has been recorded from Panama and Costa Rica (new record) within 1510–1660 m range of elevation (Fig. 41).

Bionomics. It was collected from “moss and fungi on trees” (SHARP 1885).

Type material (all examined). Lectotype (Fig. 1, here designated), ♂, specimen glued to white card with following Sharp’s handwriting: ‘*Linoderus gracilipes* D.S.V. de Chiriquí Champion’ and three additional labels, ‘V. de Chiriquí, 4,000–6,000 ft. Champion’ [white label], ‘B.C.A. Col. I. 2. *Linoderus gracilipes*, Sharp.’ [white label], ‘SYNTYPE’ [round white label with light blue margin], ‘Lectotype *Linoderus* | *gracilipes* Sharp, 1885 | des. Chani Posse 2011’, (BMNH). Other 28 paralectotypes, 16 ♂ and 12 ♀, with same labels as the lectotype (BMNH). Two additional paralectotypes, 1 ♂ and 1 ♀, both specimens glued to white card with following Sharp’s handwriting: ‘Bugaba. Panama. Champion’ and three additional white labels, ‘Bugaba. Panama. Champion’, ‘B.C.A. Col. I. 2. *Linoderus gracilipes*, Sharp.’, ‘Chicago Nat. Hist. Mus. (ex D. Sharp Colln. By exchange with Brit. Mus. Nat. Hist.’, ‘Paralectotypes *Linoderus* | *gracilipes* Sharp, 1885 | des. Chani Posse 2011’, (FMNH).

Other material examined. Costa Rica: San Isidro de Cor (?), “*Pescolinus laetus*” Bierig (ms name), Field Mus. Nat. Hist. 1966 A. Bierig Collection, Acc. Z. 13812, 1 ♂ (FMNH). Puntarenas: Altamira Biol. Sta., 4–7-VI-2004, J. Ashe, Z. Falin, I. Hinojosa, 1510–1600 m, 9°01’76”N, 83°00’49”W, ex. Flight intercept trap CR1AFH04 144, 1 ♂ (SEMC); Las Alturas Biol. Sta., 31-V/3-VI-2004J. Ashe, Z. Falin, I. Hinojosa, 1660 m, 8°56.17’N, 82°50.01’W, ex. Flight intercept trap CR1ABFOD 092, 1 ♂, 1 ♀ (SEMC).

3.1.2. *Linoderus alajuelensis* sp.n. (Figs. 2, 8, 16–20, 40, 41)

Diagnosis. *Linoderus alajuelensis* differs from *L. gracilipes* in the distinct colour pattern: head, thorax and abdomen reddish brown; elytra metallic blue; antennae, palpi and legs mostly reddish brown with antennomeres 1–6, apex of femora and styli, entire tibia and the first two tarsomeres dark brown to black.

Description. Body length 8.5–9.5 mm. **Colouration:** as in diagnosis. **Head** about as wide as to slightly wider than long (HW/HL = 1.0–1.1), slightly to moderately wider than pronotum (HW/PW = 1.1–1.2). Eyes moderately to distinctly shorter than temples (EL/TL = 0.7–0.8) seen from above. Antennae with 1st antennomere distinctly shorter than 2nd and 3rd combined, 3rd about $1.5 \times$ as long as 2nd. Maxillary palpus with 4th palpomere (apical) $1.8 \times$ as long as 3rd. Neck about $0.5 \times$ as wide as head at widest point. **Pronotum** slightly to moderately longer than wide (PW/PL = 0.8–0.9), dorsal rows of punctures each with

5 punctures. Prosternum with mid-longitudinal carina developed only along furcasternum. *Elytra* at sides about $1.5 \times$ as long as elytra along suture (EtL/Etl = 1.5–1.7). **Male sexual characters:** Sternum 8 with medially produced and roundly emarginate projection (Fig. 16). Aedeagus with median lobe gradually narrowed from apical fourth, apex distinctly lanceolate; paramere entire at middle (Figs. 19, 20). **Female sexual characters:** As described for genus.

Geographical distribution. *Linoderus alajuelensis* has only been recorded from Costa Rica (Alajuela) within the 800–950 m range of elevation (Fig. 41).

Bionomics. Unknown.

