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Macroevolution in Microchiroptera: Recoupling morphology and ecology with phylogeny

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ABSTRACT

No family of mammals has undergone a greater adaptive radiation than phyllostomid bats. Phylogeny combined with eco-morphological considerations of trophic structures can help understand this adaptive radiation and the evolution of Microchiroptera. Microchiropteran bats are overwhelmingly insectivorous, and constraints within the morphospace of insectivory have produced a dynamic equilibrium in bat morphologies that has persisted for 60 million years. The ability to eat fruit may be the key synapomorphy that allowed phyllostomids to escape insectivore morphospace and diversify. Although many phyllostomids have changed greatly, others that have maintained insectivory have changed little, which is equally remarkable.

Keywords: bats, craniodental patterns, dental patterns, diet, dilambdodonty, ecology, insectivory, macroevolution, mammals, Microchiroptera, phylogeny, Phyllostomidae.

INTRODUCTION

Adaptive radiations have long fascinated evolutionary biologists. Textbook examples include the cichlid fishes of the African Rift Valley (Liem, 1973) and the Cenozoic bovids (Jernvall *et al.*, 1996). An equal and perhaps more spectacular case is found in the Phyllostomidae, the leaf-nosed bats of the New World. From an ancestral diet of insectivory, descendants today can still be insectivorous, but also carnivorous (consumers of vertebrate prey), nectarivorous and pollinivorous, frugivorous, and sanguinivorous (Fig. 1). This diversification of diet and morphological form within a single family is without parallel in mammals or many vertebrates. How and why this diversification occurred, and how that diversification compares with that of bats in the suborder Microchiroptera, is the subject here. The fossil record is often useful in studying adaptive radiations (Foote, 1996; Jernvall *et al.*, 1996), but fossils of phyllostomids are rare (Dawson and Krishtalka, 1984). Cladistic reconstruction of phylogenies, when coupled with ecological and morphological data, offers an alternative and powerful tool for studying adaptive radiations. Fortunately, knowledge of the phylogeny of phyllostomids has reached a point (Baker *et al.*, 1989; Van Den Bussche, 1992) where my analysis can proceed. Traditionally, cranial and especially dental characteristics have weighed heavily in explaining ancestral–descendant relationships

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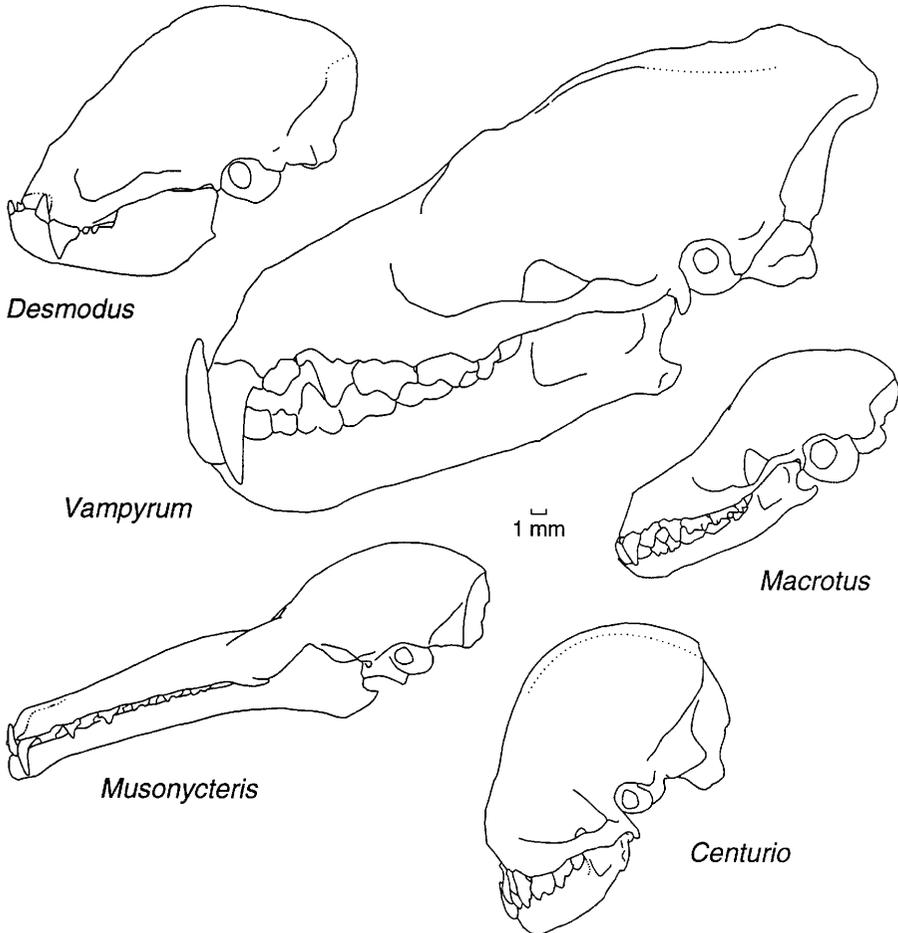


