To be biased or to be Neotropical: systematic reassessment of a megadiverse lineage of rove-beetles (Philonthina, Staphylinini, Staphylininae)

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Abstract

Classifications in the world's tropics often involve an early and sustained adoption of Holarctic-based patterns. Such is the case of the megadiverse subtribe Philonthina and its Neotropical (NT) members, for which generic limits are ill-defined due to an alleged high level of homoplasy. Although a recent total-evidence study confirmed the monophyly of a NT lineage, most of its species are assigned to the speciose genera *Belonuchus* Nordmann and *Paederomimus* Sharp, neither of them monophyletic. Here, we aim to reveal internal relationships within the NT lineage by the reassessment of characters from traditional morphology-based systematics. Specific objectives are to test the monophyly of *Belonuchus* with regards to its only junior synonym, *Musicoderus* Sharp, as well as the placement of the six South American species of *Hesperus* Fauvel, a genus of Holarctic origin. We performed a phylogenetic analysis of the subtribe with focus on its NT lineage based on 132 morphological characters (50 of them novel) including 79 taxa from genera and/or species groups relevant to our study. Most novel characters assessed herein supported clades across Philonthina and its NT lineage. We found that the NT lineage diversified into at least seven clades, each of which provides a framework for future taxonomic studies. Among them, three clades containing the type species of *Belonuchus*, *Paederomimus* and *Musicoderus* (respectively) appear to be well supported and not closely related. The currently known South American species of *Hesperus*, however, are recovered within the NT lineage. We propose to resurrect *Musicoderus* from synonymy with *Belonuchus* and to transfer *Hesperus novoteutonicus* to *Paederomimus* as a new combination: *Paederomimus novoteutonicus* (Wendeler), **comb.n.**

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Introduction

The concept of homology is at the core of any natural classification. Homologies rule and determine relationships among taxa at all hierarchical and organizational levels, so they are the alpha and omega of any phylogenetic reconstruction. Far from being trivial, the term "reconstruction" is accurate. It reminds us that evolution exists *per se* and that any classification process is subject to our understanding at a given point in time. Hypotheses are not only shaped by contemporary paradigms in science, but also by historical factors that challenge either our understanding and/or our access to knowledge. As with any human endeavour, the science of systematics can be biased.

Most paradigm changes in the history of systematics took place between the 15th and the 19th centuries. During that period, nearly all of the major contributions were made by only six or seven Western European countries, starting from an era of overseas travel and explorations that led to the establishment of vast collections of exotic organisms and the foremost need of that period: classification (Mayr, 1982). But it was the Darwinian revolution that paved the way to a "natural" classification with the criterion of grouping by common ancestry. Until that turning point,

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essentialism—with its emphasis on "typology"—had been the dominant paradigm in the western world and its spirit was continued for long after (Mayr, 1982). However, the concept of "homology", which is central to defining a natural group of organisms, arose in pre-Darwinian times. Interestingly, it was Owen (1843), one of Darwin′s main opponents of the theory of natural selection, who proposed criteria (i.e. similarity, position, connections) that nowadays remain operational for determining homologous structures (Hall, 2007). The meaning of homology, however, has been reassessed by its modern use in phylogenetics and different approaches have been proposed (see Hall, 2007; Ereshefsky, 2009; Nixon and Carpenter, 2012a, 2012b, 2012c). We do not intend to provide here a history and/or rationale of that controversy. However, we feel that it is still worthwhile to mention the most extreme approaches to the related concepts of homology/homoplasy; from that of Nixon and Carpenter (2012a, 2012b, 2012c) where homology is defined in terms of the "most recent ancestor", followed by homoplasy is "error", "not a process in nature" and "evidence of parallelism", to the "deep homology" concept (Hall, 2003) and the so-called "expanded homology" where "homology and homoplasy represent a continuum" (Hall, 2007), up to the question that summarizes these previous ideas: is deep homology a form of parallelism? (Scotland, 2010).

Classifications are products of an evolving context of concepts and methodologies. As such, we can ask about the factors that promoted our current "artificial" classifications: were they built in a time of nonevolutionary paradigms (i.e. essentialism) and/or rather utilitarian methodologies (i.e. downward or upward classification with no grouping by common ancestry)? As for non-Holarctic faunas: were classifications built upon a system well suited for their Holarctic counterparts but not accountable for the extra-Holarctic variability? As for those classifications assessed in more recent (post-Darwinian) times through phylogenetics, the question is: are homoplasies evidence of error in coding (sensu Nixon and Carpenter, 2012a, 2012b, 2012c) and may they be (eventually) reassessed as independent sources of homology? If homoplasies are parallelisms, what do they mean? Are they useful for comparative studies as proposed by several authors (e.g. Desutter-Grandcolas et al., 2005) and/or may they be evaluated as potential "deep homologies" (sensu Scotland, 2010)?

The taxonomic history of the megadiverse subtribe Philonthina (Coleoptera: Staphylinidae) and its Neotropical (NT) lineage is an example of how the above-mentioned contingent factors have affected its systematics in time and space. Philonthina accounts for 72 genera and 2819 species described worldwide (Chani-Posse et al., 2018b), and it is one of the most speciose lineages of Staphylinidae, the largest family of living animals (64 031 spp.; Newton, 2019). Within Philonthina, nearly 77% of its species belong to four highly speciose genera (Newton, 2019). Leading the list is the global and megadiverse genus *Philonthus* Stephens (1328 spp.), followed by two other genera of worldwide distribution but mostly represented in regions other than the Neotropics: *Gabrius* Stephens (450 spp.) and *Hesperus* Fauvel (209 spp.) (Newton, 2019). Finally, the genus *Belonuchus* Nordmann (190 spp.) is cited only from the Old and New World, and represented mostly in the NT region (Chani-Posse et al., 2018a). The large number of species involved has been a challenge in achieving modern concepts of these genera, which have been repeatedly shown to be nonmonophyletic (Smetana, 1995; Chani-Posse et al., 2018a). Although the species of Philonthina are most strongly represented (>70%) in extra-Holarctic (mainly tropical) areas, the taxonomic history of the subtribe reflects very uneven efforts in biogeographical terms (Herman, 2001; Newton, 2019). About 90% of its currently valid species were described by European authors at a rather steady way after Linnaeus (1758). This fact had a two-fold consequence. On the one hand, in terms of "space", generic limits were settled upon Holarctic patterns and exotic representatives were either forced to fit into them or characterized based on their distinctness with respect to them (Chani-Posse et al., 2018b). On the other hand, although "neglected" has been a commonly used expression for the study of extra-Holarctic groups (Chani-Posse, 2010), their modern knowledge also has been biased by the adoption of Holarctic-based systems (e.g. Li and Zhou, 2011; Chani-Posse, 2013). In terms of "time", generic concepts were built and "evolved" through an historical context; that is, from a "typological" perspective based on phenetic similarities to a modern homology-based approach invoking an evolutionary background.

The subtribe Philonthina was erected by Kirby (1837: 91, as "Philonthidae") for the single genus *Philonthus*, which was erected almost simultaneously by Stephens and Curtis in 1829 (Herman, 2001). Beyond the question of the authorship, these authors differed on their concepts of *Philonthus*: Curtis (1829, 1836: pl. 610) proposed a broad concept of the genus, whereas Stephens (1829a, 1829b, 1832: 226, 247, 248) gave a more restricted definition based on the shape of the protarsi. Curtis's expanded concept of *Philonthus* prevailed during the next 165 years (Smetana, 1995), justified mostly by the presence of an "entire" ligula and the position of the lateral setae at the pronotal margin (e.g. Erichson, 1840: 426; Fauvel, 1874: 207). From an historical perspective, the position of the lateral pronotal seta played a major role in the classification of Philonthina, because it separated those genera with the seta close to or touching the pronotal margin

(*Philonthus* and allies) from those with a seta distant from the pronotal margin (e.g. *Belonuchus, Hesperus*). It was not until recently that the condition of the protarsi became of relevance in the classification of the subtribe (e.g. Smetana, 1995). The configuration of protarsi involves two independent but associated characters that occur in and out of Philonthina (e.g. Chani-Posse, 2013; Gnaspini et al., 2017a, 2017b): the expansion, dilatation or width of protarsomeres and the presence/absence of modified adhesive setae on their ventral surface. These characters and their states have proved to be useful for defining natural groups not only within Philonthina (e.g. Smetana, 1995), but also across Staphylinini (Chani-Posse et al., 2018a). The lack of importance given to the protarsi in earlier classifications led to confusion, with authors describing species within not only *Philonthus*, but also *Belonuchus* and *Hesperus* (e.g. Erichson, 1840; Sharp, 1885; Bernhauer, 1906, 1921). Because an updated classification of the NT representatives lags far behind that of their Holarctic counterparts, many questions remain nowadays about the affiliation of the large number of NT species that were never revised after their original descriptions (Chani-Posse et al., 2018b).

Philonthina and its NT lineage were focal points of a recent total-evidence analysis that reconstructed phylogenetic relationships across Staphylinini, one of the most emblematic tribes of Staphylinidae (Chani-Posse et al., 2018a). That same study concluded that the need of more taxonomic work in the subtribe "may be most efficiently guided by molecular evidence given the high level of morphological homoplasy". In the case of the NT lineage, notwithstanding, there is a broad range of morphological variability not yet explored (Chani-Posse et al., 2018b) that may yield further phylogenetic signal after a deeper reassessment of characters, including those traditionally used in the systematics of the group. The so-called "*Belonuchus*-complex" (Chani-Posse et al., 2018a) appears to be the main lineage of NT Philonthina, but the generic affiliation of at least one hundred of its species is doubtful (Chani-Posse et al., 2018b). Many of them are currently assigned to *Belonuchus,* but outside of the "*Belonuchus-haemohrroidalis* clade" or "true" *Belonuchus* (Chani-Posse et al., 2018b). Also, a question remains in the Neotropics about the status of *Musicoderus* Sharp, the only junior synonym of *Belonuchus* at present, which was erected by Sharp (1885) for two species, *M. cephalotes* and *M. gracilis*. The other 16 species of *Musicoderus* were described at different times afterwards, either as genus or subgenus of *Belonuchus* and eventually synonymized with it (Chani-Posse et al., 2018b). However, *Hesperus* or alternatively the "*Hesperus*-complex" is a Northern Hemisphere lineage with ten species recorded from the NT region (Chani-Posse et al., 2018b). Among them,

only two Mexican species, *H. fasciatus* (Sharp) and *H. pollens* (Sharp), do belong to *Hesperus* after its current monophyletic concept (Chani-Posse et al., 2018a, 2018b). Another species (*H. heynei* Wendeler from Costa Rica) has been recently transferred to *Paederomimus* Sharp (Chani-Posse and Ramírez-Salamanca, 2019). The remaining seven species (*H. ornaticornis* Wendeler from Costa Rica and six South American species) do not belong to *Hesperus,* and their affiliation is uncertain (Chani-Posse et al., 2018b).

The current classification of Philonthina and its NT representatives should be considered as a result of conceptual and methodological factors and/or biases that have interacted through space and time. The main objectives of this work are: (i) to reassess characters associated with traditional morphology-based systematics, including those from secondary sexual dimorphism; (ii) to resolve the phylogenetic position of the NT species of *Hesperus* with uncertain affiliation; and (iii) to reassess the monophyly of *Belonuchus* and its "*Belonuchus-haemohrroidalis* clade" with respect to *Musicoderus* Sharp, the only current junior synonym of *Belonuchus*. Our ultimate goal is to provide new insights into the diversification and evolution of the NT lineage in order to guide future taxonomic work on this megadiverse group.