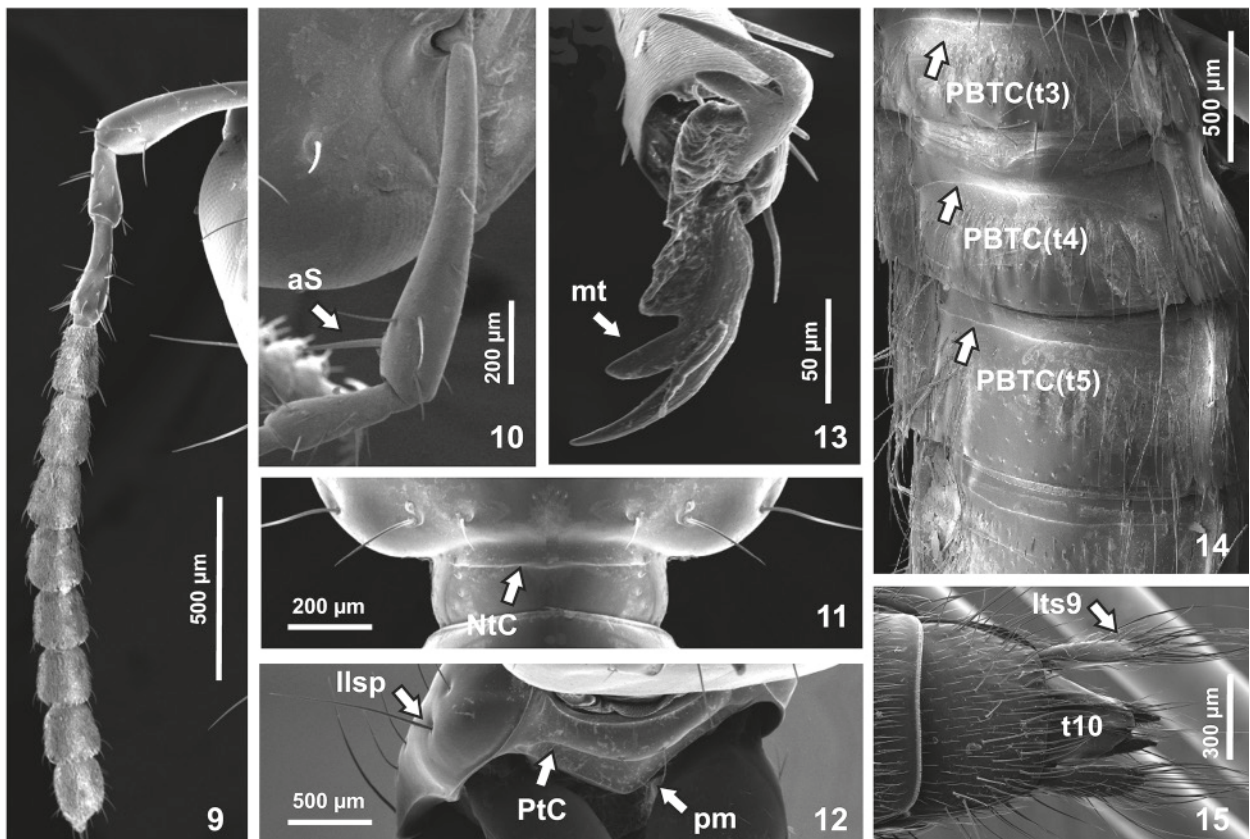
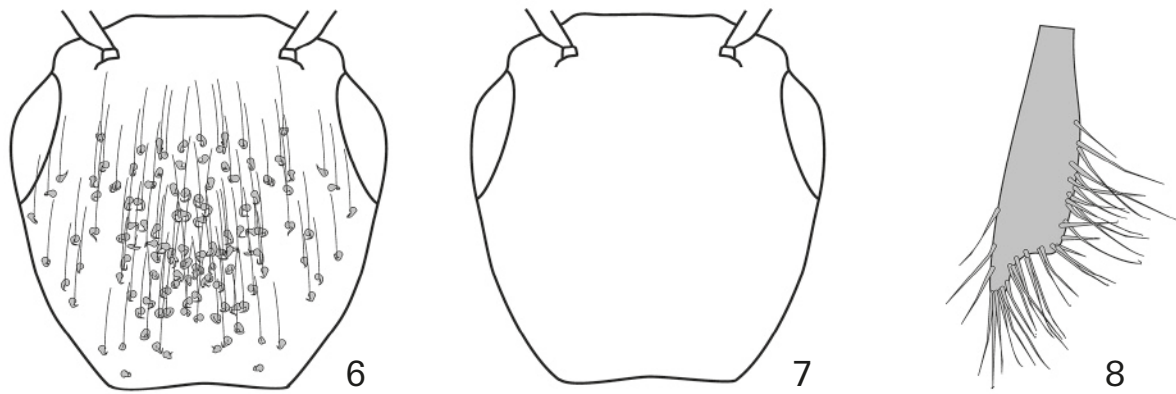
Etymology. The specific name refers to Alajuela, Costa Rica, where this species was found.

Type material (all examined). Holotype, ♂ with labels ‘Costa Rica: Alajuela, R. San Lorencito, | R. F. San Ramon, 5 km de Colonia | 13-jun-93 | Curso Scarabaeidae | 900 m L-N-244500, 470700’, ‘Holotype *Linoderus* | *alajuelensis* | Chani Posse & Solodovnikov, 2017’ (INBio). Two paratypes: 1 ♀, with labels: ‘Costa Rica: Alajuela, E. B. San Ramon, | R. B. San Ramon 27km .N&8km, | W San Ramon, 10°13’30”N, 84°35’30”W | 850–950 m, 29-VI-6-VII-1999 | R. Anderson, in rotting palm trunk CR1A99-108C’ (SEMC); 1 ♀, with labels ‘Costa Rica | Turrialba 800 m | ex coll. A. Heyne’ (yellow label), female symbol (white label), ‘Paederomimus | bicolor n. sp. | Wendeler det.’ (white label), HOLOTYPE (red label), ‘bicolor Wdlr’ (handwritten green label) (ZMHB). Paratypes with additional label ‘Paratype *Linoderus* | *alajuelensis* | Chani Posse & Solodovnikov, 2017’.

3.1.3. Species excluded from *Linoderus*

Although we were not able to see the type material of *Linoderus navarretei*, comparison of its original description (LÓPEZ-GARCÍA & MÉNDEZ-ROJAS 2014: 85) with the type material of *Belonuchus albovariegatus* Bernhauer, 1916 leaves no doubt that *Linoderus navarretei* is a **new junior synonym** of the former species. Results of the phylogenetic analysis here indicate that *Belonuchus albovariegatus* does not fit inside or near the genus *Linoderus*. Naturally, it does not match the diagnosis provided for *Linoderus* (see above) in the following characters: head with punctuation sexually dimorphic and antennal insertions at about equal distance to both the anterior margin of frontoclypeus and eyes. *Belonuchus albovariegatus* does not form a monophyletic group with either *B. haemorrhoidalis* (type species of the genus) or any other *Belonuchus* species sampled for this analysis, and there is no robust evidence for it being included in *Odontolinus* (see section 4.) either. Until we have a better systematic understanding of what should form the genus *Belonuchus* and other related Neotropical lineages, we prefer to maintain *Belonuchus albovariegatus* in this genus.

