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SYSTEMATIC PATTERNS AND THE EVOLUTION OF FEEDING HABITS IN CHIROPTERA (ARCHONTA: MAMMALIA)

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Abstract. *Ferrarezzi, H. & Gimenez, E.A. 1996. Systematic patterns and the evolution of feeding habits in Chiroptera. (Mammalia: Archonta) . J. Comp. Biol. 1(3/4): 75-94.* The evolution of Chiroptera feeding habits is reconsidered under a phylogenetic approach. The terminal taxa selected for the analysis within the Chiroptera range from family to species levels. A transformation series is proposed for the different feeding habit conditions in the family. The character evolution was reconstructed with the use of parsimonious optimization on the cladograms previously proposed for major archontan lineages and on several levels of the Chiroptera phylogeny. This led to a proposed history of the feeding habits evolution from the base of the Archonta to the terminal taxa within the Chiroptera. Feeding habits could be attributed to each ancestral node of the cladogram of the group. The theories to explain the major shifts in the evolution of bat feeding habits are revisited. The insectivorous condition at the Chiroptera ground plan, widely accepted in the literature, finds scarce support in our analysis. A new hypothesis of a herbivorous ancestor for the Chiroptera and Volitantia is proposed. This condition may have been originated from an even earlier level in the archonta phylogeny. From this herbivorous chiropteran ground plan condition, the insectivorous feeding habit was acquired as a synapomorphy of the Microchiroptera. The origin of the other feeding habits in Megachiroptera and Microchiroptera is explained in a more parsimonious reconstruction. With some few exceptions, the theory emphasizing the importance of the diet duality to explaining the major shifts in bat feeding habits is compatible with the recovered pattern. The question of the evolution of sanguivory is particularly considered. Previous hypotheses assuming that sanguivory originated through ancestral habits of feeding on arthropods associated with large mammals are disclaimed. The hypothesis of a desmodontine ancestor preying on birds in trees is well-supported by this analysis.

Key Words. Chiroptera; Archonta; phylogeny; feeding habits; evolution.

Introduction

No other mammal group achieved the feeding habits diversity found within the Chiroptera, including a unique specialization among terrestrial vertebrates, the sanguivory. Most of this diversity occurs in a single New World bat family, the Phyllostomidae, but several other interesting feeding strategies are found within other bat groups. Specializations to exploitation of different food resources demanded great diversification of morphological and behavioral adaptations functionally related to feeding strategies. These changes with no doubt played a major role in the history of chiropteran evolution.

The bats of the suborder Megachiroptera (Pteropodidae) are well-known to be herbivorous and generally frugivorous, as opposed to the Microchiroptera, of which most members are insectivorous. This difference in feeding habits is so marked that in the earliest classifications proposed for the Chiroptera, Megachiroptera and Microchiroptera were respectively called the Fructivorae (or Frugivora) and the Insectivorae (or Animalivora) (Gray, 1866; Gill, 1872).

Within the Microchiroptera, however, the superfamily Noctilionoidea (=Phyllostomoidea)

—but especially the family Phyllostomidae— represents by far the bat group exhibiting the greatest diversity of feeding habits, including insectivorous, omnivorous, frugivorous, nectarivorous, carnivorous, sanguivorous, and piscivorous species. Thus, it encompasses all variation found in the whole order.

The present study is the first comprehensive phylogenetic approach attempting to determine the systematic pattern of variation in feeding habits within Chiroptera, with special reference to the members of the family Phyllostomidae. Its main purpose is to evaluate whether or not the detected pattern is congruent with the current theories explaining the transition from one habit to another, and to contribute to the study of evolutionary processes determining the major trends in the evolution of feeding strategies in bats.

Theories about the evolution of feeding habits in bats

The ancestral feeding habit of Chiroptera. It has been quite well-demonstrated, as seen below, that both Microchiroptera and Megachiroptera are monophyletic. The Megachiroptera, as stated above, can be characterized by a herbivorous diet, whereas Microchiroptera can be characterized by

an insectivorous diet. Although some inclusive groups within Microchiroptera exhibit a diversity of feeding habits, including herbivory, all the evidence indicates that herbivory is a secondary achievement within the group. Considering the generalized distribution of insectivory in the Microchiroptera families, there would be little doubt that insectivory represents the ancestral feeding habits for the group, whereas herbivory (or more properly frugivory) would be the ancestral condition for Megachiroptera. Thus, the question is which of these two major conditions was present in the most recent common ancestor of the two suborders.

The feeding habit traditionally hypothesized to be present in the common ancestor of the Chiroptera is insectivory (*e.g.*, Romer, 1956; Gillette, 1975; Smith, 1976; Emmons, 1991) Arguments derived from independent sources of evidence, from systematics to functional anatomy and paleontology, have been used to justify this assumption. Romer (1956) stated: "Developed from insectivorous ancestors is the one group of mammals which has attained true flight - the bats ... The majority of bats have *remained insectivorous* in habits; however, one major group, ... consists of relatively large fruit-eaters" (our italics). Similarly, Gillette (1975) stated that: "Whereas the Microchiroptera evolved increasingly more efficient means of capturing insect food, the Megachiroptera early shifted their insectivorous habits to a herbivorous diet." The idea of an insectivorous ancestor for bats was also implicit in Emmons' (1991) comment: "...the same pattern of frugivory evolved independently at least twice in bats [referring to Megachiroptera and stenodermatine phyllostomids] and, evidently, a third time in tree shrews."

In reviewing this subject, Smith (1976) better justifies this assumption: "Based on dental morphology of extant species as compared with that of early fossils, it is generally assumed that aerial insectivory was the initial impetus for chiropteran evolution. Subsequent diversification has been associated with the further partitioning and specialization of this generalized feeding strategy into carnivory, piscivory, foliage gleaning, frugivory, nectarivory, and sanguivory." On the other hand, Smith (1976) suggested that the arguments used in favor of an insectivorous ancestor are open to question, and cautiously discussed the possibility of an omnivorous, rather than insectivorous, chiropteran ancestor.

As exposed above, there are several reasons

for which the traditional assumption that insectivory is the ancestral habit for Chiroptera has been accepted and maintained. The gradistic evolutionary viewpoint considering the order Insectivora as an ancestral group (or stock), from which the other orders of placental mammals independently originated is certainly one important factor. The fact that insectivory represents the most common feeding habit among bat families or even among bat species is perhaps another reason. However, the fact that the oldest fossil bats have a typical insectivorous (dilambdodont) pattern of molar cusps seems to have been the strongest argument favoring the view that insectivory is the plesiomorphic habit for Chiroptera (Smith, 1976). The view that all advanced placental mammals derived from insectivores is an old, simplistic evolutionary scenario in mammalogy. More recently, there has been a search for a more precise and well-resolved pattern for the interrelationships between the mammal orders. We now know that the extant Insectivora have no closer affinity with the Chiroptera. Although insectivory is the generalized habit of more than two thirds of bat species, the principle of communality has been widely rejected as a valid criterion for assessing character polarity (Watrous & Wheeler, 1981). The importance of the fossil evidence will be discussed in more detail below.

Processes to explain the evolution of feeding habits. Although divided in a few basic classes, such as insectivory, frugivory, nectarivory, etc., the diversity of feeding habits is considerably larger, including taxa exploiting more than one food source without strong specialization to any of then. The occurrence of species with intermediate conditions between the major kinds of habits is relatively common, and it is well-known that even bats with more specialized feeding habits frequently use other complementary food resources.

Gillette (1975) emphasized the role of the feeding habits 'duality' in the process of evolution from the primitive insectivory to some other kinds of feeding habit specialization. The mechanism proposed by this author to explain the major shifts in feeding habits that occurred in bats involves a sequence of steps: (1) generalized insectivory, followed by (2) specialized insectivory (including feeding on insects associated with or located on "potential" food sources), which can have provided

opportunities to (3) utilization of a dual food source (including insects and the new food source), which could then have conduced to (4) specialization to the new food source. This adaptation mechanism causing the transition from one major food source to another through intermediate stages was used to explain all supposed events that occurred in the evolutionary history of bat feeding habits, like the independent transition from strict insectivory to other kinds of specialized diet. Hence, Gillette (1975) hypothesized, for example, that both frugivory and nectarivory are specializations originated from the habits of eating insects + fruits and insects + flowers, respectively, which were independently derived from a common ancestral stage of specialized insectivory, that is, preying on insects associated with plants. Apparently, it has not been confirmed whether the insects eaten by frugivorous phyllostomids are caught on fruits or on other kinds of vegetation substrates, which would be an important piece of testing information for this hypothesis. Gillette's (1975) hypothesis provided a reasonable explanation for the origin of piscivory, beginning with an ancestral stage of specialized insectivory, in which bats capture insects on the water surface. This also applies to the origin of sanguivory from an ancestral habit of preying on mammalian ectoparasites.

In apparent agreement to the view above, there are representative taxa exhibiting possible reminiscent habits from this ancestral stage of duality, at least for piscivorous and nectarivorous bats, which act as living examples of such stages of transition. Both known extant species of Noctilionidae catch insects on the water surface, but only one is piscivorous. Also, several species of nectarivorous phyllostomids are known to eat insects found inside flowers while feeding on nectar. However, the existence of species with intermediate and/or dual habit is a necessary but not sufficient argument favoring Gillette's theory. It is also necessary to verify whether the taxa exhibiting the intermediate habit also have intermediate phylogenetic positions between the taxa characterized by more extreme habit tendencies. This procedure will provide the test of congruence necessary to verify if the recognized sequence of primary homologies defined *a priori* by ordination of the states of feeding habits corresponds to truly secondary (or evolutionary) homologies (sensu de Pinna, 1991).