Materials and methods

Taxon sampling

A matrix of 79 taxa and 132 morphological characters was analyzed. Sixty-eight taxa representing 25 genera of the subtribe Philonthina were studied, including four genera/species not represented in the NT region but endemic to other biogeographical areas (i.e. *Actinus imperialis, Agacerus pectinatus, Laetulonthus laetulus, Trapeziderus diversus*). Another 10 taxa were chosen in an attempt to broadly represent the diversity of the main lineages of Staphylinini in the NT and Andean regions (Morrone, 2014a, 2014b). Among the extant taxa, Arrowinini and Staphylinini are sister groups within the subfamily Staphylininae (Solodovnikov and Newton, 2005; Solodovnikov et al., 2013), so *Arrowinus minutus* Solodovnikov and Newton was included to root the trees. All taxa are listed in Table 1. Genera of Philonthina that are rich in species in the NT region (i.e. *Philonthus, Belonuchus* and *Paederomimus*) were represented in this analysis by at least 11 species from different species groups, as far as this knowledge is available (for *Philonthus*: Smetana, 1995; Schillhammer, 1998, 1999, 2000, 2001, 2003; Chani-Posse, 2010; for *Belonuchus*: Chani-Posse et al., 2018a, 2018b; for *Paederomimus*: Sharp, 1885: 438–439). To thoroughly test the monophyly of the "true"

Table 1
Taxon sampling for the phylogenetic analysis (79 taxa, organized alphabetically by tribe or subtribe, genera and species)

Current tribe/subtribe	Genus	Genus distribution	Species in analysis	Species distribution	Depositories of species used in analysis	Material examined Number/sex
Arrowinini	*Arrowinus* Bernhauer, 1935	South Africa	*Arrowinus minutus* Solodovnikov and Newton, 2005	South Africa	*	*
Amblyopinina	*Amblyopinus* Solsky, 1875	Neotropical	*Amblyopinus emarginatus* Seevers, 1955	Costa Rica, Panama, Colombia, Venezuela	*	*
Anisolinina	*Misantlius* Sharp	Neotropical	*Misantlius gebieni* Bernhauer, 1942	Costa Rica	* & NHMUK	* &1♀
Cyrtoquediina	*Cyrtoquedius* (Brunke et al., 2016)	Neotropical	*Cyrtoquedius* aff. *frenatus* (Erichson, 1840)	Peru (Amazonia)	IADIZA	1♀ 1♂
Hyptiomina	*Holisus* Erichson, 1839	Australia and Pacific	*Holisus prolixus* Sharp, 1885	Mexico, Guatemala	SEMC	1♀
Philonthina	*Actinus* Fauvel, 1878	Oriental	*Actinus imperialis* Fauvel, 1878	Australia and New Guinea	SEMC	2 ♂
	Agacerus Fauvel, 1895		*Agacerus pectinatus* Fauvel, 1895	India, Myanmar, Laos, China	NMW	2♂
	Belonuchus Nordmann, 1837	Nearctic, Neotropical, Old World	**Belonuchus albovarigatus Bernhauer, 1916**	**Colombia**	FMNH	**1♂ (LT)**; **2♀ (PLT)**
			Belonuchus atticida (Wasmann 1925)	Brazil, Paraguay	NMW	1♂ (LT); 4♀ (PLT)
			Belonuchus (*Musicoderus*) *barbicornis* Bernhauer, 1916	Colombia	CNC	1♀ 1♂
			Belonuchus cephalotes (Sharp, 1885)	**Panama, Venezuela**	NHMUK	1♀ 1♂
			Belonuchus cognatus Sharp, 1885	Belize, Guatemala, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Trinidad, Brazil, Argentina, St. Vincent	MLPA	1♀ 1♂
			Belonuchus gracilis (Sharp, 1885)	**Nicaragua**	NHMUK	**1♀ (HT)**
			Belonuchus haemorrhoidalis (Fabricius, 1801)	Colombia, Venezuela, French Guiana, Peru, Bolivia, Brazil, Paraguay, Argentina	MLPA	1♀ 1♂
			Belonuchus mordens Erichson, 1840	Peru, Brazil, Argentina, Bolivia	MLPA	1♂
			Belonuchus pollens Sharp, 1885	Mexico, Guatemala, Honduras	SEMC 1♀; NHMUK 1♂; ZMHB 1♂	1♀ 1♂
			Belonuchus (*Musicoderus*) *subaeneus* Bernhauer, 1916	Bolivia	CNC	1♀ 1♂
			Belonuchus rufipennis (Fabricius, 1801)	Nearctic, Neotropical	MLPA	1♀ 1 ♂
	Bisnius Stephens, 1829a	Canada to Mexico, Palearctic, Oriental, Ghana, New Zealand, intro Chile, Argentina, Australia	*Bisnius sordidus* (Gravenhorst, 1802)	Palearctic, Azores, Canary Is., Madeira, Japan, Mongolia, China, India, Nepal; intro Canada, USA, Mexico, Chile, Argentina, Australia, New Zealand, Tristan d.C.	IADIZA	2♀ 2♂
	Cafius Stephens, 1829 (Gravenhorst, 1806)	World	*Cafius seminitens* Horn, 1884	Canada, USA, Mexico	SEMC 4♀; FMNH 1♂	1♀ 1♂
			Cafius xantholoma	Europe, Ukraine, Morocco, Algeria, Tunisia, Libya, Egypt, Turkey, Azores, Canary Is., Iceland; adventive? in South Africa, Chile	SEMC	
	Chroaptomus Sharp, 1885	Neotropical	*Chroaptomus flagrans* (Erichson, 1840)	Neotropical	IADIZA	3♀ 3♂
	Delgadobius Chani-Posse & Couturier 2012	Neotropical	*Delgadobius amazonensis* Chani-Posse & Couturier, 2012	Amazonia (Peru, Brazil)	IADIZA	3 ♀ 2 ♂
	Ecitophytes Wasmann, 1923	Neotropical	*Ecitophytes coniceps* Wasmann, 1923	Brazil	FMNH	3♀ 3♂
	Flohria Sharp, 1884	Nearctic, Neotropical	*Flohria subcoerulea* (LeConte, 1863)	USA, Mexico, Honduras, Nicaragua, Costa Rica	FMNH 1♀; INBIO 1♂	
	Gabrius Stephens, 1829	World	*Gabrius picipennis* (Mäklin, 1852)	Canada	*	*

Table 1
(*Continued*)

Current tribe/subtribe	Genus	Genus distribution	Species in analysis	Species distribution	Depositories of species used in analysis	Material examined Number/sex
	Hesperus Fauvel, 1874	World	*Hesperus baltimorensis* (Gravenhorst, 1802)	USA	SEMC	1♀ 1♂
			Hesperus argentinus **Scheerpeltz, 1971**	**Argentina**	NMW	1♀ (ST)
			Hesperus bruchi **Bernhauer, 1921**	**Argentina**	FMNH	1♂ (HT)
			Hesperus ferrugineus **Bernhauer, 1925**	**Argentina**	FMNH	1♀ (HT)
			Hesperus novoteutonicus **Wendeler, 1956**	**Brazil**	MNHUB	1♀ (HT) 5♀ 2♂(PT)
			Hesperus ornaticornis **Wendeler, 1927**	**Costa Rica**	MNHUB	1♀ (HT)
			Hesperus tremolerasi **Bernhauer, 1927**	Uruguay	FMNH	1♂(HT)
			Hesperus zischkai **Scheerpeltz, 1971**	Bolivia	NMW	1♀ (ST)
	Laetulonthus Moore & Legner, 1973	Nearctic	*Laetulonthus laetulus* (Say, 1834)	Canada, USA	SEMC	1♀ 1♂
	Leptopeltoides Chani-Posse and Asenjo, 2013	Andean	*Leptopeltoides columbiensis* **Chani-Posse and Asenjo, 2013**	**Colombia**	SEMC	1♀ 1♂(HT)
	Leptopeltus Bernhauer, 1906	Andean	*Leptopeltus flavipennis* (Erichson, 1840)	Venezuela, Colombia, Ecuador Peru, Bolivia	IADIZA	1♀ 1♂
	Linoderus Sharp, 1885	Neotropical	*Linoderus gracilipes* **Sharp, 1885**	**Costa Rica, Panama**	NHMUK	1♀ 1♂(LT)
	Neopescolinus Chani-Posse, 2014b	Neotropical	*Neopescolinus nevermanni* **Chani-Posse, 2014**	**Costa Rica**	FMNH 1♀ (HT); INBIO 1♂	1♂
	Odontolinus Sharp, 1885	Neotropical	*Odontolinus fasciatus* Sharp, 1885	Honduras, Nicaragua, Costa Rica, Panama, Ecuador	SEMC	1♀ 1♂
	Ophionthus Bernhauer, 1908	Neotropical	*Ophionthus serpentinus* **Bernhauer, 1908**	**Peru**	FMNH	1♂(HT)
	Paederallus Sharp, 1885	Neotropical	*Paederallus* sp.	Peru	FMNH	1♀ 1♂
	Paederominus Sharp, 1885	Neotropical	*Paederominus aeneiceps* (Sharp, 1876)	Brazil, Peru	CNC	1♀ 1♂
			Paederominus angusticollis (Erichson, 1840)	Mexico, Guatemala	CNC	1♀ 1♂
			Paederominus capitalis Sharp, 1876	Brazil (Amazonas), Costa Rica?	IADIZA	1♀ 1♂
			Paederominus contractus Sharp, 1885	Guatemala, Nicaragua, Costa Rica	FMNH	1♀ 1♂
			Paederominus difformiceps Sharp, 1885	Guatemala	FMNH 1♀ 2♂	
			Paederominus gentilis Sharp, 1885	Mexico	CNC	1♀ 1♂
			Paederominus lustrator Sharp, 1876	Brazil	CNC	1♀ 1♂
			Paederominus nigrinus **Sharp, 1885**	**Nicaragua**	NHMUK (**HT**); MNHUB 8♀; SEMC 1♂	
			Paederominus nobilis Sharp, 1885	Panama, Nicaragua.	SEMC	1♀ 1♂
			Paederominus pectoralis **Sharp, 1885**	**Mexico, Guatemala**	NHMUK	1♀ 1♂(ST)
			Paederominus salvini Sharp, 1885	Panama	SEMC	1♀ 1♂
	Pescolinus Sharp, 1885	Neotropical	*Pescolinus palmatus* Sharp, 1885	Panama	NHMUK	1♀ 1♂
	Phileciton Wasmann, 1894	Neotropical	*Phileciton badariottii* Wasmann, 1894	Brazil	FMNH	1♀ 1♂

Table 1
(*Continued*)

Current tribe/subtribe	Genus	Genus distribution	Species in analysis	Species distribution	Depositories of species used in analysis	Material examined Number/sex
	Philonthus Stephens, 1829	World	*Philonthus bicoloristylus* Chani-Posse 2004	Argentina	MLPA	1♀ 1♂
			Philonthus bonariensis Bernhauer, 1909	Neotropical	IADIZA	1♀ 1♂
			Philonthus caeruleipennis Mannerheim, 1830	Nearctic	*	*
			Philonthus callosipennis Scheerpeltz, 1960	**Bolivia**	NMW 1♀ 1♂	
			Philonthus cyanipennis (Fabricius, 1792)	Palaearctic	IRSNB	1♀ 1♂
			Philonthus diamantinus Bernhauer 1917	Bolivia	CNC	1♀ 1♂
			Philonthus figulus Erichson, 1840	Brazil	*	*
			Philonthus flavolimbatus Erichson, 1840	Neotropical, Nearctic	IADIZA	1♀ 1♂
			Philonthus fulgipennides Sharp, 1885	Panama	CNC	1♀ 1♂
			Philonthus laetipennis Sharp, 1885	Mexico	INBIO	1♀ 1♂
			Philonthus longicornis Stephens, 1832	Cosmopolitan [adventive? in the Americas]	IADIZA	1♀ 1♂
			Philonthus lynchi Bernhauer and Schubert, 1914	Peru, Paraguay, Uruguay, Argentina	IADIZA	1♀ 1♂
			Philonthus nitidus (Gravenhorst, 1806)	Nearctic	IRSNB	1♀ 1♂
			Philonthus rectangulus Sharp, 1874	Europe, Russia, Azores, Madeira, Canary Is., Turkey, Afghanistan, Kazakhstan, Japan, Korea (S), China, Taiwan, Thailand, Nepal, Bhutan, Indonesia, New Guinea; adventive in Tahiti, Hawaii, New Zealand, Canada, USA, Mexico, Brazil, Chile, Argentina, Uruguay, Cuba, Costa Rica etc.	*	*
			Philonthus sericans (Gravenhorst, 1802)	Canada, USA, Mexico, Brazil, Argentina	MLPA	1♀ 1♂
			Philonthus splendens (Fabricius, 1793)	Palaearctic	IRSNB	1♀ 1♂
	Proxenobius Seevers, 1965	Neotropical	*Proxenobius borgmeieri* Seevers, 1965	Mexico, Costa Rica, Panama; Ecuador and Bolivia new records	SEMC	3♀ 2♂
	Trapeziderus Motschulsky, 1860	Afrotropical, Oriental	*Trapeziderus diversus* (Bernhauer, 1928)	Zaire	MRAC	1♀ 1♂
Philothalpina	*Philothalpus* Kraatz, 1857	Neotropical	*Philothalpus bilobus* Chatzimanolis and Ashe, 2005	French Guiana, Guayana, Surinam	*	*
			Philothalpus falini Chatzimanolis and Ashe, 2005	Costa Rica, Nicaragua	*	*
Staphylinina	*Creophilus* Leach, 1819	World	*Creophilus maxillosus* (Linnaeus, 1758)	World except Africa	IADIZA	1♀ 1♂
	Platydracus Thomson, 1858	World, except Australia, New Zealand and Pacific	*Platydracus chrysotrichopterus* (Scheerpeltz, 1933)	Neotropical	IADIZA	1♀ 1♂
Xanthopygina	*Nordus* Blackwelder, 1952	Neotropical	*Nordus elytsi* Chatzimanolis, 2004	Argentina, Bolivia	IADIZA	1♀ 1♂
	Xenopygus Bernhauer, 1906	Neotropical	*Xenopygus analis* (Erichson, 1840)	Neotropical	IADIZA	1♀ 1♂

Current subtribes and distributional data are given according to Chani-Posse et al. (2018b) for Neotropical Philonthina; Herman (2001) and Newton (2019) for other Staphylinini.
*After Ashe and Timm (1995), Smetana (1995), Chatzimanolis and Ashe (2005), Solodovnikov and Newton (2005), Chani-Posse (2010) and Chani-Posse et al. (2018a, 2018b). Species whose type material was examined for this study and their depositories are in bold.
HT, holotype; LT, lectotype; PLT, paralectotype, PT, paratype, ST, syntype.