Fig. 1. Four eco-morphological extremes in the Phyllostomidae: *Desmodus*, a blood-feeder; *Vampyrum*, a large carnivore; *Musonycteris*, a nectarivore; and *Centurio*, a frugivore. *Macrotus* is insectivorous and frugivorous, more central in eco-morphological space (Fig. 4), and one of the least derived phyllostomids. Skulls are drawn to scale and aligned so that the basicranial axis is horizontal (Freeman, 1984).

in mammals in general and phyllostomids in particular. Teeth and characteristics derived from bony parts are often the only fossils available to palaeontologists for determining relationships of mammals and bats (Simpson, 1945; Slaughter, 1970). Numerous phylogenies for Microchiroptera and Phyllostomidae have been constructed by both neo- and palaeomammalogists, incorporating a variety of cranial, craniodental, postcranial bony and soft tissue characteristics (Miller, 1907; Smith, 1976; Van Valen, 1979; Hall, 1981; Griffiths, 1982; Novacek, 1991; Koopman, 1993, 1994). Phylogenetically important characteristics for Microchiroptera have shifted from skulls and teeth (Miller, 1907) to a more biochemical approach to derive inter-familial relationships (Pierson *et al.*, 1986, used immunological distance). Baker (1967) began using karyological and biochemical techniques to investigate

phylogenetic diversity in Phyllostomidae that culminated in a synthesis based heavily on female reproductive morphology, immunological distance data and G-band chromosomal data (Baker *et al.*, 1989). The approach taken by the latter authors is robust for two reasons: their data comprise both biochemical and non-dental morphological characteristics, and they applied rigorous cladistic methods to determine phylogeny. Van den Bussche (1991, 1992) refined Baker's phyllostomid phylogeny further using ribosomal DNA and restriction site variation. Analyses derived from chemical data have been slow to be accepted by more traditional mammalogists (Koopman, 1994). Here, I recouple traditional craniodental characteristics of bats that have ecological and functional significance with this rigorous cladistic phylogeny, founded on non-traditional and non-dental data. Together, they help to explain how phyllostomids radiated.