Methods of Analysis

Sources of information about feeding habits. Information on feeding habits, mainly concerning food items, was compiled from the current literature, especially the revisionary studies by Wilson (1973), Gardner (1977), Emmons (1990), and Nowak (1991), as well as shorter notes on species habits (*e.g.*, Arata *et al.*, 1967; Silva-Taboada & Pine, 1969; Dwyer, 1970; Goodwin, 1970; Tuttle, 1970; Novick & Dale, 1971; Taddei, 1973, 1980; Daniel, 1976; Sazima 1976, 1978a,b; Sazima & Sazima, 1977; Sazima & Uieda, 1980; Start & Marshall, 1976; Fenton *et al.*, 1981, 1983; Marshall, 1983; Ryan *et al.*, 1983; Robson, 1984; Trajano, 1985; Greenhall, 1988; Medellín, 1988; Brosset & Charles-Dominique, 1990; Kitchener *et al.*, 1990; Emmons, 1991; Zortéa, 1993; Zortéa & Mendes, 1993; Kunz & Ingalls, 1994; Pedro & Passos, 1995). Ruschi's observations on feeding habits (see Gardner, 1977) were not considered here, since they include a number of unconfirmed and intriguing findings, which have not been accepted by most subsequent chiropterologists.

Hypotheses on bat phylogeny. The working hypotheses used to interpret and discuss the evolution of feeding habits in bats were obtained from recent cladistic analyses carried out by several authors, based on diverse comparative data, and at different hierarchical levels. As discussed in detail below, the monophyly of Archonta (including Chiroptera, Primates, Dermoptera, and Scandentia) seems to have been well-demonstrated by Wible & Novacek (1988), Novacek (1990, 1992), Beard (1993), Ammerman & Hillis (1992).

The diphyletic origin of the Chiroptera sustained especially by Smith & Madkour (1980) and Pettigrew *et al.* (1989), was strongly criticized in recent papers. The monophyly of the Chiroptera has been defended in the phylogenetic studies by Luckett (1980), Wible & Novacek (1988), Novacek (1990), Adkins & Honeycutt (1991), Minddle *et al.* (1991), Ammerman & Hillis (1992), Bailey *et al.* (1992), and Beard (1993), and is herein accepted.

The phylogeny of the large and diversified Phyllostomidae family has been extensively discussed in the recent literature, resulting in a relatively well-resolved consensus topology for the relationships among its major assemblages (see Baker *et al.*, 1989). The phylogenetic

Table I. List of conditions of feeding habits related to each possible food type (characters 1-7) and feeding behavior (character 8).

1. Insectivory: (0) absent; (1) complementary; (2) predominant; (3) strict.
2. Carnivory: (0) absent; (1) present (predominant).
3. Piscivory: (0) absent; (1) complementary; (2) predominant.
4. Sanguivory: (0) absent; (1) present.
5. Frugivory: (0) absent; (1) complementary; (2) intermediate; (3) predominant; (4) strict.
6. Nectarivory/polinivory: (0) absent; (1) complementary; (2) predominant.
7. Folivory: (0) absent; (1) complentary; (2) predominant.
8. Foraging behavior: (0) foliage gleaning; (1) aereal insectivory; (2) aquatic gleaning.

schemes adopted for the various levels considered in the analysis made here are presented and discussed in the systematic section, later in this study.

Choice of terminal taxa. The terminal taxa of the present analysis were chosen by means of two criteria: 1. All bat families should be represented; and 2. taxa exhibiting diversity of feeding habits were subdivided until monophyletic terminals with scarce or no habit variation were obtained. This procedure resulted in 59 terminal taxa (including Dermoptera), ranking from family to species levels.

Character coding. After the compilation of the data on feeding habits, especially regarding food items, we defined some characters and character states concerning major feeding habits among taxa, using the procedures described below.
1. A codification of the different food items was carried out treating each item as an independent binary or linearly ordered series. This procedure resulted in seven binaries or multistate conditions. The binary conditions correspond to more simple cases (presence/absence), that is, the utilization or not of a given food item. The ordered multistate characters involve at most four states. Each of these states refers to the relative importance of a given food item in the diet. The states are defined as strict (the only food consumed), predominant (the most important or primary food source), complementary (a secondary food source), and finally, absent (or non-utilization of such food item) (Table I). The conditions of use of food items do not properly constitute characters at this point of the analysis, since there is a certain redundancy among them and each one is rather dependent on the other. The number 8, in Table I, refers to a true character related to feeding behavior. The condition exhibited by each terminal taxon, for each food item, is presented in Table II (columns 1-8).
2. A codification was applied treating the feeding

habit as a single complex multistate character, considering the information in Table I. Each state of this large character corresponds to a unique combination of the states of the seven characters concerning each individual food item. After the definition of the states, they were ordered and interconnected in a branched transformation series or character state network (Fig. 1). The criteria applied to connect and order the feeding habit states were the existence of intermediate or mixed habits, combining dietary components of two or more major (exclusive) habits. Arguments for ordering complex multistate transformation series have been presented by several authors (Mickevich & Lipscomb, 1991; Lipscomb, 1992; Wilkinson, 1992). In this kind of study, ordering a transformation series will only in some cases restrict the possibilities of ambiguous (equivocal) assessment of the ancestral condition for a given internal tree node.

Character optimization. The feeding habits evolution was reconstructed with the use of previously constructed phylogenetic hypotheses as the independent variable and the differences regarding feeding habits as the dependent variable. The ancestral feeding habit condition for each of the hypothetical ancestors of the study group was assessed by means of parsimonious optimization on previously assumed cladogram topologies, following the criteria of Farris (1970) and Swofford & Maddison (1987). Although this procedure has been originally described for completely resolved (dichotomous) trees, it can be also adapted for the reconstruction of character evolution on trees containing polytomies (Maddison, 1989). In the case of ordered or additive characters, we have used both Wagner's and Fitch's parsimony. After the application of this procedure at different hierarchical levels within Archonta and Chiroptera, the result was a polarized transformation series for all kinds of feeding habits. This polarized series was used to critically evaluate the current hypotheses and scenarios of

Table 11. Matrix showing the taxonomic distribution of the states of the features studied in this paper (coded Table I). Column 0 represents the feeding habit state as defined in transformation series in Figure 1. "v" variable.

	0	1	2	3	4	5	6	7	8		0	1	2	3	4	5	6	7	8
Primates	v	1v	0	0	0	v	v	v	-	other Myotinae	2	3	0	0	0	0	0	0	1
Scandentia	6	2,1	0	0	0	1	0,1	0,1	-	*Myotis vivesi*	2	3	0	1	0	0	0	0	2
Dermoptera	11	0	0	0	0	1	1	2	-	*Noctilio albiventris*	2	3	0	0	0	0	0	0	2
Pteropodini	10	0	0	0	0	2	1	1	-	*Noctilio leporinus*	1	2	0	1	0	0	0	0	2
Epomophorini	10	0	0	0	0	2	1	1?	-	Mormoopidae	2	3	0	0	0	0	0	0	0
Cynopterini	10	0	0	0	0	2?	1?	1?	-	*Macrotus*	6	2	0	0	0	1	0	0?	0
Macroglossini	9	0	0	0	0	1	2	?	-	*Micronycteris*	6	2	0	0	0	1	0	0?	0
Notopterini	9	0	0	0	0	1	2	?	-	*Trachops*	4	1	1	0	0	1	0?	0	0
Emballonuridae	2	3	0	0	0	0	0	0	1	*Chrotopterus*	4	1	1	0	0	1	0?	0	0
Rhinopomatidae	2	3	0	0	0	0	0	0	1	*Vampyrum*	4	1	1	0	0	1	0?	0	0
Craseonycteridae	2	3	0	0	0	0	0	0	0	*Lonchorhina*	2	3	0	0	0	0	0	0	0
Nycteris spp	2	3	0	0	0	0	0	0	0	*Macrophyllum*	2	3	0	0	0	0	0	0	0
Nycteris grandis	3	1	0	0	0	0	0	0	0	*Tonatia*	6	2	0v	0	0	1	1?	0	0
Lavia	2	3	0	0	0	0	0	0	0	*Mimon*	6	2	0	0	0	1	?	0	0
Macroderma	3	1	1	0	0	0	0	0	0	*Phylloderma*	6	2	0	0	0	1	1?	0	0
Cardioderma	3	1	1	0	0	0	0	0	0	*Phyllostomus*	6v	2v	0v	0	0	1v	1	0	0
Megaderma	3	1	1	0v	0	0	0	0	0	*Carollia*	7	1	0	0	0	2	1	0	0
Rhinolophinae	2	3	0	0	0	0	0	0	0	*Rhinophylla*	7	1	0	0	0	2	1	0	0
Hipposiderinae	2	3	0	0	0	0	0	0	1v	*Sturnira*	7	1	0	0	0	2	1	0	0
Mystacinidae	6	2	0	0	0	1	1	0	0	*Pygoderma*	12	0	0	0	0	3	0	0	-
Molossidae	2	3	0	0	0	0	0	0	1	Stenodermatini	12	0	0	0	0	3	0	0	-
Antrozoidae	2	3	0	0	0	0	0	0	0	Artibeini	7	1	0	0	0	2	1	1	0
Myzopodidae	2	3	0	0	0	0	0	0	1	Vampyressini	7	1v	0	0	0	2	1	1?	0
Thyropteridae	2	3	0	0	0	0	0	0	1	Glossophagini	8	1	0	0	0	1	2	0	0
Furipteridae	2	3	0	0	0	0	0	0	1	Lonchophyllini	8	1	0	0	0	1	2	0	0
Natalidae	2	3	0	0	0	0	0	0	1	Phyllonycterini	8	1	0	0	0	1	2	0	0
Nyctophilini	2	3	0	0	0	0	0	0	0	Brachyphyllini	8	1	0	0	0	1	2	0	0
Plecotini	2	3	0	0	0	0	0	0	0	*Diphylla*	5	0?	0	0	1	0	0	0	0
otherVespertilioninae	2	3	0	0	0	0	0	0	1	*Diaemus*	5	0?	0	0	1	0	0	0	0
Miniopterinae	2	3	0	0	0	0	0	0	1	*Desmodus*	5	1	0	0	1	1	0	0	0
Murininae + Kerivoulinae	2	3	0	0	0	0	0	0	1										

the bat feeding habit evolution proposed in the literature.