Type material of *Belonuchus albovariegatus* (all examined), Lectotype (Fig. 3, here designated), ♂, with labels ‘Columbia Occ |



Figs. 6–15. *Linoderus gracilipes*: (6) male head (dorsal view), (7) female head (dorsal view), (8) right lateral tergal sclerite 9 (stylus). *Odontolinus fasciatus*: (9) left antenna (dorsal view), (10) first and second antennomeres (dorsal view), (11) neck (dorsal view), (12) prothorax, (13) pretarsal claws of right foreleg (oblique apical view, upper claw is the posterior one), (14) abdominal tergites 3–6, (15) female lateral tergal sclerites 9 (styli; dorsal view). — **Abbreviations:** aS, apical macroseta; llsp, large lateral setiferous puncture; lts9, lateral tergal sclerite 9; mt, medial tooth; NtC, neck transverse carina; pm, pair of macrosetae; PBTC(t3–5), posterior basal transverse carina on abdominal terga 3–5; PtC, prosternal transverse carina; t10, abdominal tergum 10.

Cali, Fassi' (printed white label), 'St. Antonio | XII Kol 2000 m' (printed white label), 'Belonuchus | albovariegatus | Bernh Typus' (Bernhauer's handwriting in yellow label), 'Chicago NHMus | M. Bernhauer | Collection' (printed white label), 'Lectotype *Belonuchus* | albovariegatus | Chani Posse, 2014' (FMNH). Two paralectotypes, ♀, one with same labels as lectotype (but 'Cotypus' in yellow label) and the other one with 'Alto de las | cruces 2200 m' (printed white label), 'Columbia Occ | Cali, Fassi' (printed white label), 'albovariegatus | Bernh cotypus' (Bernhauer's handwriting in yellow label), 'Chicago NHMus | M. Bernhauer | Collection' (printed white label), 'Paralectotype *Belonuchus* | albovariegatus | Chani Posse, 2014' (FMNH).

3.2. Genus *Odontolinus* Sharp, 1885 (Figs. 4, 5, 9–15, 28–39, 40, 41)

Odontolinus Sharp, 1885: 454; BERNHAUER & SCHUBERT 1914: 372 (catalog); BLACKWELDER 1944: 138 (checklist); BLACKWELDER 1952: 269 (type species); HERMAN 2001: 2721 (catalog); NEWTON et al. 2005: 19 (checklist, as "probable"); CHANI-POSSE 2013: 4, 8, 10, 14 (phylogenetic placement); CHANI-POSSE 2014a: 7, 10, 11, 15–18, 21 (key); CHANI-POSSE 2014b: 239, 242, 250, 252, 254 (characters, phylogenetic affinities).

Type species. *Odontolinus fasciatus* Sharp, fixed by monotypy.

Diagnosis. *Odontolinus* differs from all other genera of Philonthina by the following combination of characters: 1st antennomere distinctly longer than half of head length, with a modified, spine-like seta apically; 2nd antennomere about as long as the following segment; neck with transverse carina; sternum 8 straight to slightly emarginate medioapically, not sexually dimorphic; genital segment with lateral tergal sclerites 9 (styli) dorsoventrally flattened, distinctly dilated in both sexes and not sexually dimorphic. From *Neopescolinus* and *Pescolinus* it differs in having a rather elongate first antennomere (i.e., longer than half of its head length) (CHANI-POSSE 2014a,b).

Redescription. Length 8.0–10.0 mm. **Colouration:** Head reddish brown to dark brown; thorax reddish brown; elytra bicolorous, reddish brown in basal half and dark brown to black in distal half; abdomen with first three abdominal segments reddish brown, 4th and 5th dark brown to black and 6th light brown to yellow; antennae entirely reddish brown to light brown or with both 1st and last antennomeres slightly to distinctly lighter than others; palpi and legs reddish brown to light brown.

Head of quadrangular shape with distinctly obtuse hind angles (Figs. 4, 5), at one third from posterior end about as wide as in anterior third in both sexes; slightly to distinctly wider than long, slightly to distinctly wider than pronotum at widest point; dorsal and ventral surface of head with rather rudimentary wave-like microsculpture. Eyes moderately convex, about as long as to moderately longer than temples seen from above. Antennae inserted closer to anterior margin of frontoclypeus than to eyes, separated from each other by distinctly less than $2.0 \times$ the distance to eye, 1st antennomere distinctly longer than half of head length and antennomeres 2nd and 3rd combined, with a modified, spine-like seta apically (Fig. 10), antennomeres 3rd distinctly longer than 2nd, segments 1st–3rd with rather scarce long setae (Fig. 9). Maxillary palpus with 4th palpomere $1.5 \times$ as long as 3rd. Labrum subrectangular, moderately transverse. Mentum with anterior margin slightly emarginated and moderately longer than submentum. Labial palpus moderately long, 2nd palpomere with 3–4 setae evenly distributed medially and $1–1.5 \times$ as long as 1st, 3rd medially inflated and distinctly longer than 2nd ($Lp3L/Lp2L = 1.5–1.8$). Neck about $0.3–0.4 \times$ as wide as head at widest point.

Prothorax: Pronotum slightly to moderately longer than wide, moderately broadened anteriorly (Figs. 4, 5); front margin subtruncate, hind margin arcuate, anterior angles rather obtuse and posterior angles rounded (Figs. 4, 5); disc with dorsal rows of punctures sub-parallel to each other, each with 3–4 punctures; surface with fine microsculpture of transverse and oblique waves. Prosternum without distinct mid-longitudinal carina. **Legs:** Profemora subcylindrical in shape, with scarce setae; protarsi with first four segments flattened dorsoventrally and widened more distinct in males, with long and curved

pale (adhesive) setae underneath; 1st metatarsomere moderately to distinctly longer than 5th metatarsomere (last) ($S1/S5 = 1.3$). Hind femora and trochanter sexually dimorphic, both spinose in males. **Elytra** at suture distinctly shorter than pronotum at midline (Figs. 4, 5); punctuation fine and dense.