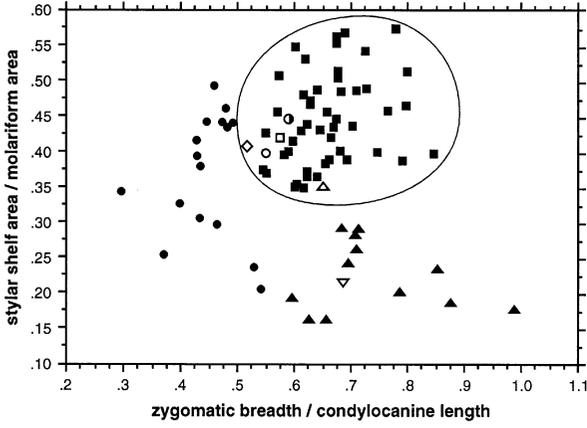
INSECTIVORE MORPHOSPACE

This story begins with eco-morphological space containing representatives of many microchiropteran genera (Fig. 2). The axes illustrated here are morphological characteristics I think are critical to differentiating feeding ecology: size, width of face, rostral length, thickness of dentary, relative size of molars, and proportion that the raised styler shelf – the W-shape – occupies on the upper molar row. These are a small subset of characteristics I have quantified for 85 species of Microchiroptera representing 63 genera across nine families (11% of 759 species and 49% of the named genera in the most speciose families; Wilson and Reeder, 1993). Position in morphological space maps function in ecological space (Freeman, 1979, 1981a,b, 1984, 1988, 1992, 1995, 1998) and the characteristics represented in Fig. 2 are reliable for separating insectivorous and carnivorous bats (sometimes lumped into a group of animalivores) from frugivorous and nectarivorous ones. This approach is not uncommon for biologists who study bats (Findley and Wilson, 1982; Fenton, 1989; Saunders and Barclay, 1992; Findley, 1993; Fleming, 1993; Barlow *et al.*, 1997; Freeman, 1998), a group which Findley (1993: 145) labelled 'among the most difficult small vertebrates to study'. Findley also furnishes evidence from many studies that 'bat morphology provides a rather accurate key to the kinds of lives bats lead'.

Non-phyllostomid microchiropteran bats are almost exclusively insectivorous. Furthermore, insectivorous bats are the earliest bats and were around 60 million years ago (Dawson and Krishtalka, 1984). Insectivory in bats is an adaptive zone comprising dental variations based on the theme of dilambdodonty, the W-shape that is the typical ancestral molar pattern of insectivorous mammals (Slaughter, 1970; Romer, 1971; Young, 1981; Vaughan, 1986; Carroll, 1988). The most pronounced morphological variation in insectivorous bats is correlated with the degree to which hard versus soft items occur in the diet (Freeman, 1979, 1981b) (Fig. 3A). Robust-skulled bats are durophagous (duro = hard + phagous = feeding) and are capable of eating harder-bodied prey such as hard-shelled insects, invertebrates and fish (Black, 1974; Husar, 1976; Freeman, 1979, 1981b; Findley and Black, 1983; Strait, 1993a,b; Brooke, 1994).

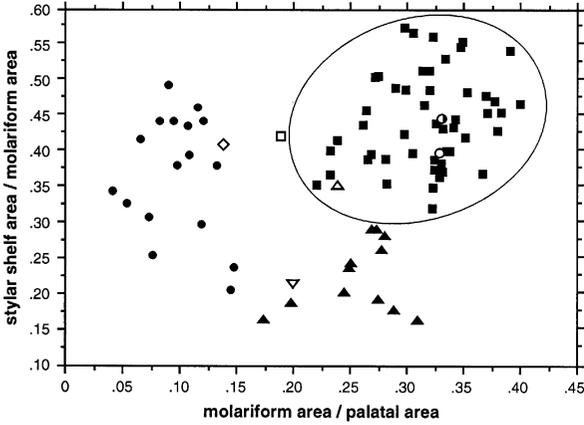
The robust bats in my insectivore morphospace all evolved durophagy independently because they are from five different families (Molossidae, Vespertilionidae, Emballonuridae, Noctilionidae and Rhinolophidae; Freeman, 1984). Characteristics of durophagy include large masseter muscle volumes, stout dentaries, tooththrows with fewer but larger teeth, the development of cranial crests, usually longer canines relative to maxillary tooththrow length, and usually wide skull widths relative to skull lengths. However, these features are expressed

