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

Gustavo Graciolli¹ & Claudio J. B. de Carvalho²

¹Departamento de Biologia, Centro de Ciências Biológicas e da Saúde, Universidade Federal de Mato Grosso do Sul, Cidade Universitária, Caixa Postal 549, 79070–900 Campo Grande-MS, Brasil. ggraciolli@yahoo.com.br
²Departamento de Zoologia, Universidade Federal do Paraná, Caixa Postal 19020, 81531–980 Curitiba-PR, Brasil. cjbcarva@ufpr.br

ABSTRACT. 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. We examined whether, like many parasite-host systems of coevolution, a group of obligate parasitic bat flies (*Trichobius phyllostomae* Kessel and related species) co-speciate 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, Megistapophysys))* 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. brevanni* Wenzel)))). When we compared phylogenies through historical association analyses, co-speciation was uncommon, while host-switching was more common and better explained the association between the *phyllostomae* group and their bat hosts.

KEYWORDS. Bat fly; co-speciation; macroevolutionary events; Trichobinaceae; *Sturnira*.


PALAVRAS-CHAVE. Dípteros ectoparásitos de morcegos; co-especiação; eventos macroevolucionários; Trichobinaceae; *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 coevolutionary 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
Do fly parasites of bats and their hosts coevolve?

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*, *Sturnira*, *Platyrrhinus*, *Speiseria*, *Dick & Wenzel*, 2006, *Megistotipoda*, *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. 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*, *phyllostoma* 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 *phyllostoma* group, *T. vampyropis* Wenzel, 1966 was related to *T. hispidus* Wenzel, 1976 while *T. petersoni* Wenzel, 1976 and *T. phyllostoma* Kessel, 1925 were closer to *T. brennani* Wenzel, 1966 (Wenzel 1976).

The five species of the *phyllostoma* 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

The events that are used by TARZAN are cospeciations, duplications, sortings, extinctions, and (host) switching. The cost assignment used for each cophylogenic event was: cospeciation = 2, duplication = 2, sorting = 1, switch = 2. TARZAN reconciliation analysis does not allow 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 vamypropis* 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 longicus* (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. longicus*, *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
Do fly parasites of bats and their hosts coevolve?

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.

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, Megistapophys, and phyllostomae group.

4. Setae 6 of laterovertex: (0) present; (1) absent. L = 3; CI = 33, RI = 75.
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 homoplastically 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.
Do fly parasites of bats and their hosts coevolve?

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.

Cospéciation = 2  
Duplicación = 1  
Sortings = 1  
Switch = 4  
Extinctions = 0
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. longicus. In T. phyllostomae, long and triangular metasternal lobe is a synapomorphy (Figs. 2, 15).
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 Megistopophysis 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, Exastination, Noctiliostreba 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 unsclerotized.

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 cospeciation 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, pallidius, caecus, and 
phyllostoma groups and Paratrichobius, Megistopoda, 
Megistapophysis, and Neotrichobius are in the same large 
clade, while dugesii, dunnii 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 charac-
ters, such as setae on the base of the 1A(2A) vein (Fig. 17) 
and longer distal than basal gonapophyseal setae, may be 
homoplastic. Wenzel et al. (1966) also suggested the pos-
sibility that Speiseria may be related to phyllostoma 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 Megistopaphysis and the T. phyllostoma group, 
Paratrichobius, Megistopoda and Neotrichobius (Dick & 
Wenzel 2006). Thus, the following relationship among gen-
era was predicted: (T. phyllostoma 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 ma-
jor group. Here, we suggest that uniformis, dugesii, longipes, 
and dunnii 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 com-
prehensive 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 pallidius groups 
probably do not belong to Trichobius, but we prefer to wait for a 
more detailed study before renaming caecus group and 
validating Kesselia Curran, 1934 to comprise T. pallidus. 
A new genus should be given to the phyllostoma 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. brenniani, and T. petersoni is a sister-group of T. 
hispidus which is in turn a sister-group T. vampyropis. Here, 
we found that the species that are found on Sturina 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 differ-
ent 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 phyllostoma 
group have strong host specificity, which should favor 
cospeciation, and low prevalence and intensity, which should 
favor sorting, cospeciation and sorting are seldom encoun-
tered. Streblid bat flies are pupiparous, which means that 
instead of eggs, females deposit pupae around the bat roost-
ing 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. Nonethe-
less, because of host grooming behaviors and low rates of 
infestation (small population sizes of the flies), host switch-
ing may be minimal.

