
DISTRIBUTIONAL EVIDENCE FOR COSPECIATION BETWEEN NEOTROPICAL BATS AND THEIR BAT FLY ECTOPARASITES

Bruce D. Patterson, J. William O. Ballard and Rupert L. Wenzel

Department of Zoology, Field Museum of Natural History, Chicago, U S A

ABSTRACT

Distributional evidence bearing on cospeciation of New World bats (superfamily Noctilionoidea) and associated bat flies (Diptera: Streblidae) was analyzed and revealed substantial phylogenetic structure, especially when we focused on “normal” host associations and encoded the data set hierarchically. Brooks’ parsimony analyses of bat fly occurrences among hosts recovered generally accepted sets of host relationships. Putatively monophyletic host taxa provide a necessary but insufficient condition for coevolution via cospeciation.

KEYWORDS: Chiroptera, Phyllostomidae, Diptera, Streblidae, bats, bat flies, ectoparasite occurrence, cospeciation.

“The main difficulty in the way of a general use of the parasitological method is that only a minute amount of the possible knowledge of parasites and their hosts is available. Many fortunate circumstances must coincide and much difficult work be done to make known a single host-parasite relationship, and the discovery of even several new relationships scarcely promises anything very interesting. Only the comparative investigation as nearly as possible of all existing relationships will reveal the conformities to law.” W. Hennig 1979, p. 180

INTRODUCTION

Few systems involving mammals and their ectoparasites have been investigated sufficiently to identify them as products of cospeciation. We investigated

Address correspondence to: Bruce D. Patterson, Department of Zoology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago IL 60605-2496, USA. Fax: +1-312-663 5397; e-mail: bpatterson@fmnh.org

the host-parasite system of the New World bat clade Noctilionoidea (Simmons, 1998) and its bat flies, the Streblidae. This system offers various opportunities for “horizontal” transfers of parasites among hosts: (1) bat species exhibit high degrees of spatial overlap, on both geographic and habitat scales; (2) many bats are social, some roosting in dense colonies containing thousands of conspecific individuals, while others roost in characteristic multi-specific associations; and (3) pupation of the flies takes place off of the host, in the roost, forcing newly emergent parasites to become reassociated with their hosts. Horizontal transfers would disrupt associations of bat fly species with bat species, eventually lessening both the specificity and strength of their host-parasite association.

Despite this potential, bat fly assemblages on Neotropical bats exhibit a remarkable host specificity. “Increasing knowledge of the Nycteribiidae and Streblidae [the two families of bat flies] is showing ... that they are nearly always confined to a single species or genus of host” (Marshall, 1982, p. 381). In quantitative terms, fully 70% of the 94 Panamanian

streblid species covered by Wenzel et al. (1966) were monoxenous, and even non-specific flies had apparent host associations. Another necessary (but still insufficient) condition for cospeciation is that parasites be distributed on clades of hosts, and vice versa, so that distributions reflect hierarchical relationships within each group (Brooks, 1981). Here, we compare "Brooks' parsimony" trees of bats, which treat occurrences of bat flies as derived character states, to independently established host phylogenies.

MATERIALS AND METHODS

The study system

Bat flies. The dipteran families Streblidae and Nycteribiidae are blood-feeding parasites of bats, and

both spend their entire lives on bats or in their roosts. The Streblidae (31 genera and 224 species; Marshall, 1982) are especially diverse on microchiropterans and in the New World. Although phylogenies are lacking, Old and New World streblids are highly distinctive and have no taxa in common, even at the subfamily level. Brachytarsiinae ("Nycteriboscinae;" 3 genera, 45 species) and Ascodipterinae (1, 17) are found only in the Old World, whereas Nycterophilinae (2, 7), Trichobiinae (18, 114), and Streblinae (4, 32) are exclusive to the Western Hemisphere. While little is known of their ecology (Overall, 1980), American streblids exhibit enormous morphological diversity (Fig. 1), varying in numerous attributes (presence/absence of wings, variation in number of eye facets) that probably affect host-parasite relationships. Extensive surveys of streblids and their host