This approach has been extensively applied in the last years, and has been called the comparative method (Harvey & Pagel, 1991). It has been especially emphasized for the evolutionary study of ecological and behavioral characters (*e.g.*, Brooks & McLennan, 1991; 1994). It has also been used to test adaptation hypotheses (*e.g.*, Coddington, 1994; Pagel, 1994).

Feeding habits in bats. For convenience, we have accepted the trophic categories described by Wilson (1973), with some modifications and subordination, as discussed below.
Herbivory. Herbivory (or phytophagy) is referred to here as the habit of feeding exclusively or predominantly on vegetal material, including fruits, flowers, and floral products, buds, and leaves. In bats, herbivory is better represented by predominantly frugivorous and predominantly nectarivorous groups, both complementing the diet with other vegetal material, besides the primary food source. Most nectarivorous taxa

apparently do not abandon frugivory as secondary or complementary food sourc Predominantly herbivorous taxa may al complement their diet with insects (see below

Frugivory. Frugivory is characterized as the hal of feeding predominantly or solely on fruits. T Megachiroptera of the subfamily Pteropodin are strictly herbivorous and predominant frugivorous, also complementing their diet wi floral products and leaves (Marshall, 198 Utzurrum, 1984; Kitchener *et al.*, 1990). Bo Megachiroptera and Stenodermatinae phyll stomid Microchiroptera frugivorous bats e fruits in a similar manner. They suck the fr juice by chewing chunks of fruit and spitting o fibers and seeds in moist wads (Morrison, 198 Richardson *et al.*, 1987; Emmons, 1991). Mc stenodermatines, however, include a variab amount of insects as a complement to the predominantly frugivorous diet, whereas tl Megachiroptera appear to eat insects on accidentally (Thomas, 1984; Start & Marsha 1976; Marshall, 1983; Kitchener *et al.*, 1990 Apparently there is no record of insects and flor
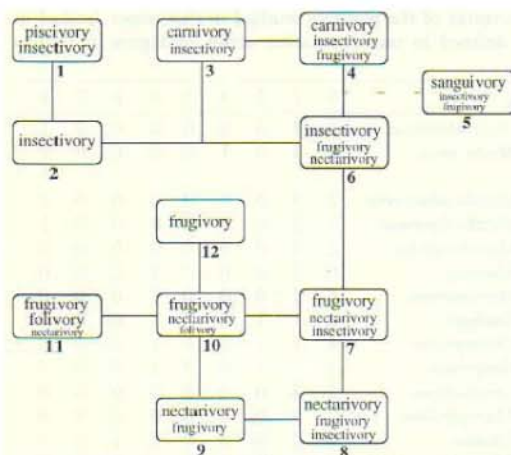
Figure 1. Ordering and coding of the different feeding habits found within the taxon Volitantia (Dermoptera + Chiroptera) in a character state tree. The series is not polarized, and the order of connection between states was decided by the occurrence of intermediate conditions. Predominant and complementary feeding habits are indicated by different sizes of letters.

products as complementary food items for the short-faced stenodermatine bats (tribe Stenodermatini), with the possible exception of *Ariteus*, which has been reported also to eat insects.

Nectarivory. Nectarivory as defined here is the habit of feeding not only on nectar, but also on other floral products and parts, such as pollen and petals. Pollen is one of the most important food sources for nectarivorous bats. Although the habit of feeding on flowers is shared by most phyllostomids and perhaps all megachiropterans, only the Glossophaginae (including brachy-phyllines, phyllonycterines, and lonchophyllines) within the former, and the Macroglossinae, within the latter, are specialized to a predominantly nectarivorous diet. Similarly to their frugivorous counterparts, the nectarivorous Glossophaginae Microchiroptera differ from the nectarivorous Megachiroptera of the subfamily Macroglossinae by including insects as an important complement to their diet (Gardner, 1977; Marshall, 1983). *Brachyphylla*, a problematic genus from the phylogenetic point of view, is now regarded as part of or at least closely related to the Glossophaginae. This genus was earlier considered primarily frugivorous, but the excellent study by Silva-Taboada & Pine (1969) demonstrated that its diet is predominantly nectarivorous, including a large amount of pollen. Its feeding habits, hence, do not differ from those of the closely related

phyllonycterines.

Folivory. Folivory is defined as the utilization of leaves, including buds and some other plant green parts. There is no Chiroptera that can be characterized as strictly folivorous and even the utilization of leaves as a complementary food item is rather uncommon among the Chiroptera. It has been reported that several Megachiroptera, especially within the Pteropodinae (Marshall, 1983), and representatives of at least two genera of stenodermatine phyllostomids (Zortéa, 1993; Zortéa and Mendes, 1993; Kunz and Diaz, 1995) use leaves as a complement to their diet. Among the Archonta, folivory apparently plays a major role in the diet of dermopterans and of several Primates groups than in that of the Megachiroptera.

Omnivory. The definition of omnivory is restricted here to a generalized diet composed primarily of both animal (usually insects) and vegetal material (usually fruits and/or flowers). Although omnivory appears to be common in Scandentia and Primates (Emmons, 1991; Nowak, 1991), its occurrence is considerably restricted among chiropteran groups. At the family level, the monotypic family Mystacinidae is the only one referred to as omnivorous (Daniel, 1976), but such case should perhaps be classified as predominantly insectivory. Within the Phyllostomidae, there are some species of *Phyllostomus* that may be referred to as truly omnivorous, but congeneric species and species of other phyllostomid genera feeding on both animal and vegetal material are used to feeding predominantly on one or another source. We prefer not to treat omnivory as a character state distinct from predominant insectivory within the Chiroptera.

Animalivory. The remaining non-herbivorous feeding habits may be grouped together in the broad sense of carnivory, which in the case of bats would be more appropriately called animalivory. This broad category includes the generalized insectivory, as well as carnivory and piscivory with an important contribution of insectivory to the diet, as well as the highly specialized sanguivory.

Insectivory. Insectivory is here defined to characterize species feeding exclusively or predominantly on insects and other arthropods.

No species of Megachiroptera are known to eat insects voluntarily. Although restricted to Microchiroptera, insectivory is widespread among its families. Even representatives of the herbivorous, piscivorous, carnivorous, and to a lesser extent sanguivorous, microchiropteran families are known to regularly or occasionally use insects as a complementary food source. Insectivory was divided into two major states (Fig. 1), one for a strictly insectivorous diet (state 2), shared by most microchiropteran families, and another for a predominantly insectivorous diet (state 6), complemented with fruits and floral products, as is characteristic of most insectivorous phyllostomids and the Mystacinidae.

Concerning the foraging behavior, the insectivorous bats have been classified as aerial insectivores or foliage gleaners. The aerial insectivory is characterized by the capture of insects in the air during open flight, whereas the foliage gleaning is characterized by the overflight, close to the vegetation and ground, in search of preys on or over these substrates. Emballonuridae, Rhinopomatidae, Molossidae, Myzopodidae, Thyropteridae, Furipteridae, Natalidae, most Vespertilionidae, and most Hipposiderinae (Rhinolophidae) are true aerial insectivores. Several taxa, however, are capable of using both aerial and foliage gleaning hunting strategies (Wilson, 1973). Most representatives of the Vespertilioninae tribes Plecotini and Nyctophylini, as well as the Rhinolophinae, Antrozoidae, and Mormoopidae (Goldman & Henson, 1977), are known to be facultatively aerial insectivores and foliage gleaners. The Phyllostomidae, Nycteridae, and Mega-dermatidae (with exception of *Lavia*) are predominantly foliage gleaners, with scarce aerial insectivory. Although the Craseonycteridae and Mystacinidae have been reported to glean on foliage, we have doubts whether or not they may be facultative aerial insectivores. It is interesting to note that the two known Noctilionidae species are specialized for a particular kind of gleaning over the water surface, in search of aquatic preys, which are captured in their feet. The foraging behavior is treated as a character independent of the diet, which allowed the adequate coding of trophic categories other than insectivory (*e.g.*, carnivory) as foliage gleaning.