Grooming is an important cause of ectoparasite mortal-
ity 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 
blasca Spiezer, 1900 and Noctiliostrebla atikeni Wenzel, 1966 
remains were found in 10% and 2% (respectively) of the fe-
ces of N. leporinus (Bordignon 2006).

Sturina evolved from a highland ancestor (Villalobos 
& Valerio 2002) such as the Andean Platyrrhinus (Velaques 
2005). Platyrrhinus spp. and Sturina bidens (Thomas, 1915) 
have been found syntopically (Molini & Soriano 1987; 
Lidner & Morawetz 2006) and both often use caves for roost-
ing (Gardner 2007; Molinari & Soriano 1987). Other spe-
cies of Sturina do not roost in caves, but rather use tunnels, 
bridges and houses (Molinari & Soriano 1987). These roost-
ing 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 under-
stand 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 brach-
hypterus genera of streblid bat flies, Joblingia and 
Anatrichobius. Joblingia includes two described species. 
Joblingia schmidt Dybas & Wenzel, 1947 parasitizes Myotis 
keaysi J. A. Allen, 1914 and M. oxytus (Peters, 1867) from 
the highlands of Guatemala and Panama (Guerrero 1995).

And the recently described Joblingia minutia 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 
sorvari Wenzel, 1966 is found on Myotis albescens Geoffroy, 
1806, M. keaysi, M. nigricans (Schinz, 1820), M. oxytus 
and occurs from Panama to Argentina (Guerrero 1995;

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.

ACKNOWLEDGMENTS

We thank the following curators and their institutions for the specimens loaned: Márcia Árzua (MHNCI), Eliana Cancello and Mirian Marques (MZSP), and Rupert L. Wenzel and Carl W. Dick (FMNH). We are grateful to Luciane Marinoni, Walter A. P. Boeger, Aricio X. Linhares, Mauricio O. Moura, Marcela Lareschi, and Silvio S. Nihei for helpful comments. We are grateful to David Notton for sending digital images of the holotype of Trichobius phyllostomae. Maureen Turcatel prepared the illustration of Sturnira in Fig. 2. This study was funded by the CNPq (#140214/00–3) and National Science Foundation (DBI-0545051) -“Digitization, Conversion, and Accessibility of The Field Museum’s Bat Fly Collection.” Carl W. Dick, PI; Bruce D. Patterson, Joanna McCaffrey, Alfred F. Newton, CoPIs. CJBC is also grateful to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), for the support provided (process # 304713/2011–2). Contribution number 1781 of Departamento de Zoologia, UFPR.