Abdomen: Abdominal terga 3–5 with posterior basal transverse carina complete and straight, punctuated or not (Fig. 14). Hind margin of tergum 8 (sixth visible) subtruncate in both sexes (Fig. 15). **Male sexual characters:** Sternum 8 straight to slightly emarginate medioapically (Fig. 34). Genital segment with lateral tergal sclerites 9 (styli) dorsoventrally flattened and distinctly dilated (Fig. 15); tergum 10 truncate to subtruncate at apex with two apical setae (Figs. 29, 36); sternum 9 with basal portion distinctly asymmetrical, about as long as distal portion and moderately emarginate apically, with several fine apical setae at each side of emargination (Figs. 29, 34). Aedeagus with parameres fused to one short sclerite, completely fused to median lobe and without sensory peg setae; median lobe elongate, with apical part narrowed into subacute apex (Figs. 31, 32, 36, 37). **Female sexual characters:** Sternum 8 straight medioapically. Genital segment with lateral tergal sclerites 9 (styli) similar to those of male; tergum 10 arcuate to subangulate apically (Figs. 32, 38); second gonocoxites each with a long macroseta at middle, with stylus bearing one long apical macroseta (Figs. 33, 39).

Immature stages. Unknown.

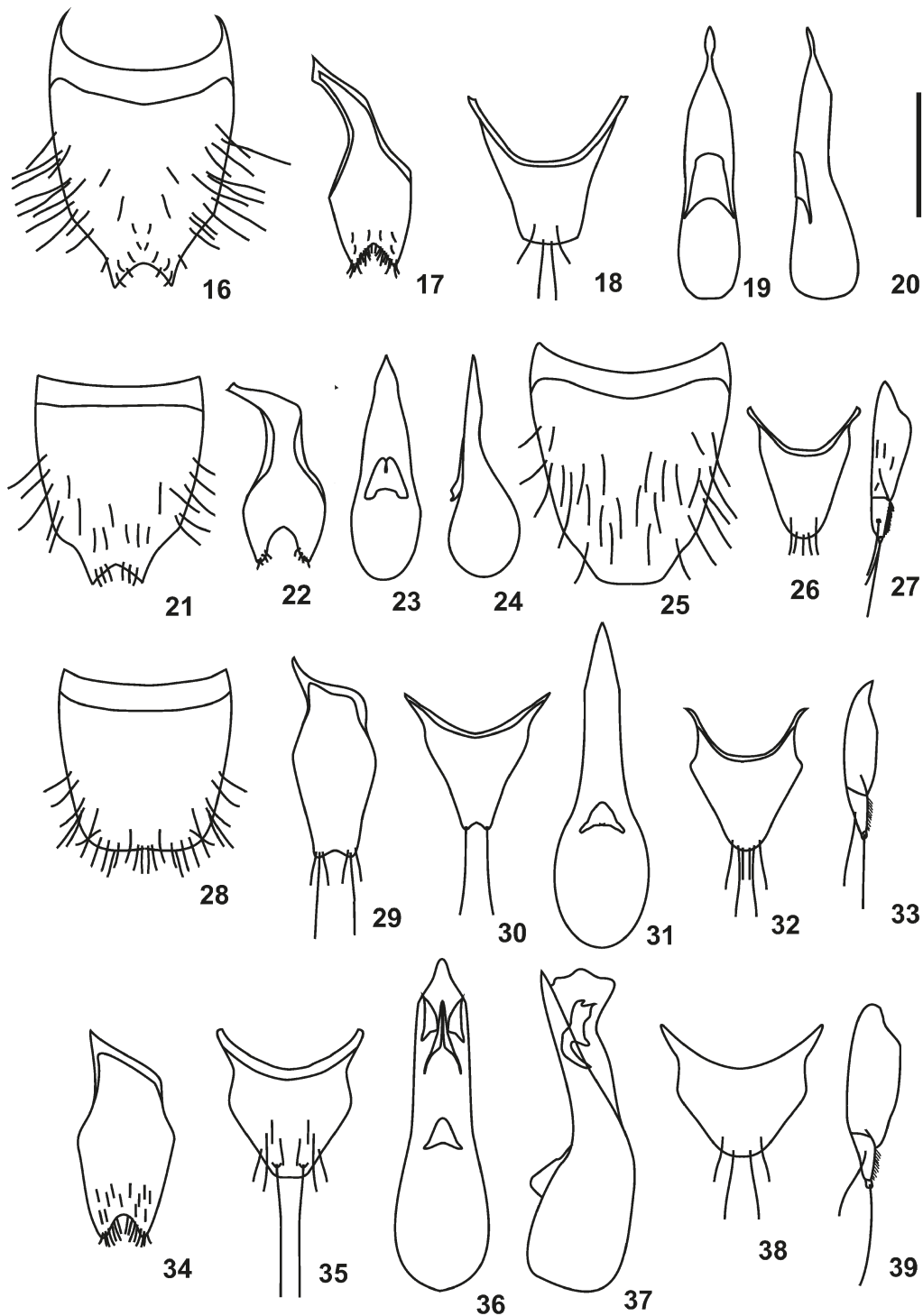
Bionomics. The species of *Odontolinus* have been reported as consistently associated with flower bracts of the genus *Heliconia* (Zingiberales: Heliconiaceae), where they prey upon dipteran larvae (FRANK & BARRERA 2010).

