Do fly parasites of bats and their hosts coevolve? Speciation in *Trichobius phyllostomae* group (Diptera, Streblidae) and their hosts (Chiroptera, Phyllostomidae) suggests that they do not

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ABSTRACT. Do fly parasites of bats and their hosts coevolve? Speciation in *Trichobius phyllostomae* group (Diptera, Strebilidae) and their hosts (Chiroptera, Phyllostomidae) suggests that they do not. We examined whether, like many parasite-host systems of coevolution, a group of obligate parasitic bat flies (*Trichobius phyllostomae* Kessel and related species) cospeciate with their hosts. We first did a cladistic analysis of the *T. phyllostomae* group and combined that analysis with a phylogenetic hypothesis from the literature for the Stenodermatinae bats. The cladistic analysis included, as outgroups, one species from each morphological group and complex of *Trichobius* Gervais, and one species from the following genera: *Paratrichobius* Miranda-Ribeiro, *Megistopoda* Macquart, *Megistapophysys* Dick & Wenzel, *Neotrichobius* Wenzel & Aitken, *Speiseria* Kessel and *Strebla* Wiedemann. The cladogram was rooted with a species of *Strebla* in the subfamily Streblinae. One cladogram was obtained and which found *Trichobius* to be polyphyletic. The phylogenetic hypothesis as follows: (*Paratrichobius,* (*Neotrichobius,* (*Megistopoda*, *Megistapophysis*)))) is the sister-group of the *phyllostomae* group and the following relationships within the ingroup, (((*T. vampyropis* Wenzel, *Trichobius* sp. 2) ((*T. hispidus* Wenzel, *T. petersoni* Wenzel) ((*Trichobius* sp. 1 (*T. phyllostomae*, *T. brennani* Wenzel))))). When we compared phylogenies through historical association analyses, cospeciation was uncommon, while host-switching was more common and better explained the association between the *phyllostomae* group and their bat hosts.

KEYWORDS. Bat fly; cospeciation; macroevolutionary events; Trichobiinae; *Sturnira*.

RESUMO. Moscas parasitas de morcegos e seus hospedeiros co-evoluem? Especiação do grupo *Trichobius phyllostomae* (Diptera, Streblidae) e seus hospedeiros (Chiroptera, Phyllostomidae) sugere que eles não fazem. Nós examinamos, como em muitos sistemas parasito-hospedeiro de coevolução, se um grupo de moscas parasitas obrigatórias de morcegos (*Trichobius phyllostomae* Kessel e espécies relacionadas) coespecia com seus hospedeiros. Primeiro, nós fizemos uma análise cladística do grupo *T. phyllostomae* e combinamos a análise com a hipótese filogenética da literatura para os morcegos da subfamília Stenodermatinae. A análise cladística incluiu, como grupo-externo, uma espécie de cada grupo morfológico de *Trichobius* Gervais, e uma espécie dos seguintes gêneros: *Paratrichobius* Miranda-Ribeiro, *Megistopoda* Macquart, *Megistapophysys* Dick & Wenzel, *Neotrichobius* Wenzel & Aitken, *Speiseria* Kessel e *Strebla* Wiedemann. O cladograma foi enraizado com a espécie de *Strebla* da subfamília Streblinae. Um cladograma foi obtido e no qual encontramos *Trichobius* como polifilético. A hipótese filogenética a seguir: (*Paratrichobius,* (*Neotrichobius,* (*Megistopoda*, *Megistapophysis*)))) é grupo-irmão do grupo *phyllostomae* e a relação dentro do grupo-interno a seguir, (((*T. vampyropis* Wenzel, *Trichobius* sp. 2) ((*T. hispidus* Wenzel, *T. petersoni* Wenzel) ((*Trichobius* sp. 1 (*T. phyllostomae*, *T. brennani* Wenzel))))). Quando comparamos as filogenias através de análises de associação histórica, co-especiação foi pouco comum, enquanto colonização de um novo hospedeiro foi mais comum e explicou melhor a associação netre o grupo *phyllostomae* e seus hospedeiros.

PALAVRAS-CHAVE. Dípteros ectoparasitos de morcegos; co-especiação; eventos macroevolucionários; Trichobiinae; *Sturnira.*

The history of host-parasite associations is often studied through reconciliation analysis and similar methods (Page 2003). For example, the Phthiraptera often have been used in this type of study because the entire lice life cycle is on their host and so their host specificity and alpha-taxonomy are very well examined and known (Table I). Although Phthiraptera is a good model system, there are some other groups that have the same potential to be a model system. Widening host-parasite analysis to include candidate groups, such as Streblidae, will enhance our knowledge of the coevolutionay process by testing hypothesis in a broad context. Of such groups, a few studies examine historical associations among fleas and ticks (parasites with a free life stage) and their hosts (Cumming 2000; Krasnov & Shenbrot 2002, respectively, Table I) and no one has yet been done in bat fly-bat system.

Bat flies (Diptera, Nycteribiidae and Streblidae) are blood-feeding, obligate ectoparasites (Dick & Miller 2010; Graciolli 2010). Of these, the streblid bat flies are mostly tropical and more species are found in the New World where their main hosts are bats in the family Phyllostomidae. In the fly family Streblidae, the American genus *Trichobius* Gervais, 1844 has the greatest number of species and subspecies. The 68 species and subspecies of *Trichobius* were divided into morphological groups and complexes by Wenzel *et al.* (1966) and Wenzel (1976) using mostly male and female post-abdomen characteristics for their classification, and in which each group or complex was monophyletic although the genus was not. This perspective places the *phyllostomae* group as a sister-group of the genera *Paratrichobius* Costa-Lima, 1921, *Megistopoda* Coquillett, 1899 and *Neotrichobius* Wenzel & Aitken, 1966 (Fig. 1).

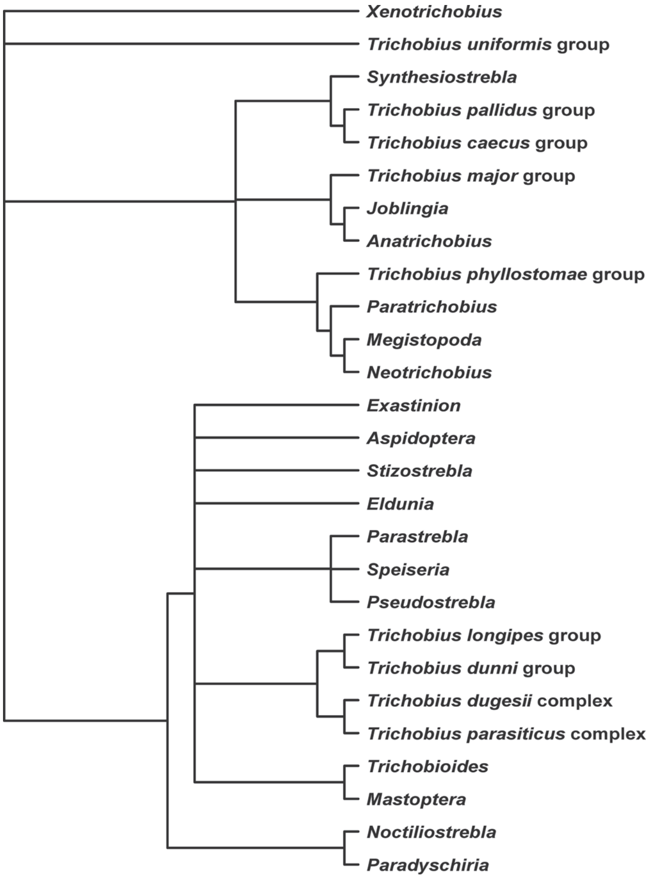


Fig. 1. Diagram showing a tentative grouping of Trichobiinae based on Wenzel *et al.* (1966) and Wenzel (1976).

A recent phylogenetic analysis of bat flies using molecular data supported the polyphyly of *Trichobius*, although the species of the *dunni*, *pallidus*, *phyllostomae* and *uniformis* groups and other streblid genera, with exception of *Strebla* Wiedemann, 1824 were not included in that analysis (Dittmar *et al.* 2006). In opposition to polyphyly of *Trichobius*, Jobling (1938) and Guerrero (1997) considered the genus a natural group and Guerrero (1997) further suggested that each morphological group within *Trichobius* should be considered as a subgenus. In regards to the *phyllostomae* group, *T. vampyropis* Wenzel, 1966 was related to *T. hispidus* Wenzel, 1976 while *T. petersoni* Wenzel, 1976 and *T. phyllostomae* Kessel, 1925 were closer to *T. brennani* Wenzel, 1966 (Wenzel 1976).

The five species of the *phyllostomae* group (not including two undescribed species) have been found above 800 meters elevation in Central America and northern South America and southern Brazil. These species are host-specific parasites of bats in the genera *Sturnira* Gray, 1842 and *Platyrrhinus* Saussure, 1860 (Fig. 2) (Wenzel *et al.* 1966; Wenzel 1976), both in the subfamily Stenodermatinae (Phyllostomidae). In that subfamily there are 15 species in two subgenera (Simmons 2005), all of which are frugivorous (Molinari & Soriano 1987; Gannon *et al.* 1989; Giannini 1999). Most species roost in the forest canopy or in hollow trees, while one species, *Sturnira bidens* (Thomas, 1915) uses caves (Molinari & Soriano 1987). Species of *Sturnira* may often be sympatric and syntopic (Tamsitt & Häuser 1985; Soriano & Molinari 1987; Gannon *et al.* 1989; Pacheco & Patterson 1992; Giannini 1999). The genus *Platyrrhinus* includes 14 species restricted to the Neotropics (Velazco 2005). All species are frugivorous and roost in the canopy or hollow trees (Novak 1994).

Here, we develop a phylogenetic hypothesis for the *Trichobius phyllostomae* group and examine their associations with their hosts using a historical perspective by means of reconciliation analysis.

MATERIAL AND METHODS

Host phylogeny. We used the phylogenetic hypotheses for the genera of stenodermatine bats of Wetterer *et al.* (2000) as a template. The phylogenetic hypothesis of *Sturnira* (Villalobos & Valerio 2002) and *Platyrrhinus* (Velazco 2005) were merge to the template phylogeny to improve historical scenarios.

Parasite (*phyllostomae* group) phylogeny. To achieve a parsimonious phylogenetic hypothesis for *Trichobius* (and thereby allow for the possibility of paraphyly) to associate with the bat flies, we included as outgroups one species from each morphological group and complex of *Trichobius*, including *Trichobius parasiticus* Gervais, 1844 the type species of the genus, and one species of the genera *Paratrichobius*, *Megistopoda*, *Megistapophysis* Dick & Wenzel, 2006, *Neotrichobius*, and *Speiseria* Kessel, 1925. To root the cladogram we used a species of *Strebla* Wiedemann, 1844 in the subfamily Streblinae (Appendix 1). Nexus 0.5.0 (Page 2001) was used for the morphological data matrix, which comprised 44 characters (19 binary, 25 multistate) of which one was polymorphic.