Belonuchus (i.e. the "*Belonuchus-haemohrroidalis* clade") with respect to *Musicoderus*, their type species (*B. haemohrroidalis* and *M. cephalotes*, respectively) were included as well as *M. gracilis* and another two species once assigned to *Musicoderus* (*B. subaeneus* and *B. barbicornis*). As for *Hesperus*, all of the seven Neotropical species currently considered as "not *Hesperus*" by Chani-Posse et al. (2018b) were added together with *H. baltimorensis*, a Nearctic species closely related to the type species of the genus (Smetana, 1995; Chani-Posse et al., 2018a).

Morphological study

Beetle specimens were examined using a Nikon SMZ745 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. The right protarsus was removed directly from each adult specimen and examined using SEM. Typically, one male specimen of each species was examined; and we also analysed females, if available (see Table 1). Detached protarsi (and in a few cases also entire specimens) were cleaned through an ultrasonic bath for 5 min. They were air-dried and then mounted on metal stubs using Z-Axis conductive tape. In the case of fragile or old material with a few specimens, especially those represented by small individuals, they were not cleaned using the procedure described in order to avoid damage; they were directly mounted on stubs. The material was sputter-coated with gold and examined in a JSM-6610 scanning electron microscope. Specimens were borrowed from and/or are deposited in the following collections (acronyms used throughout the text): CNC, Canadian National Collection, Ontario, Canada (P. Bouchard, A. Brunke, J. Buffam); FMNH, Field Museum of Natural History, Chicago, IL, USA (A. F. Newton, M. K. Thayer, C. Maier); IADIZA, Instituto Argentino de Investigaciones de las Zonas Aridas, Mendoza, Argentina (S. Roig Juñent); INBio, Instituto Nacional de Biodiversidad de Costa Rica (A. Solís); IRSNB, Institut Royale des Sciences Naturelles de Belgique (Y. Gérard); MLPA, Museo de La Plata, La Plata, Argentina (A. Lanteri, N. Cabrera); MNHUB, Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, Germany (J. Frisch, B. Jaeger, J. Willers); MRAC, Musée Royal de l'Afrique centrale (Didier Van den Spiegel, Stéphane Hanot); NHMM, Natuurhistorisch Museum Maastricht (P. Beuk); NHMUK, The Natural History Museum, London (M. Barclay); NMW, Naturhistorisches Museum Wien, Austria (H. Schillhammer); and SEMC, Snow Entomological Collection, Natural History Museum/ Biodiversity Research Center, University of Kansas, Lawrence, USA (Z. Falin).

Morphological characters

The selection of characters mainly followed Brunke et al. (2016) and Chani-Posse et al. (2018a) in their exploration of morphological characters for the phylogenetic reconstruction of the tribe Staphylinini. Among the 132 characters used, 119 were derived from external morphology, ten from male genitalia and three from female genitalia. Eighty-two characters were included and illustrated in previous studies (see character list below), and 50 characters are novel (i.e. newly discovered and/or used for the first time in a phylogenetic analysis) and therefore marked in the character report with an asterisk (*). Among them, 16 sexually dimorphic characters (SD) were evaluated after morphological differences other than those traditionally associated with male or female genitalia in Staphylinini (e.g. sternum 8), and distinguished as such from other characters belonging to the same structure. Following Sereno (2007, 2009), neomorphic (presence/absence) and transformational (transformation from one state to another) characters referring to the same structure were coded separately. Characters are listed below in sections according to their corresponding body parts.

General body

1. * Head and pronotum, spine-like setae: (0) absent; (1) present.

Head and mouthparts (characters 2–39)

2. Antennal insertions (ai), position in relation to frontoclypeus and eye: (0) ai situated at the anterior margin of frontoclypeus, i.e. anterior margin of antennal cavity touching the anterior margin of frontoclypeus (Chani-Posse, 2013: fig. 1B,C); (1) ai situated closer to frontoclypeus than to eye (Chani-Posse, 2013: fig. 1A); (2) ai situated at equal distance or closer to eye (Chani-Posse, 2014a: fig. 11D).
3. * Sexual dimorphism, antennal insertions, distance between each other in relation to eye (ai-ai/ ai-e): (0) absent (both male and female with same ai-ai:ai-e ratio); (1) present (only males with antennal insertions equidistant from each other and eye or closer to each other than to eye).
4. * Sexual dimorphism, antennal length: (0) absent (both male and female with same length); (1) present (i.e. longer in males).
5. * Sexual dimorphism, antennomere 1, setation: (0) absent (i.e. both male and female with same setation); (1) present (i.e. denser in males).
6. Antennae, relative length of antennomere 1 (a1), and antennomeres 2 (a2) and 3 (a3) combined: (0) a1 distinctly shorter than a2 and a3 combined; (1) a1 as long as or longer than a2 and a3 combined.

7. Antennae, length of antennomeres 3 and 2 ratio (a3:a2): (0) a3 not longer than a2 (maximum a3/a2 ratio 1.0; (1) a3 moderately longer than a2 (a3:a2 ratio 1.2–1.5); (2) a3 distinctly longer than a2 (a3: a2 ratio ≫ 1.5).

8. Antennae, antennomere 3, tomentose pubescence (see Chani-Posse, 2013): (0) absent (fig. 1D); (1) present (fig. 1C).

9. Antennnae, antennomere 6, apical long setae (see Chani-Posse, 2014b): (0) absent (fig. 10); (1) present (fig. 11).

10. * Sexual dimorphism, head, punctation, dorsal view (see Chani-Posse, 2014a): (0) absent (i.e. both male and female with same punctation); (1) present (i.e. with dense punctation in males, scarcely punctuate to almost glabrous in females) (fig. 12E).

11. * Sexual dimorphism, head, punctation, ventral view: (0) absent (i.e. both male and female with same punctation); (1) present (i.e. with dense punctation in males, scarcely punctuate to almost glabrous in females).

12. * Sexual dimorphism, head, setation, ventral view: (0) absent (i.e. both male and female with same setation); (1) present (i.e. with dense setation in males, scarce setae to almost glabrous in females).

13. * Sexual dimorphism, head, width: (0) absent (both male and female with about the same width); (1) present (distinctly wider in males).

14. * Sexual dimorphism, frontoclypeus, emargination (see Chani-Posse, 2006): (0) absent (i.e. both male and female without emargination); (1) present (emarginate in males) (fig. 1).

15. Head, neck constriction: (0) neck distinct at sides only (Solodovnikov and Newton, 2005: fig. 16A, D); (1) neck constriction fully developed, distinct all around (Chani-Posse, 2013: fig. 1A,B,F); (2) neck region indistinct.

16. Head, dorsal basal ridge (see Li and Zhou, 2011): (0) absent (fig. 3A,F); (1) present (fig. 3B,E).

17. Head, ventral basal ridge (vbr), development: (0) vbr along considerable portion of its length confluent with ventral portion of postoccipital suture (Chani-Posse, 2014a: fig. 2I); (1) vbr extending more or less parallel to ventral portion of postoccipital suture (Fig. 1a,c–f).

18. Head, postgenal ridge: (0) absent (Solodovnikov and Newton, 2005: fig. 9D); (1) present (Fig. 1a, c–f).

19. Head, postgenal ridge (pgr) relative to ventral basal ridge (vbr), development: (0) pgr developed ventrally but not joining vbr medially (Fig. 1a,c,e,f); (1) pgr joined vbr medially (Fig. 1d,i); (2) pgr slightly developed ventrally (rather laterally) and not joining vbr.

20. Head, postmandibular ridge: (0) absent (Fig. 1a,c,e, f); (1) present (Fig. 1b,d,i).

21. Head, postmandibular ridge (pmr) relative to mandibular base (mb): (0) pmr bordering mb almost completely (Fig. 1b); (1) pmr bordering mb only laterally; (2) pmr and mb separate (Fig. 1d).

22. Head, postmandibular sulcus (see Chani-Posse, 2014a): (0) absent (fig. 2B, D, H); (1) present (fig. 2A).

23. Head, infraorbital ridge: (0) absent (Fig. 1a,c,e,f); (1) present (Fig. 1i).

24. Head, infraorbital ridge (ior), development: (0) ior complete (Chani-Posse, 2014a: fig. 2F,K); (1) ior extending far beyond postgenal ridge; (2) ior reaching postgenal ridge or slightly extending beyond postgenal ridge (Fig. 1D,E,I).

25. Head, ligula, shape (see Li and Zhou, 2011): (0) more or less bilobed, with variously developed rounded lobes (fig. 7C); (1) small, entire (or at most slightly notched medially) (fig. 7A,B).

26. Head, mandibles, dorso-lateral groove: (0) absent; (1) present (Chani-Posse, 2013: fig. 1A).

27. Labial palpus, relative length of palpomeres 3 (p3, apical) and 2 (p2, preapical) (p3/p2): (0) p3 distinctly shorter than p2; (1) p3 and p2 subequal in length; (2) p3 distinctly longer than p(2)

28. * Labial palpomere 2 (when p3 distinctly shorter than p2), setae: (0) basal; (1) mediobasal.

29. * Labial palpomere 2, shape: (0) cylindrical (Fig. 1c); (1) slightly expanded apically (Fig. 1a,b, d,f).

30. * Sexual dimorphism, labial palpomere 2–3: (0) absent (i.e. subcylindrical in both male and female); (1) present (i.e. medially expanded in males, subcylindrical in females) (Fig. 1f).

31. * Maxillary palpus, relative length of palpomeres 4 (p4, apical) and 2 (p2) (p4/p2): (0) p4 as long as or longer than p2; (1) p4 distinctly shorter than p(2)

32. * Sexual dimorphism, maxillary palpomere 3: (0) absent (i.e. subcylindrical in both male and female); (1) present (i.e. apically expanded in males, subcylindrical in females).

33. Maxillary palpus, palpomere 4 (apical), shape: (0) subacute, i.e. narrowed at base and evenly converging towards apex; (1) fusiform to expanded apically, i.e. narrowed at base but not (or not evenly) converging towards apex; (2) subcylindrical "rod-like", parallel-sided along most of its length, apex subtruncate; 3 subcylindrical "rod-like", parallel-sided along most of its length, apex acute.