Distribution and remarks. With its two species known at present, *Odontolinus* is distributed in the biogeographical provinces of Eastern Central America, Western Panamanian Isthmus and Western Ecuador (MORRONE 2014) from elevations of 10–1450 m as indicated by trapping data (Fig. 41). *Odontolinus* was previously known only from Costa Rica and Panama; thus Ecuador, Honduras and Nicaragua are new country records.

3.2.1. *Odontolinus fasciatus* Sharp, 1885 (Figs. 4, 34–39, 40, 41)

Odontolinus fasciatus Sharp, 1885: 454; BERNHAUER & SCHUBERT 1914: 372 (catalog); HERMAN 2001: 2721 (catalog); CHANI-POSSE 2013: 4, 8, 10, 14 (phylogenetic placement); CHANI-POSSE 2014a: 7, 10, 11, 15–18, 21 (key); CHANI-POSSE 2014b: 239, 242, 250, 252, 254 (characters, phylogenetic affinities).

Diagnosis. *Odontolinus fasciatus* differs from *O. campanensis* in the pretarsal claws toothed and the abdominal terga 3–5 with the posterior basal transverse carina not punctuated.



Figs. 16–39. *Linoderus alajuelensis*: (16) male sternum 8, (17) male sternum 9, (18) male tergum 10, (19) aedeagus (dorsal view), (20) aedeagus (lateral view). *L. gracilipes*: (21) male sternum 8, (22) male sternum 9, (23) aedeagus (dorsal view), (24) aedeagus (lateral view), (25) female sternum 8, (26) female tergum 10, (27) gonocoxites of female genital segment. *Odontolinus campanensis*: (28) male sternum 8, (29) male sternum 9, (30) male tergum 10, (31) aedeagus (dorsal view), (32) female tergum 10, (33) gonocoxites of female genital segment. *O. fasciatus*: (34) male sternum 9, (35) male tergum 10, (36) aedeagus (dorsal view), (37) aedeagus (lateral view), (38) female tergum 10, (39) gonocoxites of female genital segment. (Orientation: anterior is consistently at the top; scale bar = 0.8 mm)

Redescription. Body length 8.0–10.0 mm. **Colouration:** Head reddish brown to dark brown; thorax reddish brown; elytra bicolorous, reddish brown in basal half and dark brown to black in distal half; abdomen with first three abdominal segments reddish brown, 4th and 5th dark

brown to black and 6th light brown to yellow; antennae entirely reddish brown to light brown or with both first and apical segments slightly lighter than inner segments, palpi and legs reddish brown to light brown. **Head** slightly to moderately wider than long (HW/HL = 1.1–1.2),

slightly to distinctly wider than pronotum (HW/PW = 1.1–1.3). Eyes about as long as to moderately longer than temples (EL/TL = 1.0–1.2) seen from above. **Pronotum** slightly to moderately longer than wide (PW/PL = 0.8–0.9). **Elytra** at sides more than 1.5 × as long as elytra along suture (EtL/Etl = 1.6–1.9). **Male sexual characters:** Sternum 8 straight medioapically. Tergum 10 subtruncate at apex with two apical long setae (Fig. 35). Aedeagus with median lobe gradually narrowed from apical fifth (Figs. 36, 37). **Female sexual characters:** Sternum 8 similar to that of male. Tergum 10 arcuate apically (Fig. 38); second gonocoxites each as for genus (Figs. 33).

Geographical distribution. *Odontolinus fasciatus* has been recorded from Costa Rica and Panama (HERMAN 2001; Newton, unpublished database), Ecuador, Honduras and Nicaragua (new records) between 10–1450 m of altitude (Fig. 41).

Bionomics. Adults of *Odontolinus fasciatus* were consistently found in association with *Heliconia* bracts, where they have been reported as being able to immerse completely in water to capture larvae and/or pupae of mosquitoes (Culicidae) (FRANK & BARRERA 2010).

Type material examined. Lectotype (here designated, Fig. 4), ♀, specimen glued to white card with labels: 'Bugaba, 800–1,500 ft. Champion', 'B.C.A. Col. I. 2. *Odontolinus fasciatus*, Sharp.' [white label], 'SYNTYPE' [round white label with light blue margin], 'Lectotype *Odontolinus fasciatus* Sharp, 1885 | des. Chani Posse 2011', (BMNH). Two paralectotypes, 1 ♂ and 1 ♀ glued to white card in one pin and Sharp's handwriting 'Bugaba, 800–1,500 ft. Champion', other labels same as lectotype (BMNH). Another 6 paralectotypes, 4 ♂ and 2 ♀, with labels, 'Bugaba, Panama. Champion.', 'B.C.A. Col. I. 2. *Odontolinus fasciatus*, Sharp.' [white label], 'SYNTYPE' [round white label with light blue margin]; from those 1 ♂ and 1 ♀ glued to white card in one pin and Sharp's handwriting 'Bugaba, 800–1,500 ft. Champion', and additional label, 'TYPE' [round white label with red margin], another pin, 1 ♂, with additional label 'Sp. figured' [white label] (BMNH). Two additional paralectotypes, 2 ♂, each specimen glued to a white card with following Sharp's handwriting: 'Bugaba Champion, *Odontolinus fasciatus* D.S. male' and three additional white labels, 'Bugaba. Panama. Champion' | 'B.C.A. Col. I. 2. *Odontolinus fasciatus*, Sharp.' | 'Chicago Nat. Hist. Mus. (ex D. Sharp Colln. By exchange with Brit. Mus. Nat. Hist.)'. Each with additional label 'Paralectotype *Odontolinus fasciatus* Sharp, 1885 | des. Chani Posse 2011', (FMNH).