Phylogenetic analysis used NONA (Goloboff 1998) and Winclada ver. 1.00.08 (Nixon 2002). For tree reconstruction, all characters were equally weighted and unordered (non additive) with the following commands: Tree- bisection-reconnection (TBR) branch-swapping with 10,000 heuristic random addition replicates. Bootstrapping with 1,000 replicates with random addition with TBR branch-swapping was used to examine the resulting tree. To character optimization we used Acctran.

The specimens examined in this study were lent by Coleção de Entomologia Padre Jesus Santiago Moure, Curitiba, Brasil (DZUP); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil (MZSP); Field Museum of Natural History (FMNH), Chicago, USA.

Cophylogenetic Analyses. To compare host and parasite trees we used a method reconciliation in which an event-based concept is used where each event is assigned a cost and costs are minimized in the program TARZAN 0.9 (Merke

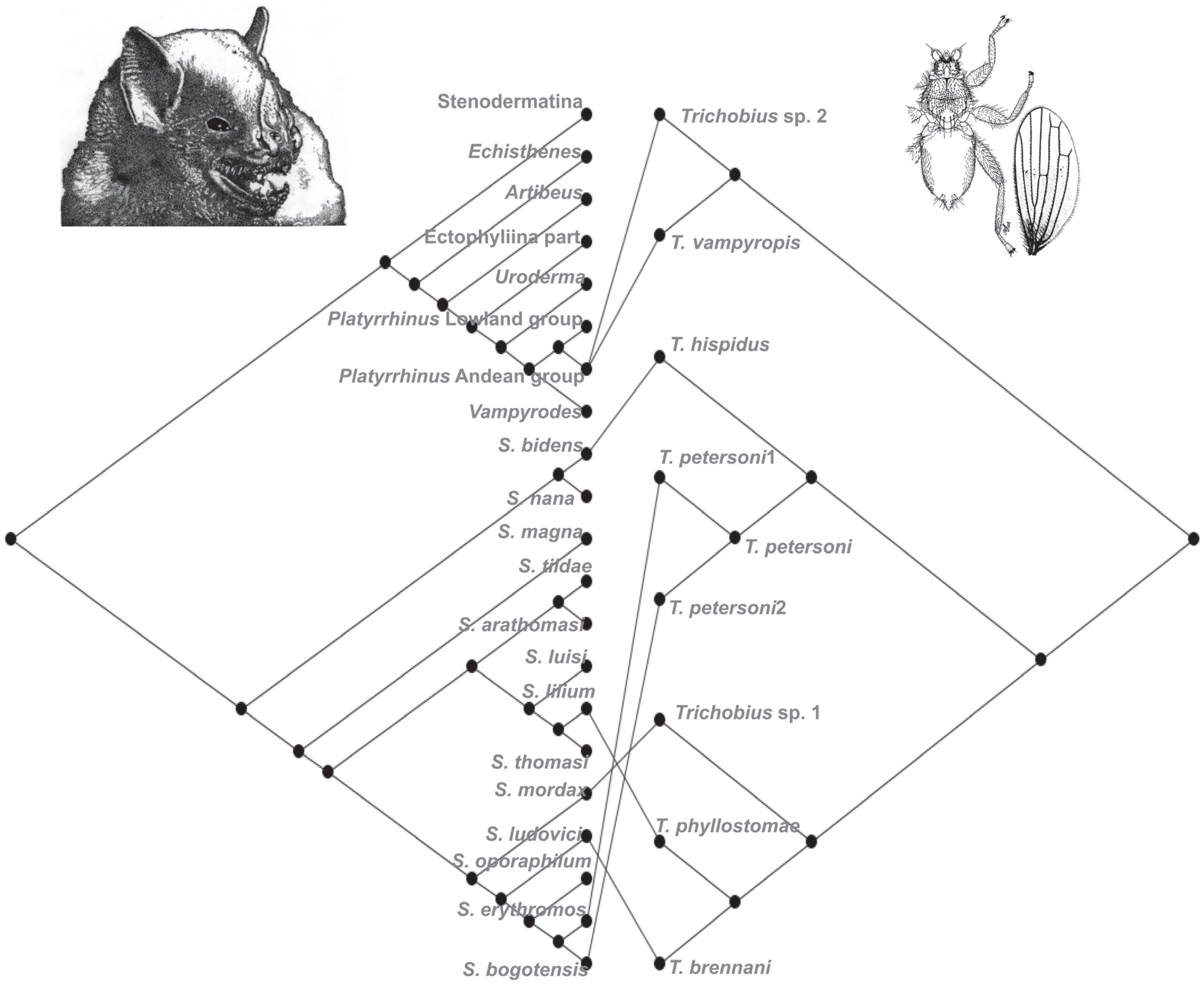


Fig. 2. Pattern of stenodermatine bats and *Trichobius phyllostomae* association.

& Middendorf 2005). The events that are used by TARZAN are cospeciations, duplications, sortings, extinctions, and (host) switching. The cost assignment used for each cophylogentic event was: cospeciation = 2, duplication = 2, sorting = 1, switch = 2. TARZAN reconciliation analysis does not allowed for multi-host associations.

To avoid "noise" in our analysis we considered two terminal branches for the species of *Platyrrhinus* (lowland and andean) following Velazco (2005), because *Trichobius vampyropis* and *Trichobius* sp. 2 are each associated with > 1 species of Andean *Platyrrhinus*. *Trichobius petersoni* is associated with two species of *Sturnira*. We considered *T. petersoni* as two populations (*T. petersoni* 1 and *T. petersoni* 2), each with its own associated host species.

RESULTS

Phylogeny of *phyllostomae* group. One most parsimonious tree was found (Fig. 3), with 144 steps, consistence index 65 and retention index 77. Eight out of 21 branches in this tree were recovered in > 70% of the bootstrap replicates (Fig. 4). The genus *Trichobius* is not a monophyletic group, but rather is separated into three clades (Fig. 3). The first clade is formed by *T. tiptoni* Wenzel, 1976, *T. parasiticus* Gervais, 1844 (*dugesii* group), *T. lonchophyllae* Wenzel, 1966 (*uniformis* group), *T. longipes* (Rudow, 1871) (*longipes* group), and *T. jubatus* Wenzel, 1976 (*dunni* group) (Fig. 3). The second clade includes *T. major* Coquillett, 1899 (*major* group), *T. galei* Wenzel, 1966 (*caecus* group), *T. pallidus* (Curran, 1934) (*pallidus* group). The remaining species of *phyllostomae* group are the sister-group of *Paratrichobius longicrus* (Miranda-Ribeiro, 1907), *Megistopoda aranea* (Coquillett, 1899), *Megistapophysis mordax* Wenzel & Dick, 2006, and *Neotrichobius delicatus* (Machado-Allison, 1965) (Fig. 3). Synapomorphies shared among the *phyllostomae* group (*P. longicrus,* (*N. delicatus,* (*M. aranea*, *M. modax*))) are pointed maxillar palp, laterovertex without setae in front of the eyes, eyes having more than 18 facets, and transverse

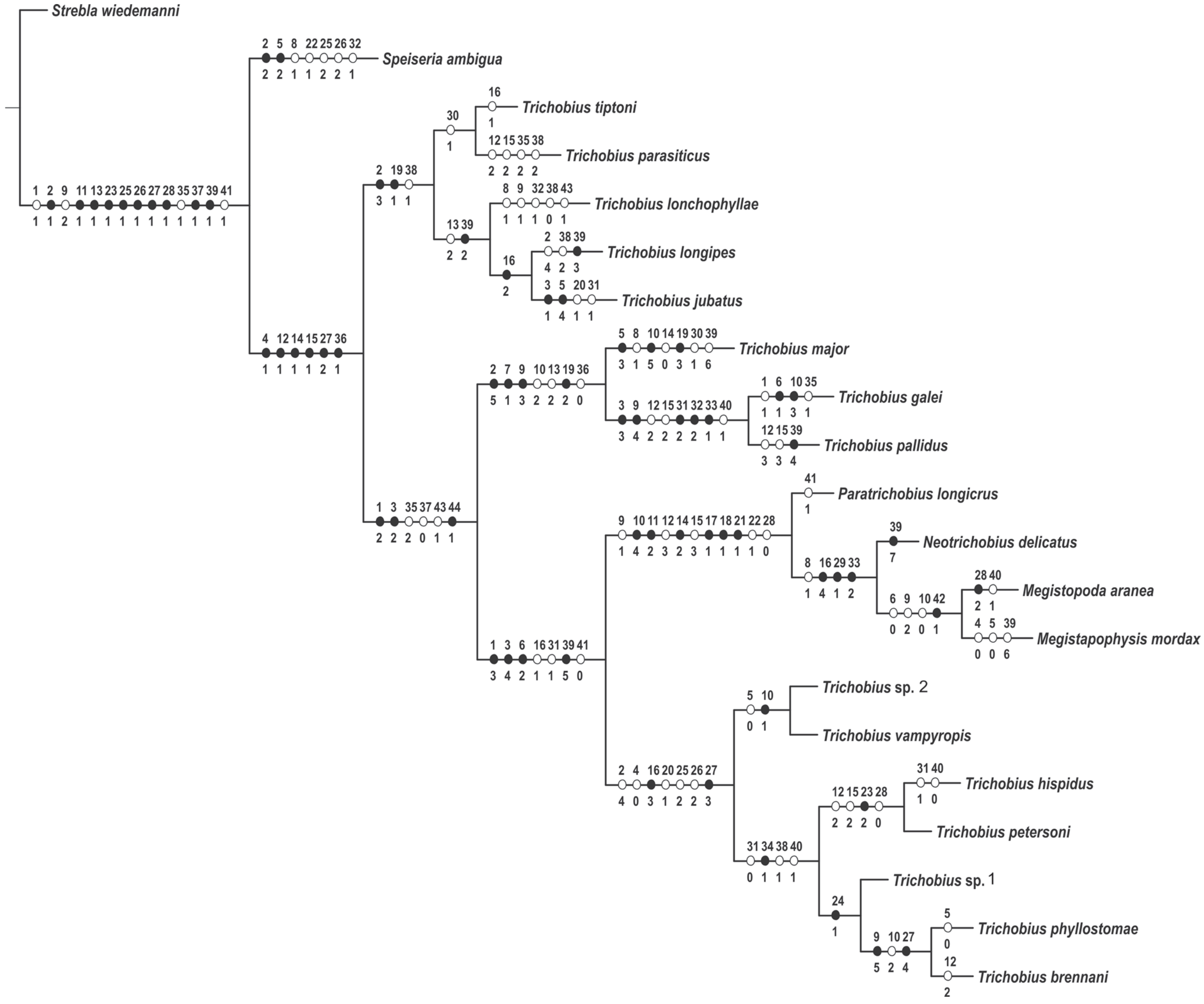


Fig. 3. Single most-parsimonious tree (length = 144, consistency index = 65, retention index = 77) from morphological data, showing Acctran optimization characters. Solid circles = synapomorphies, blank circles = homoplasies.

and elliptical tergite 7 (Fig. 3). This branch has a support of 66% in the bootstrap replicates (Fig. 4).