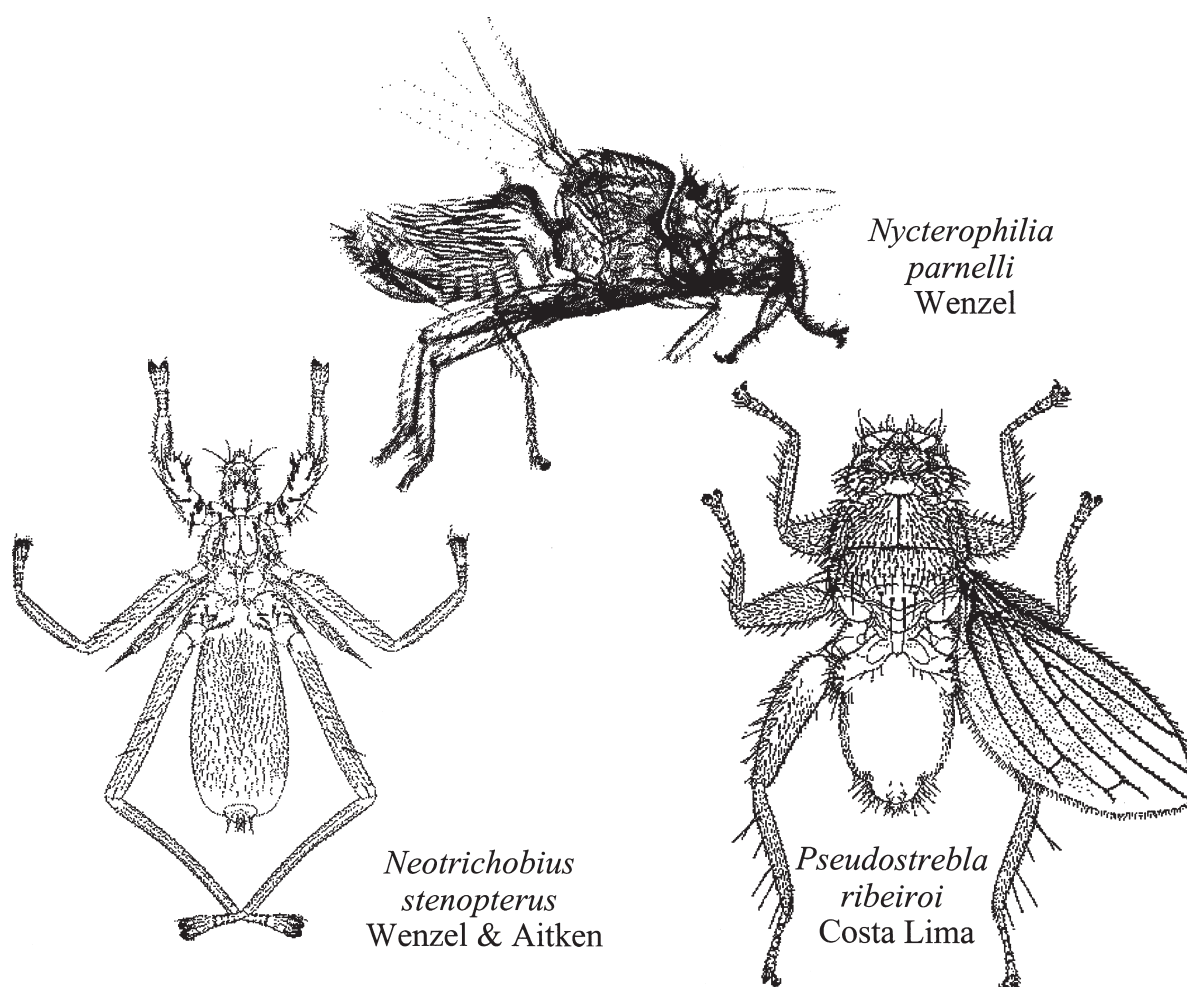


Fig. 1. Morphological diversity of American Streblidae (Diptera), showing winged and wingless species, as well as forms convergent on fleas (after Wenzel et al., 1966).

relationships by Wenzel and associates (Wenzel et al., 1966; Wenzel, 1976) offer meaningful summaries of their distributions among New World bats.

Bats. American streblids are most diverse on Noctilionoidea, a Neotropical clade that includes the leaf-nosed bats, Phyllostomidae (49 genera, 143 species listed in Koopman, 1993), and their sister clade, Noctilionidae (1, 2) + Mormoopidae (2, 8; see Simmons, 1998). Local assemblages of these bats are the world's richest, potentially exposing dozens or scores of syntopic species to a given parasite (Patterson et al., 1996). The bats vary in numerous traits that affect their suitability and susceptibility as hosts. For example, trophic and microhabitat differentiation (Baker et al., 1977) has in turn led to variation in physiological parameters (McNab, 1982) and in reproductive and social systems (Kunz & Racey, 1987). Noctilionoids also use roosting structures that vary in size, dispersion, and predictability, from rocky caves and crevices through termite mounds and tree boles to ephemeral "tents" regularly fashioned from plant leaves. Variation in any of these traits could affect the suitability and susceptibility of potential hosts.

