Towards a natural classification of the subtribe Philonthina (Coleoptera: Staphylinidae: Staphylinini): a phylogenetic analysis of the Neotropical genera

M A R I A N A   C H A N I - P O S S E

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Abstract. Philonthina, the largest subtribe of the rove beetle tribe Staphylinini, is a hyperdiverse group in the Neotropical Region, accounting for about half of the genera of the subtribe. Despite such diversity, Neotropical Philonthina have never been analysed phylogenetically, deterring formulation of a modern classification of the Staphylinini. A cladistic analysis of Neotropical Philonthina was performed based on 110 morphological characters and 77 terminal taxa. Representatives of Philonthina from other regions and other main lineages of Staphylinini, Arrowinini and Platyprosopini were included to test their relationships with Neotropical Philonthina. The major results are the monophyly of 11 of the 17 endemic Neotropical genera of Philonthina, the placement of *Holisus* Erichson (Hyptiomina) into this clade showing a sister group relationship to myrmecophile genera, and the position of *Erichsonius* Fauvel outside of Philonthina within Staphylinini. Six of the current seven species of *Endeius* Coiffait & Sáiz group with Neotropical species of *Philonthus* Stephens. The separation of Gondwana about 65 my and major landscape modifications in the vast interior of northern South America during the past 25 my is proposed to explain the evolution of the endemic Neotropical genera of Philonthina. The following taxonomic changes are proposed: *Erichsonius* Fauvel, 1874 now placed as *incertae sedis* in Staphylinini; *Endeius* Coiffait & Sáiz, 1968, **n.syn.** of *Philonthus* Stephens, 1929 and *Endeius nitidipennis* (Solier, 1849) placed as *incertae sedis* in Philonthina. The following new combinations are proposed: *Philonthus franzi* (Sáiz, 1971), **comb.n.**, *Philonthus loensis* (Coiffait & Sáiz, 1968), **comb.n.**, *Philonthus lugubris* (Sáiz, 1971), **comb.n.**, *Philonthus ovaliceps* (Coiffait, 1981), **comb.n.**, *Philonthus punctipennis* (Solier, 1849), **comb.res.** and *Philonthus subpunctipennis* (Coiffait & Sáiz, 1968), **comb.n.** *Philonthus herberti*, **n.nov.,** is proposed for *Philonthus franzi* Schillhammer, 1998, which is a junior secondary homonym of *Philonthus franzi* (Sáiz, 1971).

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Introduction

Staphylinini, the largest tribe within the subfamily Staphylininae, includes over 200 genera distributed in nine subtribes (Herman, 2001; Newton & Thayer, 2005; Bouchard *et al.*, 2011). Five subtribes account for about 80% of the total genera: Philonthina (65), Staphylinina (39), Xanthopygina (32), Amblyopinina (18) and Quediina (14) (after Chatzimanolis *et al.*, 2010). Recent morphological and molecular-based analyses support monophyly of Philonthina, Staphylinina and Xanthopygina within the tribe (the latter as far as the Neotropical core is concerned), resulting in Philonthina as possible sister group to Xanthopygina and both together as sister group to Staphylinina (Solodovnikov & Schomann, 2009; Chatzimanolis *et al.*, 2010; Solodovnikov & Newton, 2010).

As far as Philonthina is concerned, all previous studies were based either on rather limited taxon sampling of the subtribe (Solodovnikov & Newton, 2005, 2010; Solodovnikov & Schomann, 2009; Chatzimanolis *et al.*, 2010) or have not included an adequate representation of the Neotropical fauna to allow a conclusion about monophyly to be made (Smetana, 1995; Smetana & Davies, 2000; Li & Zhou, 2011). Furthermore, the placement of *Erichsonius* Fauvel within Philonthina as well as the phylogenetic position of the monotypic subtribe Hyptiomina (all but one of its currently known species are Neotropical) have been questioned, with Hyptiomina appearing as nested within Philonthina (e.g. Solodovnikov & Schomann, 2009; Li & Zhou, 2011).

Among the 65 genera of Philonthina, 28 genera occur in the Neotropical Region (Herman, 2001; Newton & Thayer, 2005), of which 17 are Neotropical endemics, most of them not studied critically since their original descriptions more than a century ago. Most of the remaining 11 genera are distributed worldwide (Herman, 2001; Newton & Thayer, 2005) but have been studied only on restricted regional scales (e.g. Smetana, 1995; Schillhammer, 1997, 1998, 1999, 2000, 2001, 2003; Hromádka, 2008a,b, 2009, 2010a,b,c; Li *et al.*, 2010). Thus, their systematic position has been difficult to assess given the scarce and fragmentary knowledge of their pantropical fauna. Although attempts have been made to clarify the taxonomic position of each of these genera within Philonthina (Smetana, 1995), their inter- and intra-generic relationships have yet to be elucidated (Smetana, 1995; Li & Zhou, 2010b). Consequently, no framework exists to provide for the development of phylogenetic hypotheses among the Neotropical members of Philonthina, or between them and the other genera of the subtribe. Moreover, the supra-generic classification of the tribe Staphylinini is currently under discussion and revision (Assing, 2000; Solodovnikov & Newton, 2005; Solodovnikov & Schomann, 2009; Chatzimanolis *et al.*, 2010; Li & Zhou, 2011). Because morphology-based studies have shown broad consensus on the treatment of characters since Smetana & Davies (2000), the lack of a new phylogenetic classification of the Staphylinini may be attributed mainly to the lack of knowledge of extra Holarctic genera, and especially pantropical elements rather than to different ideas about groupings. Therefore, the internal systematics of both the tribe and its subtribes are in need of a reclassification that includes extra-Holarctic faunas. The Neotropical region still lacks systematic collections from large areas in the forests of the Amazon basin (e. g. Basset, 2001). Considering the number of taxa yet to be discovered, an evaluation of the systematic relationships of the Neotropical Philonthina is needed to avoid a classification incompatible with the phylogeny and evolution of the subtribe.

The main objectives of this work are to test whether the Neotropical endemic genera of Philonthina belong to a single lineage and to establish the relationships both among them and with genera from other regions.

This paper constitutes a step towards a phylogenetic taxonomy of Philonthina of the Neotropical Region, and towards further studies on the phylogenetic classification of the tribe Staphylinini.

Study area

The geographical area covered in this study comprises the Neotropical Region, Chile and southern Argentina, as shown in the 12-region system used by Newton & Thayer (2005). Such a system is in agreement with the primary divisions in the biogeographic regionalization of the world given by Morrone (2009).

Material and Methods

Specimens and collections

Specimens were borrowed from and/or are deposited in the following collections (acronyms used throughout the text): BMNH, The Natural History Museum, London, (R. Booth); CNC, Canadian National Collection, Ontario, Canada (P. Bouchard, A. Davies); FMNH, Field Museum of Natural History, Chicago, IL, U.S.A. (A. F. Newton, M. K. Thayer, J. Boone); IADIZA, Instituto Argentino de Investigaciones de las Zonas Aridas, Mendoza, Argentina (S. Roig Juñent); MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (A. Roig Alsina); MLPA, Museo de La Plata, La Plata, Argentina (A. Lanteri, N. Cabrera); MNHUB, Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, Germany (M. Uhlig, B. Jaeger); NHMM, Natuurhistorisch Museum Maastricht (P. Beuk); NMW, Naturhistorisches Museum Wien, Austria (H. Schillhammer); SEMC, Snow Entomological Collection, Natural History Museum/ Biodiversity Research Center, University of Kansas, Lawrence, U.S.A (Z. Falin).

Examination of specimens

Beetle specimens were examined using a Leica MZ6 dissecting microscope. They were examined mostly as pinned dry specimens, but some were relaxed first in warm soapy water, rinsed, disarticulated and examined as wet preparations

in glycerin. SEM pictures were obtained by using a JSM-6610 system. Measurements were taken with an eyepiece linear micrometer and abbreviated as follows: AA, distance between antennal insertions; AE, distance between antennal insertion and anterior margin of eye (in dorsal view, right side); AF, distance between antennal insertion and anterior margin of frontoclypeus (in dorsal view, right side); A [1–3]L, antennal [segment] length; A [1–3]W, antennal [segment] (maximum) width; MP [3,4]L, maxillar [segment] length; MP [2,3]W, maxillar [segment] (maximum) width; LP [2,3]W, labial [segment] (maximum) width; HL, length of head capsule, from anterior margin of frontoclypeus to neck constriction (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); S1, first segment of hind tarsus length; S5, last segment of hind tarsus length.

Terminology

As in previous studies (e.g. Solodovnikov & Newton, 2005; Solodovnikov & Schomann, 2009) that were used as main references for the completion of this work, morphological terms follow Blackwelder (1936), Naomi (1987–1990), Smetana & Davies (2000) and Kukalova-Peck & Lawrence (1993): fig. 46).

Biogeography

Few of the Neotropical endemic genera of Philonthina were revised after their original description and no keys are available that allow their identification at least at the generic level. Because current records are mostly restricted to type localities with no further information about distributional range, they do not provide a robust basis for conducting a formal biogeographical analysis. It is still possible, however, to evaluate the phylogenetic signal of the resulting analysis for the Neotropical Philonthina based on two external criteria. First, recent data about the age of the tribe Staphylinini and its main subgroups suggest that the subtribe Philonthina originated some time later than the Early Cretaceous (Solodovnikov *et al.*, 2012). Second, the geological history of the Neotropical Region provides evidence for large-scale biome shifts (e.g. Benedetto, 2010) and a cyclic re-assortment of Andean and lowland species that, combined with changes in forest structure in response to climate change, would have contributed to cladogenetic events (Mayle *et al.*, 2009). Biogeographical considerations presented here are placed in a narrative context within which the evolution of the Neotropical Philonthina may have occurred.