The species of the *phyllostomae* group are monophyletic, supported by two synapomorphies, which are the long, triangular metasternal lobe and the spiniform setae that are shorter than the tarsomere on the ventral side of basitarsum 3 (Fig. 3). These had robust branch support in > 80% of the bootstrap replicates (Fig. 4).

We presented below characters and character states with length (L), consistence index (CI), and retention index (RI) used in the cladistic analysis of the *phyllostomae* group.

1. Apex of maxillar palpus: (0) wide and irregular; (1) with a small concavity; (2) rounded; (3) pointed. L = 4; CI = 75, RI = 85.

2. Shape of laterovertex: (0) Streblinae-like; (1) trapezoid; (2) subtriangular; (3) trapezoid with a posterior lobe on inner margin; (4) trapezoid with a small posterior lobe on inner margin; (5) transverse. L = 6; CI = 83, RI = 87.

The long posterior lobe (state 3) is found in *dugesii* (*T. parasiticus* and *T. tiptoni*), *uniformis* (*T. lonchophyllae*) and *dunni* (*T. jubatus*) and is very evident and more developed in the brachypterous genera *Aspidoptera* Coquillett, 1899 and *Exastinion* Wenzel, 1966. Wenzel (with collaborators 1966, 1976) considered the *dugesii* group to be closely related to these genera (Fig. 1).

3. Number of short setae on anterior margin of laterovertex in front of the eye: (0) 1; (1) 3; (2) more than 3; (3) 2; (4) 0. L = 4; CI = 100, RI = 100 (Figs. 6–9).

Setae in front of the eyes seems to be a plesiomorphic character in Trichobiinae that is lost in the clade formed by *Paratrichobius*, *Neotrichobius*, *Megistopoda*, *Megistapophysis*, and *phyllostomae* group.

4. Setae 6 of laterovertex: (0) present; (1) absent. L = 3; CI = 33, RI = 75.

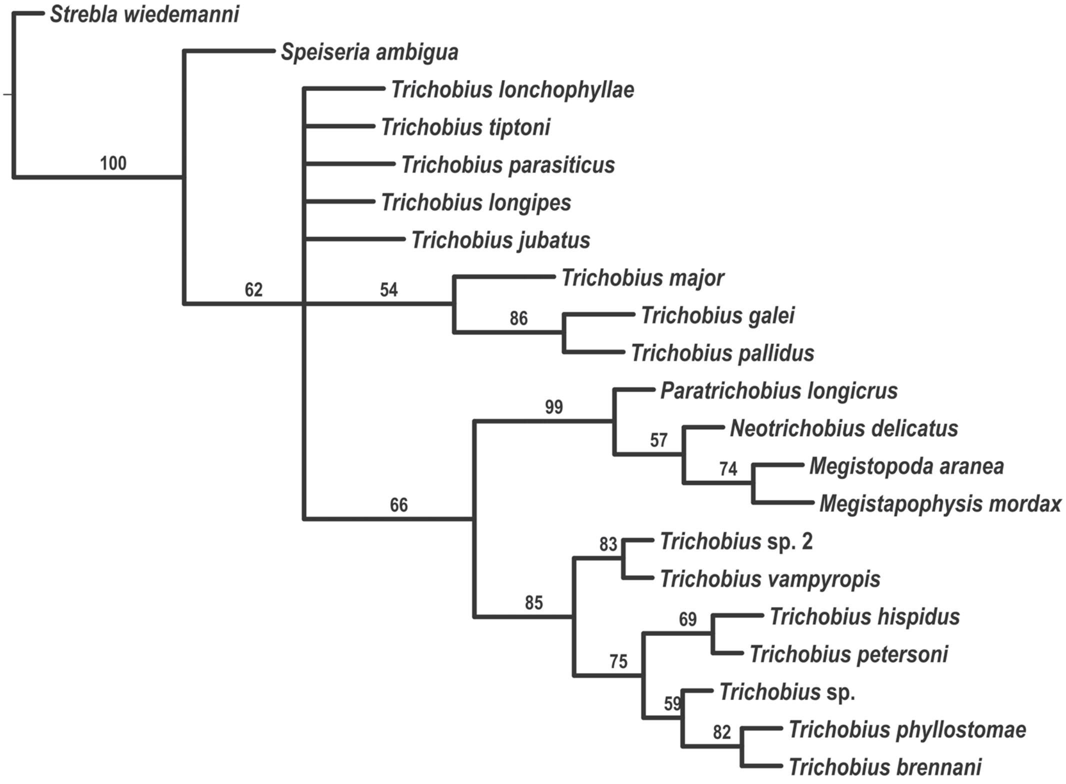


Fig. 4. Tree showing results for 10,000 bootstrap replicates. Branches values <50% are collapsed.

Several setae can be found in the laterovertex of all Trichobiinae, but some apparently have fixed positions and similar shapes. Here we tentatively consider these setae homologous and make a map of the setae. We name the setae 1 to 6 (Figs. 10–12). Only setae 6 may be absent in *Speiseria* and homoplasically in *Megistapophysis mordax* and the species of the *phyllostomae* group. It is not possible to make homologous associations of the laterovertex setae of *Strebla wiedemanni*, because they have various extra setae. Therefore we considered these as "–" (inapplicable) for this taxon.

5. Accessory setae on posterior margin of laterovertex: (0) absent; (1) 1; (2) 2; (3) 4; (4) 5. L = 6; CI = 66, RI = 33.

Normally, one accessory setae is found in the Trichobiinae. However, a single accessory setae can also be found in other genera, such as *Aspidoptera* and *Exastinion*. The number of accessory setae may be a good diagnostic character for generic or specific levels.

6. Number of eye facets: (0) 9 to 15; (1) one; (2) greater than 18. L = 3; CI = 66, RI = 87.

7. Occipital lobes: (0) sclerotized; (1) lesser sclerotized. L = 1; CI = 100, RI = 100.

8. Longitudinal and transverse sutures: (0) not united; (1) united. L = 4; CI = 25, RI = 25.

9. Number of episternal setae: (0) 2; (1) 3; (2) 4; (3) about 14; (4) 6; (5) 5. L = 7; CI = 71; RI = 50 (Figs. 22–28).

10. Setae next to episternal cleft: (0) one long and one short setae; (1) two long setae; (2) one long and two short setae; (3) two long and one short setae; (4) one long setae; (5) three long setae. L = 7; CI = 71; RI = 50. (Figs. 22–28).

Zeve & Howell (1963) studied the external thorax morphology in three species of the *major* group, describing the pattern of episternal setae, but they did not comment on chaetotaxy. Aside from that study, episternal setae have not been cited as being used for generic or specific identification. This character might be useful for specific identification, especially for the *phyllostomae* group. The state 0 (Fig. 22) is basal in Trichobiinae, in which length is modified and setae may be lost (Fig. 3), especially in ((*T. major*, (*T. galei*, *T. pallidus*)), ((*P. longicrus*, ((*M. aranea*, *M. mordax*) *N. delicatus*)), ((*Trichobius* sp. 2, *T. vampyropis*), ((*T. petersoni*, *T. hispidus*), (*Trichobius* sp. 1, (*T. phyllostomae*, *T. brennani*)))))).

11. Thoracic sternum: (0) with longitudinal bare areas on each side; (1) setose; (2) almost bare. L = 2; CI = 100, RI = 100.

12. Anterior margin of male thoracic sternum in ventral view: (0) past coxae 1 and over base of trochanter; (1) past the insertion of the trochanter; (2) not on insertion of the trochanter; (3) past and over coxae 1. L = 7; CI = 42, RI = 55.

13. Shape of the anterior margin of thoracic sternum: (0) concave; (1) truncate; (2) blunt. L = 3; CI = 66, RI = 80.

14. Posterior margin of the metasternum in ventral view: (0) not expanded over base of coxae 3, rounded margin; (1) not expanded over base of coxae 3, truncate margin; (2) expanded over base of coxa 3. L = 3; CI = 66, RI = 80.