Piscivory. No bats have a diet based only on fish. Piscivory is the most restricted specialized feeding habit within bats. All piscivorous bats complement their diet with a large amount of insects. Aquatic insects and non-aquatic insects fallen on the water surface, as well as crustaceans (a novel food item unexploited by other bats) may complement their diet (Goodwin, 1970; Robson, 1984; Nowack, 1991). Piscivorous bats utilize a foraging behavior here called aquatic gleaning. This behavior may be characterized by overflight close to the water surface in search of aquatic preys, which are captured in the extremely elongated feet and claws of the bats (Dwyer, 1970; Novick & Dale, 1971; Robson, 1984). The aquatic gleaning behavior is not exclusive of piscivorous species and it is also present in a few other species closely related to the piscivorous bats. Only *Noctilio leporinus* (Noctilionidae) and *Myotis vivesi* (Vespertili-onidae: Myotinae) are known to regularly prey on fish, utilizing the same foraging behavior. *M. adversus*, a predominantly insectivorous aquatic gleaner, is reported to occasionally eat fish (Robson, 1984). Although *N. albiventris* is truly an aquatic gleaner, it apparently has an insectivorous diet, also including aquatic arthropods.

At least two other species, *Megaderma lyra* (Megadermatidae) and *Nycteris grandis* (Nycteridae), are known to include fish as an occasional complement to their diet (Fenton *et al.*, 1981; Nowak, 1991), although the method by which they catch fishes is not known. Both species are better characterized as carnivorous or carnivorous and insectivorous. Due to the great similarity in the diet and the fishing behavior of the piscivorous representatives of Noctilionidae and Vespertilionidae, we have coded piscivory as a single state for both (Fig. 1, state 1). It represents one of the extremes of the series, linked to a strictly insectivorous habit.

Carnivory. Carnivory is here restricted to predation on other small terrestrial vertebrates. Carnivorous bats are not highly specialized for this kind of feeding, and all of them exploit other food sources, especially insects and other arthropods. Carnivorous phyllostomids include fruits as a complement to their diet. All carnivorous bats behave as typical foliage gleaners while foraging, and they complement their diet with insects. This shows how inadequate restricting this category to insectivorous bats may be.

Carnivory is known to be the predominant

feeding habit of most members of the family Megadermatidae (with the exception of the monotypic *Lavia*), and of the phyllostomid genera *Trachops, Chrotopterus,* and *Vampyrum* (Gardner, 1977; Sazima, 1978; Medellín, 1988) which constitute the subfamily Vampyrinae. Other phyllostomid genera occasionally preying on small vertebrates as *Phyllostomus hastatus* and *Tonatia bidens* (Martuscelli, 1995) have been recorded, but they cannot be characterized as truly carnivorous. The large *P. hastatus* is recognized as an omnivorous species, where as *Tonatia* feeds predominantly on insects. *Nycteris grandis* (Nycteridae) is a large species compared to its strictly insectivorous congenerics. This species is known to prey regularly on small vertebrates (Fenton *et al.*, 1981, 1983) and could be regarded at least as partially if not predominantly carnivorous.

The carnivorous diet of the Megadermatidae and of *N. grandis* differs from that found in the Vampyrinae. In this latter group, like in most insectivorous members of the family Phyllostomidae, fruit dietary complement has been occasionally recorded (Gardner, 1977). These two conditions of carnivory were treated as different, but linked character states (Fig. 1, states 3-4).

Sanguivory. Sanguivory (or hematophagy) is feeding strictly or nearly exclusively on blood. It represents a unique feature among terrestrial vertebrates, being perhaps the most specialized feeding habits found in bats, requiring extensive morphological, behavioral, and physiological modifications. Sanguivory is restricted to the species of vampire bats of the Phyllostomidae subfamily Desmodontinae. A few interesting records indicate that the common vampire (*Desmodus rotundus*) occasionally complements its diet with insects and ectoparasites (Arata *et al.*, 1967) or even with some vegetal material and fruits (Trajano, 1985). The two other monotypic vampire genera are not known to complement their blood diet, but it must be considered that their feeding biology is much less studied than that of the common vampire. Such records are scarce even for *D. rotundus* (Greenhall, 1988).

The monotypic genera *Diphylla* and *Diaemus* are known to prey preferentially on birds. However, at least *Diaemus* may occasionally feed on mammalian blood (Gardner, 1977; Sazima, 1978; Greenhall, 1988). There are some doubts

concerning the few records of *Diphylla* preying on domestic mammals (*e.g.*, Ruschi, 1951) and it is possible that this genus is specialized in bird preying. In contrast, *Desmodus* preferentially feeds on mammalian blood, but frequently preys on birds as well (Greenhall, 1988). The foraging site and behavior of *Diphylla* and *Diaemus* also differ from those of *Desmodus* (Sazima, 1978; Sazima & Uieda, 1980; Greenhall, 1988). The former forage in trees, approaching the prey from below, whereas the latter forages both on the ground and in trees, approaching the prey from above.

Chiroptera Phylogenetic Relationships

The grandorder Archonta. Although bats are usually considered derived from the "primitive" order Insectivora by gradist systematists, all the studies on phylogenetic relationships between placental mammals have indicated that both groups are not closely related. According to the most recent developments in mammalian systematics, the orders Chiroptera, Dermoptera (flying lemurs), Primates and Scandentia (tree shrews) are grouped together on the taxon Archonta, usually ranked as "grandorder". The monophyly of the taxon Archonta has been corroborated by independent cladistic analyses based on morphological and molecular comparative data (Wible & Novacek, 1988; Novacek, 1990, 1992; Beard, 1993; Ammerman & Hillis, 1992).

The monophyly of Chiroptera and its interrelationships with archontan orders have been extensively studied and debated in the last years. These studies used general morphology and osteology (Smith & Madkour, 1980; Wible & Novacek, 1988; Novacek, 1990, 1992; Beard, 1993; Simmons, 1993), central nervous system features (Pettigrew *et al.* 1989) and molecular biology (Adkins & Honeycutt, 1991; Mindell *et al.*, 1991; Ammerman & Hillis, 1992; Bailey *et al.*, 1992) as sources of information. The most accepted conclusions of these studies, as summarized by Simmons (1993), are that Chiroptera really constitutes a monophyletic group, that its sister group is represented by the Dermoptera, and that both orders compose together the taxon Volitantia (Fig. 2). The monophyly of both chiropteran suborders, the Microchiroptera and the Megachiroptera, also has been corroborated by all these and other previous studies. The relationships among
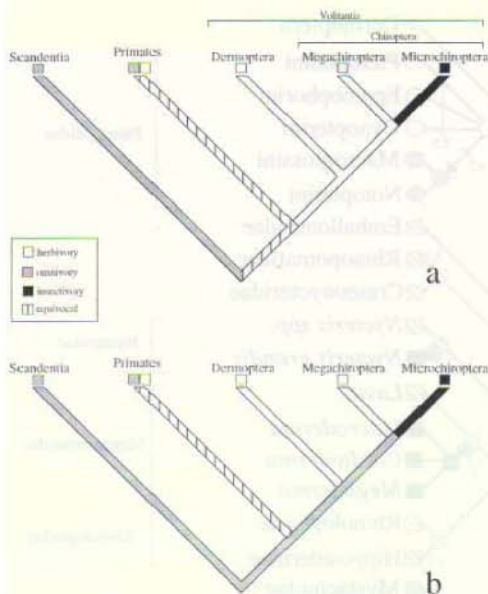
Figure 2. Hypothesis of phylogenetic relationships of members of the Grandorder Archonta (from Simmons, 1993), with the optimization of the major classes of feeding habits. (a) Most parsimonious hypothesis under the assumption of character additivity (3 steps) and non-additivity (2 steps), considering the chiropteran ancestor as herbivorous. (b) An alternative hypothesis under the assumption of character additivity (3 steps), considering the chiropteran ancestor as omnivorous.

Volitantia, Primates and Scandentia are still under debate, especially concerning the position of the "Plesiadapiformes" fossils. Regarding only the extant lineages, the most recent analyses indicate that Scandentia is either the sister group of Primates (Novacek, 1992), or the most basal archontan group, Primates and Volitantia corresponding to sister groups (Simmons, 1993).

Chiropteran paleontology and feeding habits. There seems to be no disagreement that the oldest known fossil bats (genera *Icaronycteris* and *Palaechiropteryx*, from Early and Middle Eocene) were insectivorous (Smith, 1976; Novacek, 1987). This is evidenced especially by their dilambdodont pattern of molar cusps, which are functionally specialized for the mastication of hard insect parts. Although they were earlier considered as the possible ancestors of all extant Chiroptera, it seems now clearly demonstrated that both of these fossil genera should be referred to as Microchiroptera (Novacek, 1985, 1987; Habersetzer and Storch, 1992; Simmons, 1994).

The oldest known megachiropteran fossil

dates from late Oligocene (Novacek, 1987; Simmons, 1994), including a tooth similar to that of modern members of this suborder (Ducrocq *et al.*, 1993). *Archaeopteropus* is an Oligocene taxa of putative megachiropteran affinity, whose badly damaged dentition has been suggested to be similar to an insectivorous-type (Slaughter, 1970). The relationships of this taxon to the Megachiroptera, which is based on (possibly plesiomorphic) postcranial similarities regarding wing morphology, are open to question (Smiths, 1976). Insectivorous species appeared earlier in the fossil record than frugivorous ones, but it is widely known that only stratigraphic age is not an accurate indicative of character polarity. Since the Eocene oldest bats are representatives of the two major extant lineages, apparently having the same feeding habit as their living relatives, the available paleontological information gives no contribution to the understanding of feeding habit evolution.