Taxa

A matrix of 77 taxa and 110 morphological characters was analysed. Sixty-three taxa representing 38 genera belonged to the subtribe Philonthina (including all the 'New World' genera,

with exception of *Remus*). Another 14 taxa were chosen in an attempt to broadly represent the diversity of the main lineages of Staphylinini in the Neotropical Region; two sister taxa to Staphylinini were also included. All taxa of the in- and outgroups are listed in Table S1. Those genera of Philonthina which are rich in species in the Neotropical Region (i.e. *Belonuchus*, *Hesperus*, *Paederomimus* and *Philonthus*) were represented in this analysis with at least three species each from different species groups, as far as this knowledge is available (for *Philonthus*: Smetana, 1995; Schillhammer, 1998, 1999, 2000, 2001, 2003; Chani-Posse, 2010) or an hypothesis about species groups exists (for *Paederomimus*: Sharp, 1885: 438-439). In the case of those genera with broader distribution (*Belonuchus*, *Hesperus* and *Philonthus*), taxa from other zoogeographical regions were also considered (Table S1). To analyse the relationships of the Neotropical/southern South American genera within the subtribe, genera from other regions were included (Table S1). Because there is no evidence of close sister group relationships between the Neotropical genera and those of other regions, the latter were selected among other Philonthina based on current hypotheses on the relationships between areas that arise from cladistic biogeography (Morrone, 2009).

Characters

Selection of characters mainly followed the character system developed by Smetana & Davies (2000), Solodovnikov & Newton (2005, 2010) and Li & Zhou (2011) in their exploration of morphological characters for the phylogenic reconstruction of the tribe Staphylinini. Character/character-state descriptions are shown below together with further discussion of characters previously not included and whose statements have been modified from the originals in the above-mentioned studies. Following Sereno (2007, 2009), neomorphic (presence/absence) and transformational (transformation from one state to another) characters where treated as separate, independent patterns. Such character treatment constitutes another modification from that of previous authors (Solodovnikov & Schomann, 2009; Li & Zhou, 2011).

1. Antennal insertions, distance to frontoclypeus relative to distance to eye (AF/AE): 0. at the anterior margin of frontoclypeus, i.e. ∼ 0 (Fig. 1B, C); 1. closer to frontoclypeus or at equal distance at most, i.e. ∼ 1 (Fig. 1A); 2. far from frontoclypeus, i.e. ∼ 1.5; 3. far from frontoclypeus, i.e. ∼ 2.0.
2. Antennal insertions, distance between relative to distance to eye (AA/AE), male: 0. distinctly closer to each other, i.e. ∼ 0; 1. far from each other, i.e. 1.5–4.5 (Fig. 1A–C); 2. far from each other, i.e. ∼ 5; 3. distinctly >6.0.
3. Antennae, pubescence: 0. lacking on antennomere I (with only longer sparse setae), starting on antennomere II; 1. lacking on antennomeres I–III (with only sparse longer setae), starting on antennomere IV (Fig. 1D); 2. lacking on antennomeres I–IV (with only longer sparse setae),
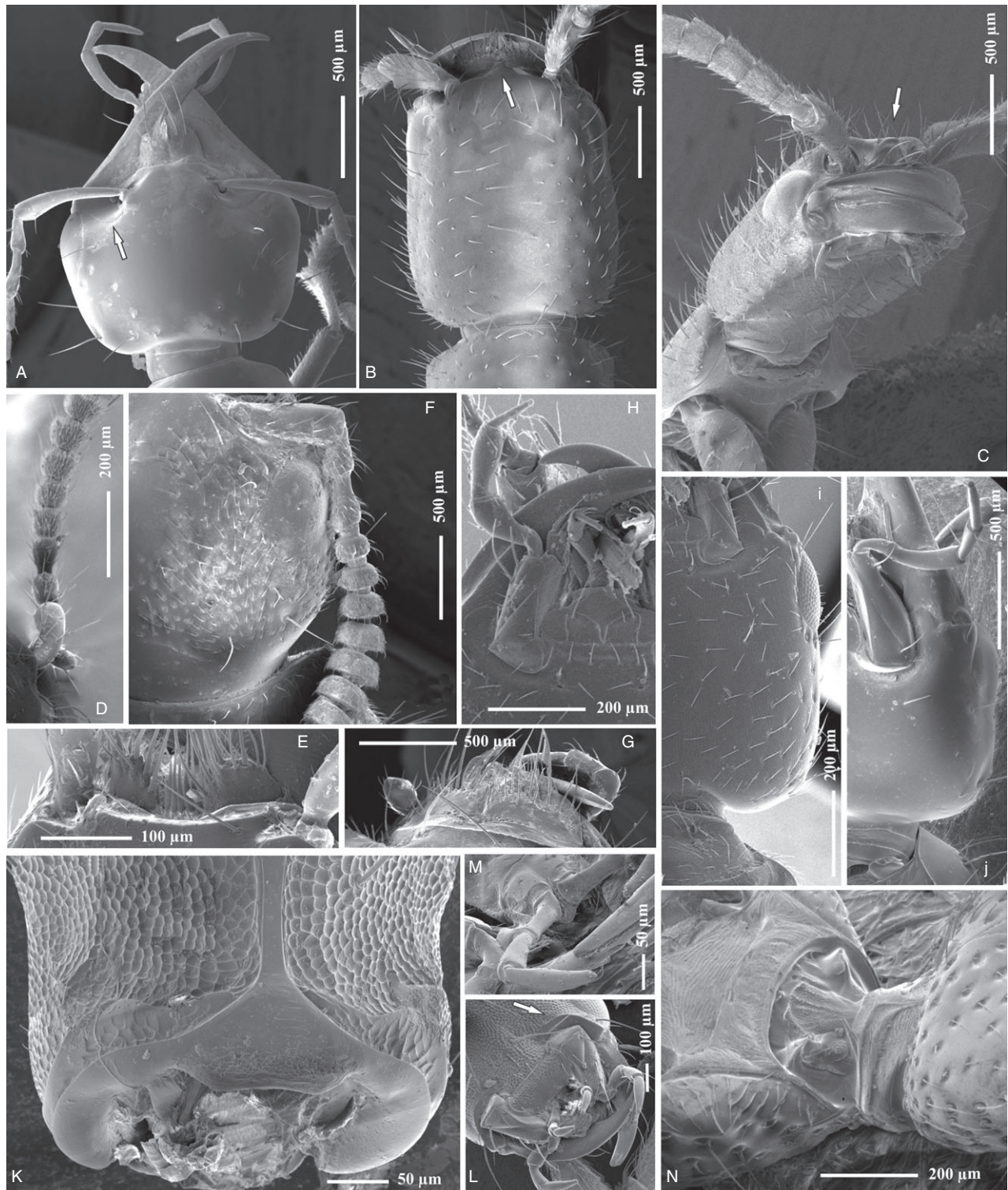
Fig. 1. (A) *Odontolinus fasciatus*, head in dorsal view. (B, C) *Proxenobius borgmeieri*: head in dorsal view (B), head in ventral view and prosternum (C). (D, E) *Erichsonius brachycephalus*: antenna (D), labrum (E). (F, G) *Flohria laticornis*: antenna (F), labrum (G). (H, I) *Holisus humilis*: maxillary and labial palpi (H), head in ventral view (I). (J) *Belonuchus mordens*. (K, L) *Ecitophytes coniceps*: base of head in ventral view (K), maxillary and labial palpi (L). (M, N) *Paederomimus contractus*: ligula and labial palpi (M); base of head in ventral view and prosternum (N).

starting on antennomere V (Fig. 1F); 3. lacking on antennomeres I–V (with only longer sparse setae), starting on antennomere VI; 4. lacking on antennomeres I–VI (with only longer sparse setae), starting on antennomere VII; 5. dense on all antennomeres; 6. lacking on antennomere I and II (with only longer sparse setae), starting on antennomere III (Fig. 1C).

4. Antennae, antennomere I, apical spine-like seta: 0. absent; 1. present.

5. Antennae, antennomere I, length relative to head length (AL1/HL): 0. ≤ 0.5 (Fig. 1B-D, F); 1. distinctly > 0.5 but < 1.0 (Fig. 1A); 2. ~ 1.

6. Antennae, antennomere I, width relative to width of antenonomere II (AW1/AW2, at widest point): 0. ≤ 1.5 (Fig. 1A-D); 1. distinctly > 1.5 (Fig. 1F).

7. Antennae, antennomere II, width relative to width of antenonomere III (AW2/AW3, at widest point): 0. ≤ 1.2 (Fig. 1A, C, F); 1. ~ 1.5 (Fig. 1D).

8. Antennae, antennomere III, length relative to length of antenonomere II (AL3/AL2): 0. ≤ 2.0; 1. distinctly > 2.0.

9. Antennae, antennomere I, apical groove: 0. absent; 1. present.

10. Antennae, last antennomere, shape of apex: 0. subtruncate; 1. subacute; 2. convex.

11. Head, antero-lateral ridge: 0. absent (Fig. 1B); 1. present (Fig. 1A).

12. Head, microsculpture on disc: 0. well developed (distinct and profound) (Fig. 1B); 1. rudimentary; 2. indistinct (Fig. 1A, F).

13. Head, neck constriction: 0. distinct at sides only; 1. fully developed, distinct all around (Fig. 1A, B, F); 2. neck region indistinct.

14. Eyes, size relative to size of temples (EL/TL): 0. highly reduced; 1. distinctly < 0.5 (Fig. 1B); 2. ≥ 0.5 (Fig. 1A, F).

15. Frontoclypeus, anterior margin, macrosetae: 0. absent; 1. present.

16. Frontoclypeus, macrosetae at anterior margin, inclination: 0. straight; 1. convergent, not crossing each other; 2. convergent, crossing each other (Fig. 1C).