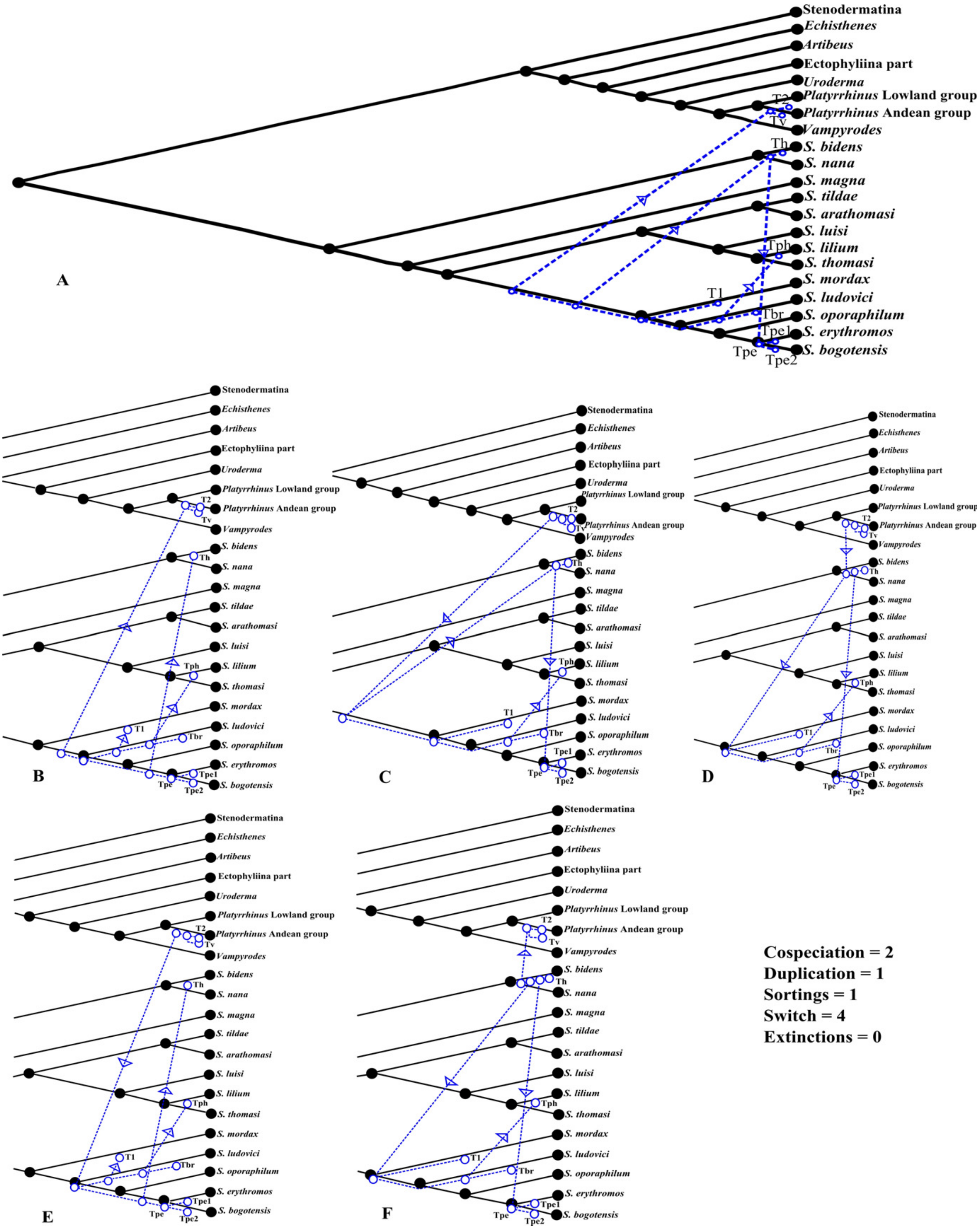
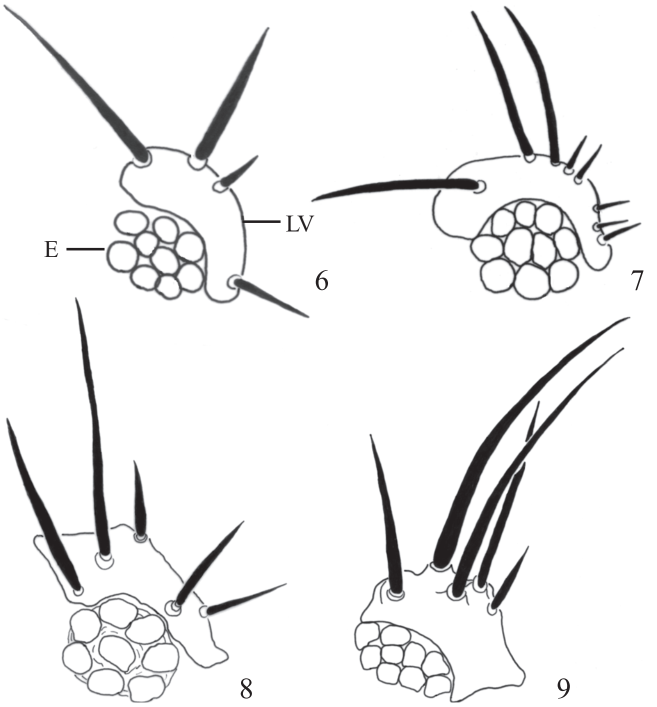
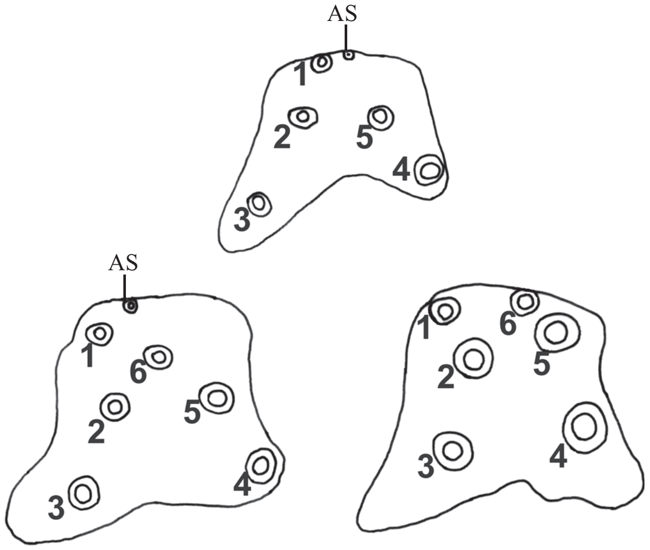


Fig. 5. Lesser cost cophylogenetics scenarios. T1 = *Trichobius* sp. 1, T2 = *Trichobius* sp. 2, Tbr = *Trichobius brennani*, Th = *Trichobius hispidus*, Tpe = *Trichobius petersoni*, Tph = *Trichobius phyllostomae,* Tv = *T. vampyropis*.



Figs. 6–9. Eye and laterovertex, lateral view. 7. *Trichobius longipes* (Rudow). 8. *Trichobius jubatus* Wenzel. 9. *Trichobius pallidus* (Curran). 10. *Megistopoda aranea* (Coquillett). E = eye, Lv = Laterovertex.

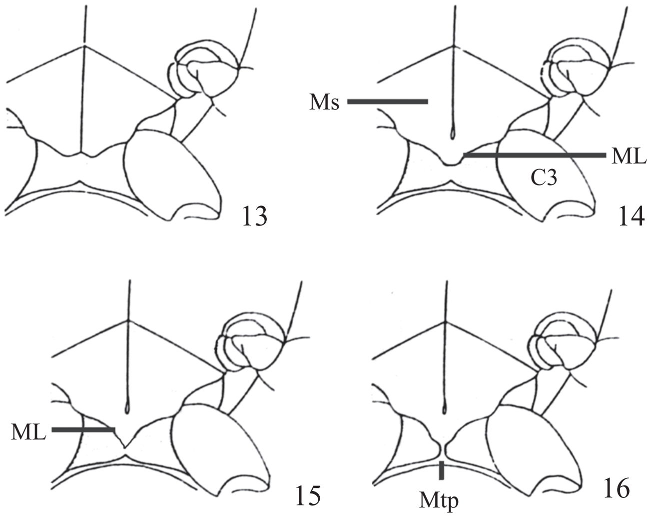


Figs. 10–12. Laterovertex with the position of the setae (1–6) and the accessory setae that are omitted. 10. *Trichobius tiptoni* Wenzel. 11. *Trichobius brennani* Wenzel. 12. *Trichobius vampyropis* Wenzel.

15. Anterior margin of female thoracic sternum in ventral view: (0) past the coxae 1 and on base of trochanter; (1) past the trochanter insertion; (2) not on trochanter insertion; (3) past and on coxa 1. L = 6; CI = 50, RI = 62.

16. Metasternal lobe: (0) absent; (1) blunt and trapezoid; (2) united with metepimere; (3) long and triangular; (4) short. L = 5; CI = 80, RI = 90. (Figs. 13–16).

The metasternal lobe was considered by Wenzel (and collaborators 1966, 1976) to be an important character to identify the groups and complexes of *Trichobius*. The blunt, trapezoidal metasternal lobe arose three times independently (Figs. 2, 14). The lobe blunt and trapezoid have arisen homoplasically in *T. tiptoni* (*dugesii* group) and *P. longicrus.* In *T. phyllostomae*, long and triangular metasternal lobe is a synapomorphy (Figs. 2, 15).



Figs. 13–16. Posterior portion of thorax in ventral view showing state in respect to metasternal lobe (modified from Wenzel *et al.* (1966)). 13. Lobe absent. 14. Lobe, short, trapezoid and blunt, not united with metepimeron. 15. Lobe, triangular and long, not united with metepimeron. 16. Lobe united with metepimeron. C3 = Coxa 3, Ms = Metasternum, ML = metasternal lobe, Mtp = metepimeron.

17. Ventral face of coxa 3: (0) setose; (1) not setose. L = 1; CI = 100, RI = 100.

18. Diagonal rows of setae on inner surface of femur 1: (0) rows with similar setae; (1) inner row with thick spines. L = 1; CI = 100, RI = 100.

19. Number of setae on inner surface of femur 1 whose apex is directed towards anterior surface: (0) none; (1) 2; (2) 3; (3) more than 3. L = 3; CI = 100, RI = 100.

20. Lateroventral setae on femur 2: (0) as long as other setae: (1) longer and thick, similar to the long dorsal setae. L = 2; CI = 50, RI = 85.

21. Unpigmented transverse ventral stripe on femur 2: (0) absent; (1) present. L = 1; CI = 100, RI = 100.

22. Unpigmented transverse ventral stripe on femur 3: (0) absent; (1) present. L = 2; CI = 50, RI = 75.

23. Tibiae 1: (0) with anterolateral and posterolateral rows of spiniform setae higher than tibiae 1; (1) with an anterolateral row of setae that are as long as the dorsal setae; (2) with an anterolateral row of spiniform setae shorter than tibia 1. L = 2; CI = 100, RI = 100.

24. Tarsomere: (0) rectangular; (1) moniliform. L = 1; CI = 100, RI = 100.

25. Thorn-like setae on ventral surface of basitarsum 1: (0) as long as the basitarsum; (1) absent; (2) shorter than the basitarsum. L = 3; CI = 66, RI = 85.

26. Thorn-like setae on ventral surface of basitarsum 2: (0) as long as the basitarsum; (1) absent; (2) shorter than the basitarsum. L = 3; CI = 66, RI = 85.

27. Thorn-like setae on ventral surface of basitarsum 3: (0) two rows; (1) as long as the basitarsum; (2) absent; (3) shorter than the basitarsum; (4) two setae. L = 4; CI = 100, RI = 100.

28. Length of basitarsum 3: (0) as long as the two preceding tarsomeres together; (1) as long as the preceding tarsomere; (2) as long as the three preceding tarsomeres together. L = 4; CI = 50, RI = 60.

29. Wing: (0) macropterous; (1) stenopterous. L = 1; CI = 100, RI = 100.

Other genera of Trichobiinae, for example *Aspidoptera*, *Joblingia* Dybas & Wenzel, 1947, and *Exastinion*, have reduced wings. Normally these wings are oval-shaped or as wide as long and are called brachypterous (Wenzel *et al.* 1966, Wenzel 1976). In *Megistopoda, Neotrichobius* and *Megistapophysis* the wings are much longer than wide.