There is a growing literature on the phylogenetics of various New World bat groups. Although much remains to be done, existing bat phylogenies can be used to evaluate the nature and scope of cospeciation with streblids. Family diagnosis and outgroup selection follows from Simmons (1998), relationships among Mormoopidae from Smith (1972), phylogeny for the tribes and subfamilies of Phyllostomidae from Baker et al. (1989), and analyses of the tribe Stenodermatini from Van Den Bussche (1992). Various authors have elucidated relationships of species within polytypic phyllostomid genera, including *Micronycteris* (Simmons, 1996), *Phyllostomus* and *Phyllostoma* (Baker et al., 1988; Van Den Bussche & Baker, 1993), *Sturnira* (Pacheco & Patterson, 1991), *Artibeus* (Patterson et al., 1992; Van Den Bussche et al., in press), and *Chiroderma* (Baker et al., 1994).

Analytical procedures

If the distributions of parasites are established by the "vertical" or genealogical transfers on which cospeciation depends, then they should be congruent with host phylogenetic patterns. Each bifurcation in the host tree will be mirrored by a corresponding fork in the parasite tree. However, even if speciation of hosts and parasites is asynchronous, parasite species will

be distributed on monophyletic groups of hosts. This reasoning underlies the approach taken by Brooks (1981), now known as "Brooks' parsimony." Here, the presence of a given bat fly taxon on two or more host taxa is taken to represent a shared derived condition, one that evolved *in situ* and persists until further speciation eliminates this synapomorphy.

Although host-parasite information for New World Streblidae is available from various sources, we based our analyses on those records established in Wenzel et al. (1966) and Wenzel (1976) for the faunas of Panamá and Venezuela. These records are: (1) Comprehensive – by including all bats and bat flies that could be sampled, these surveys avoid the taxonomic bias introduced by intensive studies of selected groups. (2) Strictly comparable – in terms of host and parasite nomenclature. (3) Well documented – typically with vouchers for both flies and bats. (4) Annotated – each accompanied by the authors' judgement on whether the associations were "normal," or instead were accidental or the result of contamination. We excluded from analysis bat flies that occurred on only a single host (as being uninformative) and bats supporting no more than a single streblid species (as likely to be under sampled and prone to spurious association in the parsimony analysis). We recognize that the latter criterion may cause us to exclude from analysis some complete parasite faunas. The bat fly species used in analyzing bat species are listed (Table 1).

This collection of host records was then filtered by two different sets of criteria to create four data matrices. One criterion distinguished "normal" (= not accidental or the product of contamination; *sensu* Wenzel et al., 1966) from total host records. The second distinguished normal and total records at different taxonomic levels: bat fly species on species of bat, and bat fly genera on genera of bats. If cospeciation characterizes a host-parasite system, contemporaneous speciation progressively eliminates synapomorphies for more distantly related hosts. On logical grounds, then, the genera-genera matrix should better retrieve the deeper nodes in the host tree by helping to extend the synapomorphies from the distal tips to lower branches. This encoding scheme implicitly assumes the monophyly of both bat and bat fly genera, so that our results cannot be construed as offering support for them.

All "characters" were treated as unordered. Four species of *Pteronotus* (Mormoopidae) were treated

TABLE 1. Distributions of the following bat fly species were used in analyses of bat species. All were taken from Wenzel et al. (1966) and Wenzel (1976). Different sets and subsets were used in analyses of “normal” associations and bat genera according to criteria given in Materials and Methods.