Other material examined. Costa Rica: Alajuela: 5mi SE Portina, 21-jul-66, J. B. Karren, taken on *Heliconia* sp., 1 ♀ (SEMC); Upala, PN Volcán Tenorio, 17 Abr. 2001, A. López 700 m, Alb. Heliconias S. Heliconias, Manual LN_422600_299100 # 62012, 1 undet. (INBio). Cartá: Monumento Nacional Guayabo, Oct 1994, G. Fonseca, 1100 m, L.N 217400, 570000 #3286, 1 undet. (INBio). Heredia: La Selva, 2mi E Puerto Viejo on Rio PV, 07-mar-65, J. B. Karren, 100 m, taken on Museaceae, 1 ♀ (SEMC); 19 May 1993, J. & A. Ashe, 80 m, ex. *Heliconia* flowers #025, 1 ♂, 3 ♀ (SEMC). Limón: ca. 2 km W. Pto Viejo, 15/16-may-93, J. S. & A. K. Ashe, 20 m, ex. *Heliconia* flowers #011, 5 ♂, 4 ♀ (SEMC); Amubri, 2–31 ENE 1996/ 8–30 MAR 1994/SET 1996, G. Gallardo, 70 m, LS385000_578100#7509/ _578100#2823/ _578100#8397, 3 undet. (INBio); Farm Castilla, VIII.38, Field Mus. Nat. Hist. 1966 A. Bierig Collection, Acc. Z. 13812, 1 ♂, 1 without genitalia (FMNH), 1 ♀ (BMNH); Manzanillo RNFS Grandoca y Manzanillo, 9 set a 13 oct 1992, K. Taylor, 0–100 m, LS_398100, 610600, 2 undet. (INBio); Pto. Limón, 2.III.1940, Field Mus. Nat.

Hist. 1966 A. Bierig Collection, Acc. Z. 13812, 1 ♂ (FMNH); Reventazon, Hamburg Farm, II.I.1933, *Heliconia*, leg. F. Nevermann, *Odontolinus fasciatus* Shp. Det. Newton 1994, 1 ♂ (FMNH); V. de la Estrella, R.B Hitoy Cerere. En Catarata, saliendo de F. Espavel, 22–24 Jul 1999/15–27 Feb 1993, W. Arana/G. Carballo, 160 m/100 m, 3 undet. (INBio). Piedras Blancas: 16mi NW of Piedras Blancas, 8 Aug 1966, J. B. Karren, taken in *Heliconia* leaf, 1 ♂, 1 ♀ (SEMC). Puntarenas: Corcovado, Est. Sirena Set. 1990, G. Fonseca, 0–100 m, 270500, 508800, 15 undet. (INBio); Est. Queb. Bonita, Res Biol. Carara, 4–26 ene 1993/10–28 Ago 1992, R. Guzmán, 50 m, L_N_194500_469850, 2 undet. (INBio); Golfito, 28 May 1993, J. & A. Ashe, 10–200 m, ex. *Heliconia* #66, 8 ♂, 5 ♀ (SEMC); Wilson Bot. Garden (Las Cruces Biol Sta.) nr. San Vito, 26 May 1993, J. S. & A. K. Ashe, 1200 m, ex. *Heliconia* flowers, 2 ♂ (SEMC). Ecuador: Pichincha, Pedro Vicente Maldonado, 3.5km N, 29 Marzo 1999, R. Brooks, 530 m, ex. *Heliconia*, rolled leaves, 1 ♂ (SEMC). San Jose: Las Nubes, Est. Santa Helena, 4–15 ene 1996, E. Alfaro, 1210 m, Interseccion L.S 217400, 570001 # 6857, 1 undet. (INBio). Honduras: Atlántida, Lancetilla Bot. Grd., Tela, 23-jun-94, J. Ashe, R. Brooks, 10 m, ex. *Heliconia* flowers #197, 1 ♂ (SEMC). Nicaragua: Rio San Juan Dept., 60km, SE San Carlos, Refugio Bartola, 26.05.2002, R. Brooks, Z. Falin, S. Chatzimanolis, 100 m, 10°58'40"N, 84°20'30"W, ex. ginger fruits, 1 ♀ (SEMC). Panamá: Chiriquí, 27.7km W Volcán, Hartmann's Finca, 14–17/06/1995, J. Ashe, R. Brooks, 1450 m, 8°45'N, 82°48'W, ex. *Heliconia* flowers #232, 1 ♂ (SEMC).

3.2.2. *Odontolinus campanensis* sp.n. (Figs. 5, 28–33, 40, 41)

Diagnosis. *Odontolinus campanensis* differs from *O. fasciatus* in the pretarsal claws simple, not toothed, and the abdominal terga 3–5 with the posterior basal transverse carina distinctly punctuated.

Description. Body length 7.3–8.0 mm. **Colouration:** Head and thorax reddish brown; elytra bicolorous, reddish brown in basal half and dark brown to black in distal half; abdomen with first three abdominal segments reddish brown, 4th and 5th dark brown to black and 6th light brown to yellow; antennae, palpi and legs mostly light brown, with antennomeres 5th to 9th distinctly dark brown. **Head** moderately wider than long (HW/HL = 1.2–1.3), distinctly wider than pronotum (HW/PW = 1.3–1.4). Eyes about as long as to slightly longer than temples (EL/TL = 1.0–1.1) seen from above. **Pronotum** slightly longer than wide (PW/PL = 0.9). **Elytra** at sides more than 1.5 × as long as elytra along suture (EtL/Etl = 1.8–1.9). **Male sexual characters:** Sternum 8 slightly emarginate medioapically (Fig. 28). Tergum 10 truncate at apex with two long apical setae (Fig. 30). Aedeagus with median lobe gradually narrowed from apical third (Fig. 31). **Female sexual characters:** Sternum 8 straight medioapically. Tergum 10 subangulate apically (Fig. 32). Second gonocoxites each as for genus (Fig. 33).

Geographical distribution. *Odontolinus campanensis* is at present only known from one collecting site in Costa Rica (Cerro Campana).

Bionomics. It was found in association with *Heliconia* flowers.