30. R vein: (0) straight; (1) sinuose, curved or bent. L = 2; CI = 50, RI = 50. (Figs. 18–22).

Although the sinuose R vein appears independently in *T. dugesii* and *T. major* groups, it is an important synapomorphy that groups the species of the *T. dugesii* group.

31. M1+2 vein: (0) setose throughout its length; (1) one long basal setae follow a bare area; (2) no basal setae. L = 5; CI = 40, RI = 40. (Figs. 17–21).

32. 1A(2A) vein: (0) basal setae absent; (1) setose throughout its length; (2) basal half without setae. L = 3; CI = 66, RI = 50. (Figs. 17–21).

Most species of Trichobiinae and Streblinae have no basal setae (state 0).

33. Dorsal abdominal connexivum: (0) almost totally bare; (1) setose on distal half; (2) almost totally setose. L = 2; CI = 100, RI = 100.

34. Male with long setae on the lateral abdominal connexivum posterior to sintergite 1+2 lobule: (0) absent; (1) present. L = 1; CI = 100, RI = 100.

35. Sternite VI: (0) wide; (1) tread-like; (2) absent. L = 4; CI = 50, RI = 60.

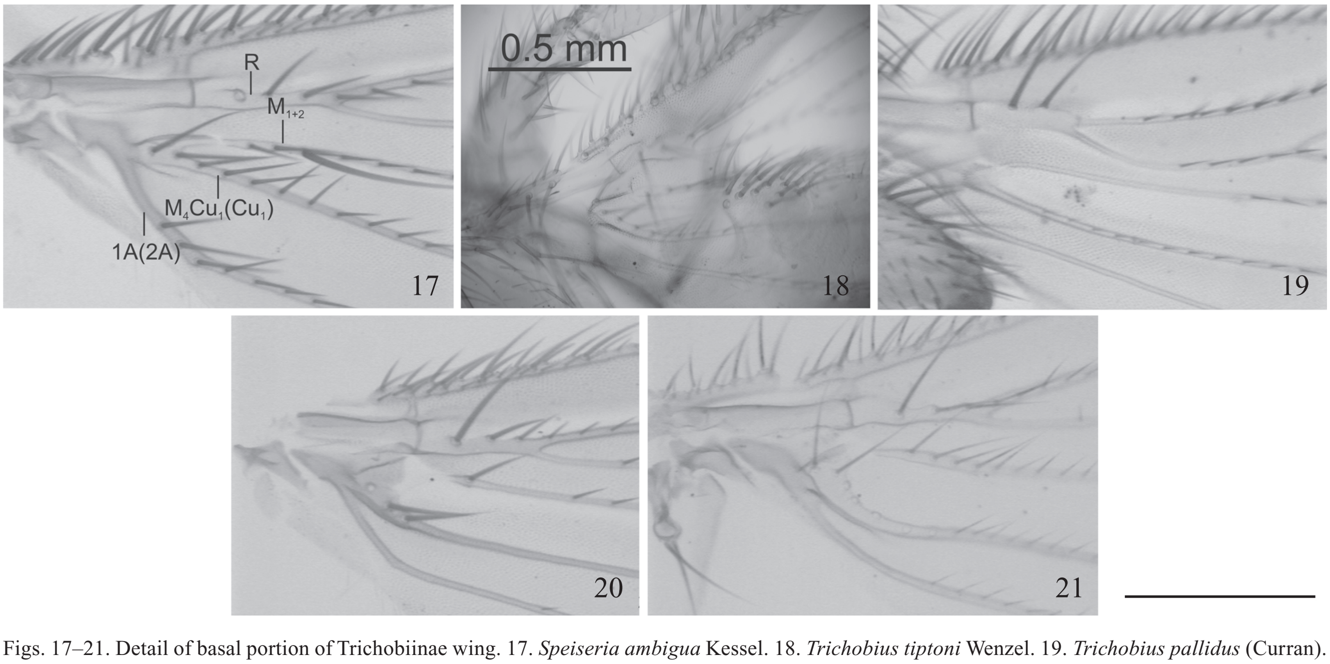
36. Gonopods: (0) symmetrical; (1) asymmetrical. L = 2; CI = 50, RI = 75.

Asymmetrical gonopods seem to be common in Trichobiinae, contrary to Streblinae, in which gonopods are symmetrical. Here, *S. ambigua* and the clade (*T. major* (*T. galei*, *T. pallidus*)) have symmetrical gonopods. Other taxa in the Trichobiinae that have symmetrical gonopods are the brachypterous genera, such as *Aspidoptera*, *Exastinion*, *Noctiliostrebla* Wenzel, and the full-winged *Paratrichobius americanus* Peterson & Ross, 1972 (Peterson & Ross 1972).

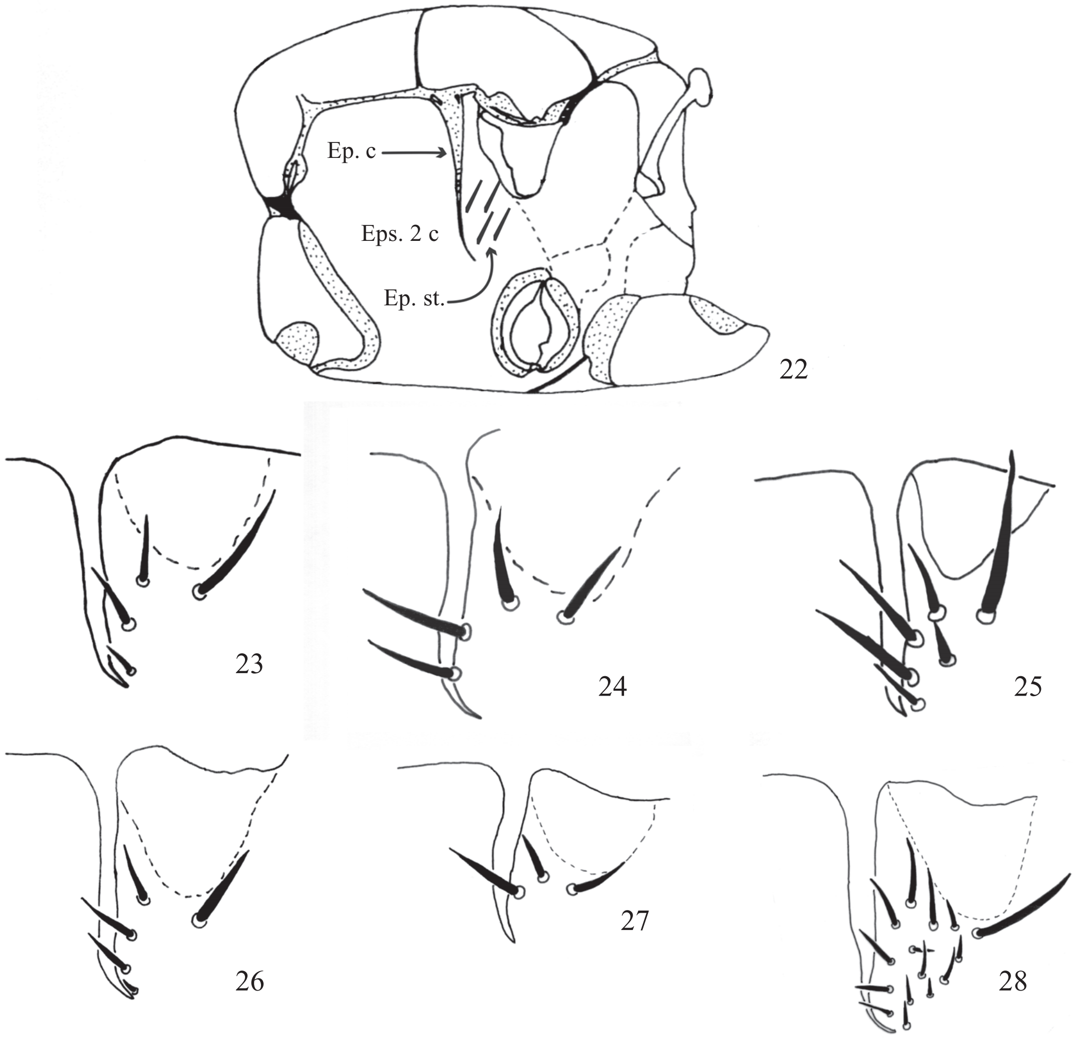
37. Gonopophyseal setae: (0) proximal seta longer than distal; (1) distal seta longer than proximal. L = 2; CI = 50, RI = 80.

38. Female with long setae on the lateral abdominal connexivum posterior to the sintergite 1+2 lobule: (0) absent; (1) a transversal row with three to four; (2) a patch. L = 5; CI = 40, RI = 57.

39. Shape of tergite 7: (0) pentagonal; (1) inverted drop-like with truncate posterior margin; (2) small and unscleroti-



Figs. 17–21. Detail of basal portion of Trichobiinae wing. 17. *Speiseria ambigua* Kessel. 18. *Trichobius tiptoni* Wenzel. 19. *Trichobius pallidus* (Curran). 20. *Paratrichobius longigrus* (Miranda-Ribeiro). 21. *Trichobius brennani* Wenzel. Scale bar: 0.5 mm.



Figs. 22–28. 22. Lateral view thorax, Ep. c. = cleft episternal; Eps 2 = episternum 2; Ep. st. = episternal setae (modified Zeve and Hovell 1963). Episternal setae in: 23. *Speiseria ambigua* Kessel. 24. *Trichobius vampyropis* Wenzel. 25. *Trichobius pallidus* (Curran). 26. *Trichobius brennani* Wenzel. 27. *Paratrichobius longicrus* (Miranda-Ribeiro). 28. *Trichobius major* Coquillett.

zed; (3) trapezoid; (4) *pallidus* form; (5) transverse and elliptical; (6) two elliptical sclerites; (7) absent. L = 8; CI = 87, RI = 80.

40. Tergite 7 and epiproct: (0) not united; (1) united. L = 4; CI = 25, RI = 50.

In addition to the taxa studied here, some species of *Strebla* and *Anastrebla* Wenzel, 1966 (Streblinae) also have united tergite 7 and epiproct. Perhaps this character is more useful for separating species than genera.