Nycterophiliinae	<i>Nycterophilia coxata</i> , <i>N. fairchildi</i> , <i>N. mormoopsis</i> , <i>N. parnelli</i> , <i>Phalcomonus puliciformis</i>
Streblinae	<i>Anastrebla caudiferae</i> , <i>Anastrebla mattadeni</i> , <i>Anastrebla modestini</i> , <i>Anastrebla nycteridis</i> , <i>Anastrebla spurrelli</i> , <i>Metelasmus pseudopterus</i> , <i>Metelasmus</i> sp., <i>Paraeuctenodes longipes</i> , <i>Paraeuctenodes similis</i> , <i>Paraeuctenodes</i> sp., <i>Strebla almani</i> , <i>Strebla alvarezi</i> , <i>Strebla carolliae</i> , <i>Strebla christinae</i> , <i>Strebla chrotopteri</i> , <i>Strebla consocii</i> , <i>Strebla curvata</i> , <i>Strebla diaemi</i> , <i>Strebla diphyllae</i> , <i>Strebla galindoi</i> , <i>Strebla guajiro</i> , <i>Strebla harderi</i> , <i>Strebla hertigi</i> , <i>Strebla hoogstraali</i> , <i>Strebla kohlsi</i> , <i>Strebla machadoi</i> , <i>Strebla matsoni</i> , <i>Strebla mirabilis</i> , <i>Strebla obtusa</i> , <i>Strebla paramirabilis</i> , <i>Strebla tonatiae</i> , <i>Strebla vespertilionis</i> , <i>Strebla wiedemanni</i> .
Trichobiinae	<i>Anatrichobius scorzai</i> , <i>Aspidoptera buscki</i> , <i>A. delatorrei</i> , <i>A. falcata</i> , <i>Eldunnia breviceps</i> , <i>Exastinion clovisi</i> , <i>E. oculatum</i> , <i>Mastoptera guimaraesi</i> , <i>M. minuta</i> , <i>M. minuta</i> complex, <i>Megistopoda aranea</i> , <i>M. proxima</i> complex, <i>M. theodori</i> , <i>Neotrichobius delicatus</i> , <i>N. setosus</i> , <i>N. stenopterus</i> , <i>Parastrebla handleyi</i> , <i>Paratrichobius dunni</i> , <i>P. longicrus</i> , <i>P. longicrus</i> complex, <i>P. lowei</i> , <i>P. salvini</i> , <i>P. salvini</i> complex, <i>P. sanchezi</i> , <i>P. sp.</i> , <i>P. sp. A</i> , <i>P. sp. B</i> , <i>Pseudostrebla greenwelli</i> , <i>P. ribeiroi</i> , <i>P. sparsisetis</i> , <i>Speiseria ambigua</i> , <i>S. magniocolus</i> , <i>S. peytonae</i> , <i>Stizostrebla longirostris</i> , <i>Trichobioides perspicillatus</i> , <i>Trichobius affinis</i> , <i>T. angulatus</i> , <i>T. assimilis</i> , <i>T. bequaerti</i> , <i>T. bilobus</i> , <i>T. brennani</i> , <i>T. caecus</i> , <i>T. cf. joblingi</i> , <i>T. costalimai</i> , <i>T. diaemi</i> , <i>T. diphyllae</i> , <i>T. dugesii</i> , <i>T. dugesioides</i> , <i>T. dybasi</i> , <i>T. ethophallus</i> , <i>T. flagellatus</i> , <i>T. furmani</i> , <i>T. galei</i> , <i>T. handleyi</i> , <i>T. hispidus</i> , <i>T. imitator</i> , <i>T. joblingi</i> , <i>T. johnsonae</i> , <i>T. keenani</i> , <i>T. leionotus</i> , <i>T. lionycteridis</i> , <i>T. lonchophylla</i> , <i>T. longipes</i> , <i>T. macrophylli</i> , <i>T. mendezii</i> , <i>T. parasiticus</i> , <i>T. parasparsus</i> , <i>T. persimilis</i> , <i>T. petersoni</i> , <i>T. phyllostomae</i> , <i>T. propinquus</i> , <i>T. silvicolae</i> , <i>T. sp. (1)</i> , <i>T. sp. (2)</i> , <i>T. sparsus</i> , <i>T. sphaeronotus</i> , <i>T. tiptoni</i> , <i>T. uniformis</i> , <i>T. urodermae</i> , <i>T. vampyropis</i> , <i>T. yunkerii</i> .

as outgroups for the species-by-species analysis, *Pteronotus* as the sole outgroup in the genus-by-genus analysis. Matrices were subjected to heuristic searches (TBR option of PAUP 3.1.1) which minimized the steps needed to specify host relationships. We use strict consensus trees to specify topologies common to multiple equal-length trees. Bootstrap replicates were run on each data set to evaluate nodal support.