17. Head, neck, longitudinal ridge: 0. absent; 1. present.

18. Head, dorsal basal ridge: 0. absent; 1. present.

19. Head, ventral basal ridge: 0. absent; 1. present (Figs 1C, J, K, N, 3A–F)

20. Head, ventral basal ridge: 0. along considerable portion of its length confluent with ventral portion of postoccipital suture; 1. strongly (to moderately) projecting anteriad (Fig. 3E); 2. extending more or less parallel to ventral portion of postoccipital suture (Fig. 3A–D, F).

21. Head, nuchal ridge: 0. absent; 1. present.

22. Head, nuchal ridge, degree of development: 0. distinct dorsally and laterally (Figs 1F, 3C); 1. distinct dorsally, laterally and, more or less, ventrally (Fig. 1A, B, J, N); 2. distinct only dorsally, disappearing laterally (Figs 1K, 3B); 3. distinct only laterally and, more or less, ventrally, entirely obsolete dorsally; 4. distinct only laterally, entirely obsolete dorsally and ventrally.

23. Head, infraorbital ridge: 0. absent; 1. present (Fig. 3C, F).

24. Head, postgenal ridge: 0. absent; 1. present (Fig. 3A, D, E, F).

25. Head, postmandibular ridge: 0. absent; 1. present (Fig. 3A–C, F).

26. Head, postmandibular ridge, shape: 0. short, extending only ventrally, sometimes confluent with long ventral extensions of nuchal or infraorbital ridges (Fig. 3A–C, F); 1. long, extending ventrally and turning more or less dorsally behind eyes.

27. Head, postmandibular ridge relative to mandibular base: 0. bordering almost completely (Fig. 3B, C); 1. bordering only laterally (Fig. 3A); 2. separate (Fig. 3F).

28. Labrum, transparent apical membrane: 0. absent (1E); 1. present, at least laterally (1G).

29. Labrum, medio-apically: 0. deeply emarginate or bilobed; 1. very slightly or not emarginated.

30. Mandibles, dorsolateral groove: 0. absent; 1. present (Fig. 1A).

31. Mandibles, length of dorsolateral groove: 0. reaching the apex; 1. not reaching the apex (Fig. 1A).

32. Maxillary palps, segment II width relative to width of segment III (Mp2W/Mp3W): 0. ≤ 1.5; 1. distinctly > 1.5.

33. Maxillary palps, apical segment, shape: 0. fusiform (Fig. 1J); 1. gradually narrowed to acute or subacute apex (Fig. 1C, L); 2. subcylindrical (parallel-sided) (Fig. 1A); 3. acicular (Fig. 1H).

34. Maxillary palps, segment IV (apical) length relative to length of segment III (Mp4L/Mp3L): 0. ≤ 0.2; 1. between 0.5 and 0.8; 2. between 1.0. and 1.8; 3. ≥ 2.0.

35. Ligula, shape: 0. more or less bilobed, with variously developed rounded lobes; 1. small, entire (or at most slightly notched medially) (Fig. 1M); 2. strongly reduced, indistinct.

36. Labial palps, apical segment, basal width relative to basal width of preceding segment (Lp3W/Lp 2W): 0. ~ 0.3; 1. between 0.5 and 1.0; 2. distinctly > 1.0 but ≤ 1.5; 3. ~ 1.7; 4. ~ 2.0; 5. distinctly > 2.0.

37. Labial palps, apical segment, shape: 0. subcylindrical to fusiform (Fig. 1M); 1. gradually narrowed to acute or subacute apex (Fig. 1L); 2. acicular (Fig. 1H); 3. gradually broadened into an slightly inflated and subtruncate apex; 4. subquadrate and flattened laterally; 5. subacute to acute and flattened laterally.

38. Submentum, chaetotaxy: 0. apparently glabrous (i.e. with microsetae only or asetose); 1. with multiple long setae not differentiated into 'macrosetae' and smaller setae; 2. with one pair of macrosetae (if accompanied by other large setae of various number, size and arrangement, then those are distinctly smaller) (Fig. 1H, L).

39. Mentum, chaetotaxy: 0. with one pair of 'macrosetae'; 1. with two pairs of 'macrosetae'; 2. with three pairs of 'macrosetae' or more.

40. Gular sutures: 0. joined before neck (Fig. 3A, D, E); 1. not joined before neck and running close to the base (Fig. 3B, C, F).

41. Neck, middle portion of disc, punctuation: 0. absent to sparse; 1. dense.

42. Neck, transverse carina: 0. absent; 1. present (Fig. 1A).

43. Pronotum, anterior angles relative to anterior margin of prosternum: 0. not produced beyond (anterad of) (Figs 1J, 2B, C); 1. produced beyond (anterad of) (Figs 1N, 2A, D).

44. Pronotum, lateral puncture with long seta, position: 0. in superior line or at a distance no more than the diameter of puncture; 1. at a distance three times as large as diameter of puncture; 2. two times.

45. Pronotum, punctation of disc: 0. disc smooth, without setiferous punctures (if punctured, punctures without setae); 1. more or less densely punctured, setiferous punctures not arranged in longitudinal rows; 2. very sparsely punctured, these large setiferous punctures in some symmetrical arrangement, most often in longitudinal rows (sometimes also with distinctly smaller and denser punctation not arranged in rows); 3. very sparsely punctured, these large setiferous puncture not arranged in rows.

46. Pronotum, hypomeron: 0. not inflexed to slightly inflexed (visible in lateral view of prothorax); 1. fully inflexed (hardly or not visible in lateral view of prothorax).

47. Pronotum, superior marginal line of pronotal hypomeron relative to anterior angles of pronotum: 0. developed through its whole length, not deflexed under anterior angle; 1. developed through its whole length, deflexed under anterior angle (Fig. 2A–D); 2. ending at anterior corners of pronotum, not deflexed under them; 3. short, deflexed but does not extend to anterior edge of pronotum.

48. Pronotum, superior marginal line vs inferior marginal line of hypomeron: 0. inferior line not meeting superior line; 1. inferior line subcontiguous or fused to superior line behind or near to anterior angles (Fig. 2A–D).

49. Pronotum, postcoxal process of hypomeron: absent (0); present (1).

50. Prosternum, basisternum: 0. without conspicuous macrosetae; 1. with one pair of 'macrosetae';

51. Prosternum, mid-longitudinal carina: 0. absent (only medial prominence, not carinate, not longitudinal) (Fig. 2B); 1. developed only along furcasternum (Fig. 2A); 2. developed along furcasternum and at least part of basisternum; 3. developed only along basisternum.

52. Prosternum, shape of longitudinal carina: 0. forming well-defined, sharp ridge at least in its basal part; 1. more or less rounded, from obtuse ridge to smooth longitudinal prominence of prosternum.

53. Prosternum, basisternum transverse carina: 0. absent; 1. present (Figs 1N, 2D).

54. Prosternum, basisternum transverse carina (if present): 0. rudimentary to incomplete; 1. complete (Figs 1N, 2D).

55. Elytral sub-basal ridge: 0. present; 1. absent.

56. Elytral sub-basal ridge, shape: 0. immediately adjacent to elytral articulation, short, extending anteriad (not extending laterad to humerus); 1. long, extending from level of middle of scutellum to elytral humerus.

57. Sternopleural (anapleural) suture: 0. transverse, or nearly transverse (very slightly oblique) (Fig. 2E); 1. distinctly oblique (medial end of suture anterior to its lateral end) (Fig. 2B); 2. more or less curved so that medial part of suture is more longitudinal and lateral part more transverse.

58. Mesoventrite, structure of medial part (with respect to the position of mesocoxae): 0. disc of mesoventrite situated more or less in one plane with, or only slightly more ventrally than its median (mesoventral part of mesocoxal acetabula); 1. disc of mesoventrite situated distinctly more ventrally than median part (mesoventral part of mesocoxal acetabula), which is usually carinate.

59. Mesoventrite, sternacostal carina: 0. absent; 1. present.

60. Mesoventrite, medial carina in coxal acetabulum: 0. absent; 1. present.

61. Mesoventrite, medial transverse carina: 0. absent; 1. present.

62. Mesoventral intercoxal process: 0. rounded or, if pointed, forming more or less obtuse angle; 1. narrow, usually pointed, forming more or less sharp angle; 2. truncate to subtruncate; 3. metaventrite fused with mesoventrite so that mesoventral intercoxal process indistinct.

63. Mesoscutellum: 0. with one transverse carina, separating scutellum from prescutum; 1. with two transverse carinae (one posterior, separating scutellum from prescutum; another anterior, extending between anterior notal wing processes).

64. Metascutellar mid-longitudinal suture (if present): 0. well developed; 1. rudimentary, (very weak but clear at base).

65. Front femur, lateroventral spines: 0. absent (Fig. 2B); 1. present (Fig. 2C).

66. Front femur, lateroventral spines (if present): 0. dense; 1. sparse (Fig. 2C).

67. Front tibia, setae on inner surface: 0. scattered along entire length (Fig. 2I); 1. dense along entire length (Fig. 2J); 2. dense on apical half.

68. Front tarsi, shape: 0. tarsomeres I–IV more or less cylindrical, not widened distally and not flattened dorsoventrally; 1. tarsomeres I–IV more or less flattened dorsoventrally and widened distally; 2. tarsomeres I–IV more or less dorsoventrally flattened but not widened distally.

69. Front tarsi, sexual dimorphism: 0. present; 1. absent.

70. Front tarsi, adhesive setae, males: 0. absent; 1. present.

71. Front tarsi, adhesive setae, females: 0. absent; 1. present.

72. Hind coxae, shape: 0. broader concave basal part more or less gradually transforming into narrower and flatter apical part; 1. broader concave basal part abruptly and sharply separated from narrower and flatter apical part by carina or strong groove; 2. cylindrical.