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

<table>
<thead>
<tr>
<th>Authors</th>
<th>Parasite</th>
<th>Host</th>
<th>Software</th>
<th>Events</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paterson et al. (2000)</td>
<td>Phthartera (Lice)</td>
<td>Phthartera (14 spp., 6 Genera)</td>
<td>TreeMap 1.0</td>
<td>Cospeciation Switch Duplication Sorting</td>
</tr>
<tr>
<td>Jonshon et al. (2003)</td>
<td>Columbicola (19 taxa, 5 genera)</td>
<td>Columbicola (25 taxa, 22 genera)</td>
<td>TreeMap 1.0</td>
<td>9 0-1 3-4 11-14</td>
</tr>
<tr>
<td>Weckstein (2004)</td>
<td>5 subfamilies of 1 spp.</td>
<td>Toucans (11 spp.)</td>
<td>TreeMap 1.0</td>
<td>9 0 3 17-22</td>
</tr>
<tr>
<td>Banks et al. (2006)</td>
<td>Ischnocera (Austrogoniodes ) (15 spp.)</td>
<td>Penguins (17 spp.)</td>
<td>TreeMap 2.0B</td>
<td>3-4 0-1 5-7 15-22</td>
</tr>
<tr>
<td>Hughes et al. (2007)</td>
<td>Pectinopygus (17 spp.)</td>
<td>Pelecaniformes (18 spp.)</td>
<td>TreeMap 2.0B</td>
<td>10-11 0-6 5-6 3-19</td>
</tr>
<tr>
<td>Smith et al. (2008)</td>
<td>Anoplura (Hoplolopura (11 spp.), Linognathoides (1 spp)); Pteophthirius initates (2 spp.)</td>
<td>Akodonini and Oryzomyini (20 spp.)</td>
<td>TreeMap 2.0B</td>
<td>12-20 3-4 10-14 1-12</td>
</tr>
<tr>
<td>Morelli &amp; Spicer (2007)</td>
<td>Ptilonyssus sairae (6 infrapopulations)</td>
<td>Birds (5 spp.)</td>
<td>TreeMap 1.0</td>
<td>5 0 0 0</td>
</tr>
<tr>
<td>Bochov et al. (2011)</td>
<td>Avenzorainae (26 spp., 6 genera)</td>
<td>Avenzorainae (26 spp., 6 genera)</td>
<td>TreeMap 1.0</td>
<td>12-13 2 6-7 26-29</td>
</tr>
<tr>
<td>Dabert et al. (2001)</td>
<td>Avenzorainae (26 spp., 6 genera)</td>
<td>Avenzorainae (26 spp., 6 genera)</td>
<td>TreeMap 1.0</td>
<td>5 0 0 0</td>
</tr>
<tr>
<td>Liang &amp; Houyoung (2005)</td>
<td>Geusibia (12 spp.)</td>
<td>Lagomorpha (12 spp.)</td>
<td>TreeMap 1.0</td>
<td>12 0 2 2</td>
</tr>
<tr>
<td>Krasnov &amp; Shenbrot (2002)</td>
<td>Siphonaptera (19 spp.)</td>
<td>Rodentia (12 spp.)</td>
<td>TreeMap 1.0</td>
<td>0 0 18 105</td>
</tr>
<tr>
<td>Dia otra</td>
<td>Trichobius phyllostomae group (7 spp.)</td>
<td>Stenodermatine bats (21 taxa)</td>
<td>Tarzan 0.9</td>
<td>2 4 1 0</td>
</tr>
<tr>
<td>Cumming (2000)</td>
<td>Ticks</td>
<td>Tropopoda (16 taxa)</td>
<td>TreeMap 1.0</td>
<td>0 0 13 73</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>TreeMap 1.0</td>
<td>2 0 11 66</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>18 148</td>
</tr>
</tbody>
</table>
REFERENCES


Page, R. D. M. 2001. NDE – Nexus Data Editor 0.5.0. http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html


Revisva Brasileira de Entomology 56(4): 436–450, dezembro, 2012
Received 18/4/2012; accepted 26/10/2012

Editor: Marcia Souto Couri

Appendix 1. Examined specimens.

**Trichobius Gervais, 1844**

**Trichobius 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.


**Trichobius brennani Wenzel, 1966**


**Trichobius vampyrops Wenzel, 1966**


Material examined. **VENUEZU. Distrito Federal:** Los Venados, 4 km NNW Caracas, 1524m, 29/VII/1965 (1 female, host Vampyrops unbratus [ = Platyrhinus dorsalis] [SPV#334], FMNH), A. Peterson & M. Tuttle leg.; 1400m, 02/VIII/1965 (2 males, 1 female, host Vampyrops unbratus [ = Platyrhinus dorsalis] [SPV#495, 508], A. Peterson & M. Tuttle leg.; 1430m, 02/VIII/1965 (1 male, 1 female, host Vampyrops unbratus [ = Platyrhinus dorsalis] [SPV#499], A. Peterson & M. Tuttle leg.; 1463m, 03/VIII/1965 (3 males, 1 female, host Vampyrops unbratus [ = Platyrhinus vittatus] [SPV#539], FMNH), A. Peterson & M. Tuttle leg. Pico Ávila, 5km NNE Caracas, near Hotel Humboldt, 2092m, 20/VIII/1965 (1 male, host Vampyrops unbratus [ = Platyrhinus dorsalis] [SPV#676], FMNH). A. Peterson & M. Tuttle leg.