34. Gular sutures (gs), development: (0) gs joined before neck; (1) gs not joined before neck, extended close to each other at base of head capsule.
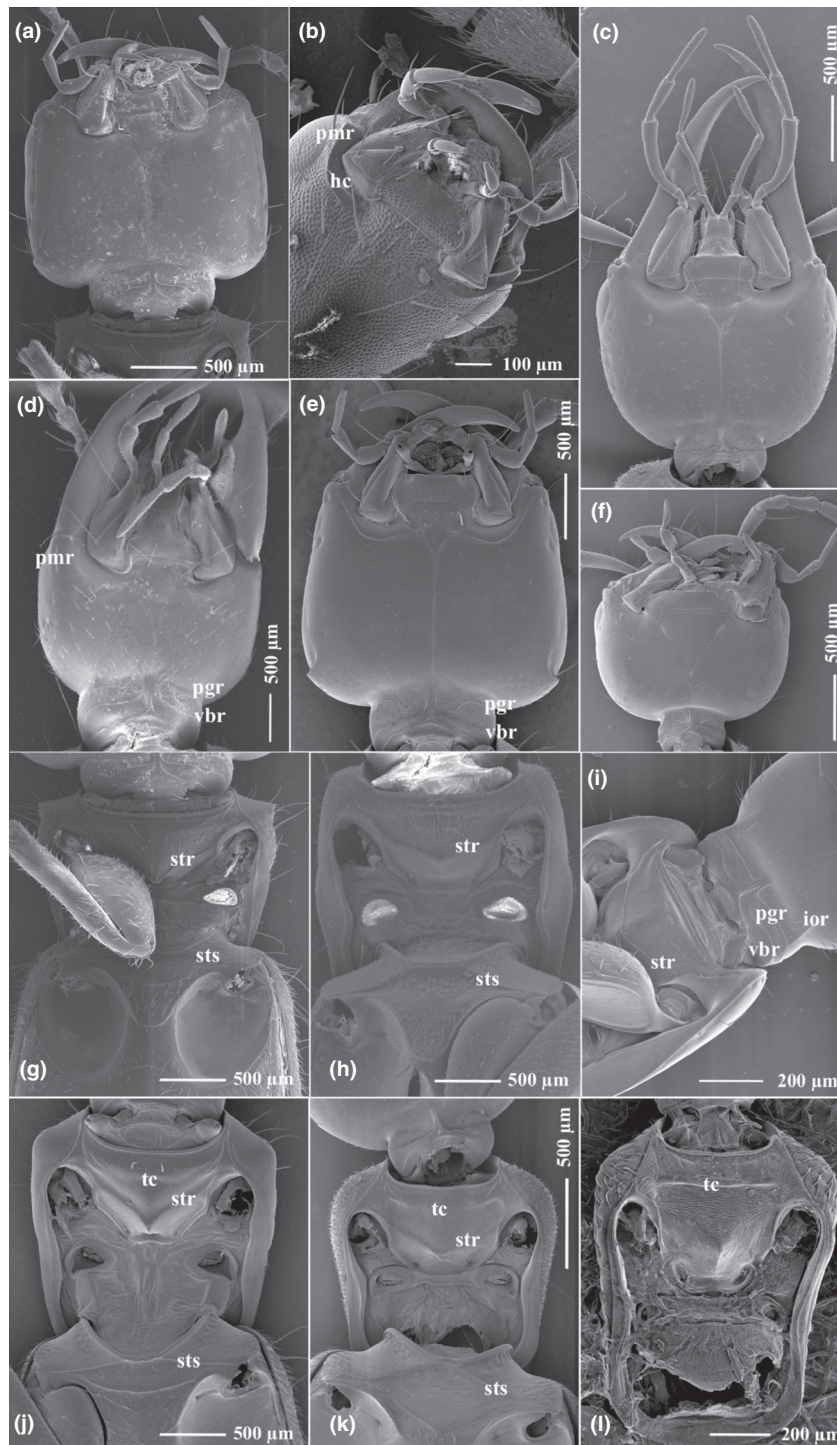
Fig. 1. (a–f) Head in ventral view: *Trapeziderus diversus* (a), *Ecitophytes coniceps* (b), *Belonuchus cephalotes* (c), *Hesperus baltimorensis* (d), *Belonuchus haemohrroidalis* (e), *Paederomimus angusticollis* (f). (g, h, j, k) Prosternum and mesoventrite: *T. diversus* (g), *H. baltimorensis* (h), *B. haemohrroidalis* (j), *B. cephalotes* (k). (i, l) Prosternum: *Philonthus bonariensis* (i), *Paederomimus contractus* (l). Abbreviations: hc, hypostomal cavity; ior, infraorbital ridge; pgr, postgenal ridge; pmr, postmandibular ridge; str, sternacostal ridge; sts, sternopleural (anapleural) suture; vbr, ventral basal ridge.

35. Gular sutures (gs), if not joined before neck, degree of separation: (0) gs slightly separated from each other; (1) gs widely separated from each other.

36. Male gular sutures, if joined before neck, joining point: (0) joined anteriorly (i.e. not >0.5× the distance between the anterior margin of mentum and

the base of head along midline); (1) joined posteriorly.

37. * Sexual dimorphism, gular sutures, if joined before neck, joining point: (0) absent (i.e. joined at same point in both sexes); (1) present (joined anteriorly in male but posteriorly in female).

38. Hypostomal cavity (hc): (0) absent; (1) present (Fig. 1b,e).

39. Hypostomal cavity (hc), if present: (0) hc distinctly delimited (i.e. cavity surface with microsculpture and/or punctation different from rest of nearby head surface); (1) hc moderately delimited (i.e. cavity surface without microsculpture or punctation different from rest of nearby head surface; Fig. 1b); (2) hc slightly delimited (cavity distinct only laterally, its surface with same microsculpture or punctation as rest of nearby head surface (Fig. 1e).

Thorax (characters 40–64)

40. Prothorax, anterior angles (aap) relative to anterior margin of prosternum (amp): (0) aap and amp at about the same level (Fig. 1g–k); (1) aap distinctly posterior to amp (Fig. 1l).

41. * Prothorax, pronotum, deflection (in ventral view): (0) absent; (1) present (Fig. 1g–l).

42. * Prothorax, pronotum, if deflected (in ventral view): (0) not visible beyond spiracles (Fig. 1g–j); (1) visible beyond spiracles (Fig. 1k,l).

43. Prothorax, large lateral setiferous puncture (llsp), position in relation to superior marginal line of pronotum (smlp): (0) llsp situated very close to smlp or at a distance ≤3× its diameter; (1) llsp situated away from smlp at a distance ≥3× as large as its diameter.

44. * Prothorax, prosternum, sternacostal ridge (str): (0) absent (Fig. 1l); (1) present (fig. 1g–k).

45. * Prothorax, prosternum, sternacostal ridge (when present): (0) joining superior line of hypomeron (Fig. 1k); (1) not joining superior line of hypomeron (Fig. 1g–j).

46. Prothorax, basisternum (bs), length relative to length of furcasternum (fs) (bs/fs, measured laterally): (0) bs slightly to moderately longer than fs (bs:fs ratio up to 1.5); (1) bs distinctly longer than fs (bs:fs ratio ≫ 1.5); (2) bs distinctly shorter than fs (bs:fs ratio ≪ (1.0).

47. Prothorax, prosternum, transverse carina on basisternum (tc): (0) absent; (1) present.

48. Prothorax, prosternum, transverse carina on basisternum, development (when present): (0) tc rudimentary to incomplete; (1) tc complete.

49. * Prothorax, prosternum, basisternum, microsculpture (when transverse carina present): (0) uniform (i.e. not different at both sides of transverse carina); (1) not uniform (i.e. distinct at both sides of carina).

50. Prothorax, prosternum, longitudinal ridge (in ventral view): (0) absent; (1) present.

51. Prosternum, keel (see Chani-Posse and Asenjo, 2013): (0) absent (fig. 2J); (1) present (fig. 2H,I).

52. Prothorax, hypomeron, superior marginal line, deflection under anterior angles (ventral view): (0) not distinct; (1) distinct.

53. Prothorax, hypomeron, inferior marginal line (iml), development: (0) iml not continued as a separate entity beyond anterior pronotal angles; (1) iml continued as a separate entity beyond anterior pronotal angles and curving around them; (2) iml continued as a separate entity beyond anterior pronotal angles and continuous with them.

54. Prothorax, degree of fusion of pronotum (pnt) and prosternum (pst) (see Li and Zhou, 2011): (0) pnt and pst not fused in procoxal cavity, pronotosternal suture complete in cavity (fig. 10C); (1) pnt and pst at least partially fused, pronotosternal suture missing in part of cavity (fig. 10A,D).

55. Prothorax, prosternum, basisternum, pair of macrosetae: (0) absent; (1) present.

56. Prothorax, prosternum, basisternum, position of pair of macrosetae (ms, if present) in relation to anterior margin of prosternum (amp) and the sternacostal suture (ss): (0) ms situated close to amp (i.e. ≤0.25× the distance between amp and the ss along midline); (1) ms situated far from amp (i.e. >0.25× the distance between amp and the ss along midline).

57. Mesothorax, mesoscutellum, posterior scutellar ridge (see Brunke and Solodovnikov, 2013): (0) absent (fig. 8A,C,D,E); (1) present (fig. 8B,F).

58. Mesothorax, elytron, humeral spines or spine-like setae: (0) absent; (1) present (Brunke and Solodovnikov, 2014: fig. 10B,E).

59. Sternopleural (anapleural) suture (sts): (0) transverse, or nearly transverse (very slightly oblique) (Fig. 1g,h,j); (1) distinctly oblique (medial end of suture anterior to its lateral end) (Fig. 1k); (2) sinuate.

60. Sternopleural (anapleural) sutures (sps), their position with respect to anterior margin of mesoventrite (amm), if oblique: (0) sps confluent at amm; (1) sps not confluent at amm.

61. Mesothorax, mesoventral cross-like ridge: (0) absent; (1) present (Chani-Posse et al., 2018a: fig. 8A, as "r(la)").

62. * Mesothorax, mesoventral longitudinal ridge: (0) absent; (1) present.

63. Mesothorax, mesoventral posterior half of prepectus, ridge connecting coxal cavities, if present: (0) absent (Fig. 1g,h); (1) present (Fig. 1j,k).

Fig. 2. Right profemur and protibia: *Trapeziderus diversus* (a). (b, c, e, g) Right profemur: *Hesperus baltimorensis* (b), *Philonthus cyanipennis* (c), *Belonuchus haemohrroidalis* (e), *Belonuchus mordens* (f), *Belonuchus (Musicoderus) barbicornis* (g). (d, h) Right protibia: *Belonuchus cephalotes* (d), *Leptopeltoides columbiensis* (h). (i–t) Right protarsus: *H. baltimorensis* (i), *Belonuchus haemohrroidalis* (j), *B. cephalotes* (k), *Ecitophytes coniceps* (l), *Proxenobius borgmeieri* (m), *Delgadobius amazonensis* (n), *Cafius seminitens* (o), *Neopescolinus nevermanni* (p), *Odontolinus fasciatus* (q), *Paederomimus aeneiceps* (r), *Linoderus gracilipes* (s), *Leptopeltoides columbiensis* (t).

64. Mesothorax, intercoxal process, apex: (0) rounded or broadly pointed, forming obtuse angle; (1) narrowly pointed forming sharp (acute) angle; (2) intercoxal process not distinct, metaventrite fused with mesoventrite.

Legs (characters 65–105)

65. Profemora, lateroventral medial spines (posterior row): (0) absent; (1) present (Fig. 2e,f,g).
66. * Sexual dimorphism, profemora, lateroventral apical spine/s (anterior row, when present): (0) absent (both sexes with spine/s); (1) present (spine/s only in males).
67. Profemora, lateroventral medial spines (anterior row): (0) absent; (1) present (fig. 2E).
68. * Profemora, chaetotaxy: (0) conspicuously denser ventrally (Fig. 2b,c); (1) sparse all over (Fig. 2e–g); (2) dense both dorsally and ventrally.
69. * Profemora, chaetotaxy, longitudinal patch of dense setae lateroventrally: (0) absent; (1) present (Fig. 2g).
70. * Sexual dimorphism, profemora, shape: (0) absent; (1) present (medially dilated or wider in males).

71. Protibiae, shape: (0) cylindrical to slightly broadened apically (Fig. 2d,h); (1) subconical to conical, moderately to distinctly broadened apically (Fig. 2a,b).
72. Protibiae, apical excavation: (0) absent; (1) present (Fig. 2d,h).
73. * Protibiae, apical excavation, spines: (0) absent; (1) present (Fig. 2d,h).
74. * Protibiae, apical excavation, spines (when present), number: (0) 5–6 (Fig. 2h); (1) 2–3 (Fig. 2d).
75. * Protibiae, lateroventral spines: (0) absent; (1) present.
76. * Protibiae, lateroventral spines, distribution: (0) irregular, not in rows; (1) in one row; (2) in two rows.
77. * Protarsi, tarsomeres 2–3, relative width: (0) as long as to longer than wide; (1) distinctly wider than long.
78. * Male protarsi, tarsomeres 2–3: (0) not bilobed (posterior margin moderately curved to straight); (1) sub-bilobed; (2) strongly bilobed.
79. * Protarsomeres 2–3, ventral surface, discal setae: (0) absent; (1) present (Fig. 2i,l,n,o).

Note: Herein we introduce the term "discal setae" for those modified setae sometimes present in Coleoptera on the ventral surface of (mostly) protarsomeres and traditionally called "adhesive" or "tenent setae" (see Stork, 1980 and Gnaspini et al., 2017a, 2017b for further references). We aim to differentiate them from the "marginal setae" (see below) as nonhomologous structures.