73. Mid and hind tibiae, shape: 0. distinctly broadened apically; 1. subcylindrical to slightly broadened apically.
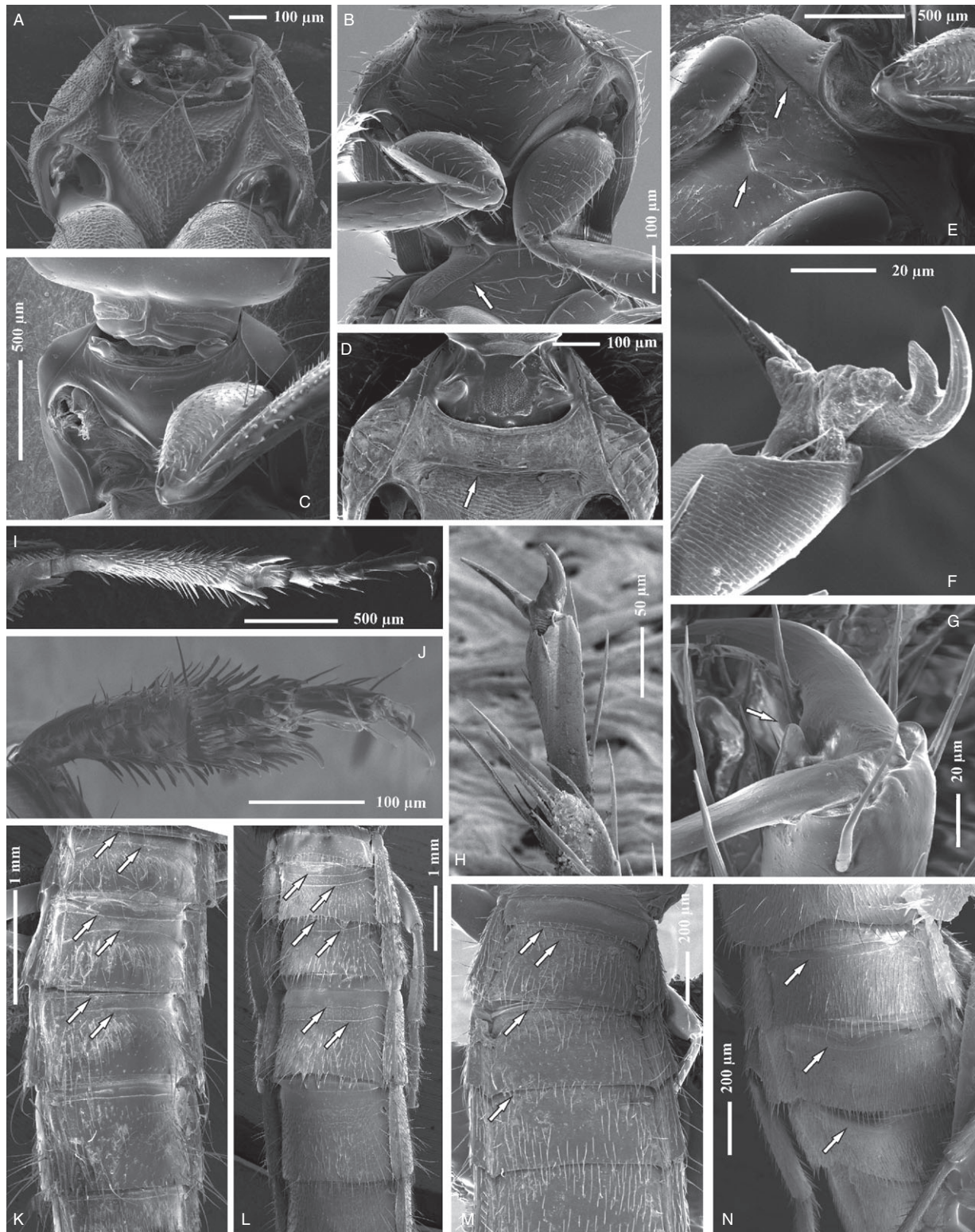
Fig. 2. (A–D) Prosternum: (A) *Ecitophytes coniceps*, (B) *Holisus humilis*, (C) *Belonuchus mordens*, (D) *Paederomimus contractus*; (E) *Belonuchus mordens*: mesoventrite. (F–H) Tarsal claw: (F) *Odontolinus fasciatus*, (G) *Proxenobius borgmeieri*, (H) *Holisus humilis*. (I, J) Front tibia and tarsus: (I) *Belonuchus mordens*, (J) *Erichsonius brachycephalus*. (K–N) Abdominal tergites: (K) *Odontolinus fasciatus*, (L) *Flohria laticornis*, (M) *Holisus humilis*; (N) *Proxenobius borgmeieri*.
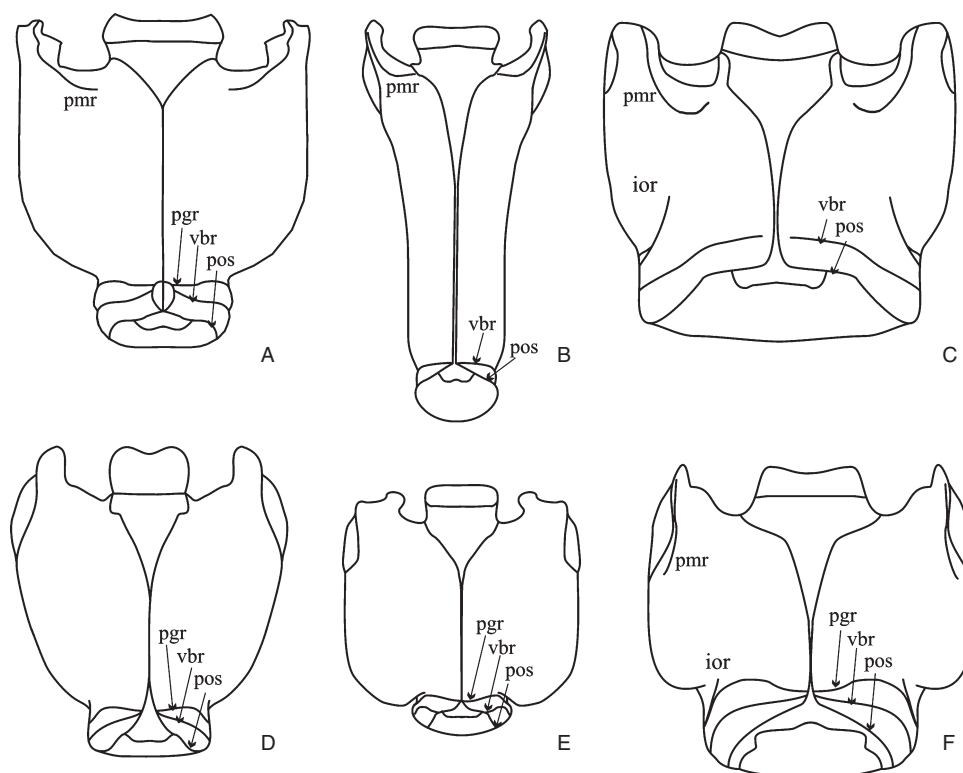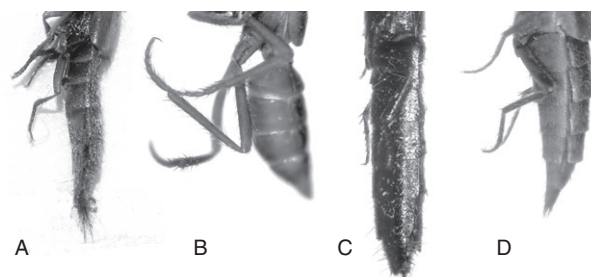
Fig. 3. (A–F) Ridges and sutures on head in ventral view: (A) *Leptopeltus flavipennis*, (B) *Ecitophytes coniceps*, (C) *Flohria laticornis*, (D) *Paederomimus contractus*, (E) *Holisus humilis*, (F) *Philonthus rectangulus*. ior, infraorbital ridge; pgr, postgenal ridge; pmr, postmandibular ridge; pos, postoccipital suture; vbr, ventral basal ridge. Setae omitted.
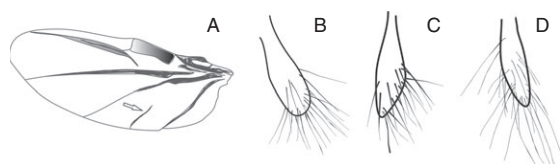
Fig. 4. (A) *Belonuchus mordens*, hind wing showing MP3 vein. (B–D) Lateral tergal sclerites IX (styles): (B) *Pescolinus schmidti*, (C) *Linoderus gracilipes*, (D) *Philonthus rectangulus*.

74. Hind tibia, setae: 0. sparse; 1. dense.
75. Hind tarsi, segment I length relative to last segment length (S1/S5): 0. distinctly < 2.0; 1. 2.0; 2. distinctly > 2.0 but < 3.0; 3. ∼ 4.0.
76. Empodial spine: 0. absent (Fig. 2H, F); 1. present (Fig. 2G).
77. Tarsal empodial setae: 0. absent; 1. present.
78. Tarsal empodial setae, length relative to length of claws: 0. about equal or longer; 1. much shorter.
79. Hind wing venation, CuA and MP4: 0. completely separate; 1. fused in one vein (although often its origin from two veins still very obvious).
80. Hind wing venation, MP3: 0. vein MP3 present, although sometimes faint (Fig. 4A); 1. vein MP3 absent.
81. Protergal glands (osmeteria), cuticular manifestation: 0. absent; 1. present.

Fig. 5. Abdominal shape in lateral view: (A) *Philonthus bonariensis*, (B) *Ecitophytes coniceps*, (C) *Flohria laticornis*, (D) *Proxenobius borgmeieri*.