RESULTS

Species-level analyses

In all, 27 species of noctilionoids (23 phyllostomids and 4 mormoopids treated as outgroups) were sampled thoroughly enough and supported diverse enough bat fly faunas to be included in this study, and 65 species of streblids have been recorded as ectoparasites of two or more of them (Table 1). Heuristic searches uncovered 514 equally parsimonious trees, each with 189 steps (CI = 0.344), and enabled us to construct a strict consensus tree (Fig. 2a). Only one of the three groupings indicated by this tree, three of the four *Anoura* species, could be real. Remaining groups combine a derived in-group member (*Artibeus lituratus*) with a designated outgroup (*Pteronotus parnellii*), or render *Phyllostomus* paraphyletic with respect to members of the Carollinae (*Carollia perspicillata*) and Stenodermatinae (*Artibeus jamaicensis*).

Analyzing the same set of bats using their “normal” complements of bat flies reduces the informative pool of streblid species to 58. Heuristic search routines identified four trees, each with 83 steps (CI = 0.807). In contrast to the earlier analysis, a strict consensus of shortest trees (Fig. 2b) much more closely approximated known relationships. It identified species belonging to all seven genera analyzed as sisters of other congeneric species. Only congeneric species were associated with one another. All four species of *Anoura* and *Carollia* were so associated, as were all three species of *Glossophaga* and *Phyllostomus*. One species of *Artibeus*, and one of *Micronycteris*, were excluded from groupings of remaining congeners, and the consensus tree united only two of the four outgroup species of *Pteronotus*. Analysis of normal parasite faunas failed to identify any intergeneric relationships; each bat genus stems from an unresolved polytomy.

Genus-level analyses

Host distributions of bat flies were also evaluated between genera of bat flies on genera of bats, tallying all of the individual records for constituent species of both host and parasite. This analysis included all 22 genera of phyllostomids from which at least two streblid genera have been recorded, a subjective and *a priori* designation of sampling intensity. An acknowledged problem with this analysis is that there are fewer characters than taxa: only 15 streblid genera were parsimony-informative. (This limitation