**Trichobius hispidus Wenzel, 1976**

Type material examined. Paratypes. **VENUEZU. Mérida:** Tabay, 6 km ESSE Tabay, Midlle Refugio, 2550 m, 06/IV/1966 (2 females [slide], host Sturnira bidens [SPV#4369, 4372], FMNH), N. E. Peterson leg.; 2640m, 08/IV/1966 (1 male, 1 female, host S. bidens [SPV#4391], FMNH), N. E. Peterson leg.; 2640m, 11/IV/1966 (1 male, host Sturnira bidens [SPV#4441], FMNH), N. E. Peterson leg.; 2640m, 11/IV/1966 (1 male, host Sturnira bidens [SPV#4447], FMNH), N. E. Peterson leg.

**Trichobius petersoni Wenzel, 1976**

Type material examined. Holotype. **COLOMBIA. Cundinamarca:** Bogota, X/1968 (1 male [slide], host Sturnira bogotensis [field #913139], FMNH), C. J. Marinkelle leg. Paratipo. **COLOMBIA. Cundinamarca:** Bogota, X/1968 (1 female [Allotype #46, slide], host S. bogotensis [field #913139], FMNH), C. J. Marinkelle leg. **VENUEZU-ELA. Mérida:** La Carbonera, 12 km SE La Azulita 2150m, 21/IV/1966 (2 males, 1 female, host Sturnira erythromos [SPV#4471, 4482], FMNH), N. E. Peterson leg.; 02/VIII/1965 (1 male [slide], host S. erythromos [SPV#4536], FMNH), N. E. Peterson leg. Tabay: 4km E Tabay, La Mucuy, 2107m, 08/III/1966 (1 male [slide], host S. bogotensis [SPV#4012], N. E. Peterson leg.)


Do fly parasites of bats and their hosts coevolve?

Trichobius sp. 1

Material examined. COSTA RICA. San José: San Gerardo, 26/II/1985 (1 male [slide] 2 females [1 slide], host Sturnia sp., MZSP), R. Eckerlin leg. Heredia: Parque Nacional Braulio Carrillo, San Miguel, 3.5 km S, 11.5 km E, 1000 m, 09/IV/1986 (1 male, host Sturnia mordax [USNM562835], FMNH), R. L. LaVal leg. Alayuela: 4.2 km SE, Cariblanco (1°16’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 Platyrhinus albericoi, FMNH), P. M. Velazco leg.; 18/IV/2001 (1 male [SS#2087], host Platyrhinus nigellus, FMNH), S. Solari leg.; 07/X/2001 (1 female [ICH#1168], host Platyrhinus 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 Platyrhinus musu, FMNH), E. Suazo leg.

cacaeus group

Trichobius galei Wenzel, 1966

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

uniformis group

Trichobius lonchophyllae Wenzel, 1966


dugesii group

Trichobius tiptoni Wenzel, 1976


parasiticus complex

Trichobius parasiticus Gervais, 1844


longipes group

Trichobius longipes (Rudow, 1871)


dunni group

Trichobius jubatus Wenzel, 1976


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)


Megistopoda Macquart, 1852

Megistopoda aranea (Coquillett, 1899)


Megistapophysis Wenzel & Dick, 2006

Megistapophysis mordax Wenzel & Dick, 2006

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


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

<table>
<thead>
<tr>
<th>Species/Genus</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strebda wiedemanni Kolenati</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Speiseria ambigua Kessel</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius tpiomi Wenzel</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius parausticus Gervais</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius lonchophyllae Wenzel</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius longipes (Rudow)</td>
<td>5</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius jubatus Wenzel</td>
<td>6</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius major Coquillett</td>
<td>7</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius galei Wenzel</td>
<td>8</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius pallidus (Curran)</td>
<td>9</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius sp. 2</td>
<td>10</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius vampyropes Wenzel</td>
<td>11</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius sp. 1</td>
<td>12</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius phyllostomae Kessel</td>
<td>13</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius brennani Wenzel</td>
<td>14</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius hispidus Wenzel</td>
<td>15</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trichobius petersoni Wenzel</td>
<td>16</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Paratrichobius longicrus (Miranda-Ribeiro)</td>
<td>17</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Neotrichobius delicatus (Machado-Allison)</td>
<td>18</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Megatopoides aranea (Coquillett)</td>
<td>19</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Megatopoides mordax Wenzel &amp; Dick</td>
<td>20</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>