Two kinds of paleontological information, of major importance to the resolution of this matter, would be especially welcome: (1) a fossil sister group to the Chiroptera whose feeding habit could be indirectly inferred; and (2) fossils representing either a basal branch of Megachiroptera having insectivore dentition, or a basal branch of Microchiroptera having non-insectivore dentition. This data is apparently lacking and for the time being any evolutionary inference on the evolution of the feeding habits has to be obtained through the study the extant fauna under a phylogenetic approach.

Bat phylogeny. The cladistic relationships among megachiropteran suprageneric taxa are poorly understood. For this reason, Koopman's (1984, 1994) classification of pteropodids was used as an approximation to a phylogenetic hypothesis for the family. We have not assumed the monophyly of the subfamily Pteropodinae, since its diagnosis is apparently based on plesiomorphic features relative to the apparently monophyletic Macroglossinae. Some other kinds of comparative data (*e.g.*, Slaughter, 1970) also indicated the possibility of Pteropodinae paraphyly relative to Macroglossinae.

The results of a recent cladistic analysis of bat families based on total evidence (Simmons, in press) are congruent with a previous phylogenetic hypothesis (Smith, 1976) and with previous classifications (Koopman, 1984, 1994)

Dermoptera
Pteropodini
Epomophorini
Cynopterini — Pteropodidae
Macroglossini
Notopterini
Emballonuridae
Rhinopomatidae
Craseonycteridae
Nycteris spp. — Nycteridae
Nycteris grandis
Lavia
Macroderma
Cardioderma — Megadermatidae
Megaderma
Rhinolophinae — Rhinolophidae
Hipposiderinae
Mystacinidae
Molossidae
Antrozoidae
Myzopodidae
Thyropteridae
Furipteridae
Natalidae
Nyctophilini
Plecotini
other Vespertilioninae
Miniopterinae — Vespertilionidae
Murininae-Kerivoulinae
other Myotinae
Myotis vivesi
Noctilio leporinus — Noctilionidae
N. albiventris
Mormoopidae
Phyllostomidae

feeding habits:

11 ⊙ herbivory
10 ○ frugivory
9 ● nectarivory
2 ▨ insectivory
1 ▣ piscivory
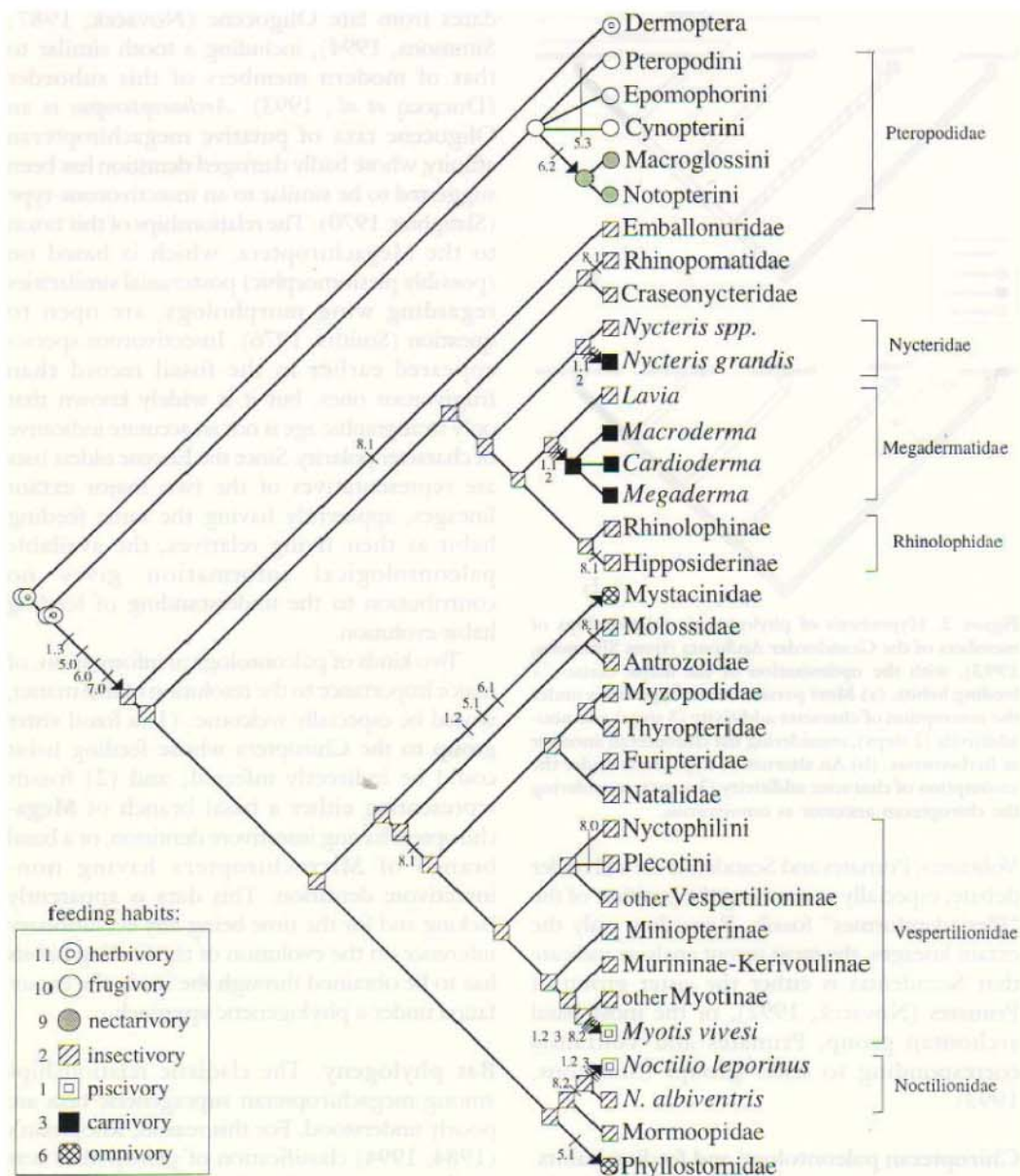3 ■ carnivory
6 ⊗ omnivory

Figure 3. Hypothesis of phylogenetic interrelationships between the Chiroptera main groups, with the optimization of the different kinds of feeding habits. The strictly insectivorous habit is symplesiomorphic within the Microchiroptera, from which carnivory has arisen in the Megadermatidae, and an omnivorous (but predominantly insectivorous diet) derived in the Mystacinidae and in the Phyllostomidae. The cladogram topology for the chiropteran interfamilial relationships is from Simmons (in press). Arrows in branches indicate major shifts in feeding habits; numbers along branches indicate minor shifts regarding food type or foraging behavior (see Tables I and II). Overlapping symbols at the basal nodes indicate ambiguous optimization for herbivory and frugivory.

of bat families, except for differences in the position of Emballonuridae and Mystacinidae. The scheme of interrelationships obtained by Simmons (in press) for bat families (and vespertilionid subfamilies) was adopted here for the study of the evolution of feeding habits at this level (Figure 3). The phylogenetic position of the megadermatid genus *Lavia* as the sister group of the set of other members of the family is in accordance with Hand's (1985) cladistic hypothesis based on dentition and osteology. For the sake of simplicity and to reduce the cladogram size, some groups were artificially collapsed in composed (probably paraphyletic) terminals
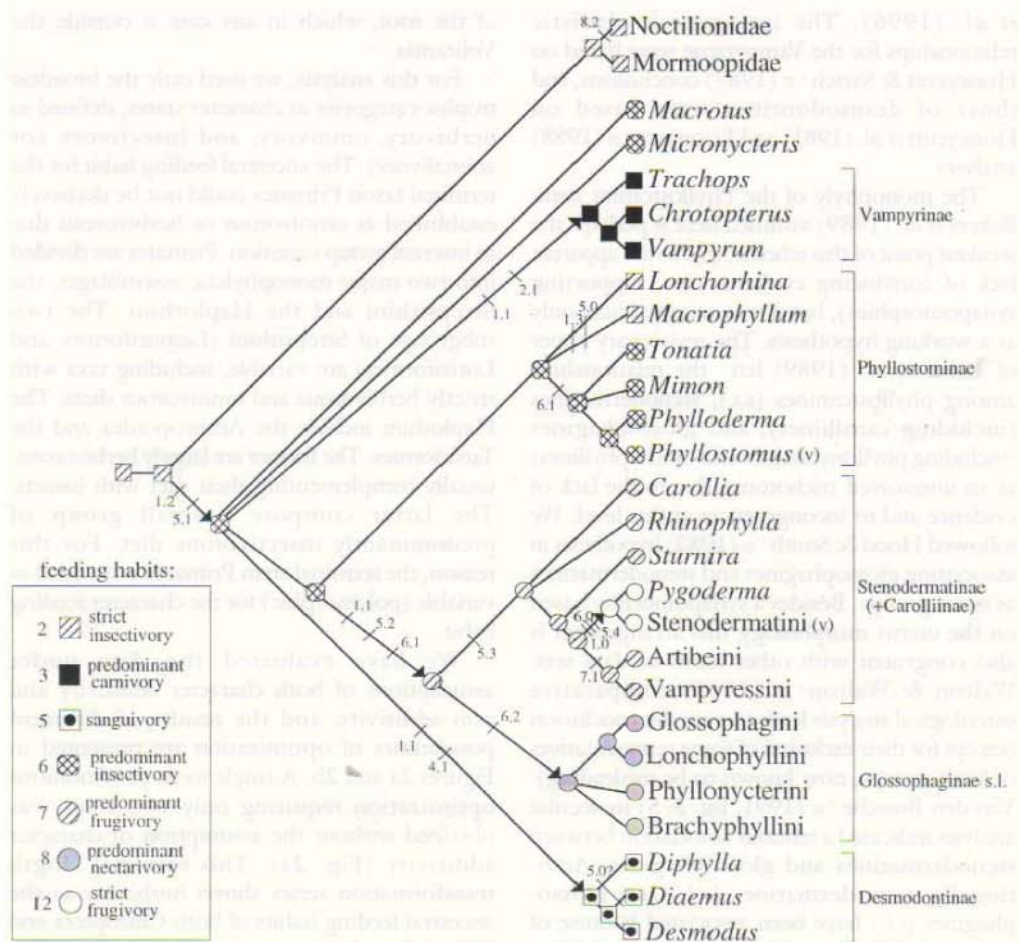
Figure 4. Hypothesis of phylogenetic interrelationships between members of the family Phyllostomidae and its closest relatives, with the optimization of the different kinds of feeding habits. The strictly insectivorous habit is symplesiomorphic for the Noctilionoidea. The cladogram topology for the phyllostomid intrafamilial relationships is a combination of data from Baker *et al.* (1989), Honeycutt & Sarich (1987), Lim (1993), Owen (1993) and Gimenez *et al.* (1996) (see text). Arrows in branches indicate major shifts in feeding habits; numbers along branches indicate minor shifts regarding food type or foraging behavior (see Tables I and II).