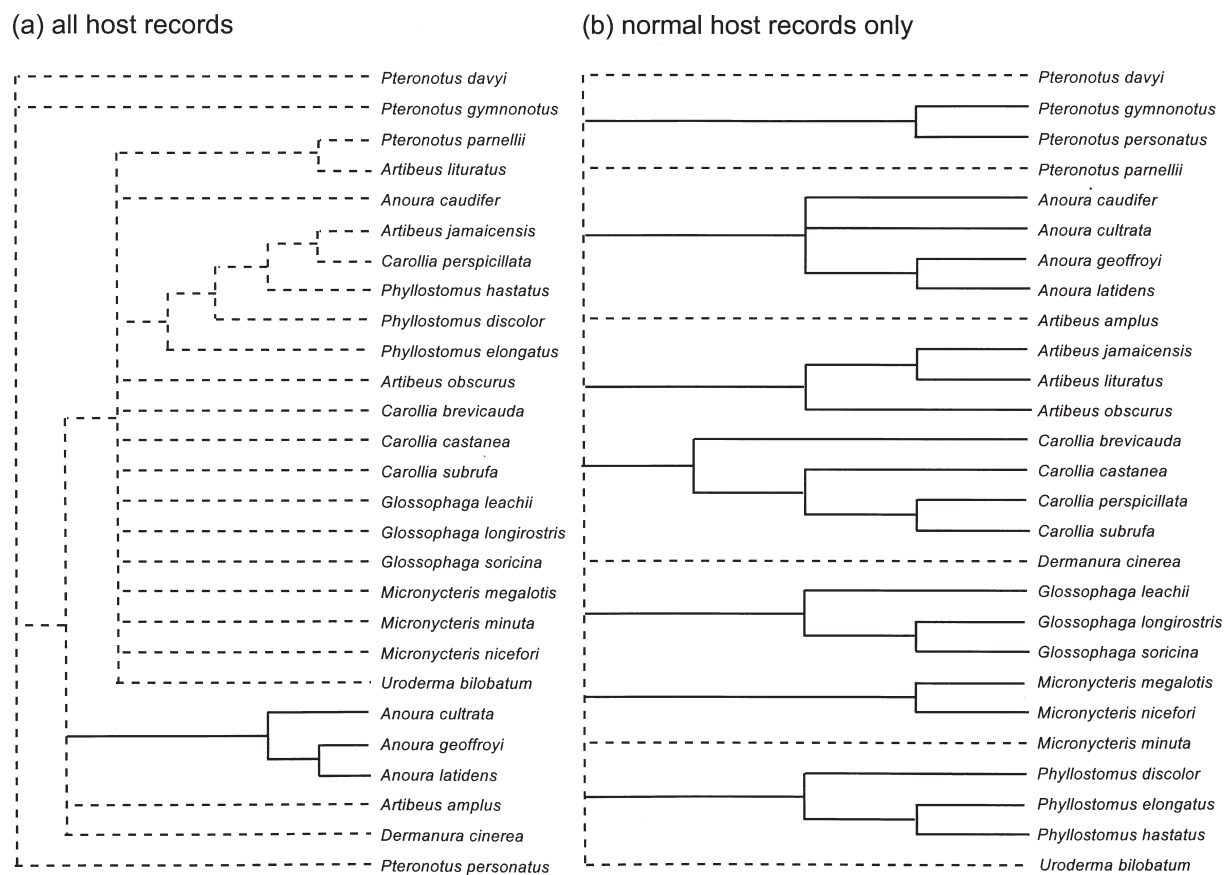


Fig. 2. Brooks' parsimony analyses of bat fly species on species of phyllostomid bats. (a) all host records: strict consensus of 514 equally parsimonious trees, each with 189 steps (CI = 0.344). (b) "normal" host records of streblids: strict consensus of four trees of 83 steps (CI = 0.807). Groupings of bat species that are plausible in terms of known phylogenetic relationships are indicated by solid lines, the remainder by dashed lines. The greater resolution afforded by "normal" host records is obvious, particularly in allying congeneric species. Nevertheless, the analysis based on species-level relationships is plainly impotent at retrieving deeper phylogenetic nodes. See text for discussion.

precluded analyses of streblid genera on bat species). Heuristic searches identified 417 minimum-length trees of 37 steps (CI = 0.405), allowing to calculate one strict consensus tree (Fig. 3a). This tree resolves very few included taxa; the only three genera allied by the analysis are all members of the Stenodermatinae.

Restricting the generic analysis to "normal" records reduces the bat fly pool to 12. Heuristic searches identified 75 minimum-length trees, each 21 steps long (CI = 0.571). The strict consensus tree (Fig. 3b) identifies three purported clades. The first contains six genera all representing the Stenodermatinae; a second unites a glossophagine (*Leptonyc-teris*) with the designated outgroup *Pteronotus* (a mormoopid); and the third unites two phyllostomine

genera, *Phyllostomus* and *Tonatia*. Relative to earlier cited analyses, there is a greater degree of higher-level structure implied in this cladogram.

DISCUSSION

Overall, there is little evidence of phylogenetic structure in the distributions of streblids on phyllostomids. Most of the nodes in consensus trees based on overall distributions remain unresolved and, worse, some apparent clades unite disparate taxa of bats. "Normal" host records of streblids provide better phylogenetic resolution. As expected, distributions of bat fly species on species of bats retrieve lower-level relationships but offer little resolution of the deeper