41. Setae across spiracle 7 in females. (0) present; (1) absent. L = 3; CI = 33; RI = 77.

42. Spiniform setae on posterior margin of sternite 2. (0) absent; (1) present. L = 1, CI = 100; RI = 100.

43. Female cerci: (0) free; (1) united with ventral arc. L = 2; CI = 50; RI = 80.

44. Postgenital sclerite: (0) absent; (1) present. L = 1; CI = 100; RI = 100.

Cophylogenetic Analyses. The cophylogenetic analysis yielded 813 scenarios, with costs ranging between 13 to 57. The number of cospeciations events in these scenarios ranged from 0 – 5, with 1 – 4 duplications, 0 – 6 host switches, 0 – 23 sorting events and 0 – 3 extinctions. The six scenarios with the lower cost (< 13) included two cospeciations events, one duplication event, four host-switches events and one sorting event (Fig. 5). Three scenarios showed that the *phyllostomae* group arose from the *Sturnira* clade (Figs. 5A, B, F) and three arose on the *Platyrrhinus* Andean group clade (Figs. 5C, D, E). In all scenarios, *T. phyllostomae* underwent speciation in moving to *Sturnira lilium* (E. Geoffroy, 1810) from *S. ludovici* Anthony, 1924 (Fig. 5).

DISCUSSION

Phylogeny of the *T. phyllostomae* group. The topological tree (Fig. 3) supported the hypothesis of relationships of the genera of Trichobiinae made by Wenzel *et al.* (1966) and Wenzel (1976) (Fig. 1). The *major*, *pallidus, caecus*, and *phyllostomae* groups and *Paratrichobius*, *Megistopoda, Megistapophysis*, and *Neotrichobius* are in the same large clade, while *dugesii*, *dunni* and *longipes* groups are included in another monophyletic group. However, contrary to one of the hypotheses of Wenzel *et al.* (1966), the *uniformis* group is unrelated to *Speiseria*, which indicates that some characters, such as setae on the base of the 1A(2A) vein (Fig. 17) and longer distal than basal gonapophyseal setae, may be homoplasic. Wenzel *et al.* (1966) also suggested the possibility that *Speiseria* may be related to *phyllostomae* group, which he later rejected (Wenzel 1976) and which is also not supported here.

The shape of thoracic sternum and the reduced wing are similar in *Megistapophysis* and the *T. phyllostomae* group, *Paratrichobius*, *Megistopoda* and *Neotrichobius* (Dick & Wenzel 2006). Thus, the following relationship among genera was predicted: (*T. phyllostomae* group (*Paratrichobius* (*Megistapophysis* (*Megistopoda* (*Neotrichobius*))))). Here, *Megistapophysis* and *Megistopoda* form a monophyletic group whose main synapomorphy is the ctenidium in the second abdominal sternite (Fig. 3).

Contrary to the morphological grouping of Trichobiinae, our results contradict the topology of Dittmar *et al.* (2006) based on molecular data. In their analysis, the *dugesii* group is paraphyletic, with the *dugesii* complex close to the *caecus* group, while the *parasiticus* complex is closer to the *longipes* group and *T. hirsutulus* Bequaert, 1933, a species of the *major* group. Here, we suggest that *uniformis*, *dugesii*, *longipes*, and *dunni* groups belong to the genus *Trichobius*, although the clade (*T. major* (*T. galei*, *T. pallidus*)) had low branch support (Fig. 4). The *major* group will require a more comprehensive analysis that includes other genera of the Trichobiinae to determine its status. Such an analysis should include the genera *Joblingia* and *Anatrichobius* because of the morphological similarity of the female terminalia among these genera. Species of the *caecus* and *pallidus* groups probably do not belong to *Trichobius*, but we prefer to wait for a more detailed study before renaming *caecus* group and revalidating *Kesselia* Curran, 1934 to comprise *T. pallidus*. A new genus should be given to the *phyllostomae* group. Thus, further study using both, morphological and molecular data, is required and should include all genera in the Trichobiinae for correct delimitation of *Trichobius*.

According to Wenzel (1976), *T. phyllostomae* is a sister-group of *T. brennani*, and *T. petersoni* is a sister-group of *T. hispidus* which is in turn a sister-group *T. vampyopis*. Here, we found that the species that are found on *Sturnira* form a monophyletic group whose sister group are found on *Platyrrhinus*.

Cophylogenetic Analysis. If host species are sympatric and syntopic, the likelihood increases for dispersal to different hosts. If survival and reproduction on these new hosts are reasonable, host-switching becomes much more likely (Clayton *et al.* 2003). Although species in the *phyllostomae* group have strong host specificity, which should favor cospeciation, and low prevalence and intensity, which should favor sorting, cospeciation and sorting are seldom encountered. Streblid bat flies are pupiparous, which means that instead of eggs, females deposit pupae around the bat roosting sites. Thus, in bat flies, host switching may have occurred during their coevolutionary histories when more than one host bat roosted in the same roosting site. Flies in the *phyllostomae* group are strong fliers, which also increases their chances of encountering a new host species. Nonetheless, because of host grooming behaviors and low rates of infestation (small population sizes of the flies), host switching may be minimal.

Grooming is an important cause of ectoparasite mortality and may reduce or eliminate colonization of new hosts (Marshall 1981). However, bats often have flies, so grooming may not be effective for bat flies and the importance of grooming for bat flies has not been studied. For example, *Noctilio leporinus* (Linnaeus, 1758) is often strongly infested by *Noctiliostrebla* Wenzel, 1966 and *Paradyschiria* Speiser, 1900 (Wenzel *et al.* 1966; Moura *et al.* 2003). *Paradyschiria fusca* Speiser, 1900 and *Noctiliostrebla aitkeni* Wenzel, 1966 remains were found in 10% and 2% (respectively) of the feces of *N. leporinus* (Bordignon 2006).

Sturnira evolved from a highland ancestor (Villalobos & Valerio 2002) such as the Andean *Platyrrhinus* (Velazques 2005). *Platyrrhinus* spp. and *Stunira bidens* (Thomas, 1915) have been found syntopically (Molinari & Soriano 1987; Lidner & Morawetz 2006) and both often use caves for roosting (Gardner 2007; Molinari & Soriano 1987). Other species of *Sturnira* do not roost in caves, but rather use tunnels, bridges and houses (Molinari & Soriano 1987). These roosting behaviors suggest that flies have had many opportunities for host switching (Fig. 5). Off-host behavior and longevity of the *T. phyllostomae* group, or of most Neotropical streblid bat flies, is unknown and should be studied to better understand how switching may occur.

Speciation in *T. phyllostomae* was the result of a switch from *S. ludovici* to *S. lilium.* Both bats are sympatric in Central America and northern South America, but *T. phyllostomae* is from southern Brazil, where *S. ludovici* is absent. A similar distribution pattern is found in two brachypterous genera of streblid bat flies, Joblingia and *Anatrichobius*. *Joblingia* includes two described species. *Joblingia schmidti* Dybas & Wenzel, 1947 parasitizes *Myotis keaysi* J. A. Allen, 1914 and *M. oxyotus* (Peters, 1867) from the highlands of Guatemala and Panama (Guerrero 1995). And the recently described *Joblingia minuta* Graciolli & Dick, 2012 parasitize *Myotis ruber* (E. Geoffroy, 1806), a vespertilionid bat that is restricted to southern South America (Graciolli & Dick 2012). *Anatrichobius* includes two described species (Graciolli 2003) and one undescribed species (Wenzel *et al.* 1966) from Peru. *Anatrichobius scorzai* Wenzel, 1966 is found on *Myotis albescens* Geoffroy, 1806*, M. keaysi*, *M. nigricans* (Schinz, 1820), *M. oxyotus* and occurs from Panama to Argentina (Guerrero 1995;

Autino *et al*. 2009). Another species, *A. passosi* Graciolli, 2003 parasites *Myotis albescens* (E. Geoffroy, 1806), *M. levis* (I. Geoffroy, 1824), *M. nigricans*, and *M. ruber* and is restricted to southern Brazil (Graciolli 2003; Bertola *et al.* 2005). These patterns suggest a common biogeographical history among these streblid bat flies.

The lack of cospeciation in the two populations of *T. petersoni* and *S. erythromos* (Tshudi, 1844) and *S. bogotensis* Shamel, 1927 may be considered a failure to speciate even though some conditions may seem favorable. Such a scenario is possible if the parasites on both hosts continued to have genetic contact after having colonized the new host (Banks & Paterson 2005). Future studies using molecular data will be able to better understand this process.

Cospeciation may be uncommon in this group for a variety of reasons. Cophylogenetic associations among arthropods and their vertebrate hosts studied using component analysis may be divided into two groups with respect to the life-cycle biology of the parasites (Table I). In one group, the entire life cycle is on the host, and in the second group, part of the life cycle is not on the host (usually an immature stage). The second is that most common among these flies. Historical associations of lice and some mites with their hosts may have many cospeciation/codivergent events, exceptions to which may be explained by phoresia (Weckstein 2004). Cophylogenetic analyses of other, second-group, ectoparasitic arthropods (fleas and ticks) with preparasitic stages in the roost or environment of their mammal hosts, find a low probability of cospeciation. This suggests that sorting, duplication and host switching were more likely. In conclusion, we found that *Trichobius* is not monophyletic, and that during the coevolutionary history of *Trichobius phyllostomae* group and their hosts, cospeciation seldom occurred.

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Table I. Examples of cophylogenetic studies of arthropods and their vertebrate hosts using reconciliation analyses.

Authors	Parasite	Host	Software	Events			
				Cospeciation	Switch	Duplication	Sorting
Entire life cycle							
Phthraptera (Lice)							
Paterson *et al.* (2000)	Ischnocera (14 spp., 6 Genera)	Seabirds (11 spp.)	TreeMap 1.0	9	0-1	3-4	11-14
Jonshon *et al.* (2003)	Columbicola (19 taxa, 5 genera)	Pigeons (25 taxa, 22 genera)	Treemap 1.0	9	–	11	61
Weckstein (2004)	5 subtrees of 1 spp.	Toucans (11 spp.)	TreeMap 1.0	1	0	3	17-22
Banks *et al.* (2006)	Ischnocera (*Austrogoniodes*) (15 spp.)	Penguins (17 spp.)	Treemap 2.02B	3-4	0-1	5-7	15-22
Hughes *et al.* (2007)	*Pectinopygus* (17 spp.)	Pelecaniformes (18 spp.)	Treemap 2.02B	10-11	0-6	5-6	3-19
Smith *et al.* (2008)	Anoplura (*Hoplopleura* (11 spp.), *Linognathoides* (1 spp.); *Pterophthirus imitans* (2 spp.)	Akodontini and Oryzomyini (20 spp.)	Treemap 2.02B	12-20	3-4	10-14	1-12
Acari							
Dabert *et al.* (2001)	Avenzoraiinae (26 spp., 6 genera)	Birds (21 spp.)	Treemap 1.0	12-13	2	6-7	26-29
Morelli & Spicer (2007)	*Ptilonyssus sairae* (6 infrapopulations)	Birds (5 spp.)	Treemap 1.0	5	0	0	0
Bochov *et al.* (2011)	Malkialginae (9 spp.)	Strepsirrhine primates (6 taxa)	Treemap 2.02B	4	1	3	2
Non-parasitic stage							
Siphonaptera							
Krasnov & Shenbrot (2002)	Siphonaptera (19 spp.)	Rodentia (Jerboa) (21 spp.)	TreeMap 1.0	0	0	18	105
Liang & Houyoung (2005)	*Geusibia* (12 spp.)	Lagomorpha (Pikas) (19 spp.)	TreeMap 1.0	2	0	9	59
Diptera							
This study	*Trichobius phyllostomae* group (7 spp.)	Stenodermatine bats (21 taxa)	Tarzan 0.9	2	4	1	0
Acari							
Cumming (2000)	Ticks	Tetrapoda (16 taxa)	TreeMap 1.0	0	0	13	73
			TreeMap 1.0	2	0	11	66
		Artiodactyla (26 spp.)	TreeMap 1.0	1	0	18	148

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Appendix 1. Examined specimens.