relative to their sister group (*e.g.*, other Myotinae, other Vespertilioninae, *Nycteris* spp.).

The intrafamilial relationships in the Phyllostomidae, maybe the most interesting taxon for evolutionary studies on feeding habits, has also been extensively studied under diverse comparative approaches (Honeycutt *et al.*, 1981; Hood & Smith, 1982; Griffiths, 1982; Owen, 1987; Honeycutt & Sarich, 1987; Koopman, 1988; Baker *et al.*, 1989; Lim, 1993; van den Bussche, 1991,1992; Gimenez *et al.*, 1996). Unfortunately we still do not have a well-resolved (dichotomous) phylogenetic hypothesis for the members of this family, and we adopt a consensus topology derived from the results of the most important papers on higher level phyllostomid

phylogeny.

The phylogenetic hypothesis adopted here to approach the problem of the evolution of the feeding habits in the Phyllostomidae is depicted in Figure 4. The higher level relationships of this cladogram is largely based on the consensus trees presented by Honeycutt & Sarich (1987) and Baker *et al.* (1989), with few modifications.

The cladogram topology and choice of monophyletic generic and suprageneric terminal taxa for stenodermatines were largely based on the results of Lim's (1993) cladistic analysis, and secondarily on Owen's (1987) analysis. The terminal taxa and relationships among glossophagines (*s.l.*) were defined according to the results and discussions presented by Gimenez

et al. (1996). The intergeneric cladistic relationships for the Vampyrinae were based on Honeycutt & Sarich's (1987) conclusions, and those of desmodontines were based on Honeycutt *et al.* (1981) and Koopman's (1988) analyses.

The monophyly of the Phyllostomini *sensu* Bakers *et al.* (1989) assumed here is perhaps the weakest point of this scheme, due to the apparent lack of convincing evidence (*i.e.*, supporting synapomorphies), but it was accepted here only as a working hypothesis. The revisionary paper of Baker *et al.* (1989) left the relationships among phyllostomines (*s.s.*), stenodermatines (including carolliines), and glossophagines (including phyllonycterines and brachyphyllines) as an unresolved trichotomy, due to the lack of evidence and to incongruences at this level. We followed Hood & Smith's (1982) hypothesis in associating glossophagines and stenodermatines as sister groups. Besides a synapomorphy based on the uterus morphology, this arrangement is also congruent with other kinds of data sets. Walton & Walton's (1969) comparative osteological analysis leads to a similar conclusion (except for their exclusion of some representatives of both groups, now known to be misleading). Van den Bussche's (1991, fig. 3, 5) molecular analysis indicated a tenuous association between stenodermatines and glossophagines. Additionally, stenodermatines (*s.l.*) and glossophagines (*s.l.*) have been associated because of their specialized molar cusp pattern (Miller, 1907), showing a great reduction of cusps and commissures relative to the primitive pattern, which is generalized among other phyllostomid groups. As it will be discussed later, the sister group relationship between stenodermatines and glossophagines is also consistent with the shared specialized herbivorous habit.

The evolution of feeding habits in the Archonta and in bats

The Grandorder Archonta. The topology of the cladogram obtained by Simmons (1993) for the Archonta is shown in Figure 2, and it was used here in search of macroevolutionary patterns of the major kinds of feeding habits at higher levels of universality in the group. The adoption of the alternative hypothesis that Scandentia and Primates are sister groups (Novacek, 1992) would lead to a similar result of the optimization, since both cladograms differ only on the position

of the root, which in any case is outside the Volitantia.

For this analysis, we used only the broadest trophic categories as character states, defined as herbivory, omnivory, and insectivory (or animalivory). The ancestral feeding habit for the terminal taxon Primates could not be decisively established as omnivorous or herbivorous due to internal group variation. Primates are divided into two major monophyletic assemblages, the Strepsirhini and the Haplorhini. The two subgroups of Strepsirhini (Lemuriformes and Lorisiformes) are variable, including taxa with strictly herbivorous and omnivorous diets. The Haplorhini include the Anthropoidea and the Tarsiiformes. The former are largely herbivorous, usually complementing their diet with insects. The latter compose a small group of predominantly insectivorous diet. For this reason, the terminal stem Primates was coded as variable (polymorphic) for the character feeding habit.
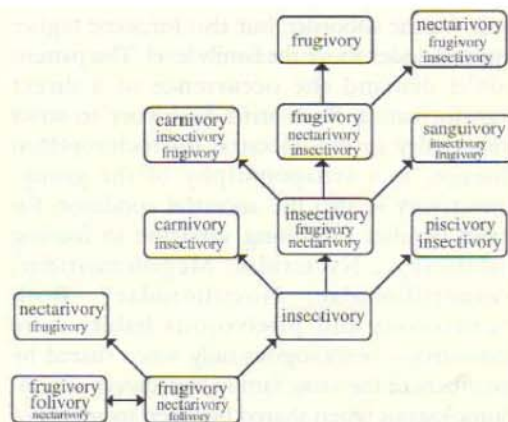
We have evaluated the data under assumptions of both character additivity and non-additivity, and the results of different possibilities of optimization are presented in Figures 2a and 2b. A single most parsimonious optimization requiring only two steps was obtained without the assumption of character additivity (Fig. 2a). This minimal length transformation series shows herbivory as the ancestral feeding habits of both Chiroptera and Volitantia, whereas insectivory is indicated as uniquely derived (at this level) for Microchiroptera. The ancestral condition for Primates and for Archonta could not be decisively inferred as herbivory or omnivory, and it was regarded as ambiguous or equivocal.

Under the assumption of character additivity, and ordering omnivory as intermediate between herbivory and insectivory there are, on the other hand, two equally parsimonious optimizations possible for the same topology, requiring three steps each. One of these alternatives is exactly the same obtained under non-additivity (Fig. 2a), and the other is depicted in Figure 2b. This last alternative is similar to the former in considering insectivory as derived for Microchiroptera, but differs from it in considering omnivory the ancestral condition for all internal nodes, from which frugivory was independently derived in Dermoptera and Megachiroptera, whereas insectivory was derived in Microchiroptera.

The coding of Primates as omnivorous (rather

than polymorphic) would lead to a similar optimization under non-additivity, not affecting the results obtained for Chiroptera and Volitantia, but it will favor a hypothesis in which it would be more parsimonious to accept both the Archonta and the (Primates + Volitantia) ground plans as omnivorous. The alternative coding of Primates as herbivorous would lead to a single most parsimonious hypothesis, in which herbivory would be the plesiomorphic habit not only for Chiroptera and Volitantia (Fig. 2a), but also for the node of the (Primates + Volitantia).

The hypothesis considering insectivory plesiomorphic at some level would require additional steps under the assumption of both additivity and non-additivity, and is thus less parsimonious. If we consider the ancestors of Chiroptera and Volitantia as insectivorous, we would have to assume at least two independent origins of herbivory from insectivory, in both Megachiroptera and Dermoptera, and perhaps again within Primates.

In summary, we can state that the hypothesis of a herbivorous ancestor for both Chiroptera and Volitantia is better congruent with the systematic pattern as recovered by a cladistic analysis based on other independent comparative evidence. However, the alternative assumption of omnivorous ancestors could not be discarded if one considers character additivity. On the other hand, assuming insectivory as the generalized feeding habit for Archonta would be incongruent with our present knowledge on the cladistic relationships in the group.

The order Chiroptera. The result of the parsimonious optimization of the 12 feeding habits states (Fig. 1) and of the independent character states concerning the relative utilization (consumption) of each food item (1-7) and foraging behavior (8) on the Chiroptera cladogram is presented in Figures 3 and 4. After optimization, the once ordered, unpolarized transformation series (Fig. 1) acquires a temporal direction. The shared primary homologies can now be tested by congruence with the tree topology, and the secondary (or evolutionary) homologies can be discerned from the homoplasies, then.