80. * Protarsomeres 2–3, ventral surface, discal setae (when present), shaft microsculpture: (0) smooth (Fig. 3a–e); (1) striate (Fig. 3g–i).
81. * Protarsomeres 2–3, ventral surface, discal setae (when present), shaft shape: (0) cylindrical, distinctly broadened apically (Fig. 3a–d); (1) subcylindrical, gradually narrowed apically (Fig. 3e–h).
82. * Protarsomeres 2–3, ventral surface, discal setae (when present), terminal plate: (0) absent; (1) present (Fig. 3a–d).
83. * Protarsomeres 2–3, ventral surface, discal setae, terminal plate (when present) shape: (0) rounded to ovoid to subquadrate (Fig. 3a–c); (1) subfusiform to leaf-like (Fig. 3d,f,h); (2) not distinct, fused to adjacent plates.
84. * Protarsomeres 2–3, ventral surface, marginal setae: (0) absent (if present only 1–2 fine setae at each lateroposterior angle); (1) present (Fig. 2j,k, m,p–t).
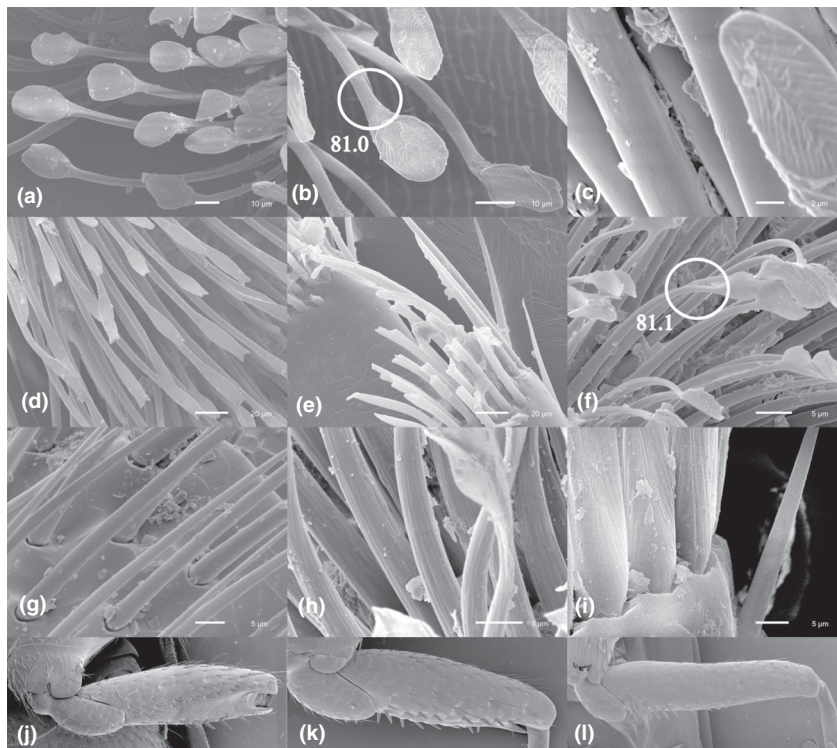

Fig. 3. (a–g). Discal setae, ultrastructure: *Trapeziderus diversus* (a), *Hesperus baltimorensis* (b), *Platydracus chrysotrichopterus* (c), *Philonthus cyanipennis* (d) *Flohria subcoerulea* (e), *Delgadobius amazonensis* (f), *Ecitophytes coniceps* (g), *Philonthus callosipennis* (h). Marginal setae, ultrastructure: *Neopescolinus nevermanni* (i). (j–l) Left metafemur: *T. diversus* (j), *Belonuchus haemohrroidalis* (k), *Belonuchus cephalotes* (l).

85. * Protarsomeres 2–3, ventral surface, marginal setae, distribution (when present): (0) posteriad (Fig. 2p,q); (1) laterally (Fig. 2j,k,m,r,s,t).

86. * Protarsomeres 2–3, ventral surface, marginal setae, distribution (when present and posterior): (0) continuous along margin (Fig. 2p,q); (1) interrupted medially.

87. * Protarsomeres 2–3, ventral surface, marginal setae, number at each side (when present and lateral): (0) 3 (Fig. 2k,m); (1) 4; (2) >4 (Fig. 2s,t); (3) 2 (Fig. 2j,r).

88. * Protarsomere 5, chaetotaxy: (0) several fine setae (Fig. 2i,o,n,l); (1) scarce (very few fine setae, almost glabrous) (Fig. 2j,m,p–t).

89. Apical tarsomere, empodial setae: (0) absent; (1) present.

90. Metacoxae, transverse carina: (0) absent; (1) present.

91. Metacoxae, ventral spines: (0) absent; (1) present.

92. * Male metatrochanter, spines: (0) absent (or only one at most); (1) present.

93. * Male metatrochanter, spines, distribution (when present): (0) posteroapical; (1) anteromedial.

94. * Sexual dimorphism, metatrochanter, spines (when present in males): (0) absent (i.e. male and female with spines); (1) present (i.e. only in males).

95. Male metafemora, spines: (0) absent; (1) present (Fig. 3j–l).

96. * Male metafemora, spines, rows (when present): (0) one row; (1) two rows (Fig. 3j–l); (2) not distinct.

97. * Male metafemora, spines, shape (when present): (0) as strong, seta-like (i.e. same orientation as nearby finer setae); (1) as true spines (Fig. 3j–l).

98. * Male metafemora, spines, distribution (when present as "true spines"): (0) entire posterior margin (Fig. 3j,k); (1) basal half of posterior margin (Fig. 3l); (2) basal fifth of posterior margin.

99. * Sexual dimorphism, metafemora, spines (when present in males): (0) absent (i.e. male and female with spines); (1) present (i.e. only in males).

100. Metatibiae, spines: (0) absent, or at most one or two spines present; (1) always several spines present.

101. Metatarsi, relative length of tarsomeres 1 (t1) and 5 (t5) (t1:t5): (0) t1 shorter than t5 or at most both tarsomeres subequal (t1:t5 < 1.0); (1) t1 moderately longer than t5 (t1:t5 ≫ 1.0 but < 2.0); (2) t1 significantly longer than t5 (t1:t5 ≫ 2.0 but <3.0); (3) t1 much longer than t5 (t1:t5 = 4.0).

102. * Sexual dimorphism, metarsomere 1 (t1), length: (0) absent (i.e. male and female with same t1 length); (1) present (i.e. t1 in male distinctly longer than in female).

103. Metatarsi, tarsomeres 3–5, dorsal surface, chaetotaxy: (0) developed only at margins, dorsal surface of tarsomeres glabrous along midline; (1) tarsomeres dorsally setose (setae not restricted to marginal series).

104. Hind wing, venation, veins CuA and MP4: (0) completely separate; (1) fused in one vein (although often its origin from two veins still very obvious).

105. Hind wing, venation, MP3: (0) vein MP3 present, although sometimes faint; (1) vein MP3 absent.

Abdomen (characters 106–116)

106. Abdomen, protergal glands, cuticular manifestation: (0) shallow impression; (1) well-developed acetabula; (2) more or less invaginated capsules with smaller openings.

107. Abdomen, tergites 3 and 4, anterobasal transverse carina (ABTC), pair of accessory ridges: (0) absent; (1) present.

108. Abdomen, tergum 3, posterobasal transverse carina (PBTC): (0) absent; (1) present.

109. Abdomen, tergum 5, ABTC, pair of accessory ridges: (0) absent; (1) present.

110. Abdomen, tergum 4, PBTC: (0) absent; (1) present.

111. Abdomen, tergum 5, PBTC: (0) absent; (1) present.

112. Abdomen, tergum 3, curved ridge on disc: (0) absent; (1) present.

113. Abdomen, tergum 4, curved ridge on disc: (0) absent; (1) present.

114. Abdomen, tergum 5, curved ridge on disc: (0) absent; (1) present.

115. Abdomen, sternum 3, basal transverse carina, shape of its lateral area: (0) not sinuate; (1) sinuate; (2) descending medially.

116. Abdomen, male sternum 7, patches of setae on disc: (0) absent; (1) present.

Male and female genitalia (characters 117–132)

117. Male sternum 8, apical margin, distinct medial projection: (0) absent; (1) present (Chani-Posse, 2014b: figs 21, 30, 47, 51, 59).

118. Male sternum 8, apical margin, medial emargination: (0) absent; (1) present.

119. Female sternum 8, apical margin, distinct medial projection: (0) absent; (1) present (Chani-Posse, 2014b: figs 26, 35, 56).

120. * Female sternum 8, apical margin, distinct medial projection (when present): (0) straight to slightly emarginate at sides; (1) distinctly emarginate at sides.

121. Male sternum 9, relative length of basal (bp) and distal (dp) portions (bp:dp): (0) bp shorter or as long as dp at most (bp:dp = 1.0); (1) bp

moderately longer than dp (bp:dp = 1.2–1.4); (2) bp distinctly longer than dp (bp:dp ≥ 1.6)

122. Male sternum 9, distal portion, median emargination: (0) distinct; (1) not distinct.

123. Male sternum 9, distal portion, emargination (if distinct): (0) acute; (1) subangulate to concave; (2) slightly arcuate.

124. Lateral tergal sclerites 9 (styli), apical straight setae: (0) absent; (1) present.

125. Lateral tergal sclerites 9 (styli), shape: (0) dorsoventrally flattened; (1) not dorsoventrally or laterally flattened; (2) laterally flattened.

126. Sexual dimorphism, lateral tergal sclerites 9 (styli) (if dorsoventrally flattened): (0) absent (i.e. equally wide in both male and female); (1) present (i.e. distinctly wider in males than in females) (Chani-Posse, 2014b: figs 19, 20).

127. Male tergum 10, shape: (0) emarginate medio-apically; (1) apically subtruncate to wide and subangulate or arcuate; (2) concave medio-apically to apically truncate; (3) apically distinctly subacute to acute.

128. Male: aedeagus, parameres, separation: (0) paired, well separated; (1) fused into a single lobe (sometimes secondarily bifurcate)

129. Male: aedeagus, paramere(s), sensory peg setae: (0) absent; (1) present.

130. Male: aedeagus, paramere(s), degree of 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.

131. Male: aedeagus, paramere(s), shape: (0) paramere(s) not (or at most slightly) produced over apex of median lobe; (1) paramere strongly produced over apex of median lobe; (2) paramere distinctly small (short and/or thin).

132. Ovipositor, each second gonocoxite, number of macrosetae: (0) 2–5; (1) one at midline.

Phylogenetic analysis

A matrix providing the distributions of character states across the 79 terminal taxa is provided (see Appendix S1). The 132 morphological characters for the outgroup taxa are coded from the examination of specimens, with the exception of those denoted with an asterisk * which were taken from the literature (see Table 1). The matrix was prepared using MESQUITE v.3.10 (Maddison and Maddison, 2016) and computed in TNT (Goloboff and Catalano, 2016) with all characters treated as unordered and equally weighted.

Eighteen characters (in parentheses) are parsimony-uninformative; 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. 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 *A. minutus* (Arrowinini). Clade support was assessed by means of standard bootstrap (SB) analysis with frequency differences as implemented in TNT with 500 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 jack-knife (JK) analysis. Additionally, absolute Bremer support (BS) values were estimated from suboptimal trees ≤30 steps longer than the shortest trees. Phylogenetic congruence of each character was assessed by its relative performance in the traditionally used consistency index (CI) and retention index (RI). Although the CI is an appropriate measure of homoplasy (=deviation from hierarchy; Goloboff, 1991), the RI provides evidence of grouping for any given character (Kitching et al., 1998). WINCLADA v.1.00.08 (Nixon, 1999) was used for character mapping.

Results

Characters

Characters were evaluated in terms of their CI and RI (CI/RI) both individually and after their corresponding body parts. Median values of CI and RI for characters from each body part are: head and mouthparts (38 characters; 0.11/0.50); thorax (25 characters; 0.33/0.67); legs (39 characters; 0.33/0.71); abdomen (14 characters; 0.50/0.61); male and female genitalia (12 characters; 0.36/0.63). From a total of 132 characters, 40 of them showed CI and RI values ≥ 0.50, of which 13 characters were novel (*). They were distributed as follows: (i) head and mouthparts (eight characters): 1*, 4*, 8, 16, 25, 26, 35, 39; (ii) thorax (five characters): 42*, 53, 54, 57, 61; (iii) legs (16 characters): 67, 71, 72, 76*, 78*, 80*, 81*, 83*, 89, 90, 91, 94*, 97*, 98*, 99*, 103; (iv) abdomen (seven characters): 106, 107, 112, 113, 115, 116, 124; and (v) male and female genitalia (four characters): 117, 120*, 121, 123. As shown in Fig. 4, characters associated with head, mouthparts and thorax supported basal nodes of Staphylinini as well as the *Paederomimus*-complex and the myrmecophiles (*Belonuchus atticida* and allies, *Ecitophytes* + *Paederallus*) within the Neotropical lineage of Philonthina. Similarly, characters associated with abdomen defined Xanthopygina and Philothalpina as

sampled here but also the *Paederomimus* group 3 clade (*P. difformiceps* + (*P. contractus* + (*P. angusticollis* + *Hesperus novoteutonicus*))). Leg characters supported