Trichobius Gervais, 1844

phyllostomae group

Trichobius phyllostomae Kessel, 1925

Type material examined. **BRASIL. Santa Catarina.** Humboldt [= Corupá], VII/1916 (digital image of 1 female [11921–200 *Trichobius phyllostomae* Kessel TYPE], host *Phyllostoma* sp., BMNH), W. Erhardt leg.

Material examined. **BRASIL**. **São Paulo**. Ilha do Cardoso, 14/V/1991 (1 female, host *Sturnira lilium*, MZSP), S.F. Corrêa leg. 11/VI/1991 (1 female, host *Sturnira lilium*, MZSP), S.F. Corrêa leg. **Paraná.** Adrianópolis, Fazenda Primavera, Tatuapeva, 05/VI/2001 (1 male, host *Sturnira lilium*, MHNCI). Fazenda Rio Grande, Fazenda Gralha Azul, 22/II/2002 (1 female, host *S. lilium*, DZUP), G. Bianconi leg. Tijucas do Sul, Lagoa, 15/IV/2000 (1, host *S. lilium*, MHNCI), G. Bianconi leg. **Santa Catarina.** Humboldt [= Corupá], 07/VII/1918 (digital image of wing, hosp. *Phyllostoma* sp., BMNH), W. Erhardt leg. Joinville, 08/V/1929 (1 male, host *Artibeus lituratus*, CNHM), Steiger leg. **Rio Grande do Sul.** Dom Pedro de Alcântara, 20/II/1997 (1 female, host *S. lilium*, DZUP), A. M. Rui leg. Maquiné: Estação de Pesquisa e Produção de Maquiné da Fundação de Pesquisa Agropecuária da Secretaria da Agricultura do Estado do Rio Grande do Sul (FEPAGRO), 27/IX/2000 (1 female, host *S. lilium*, DZUP), A. M. Rui leg; 17/XI/2000 (1 male, 2 females, host *S. lilium*, DZUP), A. M. Rui leg.

Trichobius brennani Wenzel, 1966

Type material examined. Paratypes. **PANAMA. Chiriquí**: Casa Lewis, Cerro Punta. Elev. 5600–5700 ft., 03/II/1960 (1 female [slide], host *Sturnira ludovici* [Tipton-Handley#5878], FMNH), C. M. Keenan & V.J. Tipton legs; (1 female, host *Sturnira ludovici* [Tipton-Handley#5884], FMNH), C. M. Keenan & V. J. Tipton leg.; Casa Tilley, Cerro Punta, elev. 5300–5600 ft., 23/IV/1961 (1 male [slide], host *S. ludovici* [Tipton-Handley#7303], C. M. Keenan & V. J. Tipton leg.; 12/III/1962 (2 females [slide] 1 female [Allotype, slide], host *S. ludovici* [Tipton-Handley#10469], FMNH), C. M. Keenan & V. J. Tipton leg.; 14/III/1962 (2 males, 1 female, host *S. ludovici* [Tipton-Handley#10469], FMNH), C. M. Keenan & V. J. Tipton leg.; 01/V/1960 (1 female, host *S. ludovici* [Tipton-Handley#6176], FMNH), C. M. Keenan & V. J. Tipton leg. **Darién:** Cerro Malí, 09/II/1964 (2 males, 1 female, host *S. ludovici* [Tipton-Handley#12443], FMNH), C. O. Handley Jr. leg; Cerro Tacarcuna, el. 4100–4800ft., 29/II/1964 (1 male, 1 female, host *S. ludovici*, [Tipton-Handley#12797], MZSP), C. O. Handley Jr. leg.; 04/III/1964 (2 males, host *S. ludovici* [Tipton-Handley#5878], FMNH), C. O. Handley Jr.; 07/III/1964 (1 male, 3 females, host *S. ludovici* [Tipton-Handley#12960], FMNH), C. O. Handley Jr. leg.

Trichobius vampyropis Wenzel, 1966

Type material examined. Holotype. **PANAMA. Bocas del Toro**: nr. Rancho Mojica, 13/IX/1961 (1 male [slide], host *Vampyrops vitatus* [= *Platyrrhinus vitattus*] [Tipton-Handley#8115], FMNH), C. M. Keenan & V. J. Tipton leg. Paratypes. **PANAMÁ. Bocas del Toro:** nr. Rancho Mojica, 13/IX/1961 (1 female [Allotype, slide], host *Vampyrops vittatus* [= *Platyrrhinus vittatus*] [Tipton-Handley#8115], FMNH), C. M. Keenan & V. J. Tipton leg.

Material examined. **VENEZUELA. Distrito Federal:** Los Venados, 4km NNW Caracas, 1524m, 29/VII/1965 (1 female, host *Vampyrops umbratus* (= *Platyrrhinus dorsalis*) [SVP#334], FMNH), A. Peterson & M. Tuttle leg.; 1400m, 02/VIII/1965 (2 males, 1 female, host *Vampyrops umbratus* (= *Platyrrhinus dorsalis*) [SVP#495, 508], A. Peterson & M. Tuttle leg.; 1430m 02/VIII/1965 (1 male, 1 female, host *Vampyrops umbratus* (= *Platyrrhinus dorsalis*) [SVP#499], A. Peterson & M. Tuttle leg.; 1463m, 03/VIII/1965 (3 males, 1 female, host *Vampyrops vittatus* [= *Platyrrhinus vittatus*] [SPV#539], FMNH), A. Peterson & M. Tuttle leg. Pico Ávila, 5km NNE Caracas, near Hotel Humboldt, 2.092m, 20/VIII/1965 (1 male, host *Vampyrops umbratus* (= *Platyrrhinus dorsalis*) [SVP#676], FMNH), A. Peterson & M. Tuttle leg.

Trichobius hispidus Wenzel, 1976

Type material examined. Paratypes. **VENEZUELA. Mérida:** Tabay, 6 km ESSE Tabay, Midlle Refugio, 2550 m, 06/IV/1966 (2 females [slide], host *Sturnira bidens* [SVP#4369, 4372], FMNH), N. E. Peterson leg.; 2640m, 08/IV/1966 (1 male, 1 female, host *S. bidens* [SVP#4391], FMNH), N. E. Peterson leg.; 2640m, 11/IV/1966 (1 male [slide], host *Sturnira bidens* [SVP#4411], FMNH), N. E. Peterson leg. 2640m,15/IV/1966 (1 male [slide], host *Sturnira bidens* [SVP#4447], FMNH), N. E. Peterson leg.

Trichobius petersoni Wenzel, 1976

Type material examined. Holotype. **COLOMBIA. Cundimarca:** Bogota, X/1968 (1 male [#46, slide], host *Sturnira bogotensis* [field#cjm 13139], FMNH), C. J. Marinkelle leg. Parátipos. **COLOMBIA. Cundimarca:** Bogota, X/1968 (1 female [Allotype #46, slide], host *S. bogotensis* [field#cjm 13139], FMNH), C. J. Marinkelle leg. **VENEZUELA. Mérida:** La Carbonera, 12 km SE La Azulita 2150m, 21/IV/1966 (2 male [1 slide] 1 female, host *Sturnira erythromos* [SVP#4471, 4482], FMNH), N. E. Peterson leg.; 2180m, 23/IV/1966 (1 female [slide], host *S. erythromos* [SVP#4536], FMNH), N. E. Peterson leg. Tabay: 4km E Tabay, La Mucuy, 2107m, 08/III/1966 (1 male [slide], host *S. bogotensis* [SVP#4012], N. E. Peterson leg.

Trichobius sp. 1

Material examined. **COSTA RICA. San Jose:** San Gerardo, 26/III/1985 (1 male [slide] 2 females [1 slide], host *Sturnira* sp., MZSP), R. Eckerlin leg. **Herédia:** Parque Nacional Braulio Carrillo, San Miguel, 3.5 km S, 11.5 km E, 1000 m, 09/IV/1986 (1 male, host *Sturnira mordax* [USNM562835], FMNH), R. L. LaVal leg. **Alayuela:** 4.2 km SE, Cariblanco (10°14´N 84°10‘W), 12/II/1983 (1 female, host *S. mordax* [CM92487], FMNH), T. J. McCarthy leg.