The polarized sequence of transformation of the whole series derived from optimization on the cladograms is presented in Figure 5. The major shifts in feeding habits that occurred in

Figure 5. Transformation series of feeding habits in Volitantia (Dermoptera + Chiroptera), after polarization through optimization on the cladograms of Figures 3 and 4. Compare with the ordered, unpolarized scheme in Figure 2.

the evolutionary history of bats are described below, considering the level of generality in which they appeared.

The parsimonious optimizations are the same under the assumption of both character additivity and non-additivity. This procedure allowed a clear inference about the ancestral feeding habit for all internal nodes of the Chiroptera cladogram, except for the most basal one. The ancestral habit for Chiroptera and Volitantia can be determined as herbivorous, but the optimization of states 10 (frugivory-folivory) and 11 (frugivory) is ambiguous at both nodes. Predominant frugivory seems to be a ground plan condition for Pteropodidae (based on assumptions about order between states), from which the specialized nectarivory of the Macroglossinae derived. This view is additionally supported by the probably paraphyletic condition of the Pteropodinae relative to Macroglossinae. The relative utilization of each food item should be understood as an independent character. Hence, it would be made clear that the consumption of leaves and floral products as a diet complement and the non-consumption of insects would be plesiomorphic traits retained in Megachiroptera, shared with the outgroup Dermoptera. The predominant frugivory could not be definitely established as synapomorphic for the Megachiropteran or for the Pteropodinae, and it could even be plesiomorphic for Chiroptera.

Due to the distribution of strict insectivory among families of Microchiroptera, it should be clearly considered as the ancestral condition not

only for the suborder, but also for some higher internal nodes above the family level. This pattern could demand the occurrence of a direct transformation from strict herbivory to strict insectivory in the ancestral microchiropteran lineage, as a synapomorphy of the group. Insectivory is also the ancestral condition for most families exhibiting variation in feeding habits (e.g., Nycteridae, Megadermatidae, Vespertilionidae, Noctilionidae). Both carnivorous and piscivorous habits were indicated as homologous only when shared by members of the same family, but always as non-homologous when shared between members of different families. The aerial insectivory of Emballonuridae could not be decisively polarized as an autapomorphy for the family. However, strict aerial insectivory (8.1) was inferred to have been originated independently at least other four times: autapomorphic for Rhinopomatidae, Molossidae, and Hypposiderinae, and synapomorphic for a monophyletic group including the Nataloidea plus Vespertilionidae. Within this latter family, two tribes of the same subfamily (Vespertilioninae) apparently represent an instance of secondary reversal to foliage gleaning habits from aerial insectivorous ancestors.

Within the superfamily Rhinolophoidea, the predominant carnivorous habits have been independently originated twice. In one of them it is apparently an autapomorphy of a single species of Nycteridae, and in the other it is as a synapomorphy shared by most genera of Megadermatidae, with the notable exception of *Lavia*, which maintained the plesiomorphic insectivorous habit. The pattern of distribution of carnivory as an apomorphy is more congruent with Hand's (1985) hypothesis, in which *Lavia* is placed as the sister group of all other megadermatids, than with the hypothesis of Griffiths et al. (1992). According to the topology of intergeneric relationships obtained by Griffiths et al. (1992), carnivory would be more parsimoniously explained as a synapomorphy of Megadermatidae with reversal in *Lavia*, due to the supposedly more inclusive position accepted for this genus.

Within the large superfamily Vespertilionoidea, there are very few instances of shifts in feeding habits. The family Mystacinidae became omnivorous, including fruits and floral products in its diet, without abandoning insectivory as a major food habit.

In the subfamily Myotinae, a single species of the well-diversified genus *Myotis* became truly piscivorous, apparently as an autapomorphy, although such uncommon aquatic gleaning forage behavior is also shared by a few possibly related congeneric insectivorous species.

Among all Microchiroptera, the major modifications in the feeding habits occurred within the members of the diversified superfamily Noctilionoidea (=Phyllostomoidea). The strict insectivory, plesiomorphic for the Microchiroptera as a whole, is preserved as the feeding habit of only a few members of this superfamily (e.g., Mormoopidae, and Noctilionidae species *Noctilio albiventris*). The aquatic gleaning forage behavior is a synapomorphy shared by both species of *Noctilio*, although piscivory is autapomorphic for *N. leporinus*.

In contrast to most of the other bat families, the ancestral feeding habit of the Phyllostomidae may be inferred as more specialized to an omnivorous, but still predominantly insectivorous diet (Fig. 4). As far as we are aware, only a few phyllostomid taxa, like the genera *Lonchorhina* and *Macrophyllum,* are apparently strictly insectivorous. This is indicated as a relatively plesiomorphic condition, but if the cladogram topology of Figure 4 is assumed, this condition is better interpreted as a reversal shared by the two genera. On the other hand, further studies on the feeding biology of these poorly known genera may verify that they are actually not strictly insectivorous as it was proposed. Although the inclusion of fruits as a diet complement appears to show a more general distribution among phyllostomid subfamilies, the utilization of floral products is inferred to be an apomorphy shared by glossophagines, stenodermatines and most phyllostomines s.s. The origin of a predominantly herbivorous diet is here inferred as a synapomorphy shared by stenodermatines and glossophagines, although some omnivorous species of *Phyllostomus* have apparently developed this condition homoplastically. According to the previously established transformation series, the utilization of fruits as an important component of the diet is here interpreted as plesiomorphic in relation to the predominant nectarivorous diet of glossophagines. Therefore, predominant nectarivory is a synapomorphy shared by all major glossophagine lineages.

Apparently, a predominantly insectivorous

basal ancestral lineage, whose habits have been maintained by most phyllostomine groups, independently originated the predominant carnivory as a synapomorphy of the Vampyrinae, and the sanguivory as a synapomorphy of the Desmodontinae. It is concluded that each of the major kinds of feeding habits (or trophic categories) evolved only once in the history of the Noctilionoidea, without the need to assume convergent events to explain the sharing of the same feeding habit by different suprageneric taxa in the group.

The differences in feeding habits and foraging behavior among the three Desmodontinae vampire species are also interesting to be studied from a phylogenetic perspective. This case is depicted in Figure 6. Using *Diphylla* as an outgroup, we can polarize the transformation series of features on which the sister genera *Diaemus* and *Desmodus* differ. The habit of feeding preferentially on avian blood is clearly a simplesiomorphy shared by *Diphylla* and *Diaemus*, whereas the habit of feeding preferentially on mammalian blood is an autapomorphy of *Desmodus*. The behavior and site of foraging are also correlated with this shift in diet, since species preying on birds plesiomorphically forage in trees, approaching the victim from below. In contrast, the habit of foraging preferentially on the ground, approaching the victim from above is autapomorphic for *Desmodus*. Another argument favoring the hypothesis that preying preferentially on birds is plesiomorphic in relation to preying on mammals is the presence of a specific activator for mammalian plasminogen in the saliva of *Desmodus*, whereas that of *Diaemus* also activates avian plasminogen. Although the specificity of such activator is unknown for *Diphylla*, it is highly improbable that this genus have the same specific activator as *Desmodus*, since *Diphylla* appears to be even more specialized for preying on birds than *Diaemus*. If this is correct, the presence of a specific activator for mammalian plasminogen is another autapomorphy of *Desmodus*, whereas its absence is the plesiomorphic condition found in the common ancestor of the Desmodontinae.

Discussion. Current theories of feeding habits evolution, and adaptational hypothesis

It is proposed here that herbivory is a symplesiomorphic feeding habit for bats, since
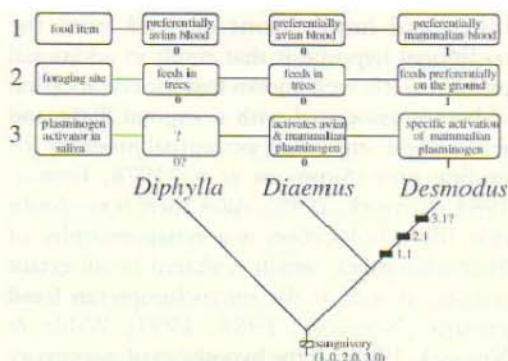

Figure 6. Evolution of feeding habits in the subfamily Desmodontinae. Top: unpolarized, binary transformation series of different conditions regarding feeding habits (characters 1,2,3); bottom: parsimonious optimization of the transformation series on the vampire bats cladogram topology. The cladogram topology, assuming *Diaemus* and *Desmodus* as sister groups, is based on Honeycutt *et al*. (1981) and Koopman (1988).

it is shared with the outgroup Dermoptera. This is presented here as an alternative hypothesis, which is more parsimonious than the traditional view considering strict insectivory as an ancestral feature for bats (*e.g.*, Romer, 1956; Gillette, 1975; Smith, 1976), maintained in the Microchiroptera. There is no immediate insectivorous outgroup for Chiroptera, and the closest related truly insectivorous archontan taxon are the tarsiiform primates, which are placed at least five internal tree nodes from the Microchiroptera. Our new hypothesis also eliminates the need to evoke multiple origins of herbivory within Archonta. If the insectivory of tarsiiforms and Microchiroptera is considered as homologous (thus plesiomorphic to most of the major archontan lineages), at least four instances of independent origin of herbivory (predominant or strict, and including frugivory) in the Archonta would have to be admitted: in Megachiroptera, Dermoptera, Anthropoidea, and in part of the Strepsirhini (the remaining Strepsirhini are omnivorous). Extending insectivory to the common ancestry of all Archonta would also imply another instance of origin of a partially frugivorous feeding habit for the Scandentia, as assumed by Emmons (1991). The morpho-physiological features associated to frugivory, shared by Scandentia and Megachiroptera (Emmons, 1991), are additional corroborations to the hypothesis that herbivory is plesiomorphic in the Chiroptera.