nodes across "Staphylinini propria" as sampled here (i.e. representatives of Anisolinina, Philonthina, Philothalpina, Staphylinina, Xanthopygina) as well as
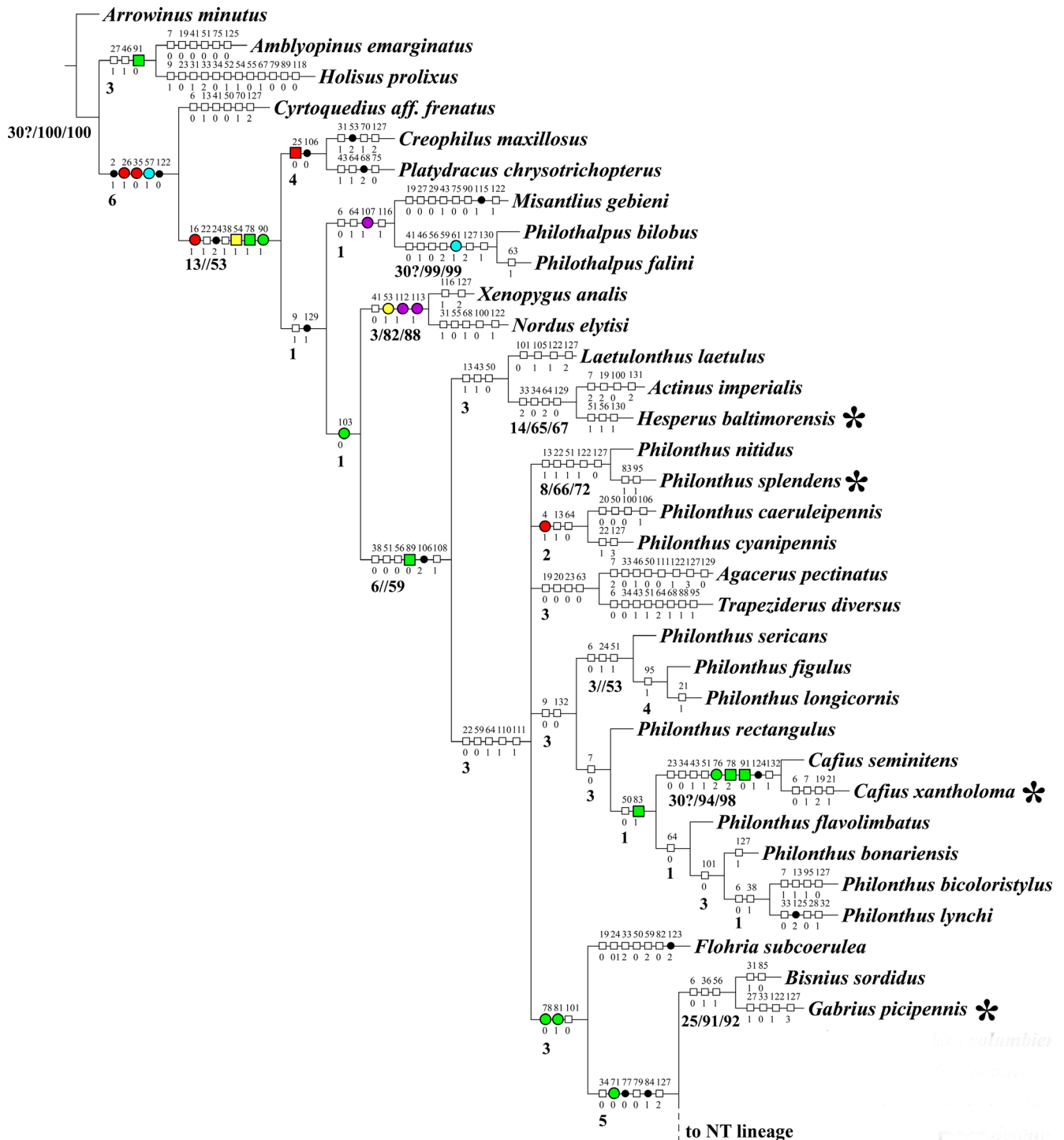

Fig. 4. Strict consensus of the four shortest trees obtained (tree length = 575; consistency index (CI) = 0.240; retention index (RI) = 0.711). Circles: exclusive synapomorphies; squares: nonexclusive synapomorphies. Support values are indicated in bold below the branches as follows: Bremer/Standard Bootstrap/Jack-knife (cut = 50 for resampling support values). Characters with CI and RI ≥ 50 are colour coded: red, head and mouthparts; yellow, prothorax; light blue, mesothorax; green, legs; lilac, abdomen; pink, genitalia. Clades of interest are in bold. * Type species of genera or close relatives.
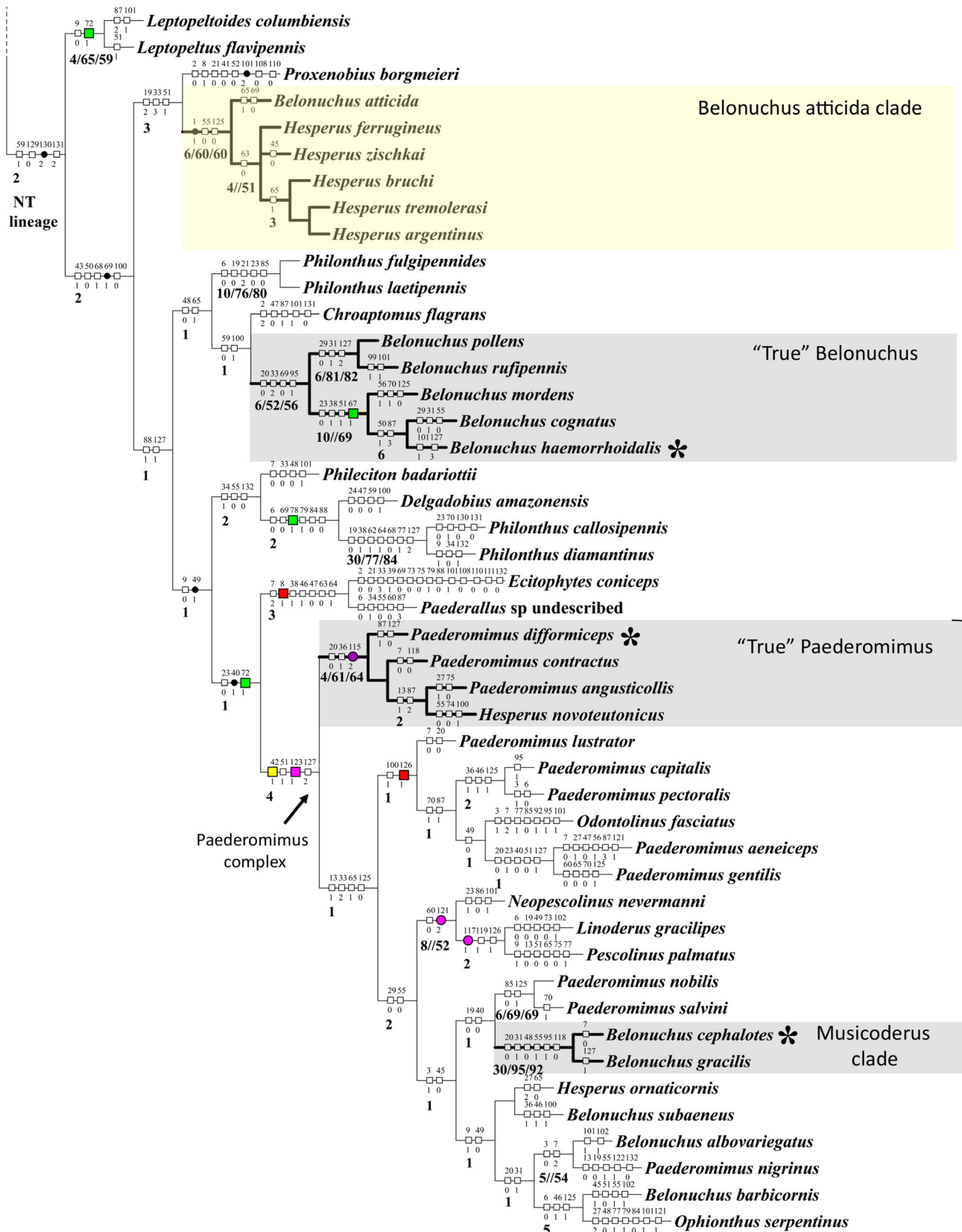
Fig. 4. Continued.

Amblyopinus emarginatus + Holisus prolixus (outgroups). Finally, character 1 from the general body defined one clade (*B. atticida* and allies) with both CI and RI of 1. Eighteen characters were noninformative (CI = RI = 0) and autapomorphic of terminal taxa within Philonthina or one of the outgroups: head and mouthparts (12 characters, eight from SD); thorax (one character); legs (three characters, one from SD); abdomen (two characters).

Phylogenetic reconstruction

Analysis of the equally weighted characters resulted in four MPTs. Each of these trees has 575 steps, a CI of 0.24 and an RI of 0.71. Figure 4 shows the strict consensus of the shortest trees with *Arrowinus* as root, four collapsed nodes and support values (BS/SB/JK) below branches. Table 2 provides details of exclusive and nonexclusive synapomorphies for Philonthina, the Neotropical lineage and its main groups. Clades well supported at the subtribal or suprageneric level were: *Amblyopinus emarginatus* (Amblyopinina) plus *Holisus prolixus* (Hyptiomina), *Cyrtoquedius* aff. *frenatus* (Cyrtoquediina) + all representatives of Staphylinini propria, Staphylinini propria, Philothalpina, Xanthopygina, Philonthina and its Neotropical lineage as sampled here. Within Philonthina, *Laetulonthus* and *Actinus* plus *Hesperus* appear as a well-supported group, sister to the remaining representatives of the subtribe which form a main clade where basal relationships are not resolved. Within this clade and outside the NT lineage, a sister-group relationship between *Agacerus* and *Trapeziderus* as well as that between *Bisnius* and *Gabrius*—each represented by one species—appears well supported. The two species of *Cafius*, however, form a monophylum that is nested in a more inclusive and well-supported group together with eight *Philonthus* species. *Philonthus*, as sampled here (16 species) is not monophyletic. Its representatives, however, form well-supported clades across Philonthina, namely *Ph. nitidus + Ph. splendens*, *Ph. caeruleipennis + Ph. cyanipennis*, *Ph. sericans +* (*Ph. figulus + Ph. longicornis*), *Ph. bonariensi*s + (*Ph. bicoloristylus + Ph. lynchi*), *Ph. fulgipennides + Ph. laetipennis*, *Ph. callosipennis + Ph. diamantinus*, the two latter within the NT lineage.

Regarding the NT lineage, neither *Belonuchus* nor *Paederomimus* (represented by 11 species each) appear as monophyletic groups. The following clades were strongly supported: *Leptopeltus + Leptopeltoides* (one species each), *B. atticida* clade (including five of the seven South American species currently placed in *Hesperus*), *B. haemohrroidalis* clade (with five species sampled, including the type species of *Belonuchus*), *Paederomimus* group 3 clade (including the type species of the genus plus other three species, one of them other South American species of *Hesperus*), *Belonuchus*

cephalotes + B. gracilis (from now on the "*Musicoderus* clade") (Table 2). Other groups with strong support were *Neopescolinus + (Linoderus + Pescolinus)* and *Pae. nobilis + Pae. salvini*. Additionally, a sister-group relationship between *Bisnius + Gabrius* and the NT lineage appears well supported as well as the sister-group relationship of *Flohria subcoerulea* with those two clades. Within the NT lineage, *Proxenobius* appears as sister group to the *B. atticida* clade and *Delgadobius* to *Ph. callosipennis + Ph. diamantinus*. Likewise, *Paederomimus* group 3 appears as sister group to a major clade that includes other *Paederomimus* representatives as well as *Odontolinus*, *Neopescolinus*, *Linoderus*, *Pescolinus*, *Ophionthus*, and species of both *Hesperus* (*H. ornaticornis*) and *Belonuchus* (including the *Musicoderus* clade).

Evolution of morphological traits

Patterns of character evolution in the NT lineage and closely related groups were investigated for those characters that showed CI and RI values ≥ 0.50 and performed as synapomorphies. Of these seven characters, four are novel (see Fig. 5): 1. * Head and pronotum with spine-like setae (*B. atticida* clade, CI and RI = 1); 42. * Prothorax with pronotum deflected beyond spiracles (*B. atticida* clade and *Paederomimus* complex, CI = 0.50 and RI = 0.96); 71. Protibiae cylindrical to slightly broadened apically ((*Bisnius + Gabrius*) + NT lineage, CI and RI = 1); 72. Protibiae with apical excavation (*Leptopeltus + Leptopeltoides* and *Paederomimus* complex, CI = 0.50 and RI = 0.96); 78. * Male protarsomeres 2–3 not bilobed (from the node joining *Flohria* with *Bisnius + Gabrius*, and the NT clade but reverts, CI = 0.50 and RI = 0.93); 81. * Protarsomeres 2–3 with shaft of discal setae on ventral surface subcylindrical, gradually narrowed apically (from the node joining *Flohria* with *Bisnius + Gabrius*, and the NT clade, CI and RI = 1); 115. Abdomen, sternum 3, basal transverse carina descending medially at sides (*Paederomimus* group 3, CI and RI = 1).