82. Protergal glands (osmeteria), morphology of cuticular manifestation: 0. shallow impressions; 1. well-developed acetabula; 2. more or less invaginated capsules with smaller openings.
83. Abdomen, shape: 0. flattened dorsoventrally (Fig. 5A); 1. conical (Fig. 5B); 2. subcylindrical (Fig. 5C); 3. subconical (Fig. 5D).
84. Abdomen, tergite II, basal longitudinal carina: 0. absent; 1. present.
85. Abdomen, tergite III–V, basal transverse carinae, anterior line: 0. absent; 1. present (Fig. 2K–N).

86. Abdomen, tergite III, basal transverse carinae, posterior line: 0. absent (Fig. 2N); 1. present (Fig. 2K–M).

87. Abdomen, tergite III, posterior basal transverse carina, medial part (if present): 0. straight, rounded, or slightly pointed; 1. sharply pointed; 2. sinuate.

88. Abdomen, tergite IV, basal transverse carinae, posterior line: 0. absent (Fig. 2M); 1. present (Fig. 2K, L).

89. Abdomen, tergite V, basal transverse carinae, posterior line: 0. absent (Fig. 2M, N); 1. present (Fig. 2K, L).

90. Abdomen, tergite V, basal transverse carinae, posterior line (if present): 0. complete (Fig. 2K, L); 1. uncomplete.

91. Abdominal segments, pubescence: 0. densely pubescent (Fig. 2N); 1. not densely pubescent, with sparse to moderate setation (Fig. 2K–M).

92. Abdomen, sternite VII, apical margin: 0. emarginate medially and projected at both sides of emargination; 1. distinctly emarginate but not projected; 2. straight; 3. slightly emarginated.

93. Male sternite VIII, apical margin: 0. medially straight to very slightly concave; 1. with single, variably developed median emargination; 2. with a pair of emarginations, medially produced between them; 3. with a medially produced emargination.

94. Male sternite VIII, medio-apical emargination, semi-membranous extension: 0. absent; 1. present.

95. Male sternite VIII, posterior margin: 0. entire; 1. pectinate.

96. Male sternite IX, basal portion: 0. more or less symmetrical; 1. strongly asymmetrical.

97. Lateral tergal sclerites IX (styles): 0. dilated (Fig. 4B, C); 1. not dilated (Fig. 4D).

98. Male tergite X, apex: 0. emarginate medio-apically; 1. subtruncate apically to wide and subangulate or arcuate apically; 2. subacute; 3. acute; 4. concave medio-apically; truncate; 5. medially projected.

99. Female tergite X, apex: 0. emarginate medio-apically; 1. subtruncate apically to wide and subangulate or arcuate apically; 2. subacute; 3. acute; 4. concave medio-apically to truncate.

100. Aedeagus, parameres: 0. paired, well separated; 1. paired, contiguous; 2. fused into a single lobe.

101. Aedeagus, paramere(s), attachment to median lobe: 0. fused to median lobe only at base, otherwise paramere(s) distinctly separated from median lobe along entire length; 1. fused to median lobe only at base and very closely appressed to median lobe along entire length; 2. fused to median lobe along its (their) entire length, paramere(s) and median lobe hardly distinguishable from each other.

102. Aedeagus, median lobe, apical part, symmetry: 0. symmetrical; 1. more or less asymmetrical.

103. Aedeagus, median lobe, apical part, shape: 0. subtruncate to acute; 1. subrectangular; 2. divided; 3. truncate and angulate before reaching apex; 4. truncate and medially projected.

104. Aedeagus, parameres relative to median lobe: 0. paramere(s) is (are) not (or at most slightly) produced over apex of median lobe, usually narrower or at most as wide as median lobe: median lobe appearing as the larger part of the aedeagus; 1. paramere strongly produced over apex of median lobe, mostly as large as or larger than median lobe: paramere appearing as a larger part of the aedeagus; 2. paramere small (short and/or thin), obviously strongly reduced.

105. Aedeagus, median lobe, face adjacent to paramere: 0. with tooth; 1. without tooth.

106. Ovipositor: 0. consisting of paired proximal and distal gonocoxites, the latter bearing styli; 1. consisting of only paired proximal and distal gonocoxites, styli absent; 2. consisting of paired proximal and single distal gonocoxite.

107. Ovipositor, distal gonocoxites: 0. with setae only; 1. with setae and spines.

108. Ovipositor, distal gonocoxites, macrosetae: 0. absent; 1. present.

109. Ovipositor, distal gonocoxites, macrosetae, number: 0. 2–5; 1. > 5; 2. 1.

110. Ovipositor, distal gonocoxites, macrosetae, location: 0. along the outer margin; 1. distal; 2. basal.

Characters of quantitative nature (1, 2, 5, 6, 7, 8, 14, 32, 34, 36, 75). These characters were those whose intraspecific variation allows relative measurements (ratios) to be made that are discrete, i.e. distinct, nonoverlapping ranges of values. Measurements were taken from the examined material (Table S1). Observations based on a unique specimen were confirmed and/or eventually completed by supporting literature. This was the case for *Hybridolinus* (Li & Zhou, 2010a), *Jurececkia, Moeocerus, Mysolius* and *Rabigus* (Li and Zhou, 2011) and *Pterygolaetus* (Bierig, 1937).

Abdominal tergites III–V, anterior and posterior lines of basal transverse carinae (characters 85–90). In the above-mentioned previous studies, criteria used on character statements describing these features suggest that the occurrence of both the anterior and posterior lines of the basal transverse carina on each segment is independent from those on the following segment. In the present study I assume that such independence may not occur between the segments but between the anterior and posterior lines themselves. I came to this observation after Li & Zhou (2011; see characters 69, 70, 71 and 73), where the anterior line, although always present, is nevertheless cited for each character/ character state. Such redundancy caught my attention and was confirmed afterwards by own observations.

Phylogenetic analysis

A matrix providing the distributions of character states across the 77 terminal taxa is provided (Table S2). The 110 morphological characters for the outgroup taxa are coded from the examination of specimens, with the exception of those of

Arrowinus phaenomenalis and *Anisolinus tsurugiensis* which were taken from the literature (see Table S1). The matrix was prepared using Mesquite v2.74 (Maddison & Maddison, 2010) and computed in TNT (Goloboff *et al.*, 2008) with all characters treated as unordered and equally weighted. Space for 99 999 trees was set in the memory. A traditional search was run with 1000 replicates of random addition sequences followed by tree bisection–reconnection, saving ten trees per replication. Trees were rooted with *Arrowinus phaenomenalis* (Arrowinini). Clade support was assessed by means of standard bootstrap analysis with frequency differences as implemented in TNT with 1000 replications of heuristic searches with 100 interactions of random addition of taxa and holding 10 trees per interaction. The same parameters were used to perform a jackknife analysis. Additionally, Bremer support was estimated by the script Bremer.run (available at http://tnt.insectmuseum.org/index.php/) from suboptimal trees up to 30 steps longer than the shortest trees. WinClada v1.00.08 (Nixon, 1999) was used for character mapping.

Results

Analysis under equal weights obtained 26 shortest trees (length = 680 steps, CI = 0.259, RI = 0.602). Figure 6 shows the strict consensus of the shortest trees with *Arrowinus* as root. The monophyly of the Staphylinini is well supported. Synapomorphies for the tribe in the current analysis are: antennal insertions closer to frontoclypeus or at equal distance at most (1); neck constriction fully developed, distinct all around (13); head with ventral basal ridge (19), postgenal ridge (24) and postmandibular ridge (25) present; labrum deeply emarginate or bilobed medio-apically (29); ligula small, entire (or at most slightly notched medially) (35); sternopleural (anapleural) suture distinctly oblique (medial end of suture anterior to its lateral end) (57); mid and hind tibiae subcylindrical to slightly broadened apically (73) and hind wing CuA and MP4 veins fused in one vein (although often its origin from two veins still very obvious) (79). The subtribe Philonthina, as sampled here, is not recovered as monophyletic. The two representatives of *Erichsonius*, currently part of Philonthina, appear as a basal lineage of Staphylinini out of the subtribe. Characters that support the exclusion of *Erichsonius* from Philonthina (all but seven homoplastic) are: antennae with antennomere II about 1.5× wider than antennomere III (7); labrum without transparent apical membrane (28) and slightly or not emarginated medio-apically (29); maxillary palp with segment IV (apical) 2.0× as long as or longer than segment III (34); ligula bilobed (35); labial palps, with apical segment gradually narrowed to acute or subacute apex (37); gular sutures joined before neck (40); pronotum with inferior lateral line fused to superior lateral line behind anterior angles (48) and postcoxal process of hypomeron (49); hind tibia with dense setae (74); tarsus without empodial setae (77); aedeagus with paired, well separated parameres (100); distal gonocoxites of ovipositor with setae and spines (107). Additionally, the two representatives of *Holisus* (Hyptiomina) appear as

nested within Philonthina, in a well-supported clade together with the myrmecophilous genera *Ecitophytes*, *Xenobius* and *Proxenobius*. Characters that support this grouping (all but 14 homoplastic) are: eyes distinctly shorter than half of temples (14); postmandibular ridge bordering mandibular base almost completely (27); prosternum with longitudinal carina forming well-defined, sharp ridge at least in its basal part (52); front tibia with dense setae on apical inner half (67); abdominal tergites IV and V without posterior line on the basal transverse carina (88 and 89). Apart from this, all other representatives of the subtribe are joined in one clade by the following characters (all but 60 homoplastic): pronotum with inferior line subcontiguous or fused to superior line behind or near to anterior angles (48); prosternum without mid-longitudinal carina (only medial prominence, not carinate, not longitudinal (51); mesoventrite with medial carina in coxal acetabulum (60) and tarsus without empodial setae (77).