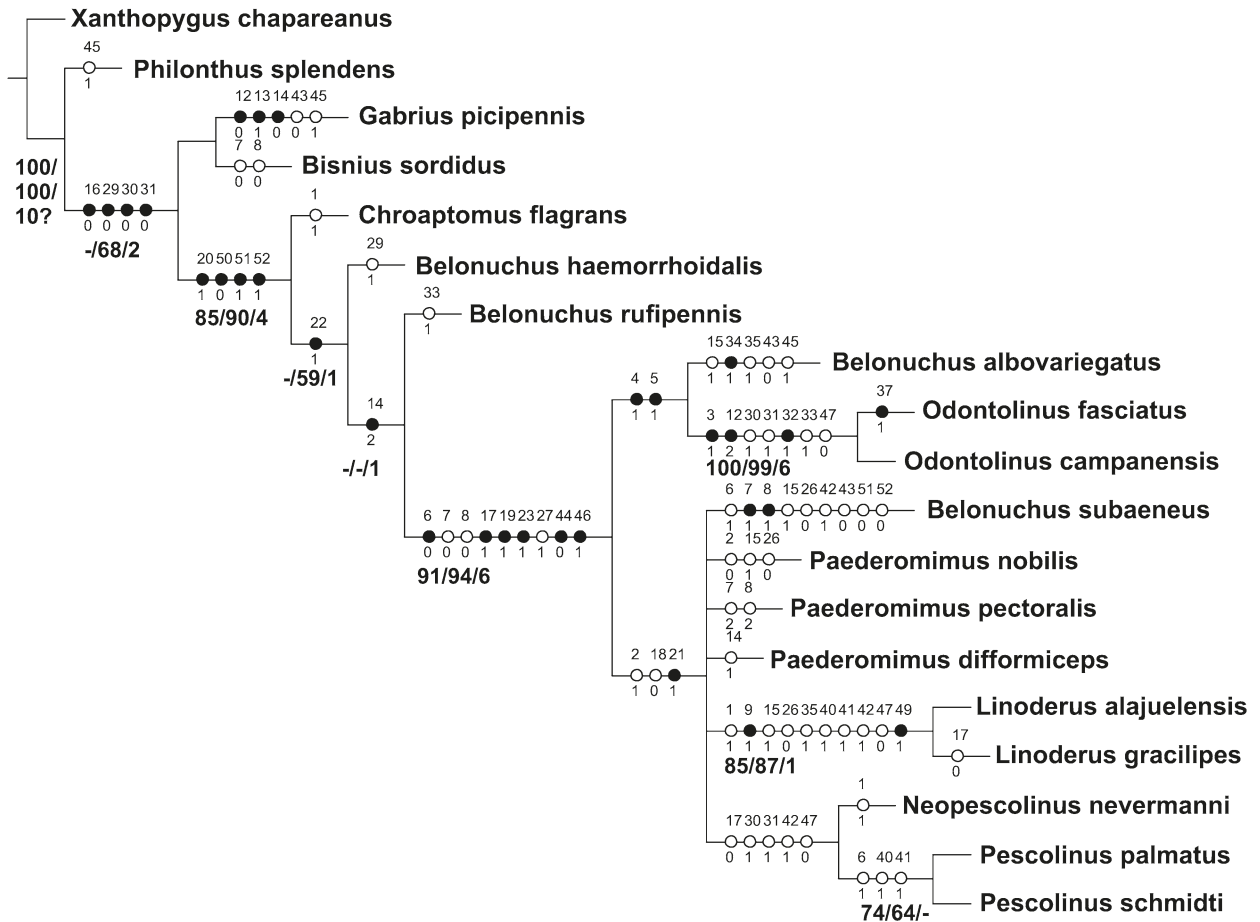


Fig. 40. Strict consensus tree showing relationships between *Linoderus*, *Odontolinus* and representatives from other Neotropical endemic genera (section 4.2.). Black circles: exclusive synapomorphies; white circles: non-exclusive synapomorphies. Numbers in bold below the branches are support values (Standard Bootstrap / Jackknife / Bremer).

Etymology. The specific name refers to Cerro Campana, Panama, where this species was found.

Type material. Holotype (Fig. 5), ♂, with labels: 'Panamá: Cerro Campana, (Capira) | 8°44'N, 79°57'W, 790 m | 1 June 1995, J. Ashe, R. Brooks | ex. Heliconia flowers #096', 'Holotype *Odontolinus* | *campanensis* | Chani Posse & Solodovnikov, 2017', (SEMC). Paratype ♀ same label as holotype and 'Paratype *Odontolinus* | *campanensis* | Chani Posse & Solodovnikov, 2017', (SEMC).

4. Phylogeny

The analysis of the data matrix (Table 1) produced four cladograms with 99 steps, a consistency index (CI) of 0.56 and a retention index (RI) of 0.71. The strict consensus from the most parsimonious trees (MPT) places both *Linoderus* and *Odontolinus* within a well-supported monophyletic group together with *Pescolinus*, *Neopescolinus*, the sampled representatives of the genus *Paederomimus* and two of a few sampled representatives of the genus *Belonuchus* (*B. albovariegatus* and *B. subaeneus*) (Fig. 40). The monophyly of *Linoderus* appears well sup-

ported and defined by two exclusive synapomorphies: head with punctuation on dorsal surface sexually dimorphic (9.1) and male with apex of lateral tergal sclerites 9 (styli) laterally emarginate (49.1). The monophyly of *Odontolinus* also shows high support measures in addition to three exclusive synapomorphies: antennomere 1 with apical macroseta spine-like, labial palpus with palpomere 3 (apical) subcylindrical (12.2) and male metatrochanter with dorsal spines (32.1). Revealed firm monophyly of both these lineages confirmed our generic assignments of both new species, respectively. Sister-group relationships of *Linoderus* are not resolved, and those of *Odontolinus* remain uncertain in terms of support values. *Odontolinus* forms the sister group to *B. albovariegatus*, and together they are sister to the rest of taxa which form a clade where only *Linoderus* and *Pescolinus* appear as well-supported and distinct genera while relationships among the *Paederomimus* representatives are unresolved. This grouping is supported by only one exclusive synapomorphy (21.1: basisternum more than 1.5 × as long as furcasternum) which has shown to be a homoplastic feature within Staphylinini (CHANI-POSSE et al. 2017). Each of the two exclusive synapomorphies supporting the subclade *Odontolinus* + *B. albovariegatus* is also recognized in the Neotropical genus *Ophionthus*