Discussion

Monophyly of the NT lineage, early diversification and main clades

Our results here confirm the monophyly of the NT lineage, which was supported by the presence of a distinctly small and asetose paramere fused to the median lobe of aedeagus along its entire length. Additionally, a sister-group relationship between *Bisnius* and *Gabrius* is corroborated. Previous studies (Chani-Posse, 2013; Chani-Posse et al., 2018a) already recovered the NT lineage as a monophylum, but a close relationship of this

Table 2
Synaphomorphies in support of Philonthina, the NT lineage and its main clades

Clades	Synapomorphies
Philonthina	**106(2) Abdomen with protergal glands as more or less invaginated capsules with smaller openings;** 38(0) Head without hypostomal cavity; 51(0) Prosternum without keel; 56(0) Prosternum with pair of macrosetae on basisternum close to the anterior margin; 89(0) Empodial setae absent; 108(1) Abdominal tergum 3 with posterior basal transverse carina
Flohria + ((*Bisnius* + *Gabrius*) + NT lineage)	**78(0) Male protarsomeres 2–3 not bilobed (posterior margin moderately curved to straight)*; 81(1) Protarsomeres 2–3 with shaft of discal setae on ventral surface subcylindrical, gradually narrowed apically*;** 101(0) Metatarsomere 1 (t1) shorter than t5 or at most both tarsomeres subequal (t1: t5 < 1.0)
Bisnius + *Gabrius*	6(0) Antennomere 1 distinctly shorter than antennomeres 2 and 3 combined; 36(1) Male gular sutures joined posteriorly; 56(1) Prosternum with pair of macrosetae on basisternum far from the anterior margin
(*Bisnius* + *Gabrius*) + NT lineage	**71(0) Protibiae cylindrical to slightly broadened apically; 77(0) Protarsomeres 2–3 as long as to longer than wide*; 84(1) Protarsomeres 2–3, ventral surface with marginal setae*;** 34(0) Gular sutures joined before neck; 79(0) Protarsomeres 2–3, ventral surface without discal setae*; 127(2) Male tergum 10 concave medio-apically to apically truncate
NT lineage	**130(2) Paramere of aedeagus fused to median lobe along its (their) entire length, paramere(s) and median lobe hardly distinguishable from each other;** 59(1) Sternopleural (anapleural) suture (sts) distinctly oblique; 129(0) Paramere of aedeagus without sensory peg setae and 131(2) distinctly small
Leptopeltus + *Leptopeltoides*	9(0) Antennomere 6 without apical long setae; 72(1) Protibiae with apical excavation
Belonuchus atticida clade	**1(1) Head and pronotum with spine-like setae*;** 55(0) Prosternum with pair of macrosetae on basisternum; 125(0) Lateral tergal sclerites 9 (styli) dorsoventrally flattened
Philonthus fulgipennides + *Philonthus laetipennis*	6(0) Antennomere 1 distinctly shorter than antennomeres 2 and 3 combined; 19(0) Head with postgenal ridge (pgr) developed ventrally but not joining ventral basal ridge (vbr) medially; 21(2) Head with postmandibular ridge (pmr) separate from mandibular base (mb) and 23(0) without infraorbital ridge; 85(0) Protarsomeres 2–3, ventral surface with marginal setae distributed posteriad*
Belonuchus haemohrroidalis clade	20(0) Head without postmandibular ridge; 33(2) Maxillary palpus, palpomere 4 (apical) subcylindrical "rod-like", parallel-sided at most of its length, apex subtruncate; 69(0) Profemora without longitudinal patch of dense setae lateroventrally*; 95(1) Male metafemora with spines
Philonthus callosipennis + *Philonthus diamantinus*	19(0) Head with postgenal ridge (pgr) developed ventrally but not joining ventral basal ridge (vbr) medially; 38(1) Head with hypostomal cavity; 62(1) Mesothorax with mesoventral longitudinal ridge*; 64(1) Mesothorax with apex of intercoxal process narrowly pointed forming sharp (acute) angle; 68(0) Profemora with setae conspicuosuly denser ventrally*; 77(1) Protarsomeres 2–3 distinctly wider than long*; 127(2) Male tergum 10 concave medio-apically to apically truncate
Paederomimus complex	42(1) Prothorax, pronotum deflected and visible beyond spiracles* (in ventral view); 51(1) Prosternum with keel; 123(1) Male sternum 9 with emargination at distal portion subangulate to concave; 127(2) Male tergum 10 concave medio-apically to apically truncate
Paederomimus group 3	**115(2) Abdominal sternum 3 with basal transverse carina descending medially at sides;** 20(0) Head without postmandibular ridge; 36(1) Male gular sutures joined posteriorly
Musicoderus clade (*Belonuchus cephalotes* + *Belonuchus gracilis*)	20(0) Head without postmandibular ridge; 31(1) Maxillary palpomere 4 (p4, apical) distinctly shorter than palpomere 2; 48(0) prosternum with transverse carina on basisternum rudimentary to uncomplete; 55(1) Prosternum with pair of macrosetae on basisternum; 95(1) Male metafemora with spines; 118(0) Male sternum 8 without medial emargination on apical margin

Exclusive synapomorphies in bold. *, novel character.

clade to *Bisnius* + *Gabrius* was supported only by molecular data (Chani-Posse et al., 2018a). One of the novel results of our study is the position of the mono-typic and relictual genus *Flohria* Sharp (currently known from southern North America to Costa Rica), as sister to (*Bisnius* + *Gabrius*) and the NT lineage, which is likewise supported by novel characters. This place-ment differs from that recovered in Chani-Posse (2013) where *Flohria* shows a rather basal position as sister group to Philonthina, supported by plesiomorphic char-acters. An alternative hypothesis for the position of *Flohria* proposes a close relationship to a terminal clade of Old World Philonthina that includes the genus

Agacerus Fauvel (Chani-Posse and Newton, 2015). Our study rejects those earlier hypotheses and provides an alternative scenario for the evolution of *Flohria* and its sister-group relationships.

Distributions of most Philonthina are still inade-quately known and prevent conclusions at this stage about the early diversification of the NT lineage. The first cladogenetic events in our analysis seem to reflect (at least in part) the pattern described by Morrone (2014a) in his general area cladogram. The first branching event within the NT lineage occurs between two Andean genera (*Leptopeltus* + *Leptopeltoides*) and a main clade composed of the rest of NT
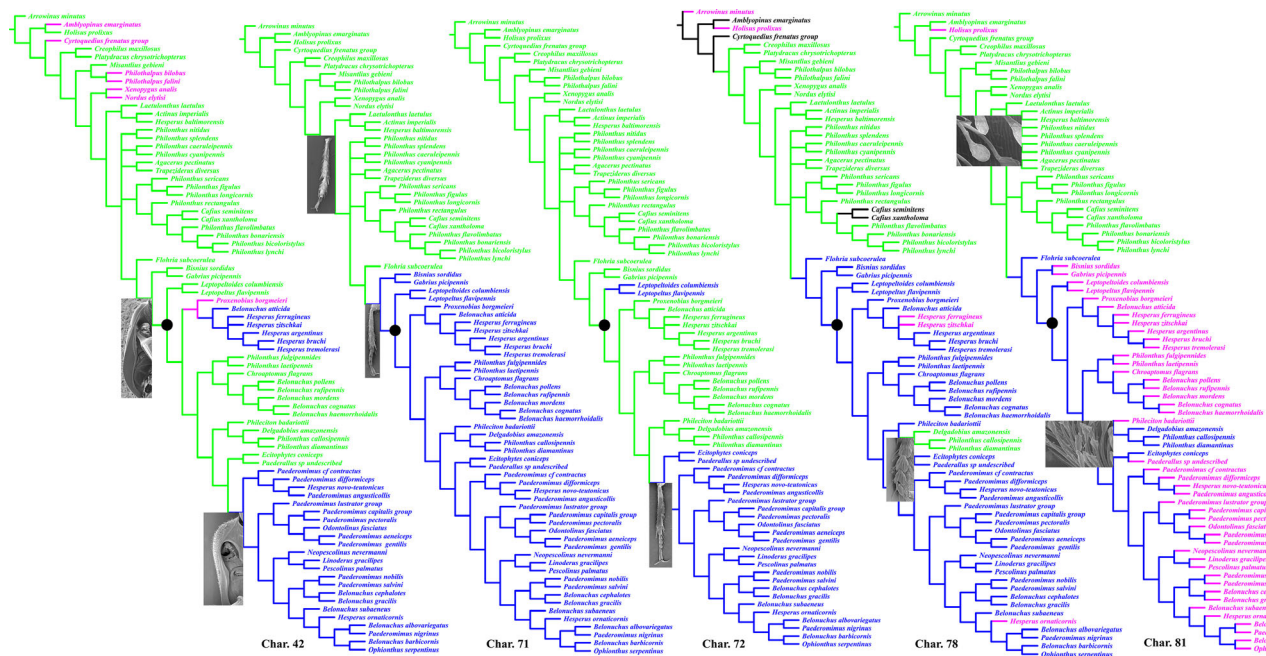
Fig. 5. Strict consensus showing patterns of evolution for most relevant characters (i.e. synapomorphies with both consistency index (CI) and retention index (RI) ≥ 50, excepting those from characters 1 and 115 which are self-explanatory). Black circle: NT lineage. [Colour figure can be viewed at wileyonlinelibrary.com]

representatives, which in turn diverges into two sub-clades: one composed of *Proxenobius* and the *B. atticida* clade, the latter showing a clear "Chacoan" affiliation, and another one represented mostly by elements from the indistinctly named "Amazonian subregion" (Morrone, 2014a: fig. 5) or "Brazilian subregion" (Morrone, 2014b: fig. 12) that includes Mesoamerica and the Andes above 26°S latitude but not the Andean highlands north of this latitude. The genera *Leptopeltus* and *Leptopeltoides* are known from altitudes mainly >3000 m above sea level (a.s.l.) in the Andean Paramo and Puna provinces of the South American Transition zone (Chani-Posse and Asenjo, 2013). Other representatives of NT Philonthina studied herein are not recorded from elevations >3000 m a.s.l. (Chani-Posse et al., 2018b). So a vicariance event between those two genera and the rest of NT representatives seems plausible. Similarly, but on a rather latitudinal scale, is our hypothesis about a cladogenetic event that separates the main clade into the "Amazonian" and the "Chacoan" subclades (with the exception of *Proxenobius*, as we discuss below). The geological history of the Neotropical Region may serve here as external criteria to date these first cladogenetic events in the NT lineage which may be explained by the uplift of the Andes and the formation of a wide epicontinental sea during the Miocene (23–7 Ma; Morrone, 2014a). Although the "Amazonian" subclade is a heterogeneous group of taxa that includes at least five monophyletic assemblages or group of species at

present, the "Chacoan" clade + *Proxenobius* is a compact group of myrmecophilous species composed of *Proxenobius* (associated with the army-ant genus *Eciton* Latreille) and the *B. atticida* or "Chacoan" clade (its species recorded in association with the leaf-cutter genera *Atta* Fabricius and *Acromyrmex* Mayr). The sister-group relationship between *Proxenobius* (known from Central to South America in the western slopes of the Andes at around 300 m a.s.l.) and the *B. atticida* clade, as well as the resulting position of *Ecitophytes coniceps* (another army-ant associated genus from the Chacoan subregion) within the "Amazonian" clade do not only imply later dispersion events between areas, but also independent origins for the *Eciton*-associated myrmecophiles in the NT lineage. The evolution of myrmecophily and/or termitophily in Philonthina has not been explored, and it is beyond the scope of the current study as it would require including further representatives from these highly adapted taxa (i.e. *Xenobius* Borgmeier, *Pridonius* Blackwelder). Recent evidence from our group of study (Chani-Posse et al., 2018a: the *Holisus* case; Maruyama and Parker, 2017) supports a molecular based approach for the study of such groups to prevent biases in the assessment of morphological characters susceptible to convergence. A well-supported group of philonthine myrmecophiles including *Proxenobius* and representatives of other related genera (e.g. *Pridonius*) was found by Chani-Posse et al. (2018a) in their combined phylogeny, but neither

Ecitophytes nor members of the *B. atticida* clade were considered there. On the one hand, the strong support exhibited by *Proxenobius* and its allies in that previous work allow us to hypothesize about their potential placement together with *Proxenobius* in our study. The *B. atticida* clade, on the other, is composed of five from the six South American species currently placed in *Hesperus* (Chani-Posse et al., 2018b). As demonstrated here, neither these species nor the remaining South American "*Hesperus*" species (*H. novoteutonicus* from Brazil) or *H. ornaticornis* (from Costa Rica) belong to *Hesperus*. So for the time being, we can conclude that there is no "true" *Hesperus* in South America. The only *Hesperus* species in the Neotropics (*H. fasciatus* and *H. pollens*) have likely come from the north and have only dispersed with higher elevation oak-pine forests (A. Brunke, pers. comm.)