Most of the Neotropical endemic genera of Philonthina (with exception of *Endeius*, *Paederallus*, *Pterygolaetus*, *Atopocentrum* and *Chroaptomus*) are in two major clades, each of which includes representatives of *Holisus* and *Belonuchus*, respectively. The consensus shows them as sister groups, but this relationship is weakly supported. The first clade includes *Holisus* and the myrmecophilous *Ecitophytes*, *Proxenobius*, *Xenobius* and *Phileciton*. The second clade includes two subclades: the first with the four representatives of *Belonuchus*, the second with seven of the Neotropical endemic genera. The genus *Belonuchus* with its four species here sampled appears as a well-supported group, defined by the following characters (all homoplastic): head without postmandibular ridge (25), front tibiae with setae on inner surface scattered along entire length (67) and hind wing venation with CuA and MP4 completely separate (79). The monophyly of the second (Neotropical) subclade is supported by the following characters: head without infraorbital ridge (23); prosternum with transverse carina on basisternum (53) and male with the apex of abdominal tergite X concave medio-apically (98). Within this group, the genera *Ophionthus*, *Paederomimus*, *Linoderus*, *Odontolinus* and *Pescolinus* constitute a monophyletic assemblage, sharing a prosternum with transverse carina (54) as synapomorphy. Additionally, *Linoderus*, *Odontolinus* and *Pescolinus* show close relationships among each other with good support values, and one synapomorphy: the lateral tergal sclerites IX (styles) dilated (97). The monophyly of *Paederomimus*, as sampled here, is well supported by the following homoplastic characters: head without postmandibular ridge (25), apical segment of maxillary palp fusiform (33), neck with transverse carina (42), mesoventrite with medial transverse carina (61), abdominal tergite III to V without posterior line on basal transverse carinae (86, 88, 89). On the other hand, *Chroaptomus* and *Atopocentrum* appear as sister groups but they are distantly related to the Neotropical clade. This relationship is rather weakly supported by three homoplastic characters: prosternum without mid-longitudinal carina (51), mesoventrite with sternopleural (anapleural) suture transverse or nearly transverse (57) and mesoventral intercoxal process forming more or less an obtuse angle (62). The tree topology supports the
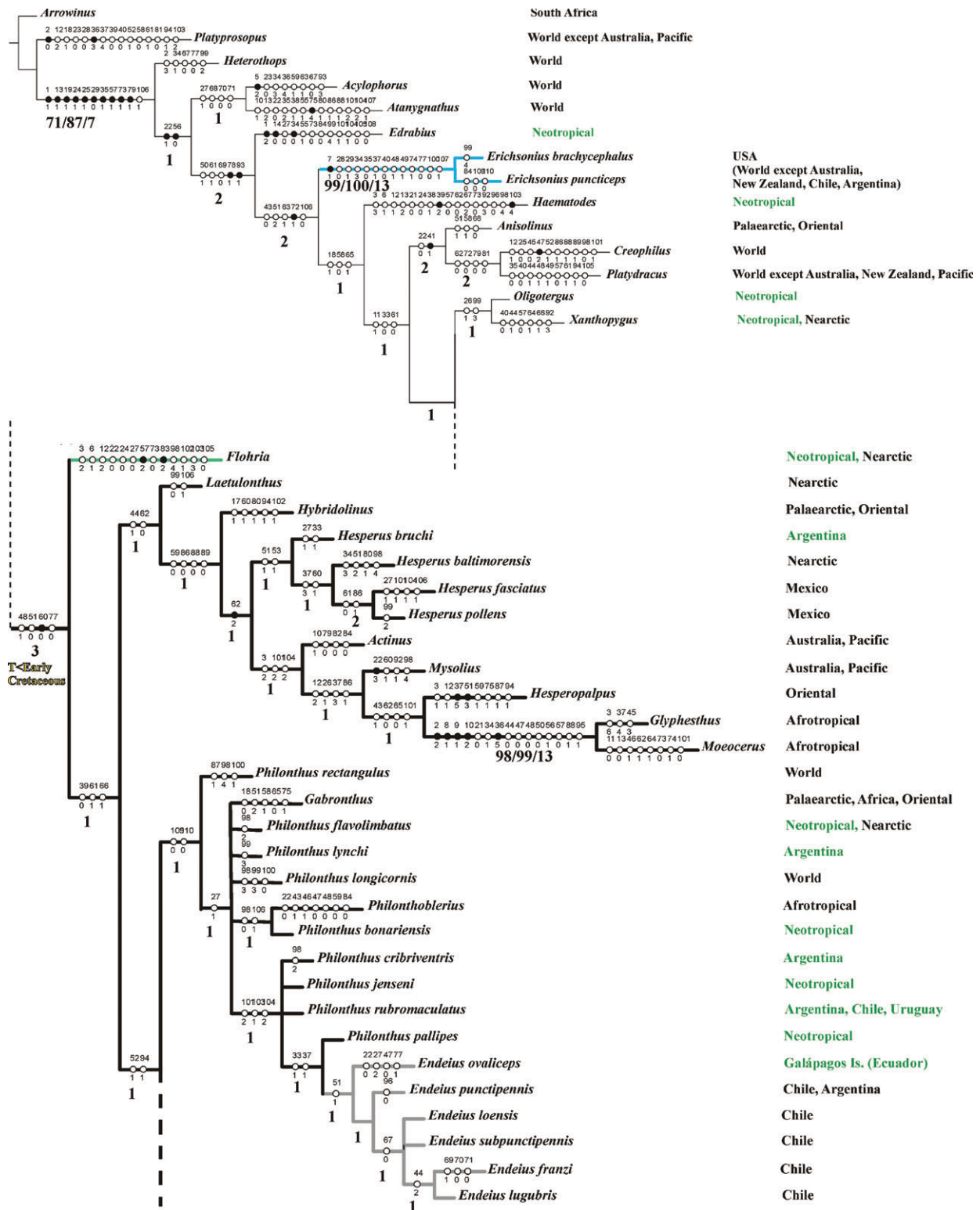
Fig. 6. Results of the parsimony-based cladistic analyses of the phylogenetic relationships of the Neotropical genera of Philonthina. Strict consensus of the 26 shortest trees obtained (tree length = 680; consistency index = 0.259; retention index = 0.602). Black circles: nonhomoplasious apomorphies; white circles: homoplasies. Support values are indicated in bold below the branches as follows: Standard Bootstrap/ Jackknife/Bremer (cut = 50 for resampling support values). Clades of interest are colour coded; distributions of the sampled genera are summarized. Neotropical endemic distributions are colour coded in green.
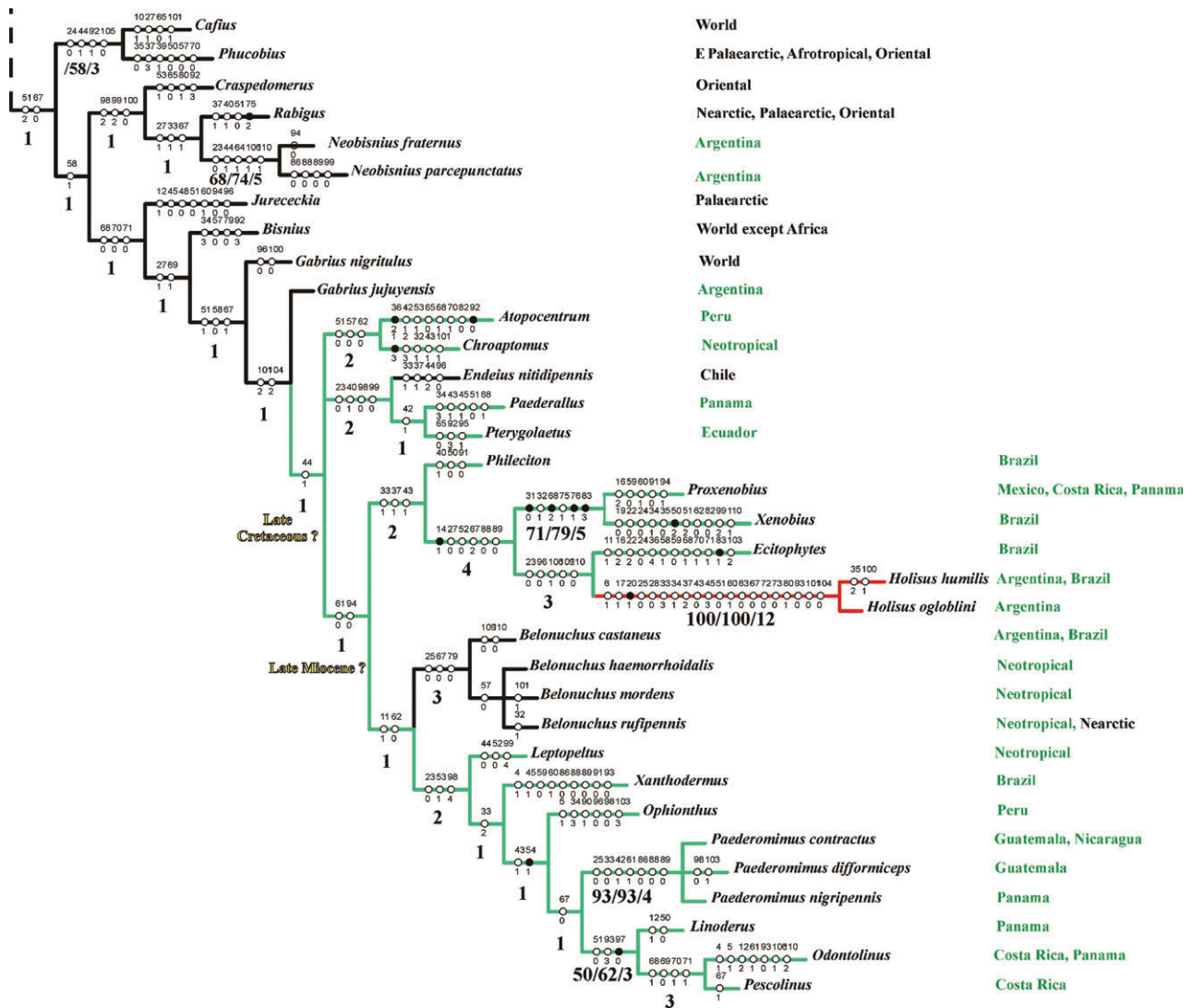
Fig. 6. Continued