Trichobius sp. 2

Material examined. **PERU. Cuzco:** Paucartambo, Pillahuata, 2460 meters, 03/IV/2001 (1 male [PMV#557], host *Platyrrhinus albericoi*, FMNH), P. M. Velazco leg.; 18/IV/2001 (1 male [SS#2087], host *Platyrrhinus nigellus*, FMNH), S. Solari leg.; 07/X/2001 (1 female [JCH#1168], host *Platyrrhinus infuscus*, FMNH), S. Solari leg.; 13/X/2001 (2 males, 2 females [BDP#4092], host *P. nigellus*, FMNH), B. D. Patterson leg.; 08/XI/2001 (2 females [CWD#P768], host *Platyrrhinus masu*, FMNH), E. Suazo leg.

pallidus group

Trichobius pallidus (Curran, 1934)

Material examined. **BRASIL. São Paulo.** Capão Redondo, Parque Estadual de Intervale, sede de pesquisa, 14/XII/1999 (1 male, host *Furipterus horrens*, DZUP), F. C. Passos & W. A. Pedro leg.; 17/XII/1999 (1 male, 1 female, host *F. horrens*, DZUP), F. C. Passos & W. A. Pedro leg.

caecus group

Trichobius galei Wenzel, 1966

Material examined. **BRASIL. Mato Grosso do Sul.** Corumbá, Instituto Agronômico, 29/I/2003 (4 males, 2 females, host *Natalus stramineus*, DZUP), M. O. Bordignon leg.

uniformis group

Trichobius lonchophyllae Wenzel, 1966

Material examined. **BRASIL. Distrito Federal.** Brasília, Gruta Fenda II, 11/VI/1998 (1 male, 1 female, host *Lonchophylla deykeseri*, DZUP), D. C. Coelho leg. Brazlândia, Gruta da Cafurinca, 02/V/1998 (10 males, host *L. deykeseri*, DZUP), D. C. Coelho leg.; 27/V/1998 (2 males, host *L. deykeseri*, DZUP), D. C. Coelho leg.

dugesii group

dugesii complex

Trichobius tiptoni Wenzel, 1976

Material examined. **BRAZIL**. **Rio Grande do Sul.** Dom Pedro de Alcântara, 24/IV/1997 (4 males, 1 female, host *Anoura caudifer*, DZUP), Graciolli, Rui & Grillo leg.; 6–7/IX/1997 (2 males, host *Anoura geoffroyi*, DZUP), H. C. Z. Grillo leg.; 08/IX/1997 (4 males, 1 female, host *A. caudifer*, DZUP), H. C. Z. Grillo leg.

parasiticus complex

Trichobius parasiticus Gervais, 1844

Material examined. **ARGENTINA. Tucumán.** Arroyo Aguas Chiquitas, Reserva Provincial Aguas Chiquitas, 31/X/1993 (1 male, 1 female, host *Desmodus rotundus*, DZUP), A. G. Autino leg. **BRAZIL. Mato Grosso do Sul.** Fazenda Rio Negro, (1 female, *D. rotundus*, MZSP).

longipes group

Trichobius longipes (Rudow, 1871)

Material examined. **BRAZIL. Distrito Federal.** Brazlândia, Gruta Dois Irmãos, 02/V/1998 (2 females, host *Phyllostomus hastatus*, DZUP), D. C. Coelho leg. **Paraná.** Fênix, Parque Estadual Vila Rica do Espírito Santo, 22/VI/2001 (1 male, host *P. hastatus*, DZUP), G. Bianconi leg.

dunni group

Trichobius jubatus Wenzel, 1976

Material examined. **BRAZIL. Paraná.** Diamante do Norte, 28/IX/1994 (1 male, 2 females, host *Molossus rufus*, MHNCI).

major group

Trichobius major Coquillett, 1899

Material examined. **USA**. **Florida:** Alachua Co., bat cave near Newberry, 04/VIII/1953 (2 males, 2 females, host *Myotis austroriparius*, MZSP), Dale W. Rice leg.

Paratrichobius Costa-Lima, 1921

Paratrichobius longicrus (Miranda-Ribeiro, 1907)

Material examined. **BRAZIL. Paraná.** Londrina, Fundo de Vale Quebec, 13/XI/1998 (2 males, 2 females, host *Artibeus lituratus*, DZUP), G. Graciolli & I. Lima legs. **Rio Grande do Sul.** Dom Pedro de Alcântara, 1997 (1 female, host *A. lituratus*, DZUP), G. Graciolli & A. M. Rui legs.; 10/V/1997 (11 males, 3 females, host *A. lituratus*, DZUP), G. Graciolli & A.M. Rui legs.

Megistopoda Macquart, 1852

Megistopoda aranea (Coquillett, 1899)

Material examined. **BRAZIL. Pará.** Santarém, Alter de Chão, 07/V/2000 (1 male, 1 female, host *Artibeus planirostris*, DZUP), E. Bernard leg. Paraná. Foz do Iguaçu, Parque Nacional do Iguaçu, 12/I/1999 (1 male, host *Artibeus fimbriatus*, DZUP), Graciolli, Lima & Rocha legs. **Rio Grande do Sul.** Dom Pedro de Alcântara, 1997 (1 female, host *Artibeus lituratus*, DZUP), G. Graciolli & A. M. Rui legs.

Megistapophysis Wenzel & Dick, 2006

Megistapophysis mordax Wenzel & Dick, 2006

Material examined. **COSTA RICA. Puntarenas.** Monteverde, 1400m (2 males, host *Sturnira mordax*, DZUP), R. K. Laval leg. **San Jose.** Cerro de La Muerte 10.5 mi N San Isidro General, 1585m, 15/VIII/1963 (2 females, host *Sturnira mordax*, FMNH), R. S. Casebeer leg.

Neotrichobius Wenzel & Aitken, 1966

Neotrichobius delicatus (Machado-Allison, 1965)

Material examined. **BRAZIL**. **São Paulo**. Ilha do Cardoso, 14/III/1991 (1 male, 2 females, host *Artibeus cinereus*, MZSP), S. F. Corrêa leg.

Speiseria Kessel, 1925

Speiseria ambigua Kessel, 1925

Material examined. **BRAZIL. Amazônia.** Reserva 1501 km 41, PDBFF Amazonas, 04/VIII/2003 (1 male, 1 female, host *Carollia* sp., INPA), F. Rocha-Mendes leg. Gavião, Dynamical Biological Forest Fragments Project, 20/X/1997 (1 male, 1 female, host *Carollia perspicillata*, MZSP), E. Sampaio leg.

Strebla Wiedemann, 1824

Strebla wiedemanni Kolenati, 1856

Material examined. **BRAZIL. Paraná.** Almirante Tamandaré, 30/IV/1985 (1 male, 1 female, host *Desmodus rotundus*, DZUP), Viana leg. Rio Branco do Sul, 21/VI/1988 (5 males, host *D. rotundus*, DZUP), Dos Santos leg. São Jerônimo da Serra, 20/VII/1987 (3 males, 4 females, host *D. rotundus*, DZUP), Dos Santos leg.

Appendix 2. Data Matrix of taxa/characters used in the cladistic analysis.

Strebla wiedemanni Kolenati	0 0 0 – – 0 0 0 0 – 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Speiseria ambigua Kessel	1 2 0 0 2 0 0 1 2 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 2 2 1 1 0 0 0 1 0 0 1 0 1 0 1 0 1 0 0 0
Trichobius tiptoni Wenzel	1 3 0 1 1 0 0 0 2 0 1 1 1 1 1 1 0 0 1 0 0 0 1 0 1 1 2 1 0 1 0 0 0 0 1 1 1 1 1 0 1 0 0 0
Trichobius parasiticus Gervais	1 3 0 1 1 0 0 0 2 0 1 2 1 1 2 0 0 0 1 0 0 0 1 0 1 1 2 1 0 1 0 0 0 0 2 1 1 2 1 0 1 0 0 0
Trichobius lonchophyllae Wenzel	1 3 0 1 1 0 0 1 1 0 1 1 2 1 1 0 0 0 1 0 0 0 1 0 1 1 2 1 0 0 0 1 0 0 1 1 1 0 2 0 1 0 1 0
Trichobius longipes (Rudow)	1 4 0 1 1 0 0 0 2 0 1 1 2 1 1 2 0 0 1 0 0 0 1 0 1 1 2 1 0 0 0 0 0 0 1 1 1 2 3 0 1 0 0 0
Trichobius jubatus Wenzel	1 3 1 1 4 0 0 0 2 0 1 1 2 1 1 2 0 0 1 1 0 0 1 0 1 1 2 1 0 0 1 0 0 0 1 1 1 1 2 0 1 0 0 0
Trichobius major Coquillett	2 5 2 1 3 0 1 1 3 5 1 1 2 0 1 0 0 0 3 0 0 0 1 0 1 1 2 1 0 1 0 0 0 0 2 0 0 0 6 0 1 0 1 1
Trichobius galei Wenzel	1 5 3 1 1 1 1 0 4 3 1 2 2 1 2 0 0 0 2 0 0 0 1 0 1 1 2 1 0 0 2 2 1 0 1 0 0 0 1 1 1 0 1 1
Trichobius pallidus (Curran)	2 5 3 1 1 0 1 0 4 2 1 3 2 1 3 0 0 0 2 0 0 0 1 0 1 1 2 1 0 0 2 2 1 0 2 0 0 0 4 1 1 0 1 1
Trichobius sp. 2	3 4 4 0 0 2 0 0 2 1 1 1 1 1 1 3 0 0 0 1 0 0 1 0 2 2 3 1 0 0 1 0 0 0 2 1 0 0 5 0 0 0 1 1
Trichobius vampyropis Wenzel	3 4 4 0 0 2 0 0 2 1 1 1 1 1 1 3 0 0 0 1 0 0 1 0 2 2 3 1 0 0 1 0 0 0 2 1 0 0 5 0 0 0 1 1
Trichobius sp. 1	3 4 4 0 1 2 0 0 2 0 1 1 1 1 1 3 0 0 0 1 0 0 1 1 2 2 3 1 0 0 0 0 0 1 2 1 0 1 5 1 0 0 1 1
Trichobius phyllostomae Kessel	3 4 4 0 0 2 0 0 5 2 1 1 1 1 1 3 0 0 0 1 0 0 1 1 2 2 4 1 0 0 0 0 0 1 2 1 0 1 5 1 0 0 1 1
Trichobius brennani Wenzel	3 4 4 0 1 2 0 0 5 2 1 2 1 1 1 3 0 0 0 1 0 0 1 1 2 2 4 1 0 0 0 0 0 1 2 1 0 1 5 1 0 0 1 1
Trichobius hispidus Wenzel	3 4 4 0 1 2 0 0 2 0 1 2 1 1 2 3 0 0 0 1 0 0 2 0 2 2 3 0 0 0 1 0 0 1 2 1 0 1 5 0 0 0 1 1
Trichobius petersoni Wenzel	3 4 4 0 1 2 0 0 2 0 1 2 1 1 2 3 0 0 0 1 0 0 2 0 2 2 3 0 0 0 0 0 0 1 2 1 0 1 5 1 0 0 1 1
Paratrichobius longicrus (Miranda-Ribeiro)	3 1 4 1 1 2 0 0 1 4 2 3 1 2 3 1 1 1 0 0 1 1 1 0 1 1 2 0 0 0 1 0 0 0 2 1 0 0 5 [0 1] 1 0 1
Neotrichobius delicatus (Machado-Allison)	3 1 4 1 1 2 0 1 1 4 2 3 1 2 3 4 1 1 0 0 1 1 1 0 1 1 2 0 1 0 – – 2 0 2 1 0 0 7 – 0 0 1 1
Megistopoda aranea (Coquillett)	3 1 4 1 1 0 0 [0 1] 2 0 2 3 1 2 3 4 1 1 0 0 1 1 1 0 1 1 2 2 1 0 – 0 2 0 2 1 0 0 5 1 0 1 1
Megistapophysis mordax Wenzel & Dick	3 1 4 0 0 0 0 1 2 0 2 3 1 2 3 4 1 1 0 0 1 1 1 0 1 1 2 0 1 0 – 0 2 0 2 1 0 0 6 0 0 1 1 1