The "Amazonian" subclade comprises at least five natural groups whose limits were chosen here based on strongly supported nodes: (i) *Ph. fulgipennides* + *Ph. laetipennis*, a clade of "false *Philonthus*" species which also appeared to be closely related to and forming a monophylum with other "false *Belonuchus*" species in Chani-Posse et al. (2018a); (ii) the *B. haemohrroidalis* clade or "true *Belonuchus*" that fits the current concept of the genus (Smetana, 1995; Chani-Posse et al., 2018a, 2018b); (iii) *Ph. callosipennis* + *Ph. diamantinus*, one of the most enigmatic clades of the NT lineage due to their widened protarsomeres with discal setae on the ventral side—the so-called "tenent" or "adhesive" setae of previous authors (e.g. Stork, 1980; Gnaspini et al., 2017a, 2017b); (iv) the *Paederomimus* group 3, here resolved as the clade containing the type species of the genus; and (v) the *Musicoderus* clade, which appears well supported and phylogenetically distant from the "true *Belonuchus*", and was recovered within a more inclusive clade, which is referred to here as the "*Paederomimus* complex". As already acknowledged, we are aware of restrictions imposed by our taxon sampling, so we are cautious about proposing broader limits or sister-group relationships for any of these groups other than those already discussed above. Notwithstanding this, our morphology-based phylogeny improves the current knowledge of taxonomic limits within the NT lineage as it provides new insights into the diversification of this group and its so-called "*Belonuchus* complex" of Chani-Posse et al. (2018a). The "*Belonuchus* complex", found by the previous study, has been revealed here as a polyphyletic assemblage, that places the "true *Belonuchus*" outside of and far from the "*Paederomimus* complex", a major clade that includes not only all the *Paederomimus* representatives (including its type species) but also those *Belonuchus* species formerly assigned to *Musicoderus* (including its type species).

Belonuchus and the *Paederomimus*-complex

The genus *Belonuchus* comprises at present 190 spp. from the Old and New World tropics (Newton, 2019). However, there is broad consensus on restricting the systematic validity of the genus to the 171 New World species (including *B. haemohrroidalis*, the type species) as the remaining 19 Old World species belong to a different lineage, far from the NT lineage (Chani-Posse et al., 2018a). Although this knowledge represents a stepping stone toward a natural classification of this megadiverse genus, the majority of New World species do not constitute a monophyletic assemblage within the NT lineage either. Until the present study, only the *B. haemohrroidalis* clade was available as a taxonomic framework to begin revisionary studies on the group. Likewise, the monophyly of *Paederomimus* (58 spp.), the most diverse of the endemic Neotropical genera, has been doubtful even from the time of its original description. In Chani-Posse et al. (2018a), representatives of both genera (including the *B. haemohrroidalis* clade) appear together in the *Belonuchus*-complex. So this more inclusive group became the main focus to start exploring generic limits in the NT lineage. Our current results do not only account for the *B. haemohrroidalis* clade (i.e. the "true *Belonuchus*") but also for two other well-supported clades, each of which contains its type species: the *Paederomimus* group 3 (or from now on the "true *Paederomimus*"), originally determined by Sharp (1885) as the group for which the name should be eventually restricted, and the *Musicoderus* clade, represented by the two species originally described in this genus by Sharp (1885). A more inclusive group containing those two clades together with the other "false *Belonuchus*" and *Paederomimus* representatives as well as those from five NT endemic genera (*Odontolinus, Neopescolinus, Linoderus, Pescolinus, Ophionthus*) is proposed here as the next main NT clade where generic limits should be further explored.

Improving efficiency of future taxonomic efforts: Paederomimus and Musicoderus

Our study rejects the monophyly of *Paederomimus*. Although its representatives appear inside the "*Paederomimus* complex", this clade also comprises taxa from other NT endemic genera whose distinctness and monophyly have been recently supported (Chani-Posse, 2014b; Chani-Posse and Solodovnikov, 2017). Such is the case of *Odontolinus* which appear together with false *Paederomimus* species, followed by *Neopescolinus, Linoderus* and *Pescolinus* whose close relationships are well supported here. However, *H. novoteutonicus* (from Brazil), the remaining South American "*Hesperus*" species, actually belongs to

Paederomimus. Although the combined phylogeny of Chani-Posse et al. (2018a) did not find a monophyletic *Paederomimus* either, they actually recovered six of their seven *Paederomimus* representatives in a well-supported group. However, they did not include the type species (*P. difformiceps*) in their study. Here, we include four of the seven *Paederomimus* species considered by that previous study as well as the other eight species of *Paederomimus*, including its type species. Among this latter group of taxa, three form the "true *Paederomimus*" clade apart from the remaining representatives which reveal otherwise similar relationships to those shown by Chani-Posse et al. (2018a). Lastly *Musicoderus*, currently a junior synonym of *Belonuchus*, is nested within the *Paederomimus* complex but not closely related to the true *Paederomimus* and far from the true *Belonuchus*. The clade containing *Musicoderus* is the most heterogeneous among those of the NT lineage as it includes representatives of *Belonuchus, Paederomimus, Hesperus* and *Ophionthus*. With the exception of *Ophionthus*, a monotypic genus only known from its male holotype, none of these species fits current phylogenetic concepts of the genera to which they are assigned. However, we will avoid the temptation to redefine *Musicoderus* to include all members of this clade at the moment. Taking into account the amount of variability that this clade displays, we prefer to be cautious and take the more conservative approach of resurrecting *Musicoderus* for its two originally recognized species and proposing those *Musicoderus*-like species as candidates to be included in future revisionary studies of the genus together with the other 16 species that were assigned at different times to *Musicoderus* (Chani-Posse et al., 2018b).

A new dress from old clothes: emergent novelties in the NT lineage

A generalized evolutionary trend toward a more elongate body, with a rather convex pronotum together with a reduction of head sutures and ridges as well as the presence of "non dilated" protarsi provided the most typical habitus among the NT Philonthina (Chani-Posse, 2013). Additionally, although only molecular data previously supported a sister-group relationship between the NT lineage and *Bisnius + Gabrius*, the presence of narrow protarsomeres was also common to both groups (Chani-Posse et al., 2018a). However, there were some issues: groups that look truly neotropical (i.e. having many of the characters described above) showed a mosaic of character states. Some of them have been traditionally associated with "Holarctic" taxa but are complex enough to be reassessed, especially those of characters from the fore and hind legs (i.e. profemora, protibiae, protarsomeres and metafemora). We noticed that such characters historically had been overlooked in

the classification: during an early stage by Curtis (1829) and his followers (the expanded *Philonthus* concept) and later by those who adopted generic limits mostly based on the Holarctic fauna. We noticed, on the one hand, that the protarsal condition was a rather conservative character at the generic level in the current classification of Staphylinini (Chani-Posse et al., 2018b). The presence of spines on pro- and/or metafemora, on the other hand, appeared highly homoplastic and/or variable within a given genus or between sexes of the same species and as such, not always considered of value (Sharp, 1885).

Herein, reassessment of characters associated with traditional morphology-based systematics of Philonthina provided new sources of information to reconstruct the evolutionary history of the subtribe in the NT region. One third of the characters used in our analysis were novel and informative across Philonthina, particularly at the generic level. Among them, most of those with high CI and RI scores are associated with the shape and chaetotaxy of protibiae and protarsomeres. One novel character derived from the head (i.e. relative length of maxillary palpomeres 2 and 4) was among those supporting the monophyly of *Musicoderus*. Sexually dimorphic characters, by contrast, exhibited limited phylogenetic signal and only at shallower levels (i.e. *Ph. cyanipennis + Ph. caeruleipennis, B. haemohrroidalis + B. cognatus*). Finally, characters derived from the integration of pronotum and prosternum (i.e. degree of deflection of pronotum, development of sternacostal ridge related to superior line of hypomeron) demonstrated once again their value to define evolutionary trends and groups within the NT lineage.

Not only did we recover new groupings within the NT lineage through character reassessment, but we also identified possible causes of the previous artificial classification. Novel characters associated with the metafemora previously acted as the source of earlier confusions among *Trapeziderus, Belonuchus, Musicoderus* and *Odontolinus*, as well as some species of *Philonthus* and *Paederomimus* that bear spinose metafemora (Sharp, 1885). The presence of metafemoral spines per se does not imply a single origin as they vary both in shape and distribution. Nonetheless, strong phenetic similarity of these nonhomologous characters was confirmed in two independent lineages of Philonthina (*Trapeziderus* and *Belonuchus*). We conclude that these characters may well deserve to be included in future comparative studies as clear cases of parallelism or even as "deep homologies" within Staphylinini. As for other cases involving the independent occurrence of a given character with strong phylogenetic signal, limitations on our taxon sampling should be acknowledged: for the protibial shape (e.g. the Oriental genus *Eccoptolonthus* Bernhauer also bears a rather cylindrical protibia) and the presence

of an apical excavation (which appears twice in the NT lineage). Finally, none of the *Hesperus* species cited from South America fitted into the current *Hesperus* concept (Smetana, 1995) or the so called *Hesperus*-complex (Chani-Posse et al., 2018a). These "*Hesperus*" species were mis-classified as a result of convergence (Bernhauer, 1921: 169) and "error in coding" (Chani-Posse, 2013). Given the potential exhibited by our exploration of morphological characters in NT Philonthina, we do believe that for the amount of NT fauna not yet explored, there is a lot of morphological information left to be built and analysed in future phylogenetic and comparative evolutionary studies.

Taxonomic changes

Musicoderus Sharp, 1885, **stat.res**

Type species. *Musicoderus cephalotes* Sharp, fixed by subsequent designation by Lucas, 1920: 425.

Musicoderus Sharp, 1885: 455; Bernhauer and Schubert, 1914: 369 (world catalog; Blackwelder, 1943: 420 (synonym of *Belonuchus*; type species: *cephalotes*); Blackwelder, 1952: 251 (type species); Smetana, 1995: 722 (synonym of *Belonuchus*); Herman, 2001: 2518 (synonym of *Belonuchus*); Chani-Posse et al., 2018b: 9 (checklist, synonym of *Belonuchus*).

Species included. Two species: *M. cephalotes* Sharp and *M. gracilis* Sharp.

Diagnosis. *Musicoderus* can be recognized by the following combination of characters: head without postmandibular ridge, maxillary palpomere 4 distinctly shorter than palpomere 2, prosternum with pair of macrosetae and transverse carina on basisternum rudimentary to incomplete, posterior margin of male metafemora with spines on its basal half, and sternum 8 straight in both sexes, without medial emargination on apical margin.

Paederomimus novoteutonicus (Wendeler, 1956), **comb.n**

Hesperus novoteutonicus Wendeler, 1956: 232; Asenjo et al., 2013: 313 (distribution within Brazil); Chani-Posse et al., 2018b: 43 (checklist, not "*Hesperus*").

Conclusions and next steps

Our morphology-based phylogeny provides further pathways to understand and reconstruct the evolutionary history of the NT lineage of Philonthina, a megadiverse group of Staphylinini whose generic limits have been biased by an artificial classification. For our group of study, the adoption and practice of Holarctic-based concepts eventually led taxonomists to premature and/or biased conclusions regarding the potential of morphological traits for further systematics studies. Morphological characters traditionally used in the classification of Staphylinini demonstrated their value at the suprageneric level. As for the generic level, structures already recognized as good sources of phylogenetic signal (i.e. head ridges and sutures, prothorax, protarsi) continued to provide most of the synapomorphies at the generic level. Although the monophyly of Philonthina and its NT lineage was confirmed once again (Chani-Posse et al., 2018a), at least seven well-supported groups of NT taxa were revealed after the inclusion of novel characters generated from a reassessment of their traditional homology. Our current reconstruction seems to suggest two basal diversification events within the NT lineage, the first associated with the uplift of the Andes and the second to the formation of an epicontinental sea. Both of them with their most conspicuous impacts during the Miocene (Morrone, 2014a). These first potential vicariance events would imply an array of different landscapes within which the evolutionary history of the NT Philonthina could have taken place: Andes, Chaco and Amazonia. Within our current framework, the "Amazonian" subclade would have experienced the main radiation, containing five of the seven natural NT groups shown herein. Among them, the *B. haemohrroidalis* clade appears once again well supported (Chani-Posse et al., 2018a) but far from the true *Paederomimus* and the *Musicoderus* clade, each of which is revealed with strong support. This new arrangement represents a significant advancement from which to direct current and future taxonomic efforts. Additionally, the six species of *Hesperus* in South America were confirmed as "non *Hesperus*" and members of the NT lineage, five of them within a "Chacoan" *B. atticida* subclade. We conclude that future efforts toward the taxonomic understanding of the NT lineage should encompass revisionary studies of the *B. haemohrroidalis* clade and the *Paederomimus* complex within which the "true *Paederomimus*" and the "*Musicoderus* clade" represent two different lineages whose limits are to be further defined. The sequence and occurrence of the biogeographical events mentioned above can only be tested through a time-calibrated molecular phylogeny. We do not deny—but rather support—the value of molecular-based studies to guide further taxonomic endeavours. Notwithstanding this, we do believe that for the breadth of NT fauna as yet not explored, there is much information left to be redefined and/or newly acquired from morphology as our most immediate and primary source of assessment.

Acknowledgements

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Morphological matrix (Mesquite).