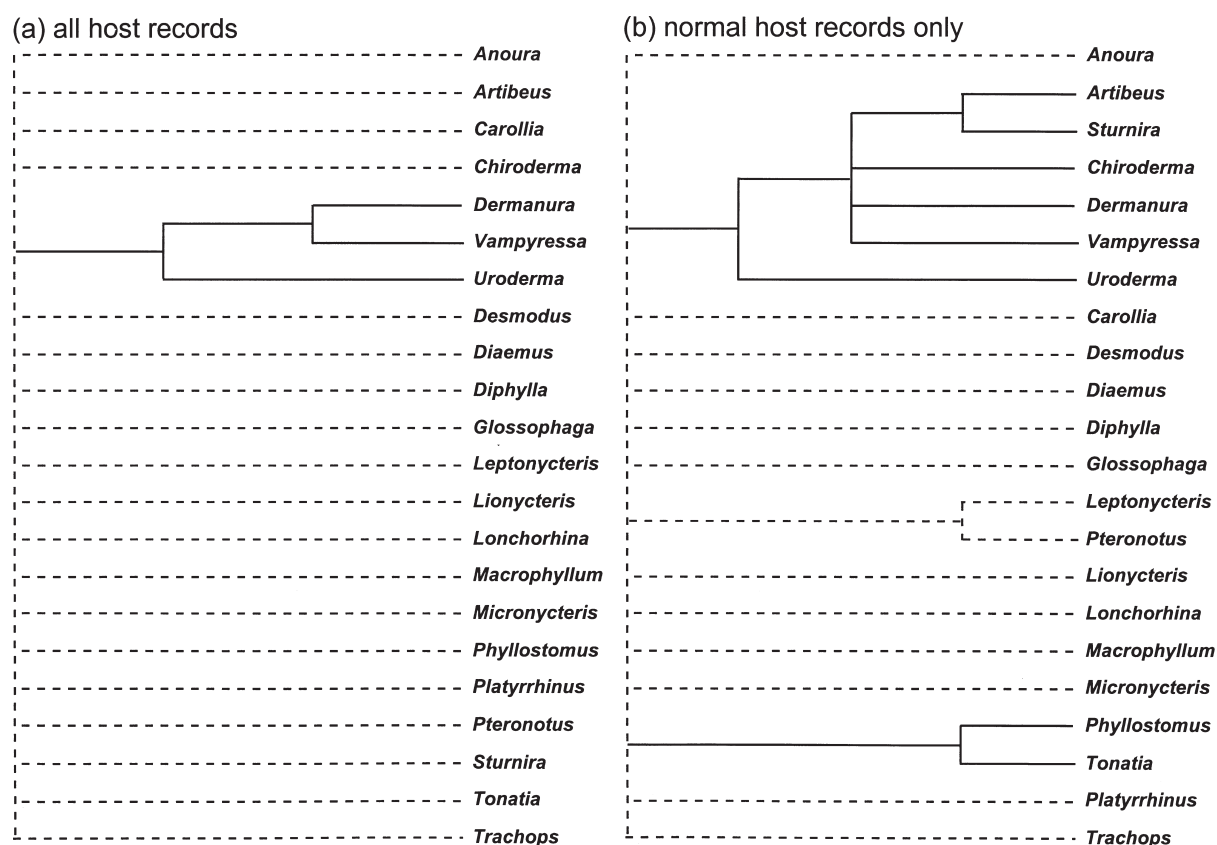


Fig. 3. Brooks' parsimony analyses of bat fly genera on genera of phyllostomid bats. (a) all host records: strict consensus of 417 minimum-length trees of 37 steps (CI=0.405). (b) "normal" host records of streblids: strict consensus of 75 minimum-length trees of 21 steps (CI=0.571). Both analyses retrieve elements of the subfamily Stenodermatinae, while that based on "normal" records a more complete cluster of stenodermatines and two additional pairs, only one of which is real. See text for discussion.

nodes. Some intergeneric relationships are recovered from the distributions of streblid genera on bat genera, while others are wholly unspecified. However, bootstrap analyses show that the phylogenetic signal uncovered by both sets of analyses is fragile. None of the nodes is retained in >75% of the replicates. This lack of support reflects homoplasy, or conflicting hierarchical patterns among the various streblid distributions.

Distribution trees and phylogeny

Trees generated using distributions of parasites normally found on Neotropical bats recover generally accepted sets of bat relationships. The species-level analyses ally congeners in each of the seven polytypic genera analyzed. In some cases (*Anoura*, *Carollia*, *Glossophaga*, and *Phyllostomus*), all allied species were included in these groupings, whereas in other cases (*Pteronotus*, *Artibeus*, and *Micronycteris*), one

or more species were excluded from these clusters. In no case did "normal parasite" data indicate that a member of one genus was allied with members of another. The analysis was flawed by lack of resolution, not false statements of relationships.

The sister-group relationship of *Phyllostomus elongatus* and *hastatus* relative to *discolor* indicated by parasite data is consistent with phylogenetic analyses of bats based on both allozymes (Baker et al., 1988) and cytochrome *b* sequences (Van den Bussche & Baker, 1993). However, the relationship identified between *Artibeus jamaicensis* and *A. lituratus* relative to *A. obscurus* is contradicted by cytochrome *b* sequence analyses by Van den Bussche et al. (in press).