hypothesis of a close relationship between all but one species of *Endeius* and four species of *Philonthus*, as previously suggested (Chani-Posse, 2010), based on characters from the apical segment of both maxillary and labial palpi (33, 37) and the aedoeagus (101, 103, 104). Furthermore, *E. nitidipennis* appears together with the Neotropical genera *Paederallus* and *Pterygolaetus* in a weakly supported clade which is defined by the following (all homoplastic) characters: head without infraorbital ridge (23), gular sutures not joined before neck and running close to the base (40), abdominal tergite X emarginate medio-apically in both sexes (98 and 99). The monophyly of the other six species of *Endeius* also appears weakly supported in the present analysis, defined only by one homoplastic character: prosternum with mid-longitudinal carina developed only along furcasternum (51). The genus *Neobisnius*, with two species represented herein, appears sister to *Rabigus* and far

from the major group containing the Neotropical endemic genera. The clade of *Neobisnius* is well supported by the following homoplastic characters: head without infraorbital ridge (23); lateral puncture of pronotum with long seta at a distance three times as large as diameter of puncture from superior lateral line (44); metascutellar mid-longitudinal suture rudimentary, (very weak but clear at base) (64); ovipositor consisting of only paired proximal and distal gonocoxites without styli (106) and single macroseta located distally (110). Finally, the four species of *Hesperus* form a monophyletic group supported by two homoplastic characters (51, 53) and sister to a clade that includes the Australian/Pacific genera *Actinus* and *Mysolius,* the Oriental genus *Hesperopalpus* and the Afrotropical *Glyphesthus* and *Moeocerus.* This sister group relationship is supported by one synapomorphy: the mesoventral intercoxal process truncate to subtruncate (62).

Discussion

The so-called 'Staphylinini propria' (subtribes Anisolinina, Staphylinina, Eucibdelina, Philonthina and Xanthopygina in the current formal system) as proposed by Chatzimanolis *et al.* (2010) also appears here as a monophyletic group, with Xanthopygina as sister to Philonthina and Anisolinina sister to Staphylinina (Eucibdelina was not included in the present study). The subtribe Philonthina, as currently known (Herman, 2001; Newton & Thayer, 2005), does not appear as monophyletic in the present study. Previous studies have already speculated about the potential exclusion of *Erichsonius* and the inclusion of Hyptiomina (e.g. Solodovnikov & Schomann, 2009; Li & Zhou, 2011).

Erichsonius shows obvious differences from other members of Philonthina, as observed by Smetana & Davies (2000) and Solodovnikov & Newton (2005) and recently confirmed by Li & Zhou (2011), whose cladistic analysis places the genus as a basal group of Staphylinini rather than a member of Philonthina. Our results agree with those concerning the systematic position of *Erichsonius*. Characters that separate this genus from Philonthina have shown to be homoplastic here, with exception of a quantitative character: the antennae with antennomere II about 1.5 wider than antennomere III. The width of the second antennomere relative to that of the following segment also constitutes a synapomorphy for the genus in Li & Zhou (2011). However, this condition would not include certain species of *Erichsonius* from the Oriental Region (Schillhammer, personal communication). This character is used to distinguish *Erichsonius* in many of the current keys to genera of Philonthina (e.g. Smetana, 1995; Newton *et al.*, 2000; Navarrete-Heredia *et al.*, 2002), with no such identification keys existing for the Oriental Region, Madagascar and the islands in the Indian Ocean except Mauritius (Uhlig & Janák, 2009).

The placement of the subtribe Hyptiomina within the core of the Neotropical Philonthina is also congruent with earlier morphological studies and the resulting hypotheses of close relationships with other representatives of Philonthina of subcortical habitats, such as most members of the genus *Belonuchus* (Solodovnikov & Schomann, 2009; Chatzimanolis *et al.* 2010; Li & Zhou, 2011). In spite of the disagreement between molecular and morphology-based data concerning the placement of Hyptiomina, Chatzimanolis *et al.* (2010) have recognized the congruence of morphological phylogenies regarding the position of *Holisus* within 'Staphylinini propria'. Thus, the clade including Philonthina plus Hyptiomina was defined as 'Philonthina propria' within a so-called 'Philonthina lineage' that also includes Xanthopygina (Chatzimanolis *et al.*, 2010). Our results are in agreement with these groupings. The synapomorphy that here supports the monophyly of Hyptiomina and the three myrmecophilous genera of Philonthina – eyes shorter than half of temples – may be an adaptation to cryptic habitats, as proposed by Solodovnikov & Newton (2005) while observing the reduction of stemmata in larvae of this subtribe. The subtribe Hyptiomina was established by Casey (1906: 359, 361, as Hyptiomae) for the genus *Hyptioma* (junior synonym

of *Holisus* Erichson, 1839) based on morphological characters related to subcortical habitats. Casey (1906) recognized the presence of a 'second fine carinal line, nearly parallel to and more abbreviated than the lower edge' regarding the deflexed side margin of pronotum. This character has been used in keys to subtribes of Staphylinini as 'additional line connecting superior and inferior line of pronotal hypomeron' (Smetana, 1995) or 'extra' (third) marginal line (Newton *et al.*, 2000). Solodovnikov & Newton (2005) agree that the three hypomeral carinae of *Holisus* correspond to the superior (uppermost) and inferior (lowermost) lines of other taxa and delimit the hypomeron, whereas the third carina 'runs obliquely along the hypomeron between these, joining the inferior line behind its junction with the superior line'. As in other Philonthina, the inferior line joins the superior line behind the anterior angles of the pronotum in *Holisus*. Therefore, this additional line, although unique in New World Staphylinini (Newton *et al.*, 2000), could be considered as derived within Philonthina. The genus *Holisus* (Hyptiomina) can be distinguished by having a conspicuously flat body, apical segments of labial and maxillary palpi aciculate, front tibia with 'ctenidium of several rows of stout setae', mesoscutellum with one transverse carina, and pronotal hypomeron with an additional oblique line connecting the superior and inferior lines (Smetana, 1995; Newton *et al.*, 2000). All of these characters appear here as homoplastic for the genus, its unique synapomorphy being the ventral basal ridge of head strongly (to moderately) projecting anteriad. Although a broad consensus exists on the affiliation of Hyptiomina, its placement within Philonthina is still controversial. The relationship of the specialized subcortical genus *Holisus* to the highly modified myrmecophilous genera of Philonthina, supported by adult morphology in the present study, is surprising. The high number of autapomorphies in these genera suggests a case of long-branch attraction (LBA), especially given the limited taxon sampling for *Holisus* (Bergsten, 2005). It is also worthwhile highlighting that a relationship of *Holisus* to the genus *Belonuchus* would be expected, given their more or less flat bodies and similar subcortical habitats (Solodovnikov & Schomann, 2009; Li & Zhou, 2011). Lacking a broader sample of both *Holisus* and its presumed allies or molecular data, this genus and its relationships need additional study. Thirty-one species of *Holisus* are currently known, with records from Mexico to northern Argentina, West Indies, Zaire (one species) and a possible record from southwestern USA (Herman, 2001; Newton & Thayer, 2005). Based on these distributional data, we may hypothesize this genus as rather Neotropical, being also nested in a Neotropical clade within Philonthina. Confirmation of the identity of the single Afrotropical species, *H. schedli* Scheerpeltz, is beyond the scope of this article but remains pending for future studies.

Philonthina, as currently defined (Smetana & Davies, 2000), does not account for the entire range of variation of some characters among the Neotropical members. Some of its representatives have empodial setae (characters 76, 77: *Endeius ovaliceps*), ligula bilobed (character 35: *Xenobius*), infraorbital ridge (character 23: *Endeius ovaliceps, Flohria*) and prosternum with transverse carina before sternacostal suture (see

characters 53 and 54, above). Genera of Philonthina from other regions that would also not fit in the current diagnosis are *Phucobius* with an emarginate ligula, *Glyphesthus, Moeocerus* and *Agacerus* with the last segment of the labial palpi distinctly broadened apically (character 37 in this study; Li & Zhou, 2011) and *Philonthoblerius* with a well-developed infraorbital ridge.