Not only the incongruence between the feeding habits and the phylogenetic pattern is to be considered in this discussion. There are

functional implications derived from the traditional hypothesis that result in additional problems. It is well-known that the echolocation in bats is associated with nocturnal flight and serves as an important perceptual modality for finding prey (Simmons *et al.*, 1978; Fenton, 1984; Novacek, 1985). Also, there is no doubt that the echolocation is a synapomorphy of Microchiroptera, which is shared by all extant species, as well as the microchiropteran fossil groups (Novacek, 1985, 1991; Wible & Novacek, 1988). If the hypothesis of insectivory as a bat ground plan condition is accepted, the common ancestor of Chiroptera would be an insectivorous species without a sonar system. This would be a considerably unlikely assumption, considering the role of the echolocation in the insect hunting in the dark. A species with such a combination of features seems unlikely to have existed. In other words, this is to say that under our model this kind of combination of features is not to be found in any extant or extinct species. On the other hand, the new hypothesis establishes both insectivory and echolocation as synapomorphies of Microchiroptera, which would have had a functional association during the early evolutionary history of this group. This is not the same as saying that the echolocation arose due to insect hunting habit. Other kinds of evidence indicate that the echolocation originated as an adaptation to a cave ecology, and its use for hunting insects would correspond to a secondary modification (Brosset, 1964; Novick, 1977). It seems reasonable that the utilization of caves precedes both insectivory and echolocation, since roosting in caves, at least facultatively, is shared by megachiropterans. Also, it has been quite well-described that one megachiropteran *Rousettus* species living in caves developed a non-homologous system of echolocation (Brosset, 1964; Novick, 1958). Thus, the echolocation may be a function derived from roosting in caves. Only after this system was established, the insectivory in nocturnal flights could originate.

Our hypothesis is also compatible with the teeth functional morphology. The primitive trituberculate pattern of molar cusps is probably the plesiomorphic condition within Archonta. It seems certainly misleading to characterize microchiropteran dentition as primitive (Novacek, 1987; Wible & Novacek, 1988). It is well-known that the dilambdodont dentition

of microchiropterans is adapted for mastication of hard parts of insects. Although not unique for Microchiroptera, the distribution pattern of dilambdodonty among archontans and other placental mammals suggests that this feature had a history of independent origins. One of these instances is a synapomorphy of Microchiroptera (Novacek, 1987; Wible & Novacek, 1988). Thus, if ancestral bats were insectivorous, they would not have a dentition functionally adapted to insectivory, as is the case of the Microchiroptera. Considering insectivory a microchiropteran synapomorphy, on the other hand, places both the specialized habit and the dentition specialized for this habit at the same level of generality, that is, originating in the same ancestral lineage of all Microchiroptera. The Megachiroptera also have a modified dentition functionally adapted to frugivory (Slaughter, 1970; Koopman & MacIntyre, 1980), and as in the case of Microchiroptera, widely divergent from the tritubercular condition found, for example, in Dermoptera (Novacek, 1987), and perhaps in the chiropteran ancestor. Although the relative apomorphy of herbivory-frugivory remained undetermined in our analysis (Fig. 3), this fact may be an indicative that megachiropteran frugivory (including nectarivory) is derived relative to a more generalized herbivorous diet of dermopterans.

Since the direction assumed for the transformation series at this level is from herbivory to insectivory, Gillette's (1975) hypothesis that frugivory originated from insectivory through a stage of a dual omnivorous habit seems misleading. Gillette's (1975) model could certainly be used to explain a modification of the feeding habit in an opposite direction. None of the two microchiropteran families with omnivorous diets (Mystacinidae and Phyllostomidae) show a basal position in the phylogeny of the group, so it seems untenable that their habits could be considered as evolutionarily intermediate (*i.e.*, relatively plesiomorphic to strict insectivory). The discovery of a fossil omnivorous sister group of the Microchiroptera would rescue Gillette's (1975) model for this shift.

If Gillette's (1975) hypothesis of intermediate stages for the change in the feeding habits seems not well founded for the base of the Microchiroptera, though it appears acceptable for other levels of universality within the group. With few exceptions (*e.g.*, at subordinal level),

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the detected shifts from a major feeding habit to another apparently occurred with intermediate stages. This is apparently true for the cases of independent origin of piscivory in *Noctilio* and *Myotis*. In both cases, their non-piscivorous closest relatives combine insectivorous diet and aquatic gleaning. They have remained as a "living testimony" of this intermediate ancestral state. The major evolutionary shift that occurred in both groups, however, was certainly the origin of aquatic gleaning, rather than the origin of piscivory. The two noctilionid species have considerably similar morphology, including the structures usually referable as "adaptations" to the particular feeding habit, as the elongated feet. The predation of fish by an originally aquatic gleaning insectivorous bat may require no significant adaptational shift and may be simply correlated with the large size of *N.leporinus*.

Aside from the large size and powerful cutting dentition, carnivory does not require major specialization other than the ones already present in insectivorous foliage gleaning ancestors of both Megadermatidae and Phyllostomidae. It seems acceptable to trace a hypothesis of transition from preying on large arthropods (as is known for *Macrotus* and other phyllostomines) to the utilization of small vertebrates as food items.

Sanguivory, the most divergent and unique of the bat feeding habits, requires extensive morphological, physiological and behavioral specializations. It is a shared homology of all desmodontine species and the only major feeding habit without homoplasies, that is, it did not evolve independently in other lineages. Diverse hypotheses and speculative scenarios have been proposed as explanation for the origin of sanguivory. Our results of inference of ancestral feeding habits for the internal nodes of the desmodontine cladogram can be used as an independent test for these hypotheses.

Slaughter (1970) proposed an origin of sanguivory from a frugivorous ancestor, specialized in cutting the rind of fruits with its large incisive teeth to suck the juice. Such an odd model may be explained by the close relationship between the desmodontines and the frugivorous carolliines accepted by Slaughter (1970, Fig. 5). This view was not supported by any of the recent phyllostomid phylogenetic studies. Due to the relatively basal phylogenetic position of the Desmodontinae within the Phyllostomidae, the assumption of a frugivorous desmodontine

ancestor is not very parsimonious and would imply another independent origin of frugivory in the Phyllostomidae.

The only possible reminiscent evidences indicating that sanguivory derived from insectivory are very sporadic records of insects and ectoparasites as complementary food items for the common vampire bat. Gillette (1975) and Turner (1975) suggested a stage of specialized "insectivory" as a hypothetical intermediate between insectivory and sanguivory. Such ancestral species would feed on large mammal ectoparasites (suc as ticks and mites), followed by a dual stage of eating both ectoparasites and blood, then leading to specialized sanguivory. Fenton (1992) presented another scenario, in which the 'protovampire' would feed on insect larvae on large mammal wounds. From this an intermediate stage of feeding on insects and body fluids, and finally on blood followed. Based on observed behavioral similarities between carnivorous bats and the common vampire when preying on small preys, Schmidt (1978), on the other hand, suggested a carnivorous origin for the desmodontine ancestor. Sazima (1978) has hypothesized that the 'protovampire' was specialized in preying on small arboreal victims, and that the feeding habits and behavior of *Diaemus* are reminiscent of this primitive habit, whereas those of *Desmodus* are derived.

It is a clear assumption of Gillette (1975), Turner (1975), and Fenton's (1992) hypotheses that the common Desmodontinae ancestor was specialized in preying on terrestrial (non-arboreal), large mammal preys. This statement is in contrast to Sazima's (1978) hypothesis of bats feeding on small arboreal preys. The conclusions derived from the present study (see Fig. 6) seem sufficient to deduce that the common ancestor of desmodontines was specialized in feeding solely or preferentially on avian blood, foraging on trees, as seen today in *Diphylla* and *Diaemus*. This certainly corroborates Sazima's (1978) hypothesis and provides sufficient grounds to reject Gillette (1975), Turner (1975), and Fenton's (1975) models. The hypothesis of a 'protovampire' specialized in feeding preferentially on blood of birds in trees, and the hypothesis of a carnivorous origin for sanguivory are not mutually exclusives. Many carnivorous species, including phyllostomids, are known to prey on birds. Since there is no indication that the Desmodontinae and

Vampyrinae are closest relatives, the evocation of a carnivorous origin for sanguivory would require an additional independent origin of the former habit in the family.

Refined analyses of minor dietary differences among species and closely related genera could help the better understanding of the processes driving the changes in feeding habits. This demands detailed studies on the feeding habits of several species of bats in search of differences between representatives of the diverse groups roughly characterized as frugivorous and nectarivorous, for example. Such knowledge would certainly be useful for the interpretation of how microevolutionary processes act during a large time scale, and produce the macroevolutionary patterns regarding the different feeding habits described here for the major chiropteran lineages.

Phylogenetically based coevolutionary studies of historical ecology, specially on coadaptation between bats and plants, and bats and preys, would be very desirable and could be illuminating. There is an exceptional amount of information available for this kind of analysis, as the cases of interactions between bats and fruits, and bats and flowers (van der Pijl, 1957, 1960; Sazima & Sazima, 1975), as well as the predator-prey relationships between carnivorous phyllostomids and frogs (Ryan *et al.*, 1990).

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