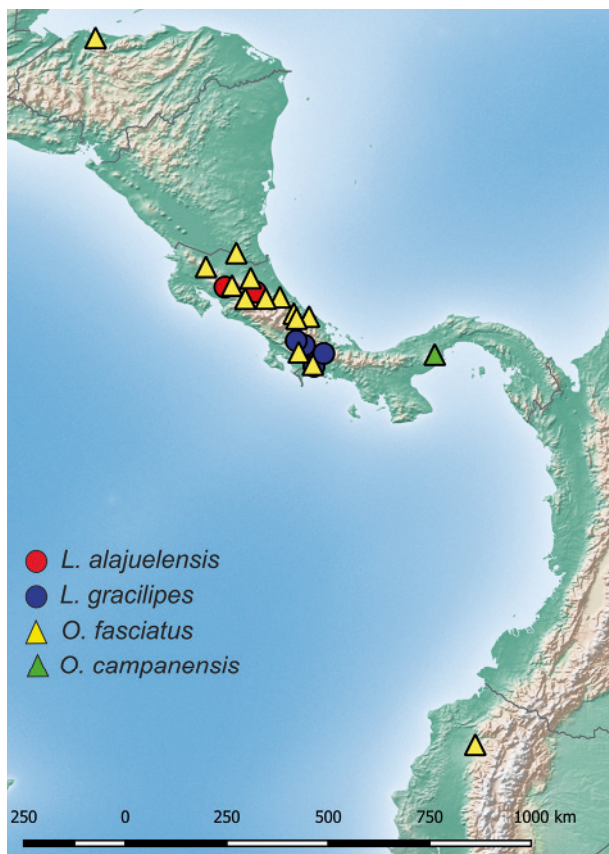


Fig. 41. Geographical distribution of *Linoderus* and *Odontolinus* species.

Bernhauer (4.1: antennomere 1 distinctly longer than half of head length) (CHANI-POSSE 2013) and the extra-Neotropical genera *Actinus* Fauvel and *Leucitus* Fauvel (5.1: antennomere 3 distinctly more than $1.5 \times$ as long as antennomere 2) (CHANI-POSSE et al. 2017). While the first character should be included in future studies exploring internal relationships within the Neotropical lineage of Philonthina, the second one should be considered as homoplastic within Philonthina.

5. Discussion

Former phylogenetic hypotheses supported *Odontolinus*, *Linoderus* and *Pescolinus* as a monophyletic group (CHANI-POSSE 2013), its sister-group relationship to *Neopescolinus* and the monophyly of *Pescolinus* (CHANI-POSSE 2014b) as well as that of *Paederomimus* (CHANI-POSSE 2013). Although in our current study these five genera and/or their representatives also appear gathered in one well-supported group, there is no agreement with previous studies (CHANI-POSSE 2013, 2014b) regarding the phylogenetic relationships among those genera. Within the context of our analysis, the currently species-rich, loosely defined genera *Belonuchus* and *Paederomimus* do not appear as monophyletic. Our phylogeny

not only confirms the suspected non-monophyly of *Belonuchus* (CHANI-POSSE 2014a; CHANI-POSSE et al. 2017) but also shows unresolved relationships among some of its species and some representatives of *Paederomimus*. When comparing this to previous results it is clear that sister-group relationships among less speciose but quite distinct genera such as *Linoderus*, *Neopescolinus*, *Odontolinus* and *Pescolinus* will not be elucidated until the most speciose and likely non-monophyletic genera such as *Belonuchus* and *Paederomimus* are better sampled in an analysis. The placement of *B. albovariegatus* is a clear example of this situation, showing no supporting evidence for a sister-group relationship to either *Odontolinus* or any *Belonuchus* representative. Characters supporting the monophyly of *Odontolinus* are not shared by *B. albovariegatus*, so the inclusion of *B. albovariegatus* in *Odontolinus* would only lead to blurred generic limits for an otherwise very distinct genus. While we acknowledge the fact that taxonomically ill-defined genera as *Belonuchus* do not provide a solid basis for classification, we advocate for keeping the current affiliation of its species until their phylogenetic position is rigorously assessed.

The systematics of the Neotropical endemic genera of Philonthina need to be assessed along a wider range of characters than those traditionally used for the Holarctic fauna. Among them, sexual dimorphism offers a source of phylogenetic and additional diagnostic characters at both generic and specific level as long as both sexes are available for study (CHANI-POSSE 2014a). A male-biased sexual dimorphism among the Neotropical philonthines was noticed as early as SHARP (1885). Sexually dimorphic characters have shown to be of phylogenetic importance in the present study. Some of them are exclusive synapomorphies defining distinct genera (*Linoderus*, *Odontolinus*), while others are homoplastic features (i.e., male with spinose metafemora, first metatarsomere distinctly longer in males than in females). We conclude that sexually dimorphic characters should not be avoided but instead studied in all their variety in order to elucidate their role in the radiation of the Neotropical Philonthina. Their systematic utility, though, should be properly tested in the course of a phylogenetic analysis.

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