The genus-level analysis of normal host distributions (Fig. 3b) identified a well marked cluster of six bat genera. All of the species included in this cluster are members of the Stenodermatinae as generally

constituted (Koopman, 1993). *Carollia*, which was treated as a stenodermatine by Baker et al. (1989) but a carolliine by Koopman (1993), is excluded from this group, as is the indisputable stenodermatine *Platyrhinus*. However, relationships within this cluster are incompatible with current understanding of New World fruit bats. *Sturnira*, universally regarded as a basal stenodermatine (Pacheco & Patterson, 1992), is united with *Artibeus* as the terminal-most pair of this analysis. Alignment of *Tonatia* with *Phyllostomus* is compatible with classifications offered by both Baker et al. (1989) and Koopman (1993). However, the postulated sister relationship of *Leptoncyteris* and outgroup *Pteronotus* derives not from their phylogenetic relationship (which lies at the superfamily level) but from joint roosting in caves, where horizontal transfers of flies have evidently occurred (Wenzel, 1976).

Lack of resolution in this analysis may be due to incomplete sampling of bat fly faunas, which would limit resolution by masking potential synapomorphies. Future analyses could be strengthened (and their resolution sharpened) by including as many parasite-host records as possible.

Assessing “normal” records

Both genus- and species-level analyses underscore the importance of identifying “normal” host associations. A host record was regarded as “normal” unless it involved an exceptional (infrequent) association of host and parasite or was thought to result from contamination (Wenzel et al., 1966; Wenzel, 1976). That trees based on “normal” distribution records are more consistent with bat phylogeny may reflect the acuity of these determinations. However, if host relationships unconsciously entered this determination, the parsimony analyses would present a circular argument for cospeciation. Future assessments of normalcy could be made objectively by using arbitrary but quantitative criteria. For example, it might be profitable to designate “normal” hosts as those with, say, >10% of known host records. Establishing quantitative thresholds for sampling may also help to reduce the homoplasy problem indicated by low bootstrap values.

Coevolution in addition to cospeciation?

Evidence for cospeciation between bats and bat flies raises numerous questions: Are the phylogenies of New World bats and their ectoparasites congruent

(do they share a common branching structure)? To what degree(s) and at which levels? What biological characteristics in bats and flies promote close correspondence in evolutionary patterns? Are “reticulations” in the bat fly trees products of accidental host transfers or regular roosting associations? Is cospeciation (Eichler, 1940) more likely in cases involving either flightless streblids or geographic isolation of their hosts? Where cospeciation is documented, do bats and flies evolve at equal rates? Because all of these questions require reference to a robust phylogenetic framework for both groups, phylogenetic analyses will be an essential component of future studies.

Correspondence between the hierarchical structures of these trees is used to gauge the nature and extent of possible cospeciation (Hafner & Nadler, 1988, 1990). Although it seems likely that blood-feeding bat flies exact a physiological cost from their hosts (and bat fly bites are certainly painful to some primates!), our analysis provides circumstantial evidence that bats affect bat fly diversification but offers no insight into the ways that flies have shaped bat evolution.

Importantly for tests of coevolutionary theory (Timm, 1983), the streblid-phyllostomid system includes enormous variation that should differentially affect the tightness of this linkage. The occurrence of this biological variation within monophyletic lineages should permit refined analyses of coevolutionary theory via the comparative method (e.g., Brooks & McLennan, 1991).

Coevolution may be considered to be a general class of evolutionary interactions that may involve cospeciation (parallel cladogenetic responses) and require coadaptations (parallel or directed anagenetic responses). Documenting coevolution is fraught with theoretical and methodological challenges (Brooks, 1979), particularly when studying host-parasite systems: the distributions of parasites among hosts must be specified, resolved phylogenies must be generated for both groups, and analyses of corresponding nodes must indicate shared structure. In addition, the specific coevolutionary links have to be proved.

Inferring host relationships

In his classical treatise on phylogenetic methods, Hennig (1979:107 ff.) identified various problems of using the “parasitological method” to uncover host

phylogenies. Besides the customary problems that accompany any character-based phylogenetic analysis, lack of resolution and rate heterogeneity, parasitological methods also admit errors stemming from horizontal transfers and their variable rates. Given the numerous ways that hosts and parasites may become uncoupled (as well as the surfeit of alternative characters that have been exposed by molecular techniques), analysis of parasite faunas can be expected to illuminate only the poorest known host groups. On the other hand, features that impair the phylogenetic usefulness of parasites promise to illuminate other aspects of their life-history. "Ironically, biologists may learn more about the evolutionary biology of hosts when host-switching has occurred" (Barker, 1994, p. 1285).

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