Among the Neotropical 'endemic' genera of Philonthina, *Chroaptomus, Leptopeltus* and *Paederomimus* are broadly distributed from Mexico up to the northern areas of southern South America (Herman, 2001; Newton & Thayer, 2005). Both *Leptopeltus* and *Paederomimus* are included here in a so-called Neotropical clade which is supported by three homoplastic characters (see above). *Paederomimus*, here represented by three of its 58 currently known species, appears as a monophyletic group. It is noteworthy that in the original description of *Paederomimus*, Sharp (1885: 438) stated 'they may be distinguished (from *Philonthus*) by the fact that the prosternum in front of the coxae is definitely divided transversely into two parts'. Such a feature is here described as the transverse carina on basisternum (54). Character 54 constitutes a synapomorphy that supports a clade where *Paederomimus* is included together with *Linoderus, Odontolinus* and *Pescolinus*–for which Sharp (1885: 452–454) also cites this character – and *Ophionthus*, later described by Bernhauer (1912) who did not take this feature into account. *Chroaptomus* as well as *Atopocentrum*, on the other hand, appear distantly related to the Neotropical clade in the present study. Both genera show striking morphological features, which in the case of *Chroaptomus* were already studied and tested for monophyly (Chani-Posse, 2006). According to current records (Herman, 2001; Newton & Thayer, 2005), only three of the ten remaining genera of Neotropical Philonthina are highly speciose in the region: the cosmopolitan genus *Philonthus* (over 200 of *c*.1250) and the broadly distributed genera *Belonuchus* (125 of 200) and *Neobisnius* (30 of 72 species). The representatives of *Belonuchus* and *Neobisnius* were grouped each in two well-supported clades, although with homoplastic characters in both cases. Smetana (1995) also recovered *Belonuchus* as monophyletic, but as his analysis was based on the fauna from America north of Mexico, he did not address the problem of *Trapeziderus* Motschulsky, 1860 (current synonym of *Belonuchus*) and its Oriental species (Li & Zhou, 2010). Given the scope of this study, I do not address this problem either but agree with these authors. Based on the placement of *Belonuchus* among other Neotropical 'endemic' genera in the current analysis, I hypothesize that a more comprehensive study on the world fauna of *Belonuchus* will confirm the Neotropical origin of this genus. The genus *Neobisnius* appears sister to *Rabigus* which is a primarily Palaearctic genus (Smetana, 1995) and far from the group that includes the Neotropical endemic genera. The nonmonophyly of the genus *Philonthus* and allies is widely accepted (e.g. Smetana, 1995; Chani-Posse, 2010) and newly confirmed in the current study: the representative of *Gabronthus* and all but one species of the South American genus *Endeius* appear nested within *Philonthus*. The monophyly of the seven currently known species of *Endeius* was previously found to be supported by one synapomorphy without further evidence, only four of its species resulting in a well-supported, monophyletic clade (Chani-Posse de Maus, 2008). Such species were included here to corroborate the rather doubtful monophyly of *Endeius* (Schillhammer, personal communication). Based on these results and the characters that the current valid species of *Endeius* share with *Philonthus* (see above), I propose that *E. franzi, E. loensis, E. lugubris, E. ovaliceps, E. punctipennis* and *E. subpunctipennis* are transferred to *Philonthus*, and that *E. nitidipennis* is placed as *incertae sedis* in Philonthina. The other four genera (i.e. *Bisnius, Cafius, Gabrius* and *Hesperus*), although speciose and distributed worldwide, are rather poorly represented in number of species in the Neotropical Region and southern South America: *Bisnius* (2 spp., introduced), *Cafius* (6 spp.), *Gabrius* (6 spp.) and *Hesperus* (11 spp.) (Herman, 2001; Newton & Thayer, 2005). Distributional records for the species of *Cafius* in the Neotropics are mostly restricted to northern areas (West Indies, Venezuela), with the exception of two species recorded from Chile, which were probably introduced. In this analysis, *Cafius* appears sister to *Phucobius*, which is congruent with previous results (Li & Zhou, 2011). As it is known in the Neotropics, *Cafius* could be a case of dispersal. Representatives of both *Gabrius* and *Hesperus* also appear out of the Neotropical clade. The genus *Gabrius*, with 363 species all over the world (Li *et al.*, 2010), seems to be primarily Holarctic and Oriental. This knowledge may change and the number of its species may increase as poorly known tropical faunas are studied (Schillhammer, 1997). The monophyly of *Hesperus* is currently under discussion (Li *et al.*, 2010; Li & Zhou, 2011). Although Smetana (1995) supports the genus as a natural group for the six Nearctic species in his analysis, he has recognized that 'changes in the generic assignment of many species are to be expected, when the Philonthina are better known at the generic level. On the other hand, some character states on the aedoeagus, such as the absence of the sensory peg setae on the paramere, or the general shape of the median lobe, seem to be rather constantly present in the species of *Hesperus*'. Finally, the presence of *Gabronthus* and *Remus* (with two and one species respectively) in Central America seems to be of introduced origin (see Frank, 1983 for *Gabronthus* and Bierig, 1934 for *Remus* after Herman, 2001). The latter was not included in the present analysis, assuming its close relationship with *Cafius* (Smetana, 1995; Li & Zhou, 2011; Jeon *et al.*, 2012). *Gabronthus* also resulted in a weakly supported group together with the representatives of *Philonthus, Philonthoblerius* and *Endeius*, out of the Neotropical clade. If we assume that the age of the basal nodes of Staphylinini phylogeny may correspond to some time later than the Early Cretaceous (Solodovnikov *et al.*, 2012), it seems reasonable to hypothesize a common ancestor of the Neotropical endemic Philonthina after South America became an isolated landmass in the Albian Age of the Early Cretaceous (Benedetto, 2010). The first cladogenetic events within the Neotropical Philonthina (Fig. 6) could be considered the result of large-scale biome shifts caused by

three major events during the Miocene in South America: the uplift of the northeastern Andes and the development of the Amazon River (Hoorn *et al.*, 1995) together with the occurrence of three marine transgressions (Hernández *et al.*, 2005). Uplift of the northeastern Andes had at least six phases of uplift and tectonic quiescence between the Late Cretaceous and the Pleistocene. The main uplift occurred between the late Oligocene and the Pleistocene, with a climax in the Pliocene–Pleistocene (Hoorn *et al.*, 1995). However, the first effects of the rise of the Eastern Cordillera were noticeable in northwest Amazonia with the development of the Amazon River: the area of the present upper and middle Magdalena Valley, previously connected to the Llanos and Amazonian lowlands, became an isolated area during the late middle Miocene (15–10 my) (Hoorn *et al.*, 1995). Later, both the final closure of the Isthmus of Panama during the Pliocene (*c*. 2.7 my) (Benedetto, 2010) and the Pleistocene climate variations triggered the Great American Biotic Interchange, an important paleozoogeographical event in which land and freshwater fauna migrated from North America via Central America to South America and vice versa. I hypothesize that this period was the moment of entrance into South America of those lineages with a presumed different origin (i.e. those of *Philonthus*, *Gabrius*, *Hesperus* and *Neobisnius*) and current distributions not endemic to the Neotropical Region. Another major consequence of this interchange would have been the colonization of Central America by some of the South American lineages, particularly those with (at that time) presumably Andean and northeastern distributions. The main radiation of the Neotropical Philonthina would have occurred over the last 370 000 years in correspondence with four cycles of regional glacial advance and retreat (Fritz *et al.*, 2007), promoting speciation events by both vicariance and dispersal in a rather dynamic environment. For the last 21 000 years (Last Glacial Maximum) recent studies suggest that there were no large-scale differences in major biome distributions (notwithstanding the Atlantic forests of SE Brazil), with biome shifts largely associated with ecotonal areas – downslope expansion of montane grasslands in the Andes at the expense of montane forest, and savanna expansion at the expense of rainforest and gallery forest at the Amazon basin margins (Mayle *et al.*, 2009). However, both spatial heterogeneity in canopy density and environmental gradients associated with differences in forest structure across the Amazonian basin could potentially have been enough to promote different modes of speciation (Mayle *et al.*, 2009).

Summary of new taxonomic changes

Based on the phylogenetic results given above, and consistent with prior phylogenetic studies that were cited in the discussion, the newly proposed formal taxonomic changes to the classification of Staphylinini can be summarized as follows:

Genus *Erichsonius* Fauvel, 1874 moved from subtribe Philonthina to tribe Staphylinini *incertae sedis*

Genus *Philonthus* Stephens, 1929 = *Endeius* Coiffait & Sáiz, 1968, **syn.n.**

Philonthus franzi (Sáiz, 1971), **comb.n.** ex *Endeius Philonthus loensis* (Coiffait & Sáiz, 1968), **comb.n.** ex *Endeius Philonthus lugubris* (Sáiz, 1971), **comb.n.** ex *Endeius Philonthus ovaliceps* (Coiffait, 1981), **comb. n.** ex *Endeius Philonthus punctipennis* (Solier, 1849), **comb.res.** ex *Endeius Philonthus subpunctipennis* (Coiffait & Sáiz, 1968), **comb.n.** ex *Endeius*

Endeius nitidipennis Solier, 1849 Moved from genus *Endeius* but placed as *incertae sedis* within subtribe Philonthina

Replacement name for *Philonthus franzi* Schillhammer, 1998

Philonthus franzi (Sáiz) is a senior secondary homonym of *Philonthus franzi* Schillhammer, 1998: 111, for whom a new replacement name, *Philonthus herberti*, is proposed here. In the original description, Schillhammer (1998) dedicated this species to Prof. Dr. Herbert Franz. The new name aims to keep that purpose.

Conclusions

The consensus tree shows most of the nodes resolved, although with relatively weak support for many of them. This fact prevents us from being over-confident in the results. However, most branches within the Neotropical clade (including 11 of the 17 endemic genera of Philonthina) show good support values which allow us both to make inferences about the evolution of the Neotropical Philonthina and to hypothesize about the origin of this lineage around the Miocene. Moreover, all but one of the endemic genera are currently known as either monotypic or species-poor genera (i.e. the outcome of the analysis should not be significantly hampered by a limited taxon sampling). Thus, the present study is aimed to provide a reliable framework for future revisionary studies of the Neotropical endemic Philonthina. Further studies on the systematics of Neotropical Philonthina with broader distribution should be carefully designed in order to address questions that provide insight into their own evolutionary history (most of them are species-rich genera currently known as nonmonophyletic) as well as the evolution of the subtribe. Concerning Philonthina, further fieldwork is required in the Neotropical Region. Information on type localities of the Neotropical species of Philonthina shows that collecting efforts have taken place mainly in the Caribbean Subregion and adjacent areas of the Amazonian Subregion. Coincidentally, Mittermeier *et al.* (2004) cited these areas (Mesoamerica, Atlantic Forest, Cerrado, Tumbes-Chocó-Magdalena, Tropical Andes) among the main 'hotspots' in terms of biodiversity. In our case, such an assumption could be biased or somehow restrictive considering that the big core of the Amazon remains largely unexplored. It is expected that the Neotropical Region contains many more taxa awaiting description which, when accomplished, will improve our understanding of the evolutionary history of the Neotropical Philonthina and the factors that have led to this highly diverse group.

Supporting Information

Table SI. Taxon sample for phylogenetic analysis.

Table S2. Data matrix.

Acknowledgements

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