A



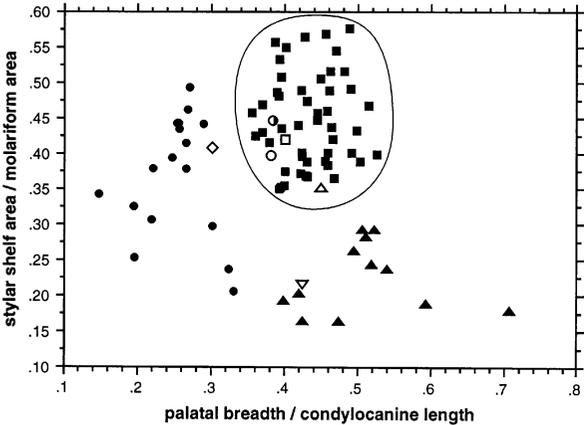
- ANIMAL
- NECTAR
- ▲ FRUIT
- ◐ *Macrotus*
- *Micronycteris*
- △ *Uroderma*
- *Carollia*
- ▽ *Sturnira*
- ◇ *Glossophaga*

B



- ANIMAL
- NECTAR
- ▲ FRUIT
- ◐ *Macrotus*
- *Micronycteris*
- △ *Uroderma*
- *Carollia*
- ▽ *Sturnira*
- ◇ *Glossophaga*

C



- ANIMAL
- NECTAR
- ▲ FRUIT
- ◐ *Macrotus*
- *Micronycteris*
- △ *Uroderma*
- *Carollia*
- ▽ *Sturnira*
- ◇ *Glossophaga*

differently with regard to how a bat's echolocation call is emitted. That the two kinds of microchiropteran echolocation are produced by characteristically different cranial morphologies has been investigated in both neonatal and adult skulls by Pedersen (1993, 1995, 1998). Robustness and durophagy in oral-emitting molossid, vespertilionids, noctilionids and emballonurids are typically wide-faced. However, nasal-emitting rhinolophids that eat hard items are typically narrower-faced but have tall sagittal crests and vertically tall mandibular rami or thick dentaries. Given that the major trophic difference that has evolved in insectivorous bats has centred around durophagous and non-durophagous feeders, these differences can be neatly summarized in a bivariate plot of dentary thickness versus skull width (Fig. 3A). These two features explain two design constraints of oral and nasal emission because durophagy is solved differently by each group. Nasal emitters have longer faces, perhaps to retain a longer nasal capsule for nasal emission that may not be shorter without sacrificing echolocation function. The most extreme durophagous, nasal-emitting bat here (the rhinolophid, *Hipposideros commersoni*) is a known beetle specialist (Vaughan, 1977). It has increased areas for jaw musculature in a vertical direction, particularly an

Fig. 2. Three bivariate plots to represent the eco-morphological space of insectivores/carnivores (ANIMAL), the circle of which includes all non-phylostomid bats from eight microchiropteran families and some phyllostomid bats; phyllostomid nectarivores (NECTAR); and phyllostomid frugivores (FRUIT). (A) Relative amount the styler shelf occupies on the molariform tooththrow vs the relative width of the skull; (B) styler shelf vs relative area that the molariform teeth occupy on the palate; and (C) styler shelf vs relative width of the palate. Blood-feeders are not included here because their presence compresses the scatter of all other points. Seventy-six percent of all possible phyllostomid genera are represented in this study. The insectivorous non-phylostomids and the percentage of genera of their respective families are: *Saccolaimus peli*, *Taphozous nudiventris*, *Peropteryx kappleri* (23% of emballonurid genera), *Rhinolophus luctus*, *Rhinolophus rufus*, *Rhinolophus blasii*, *Hipposideros commersoni gigas*, *Hipposideros c. commersoni*, *Hipposideros lankadiva*, *Hipposideros pratti*, *Hipposideros ruber* (20% of rhinolophid genera), *Scotophilus nigrata gigas*, *Ia io*, *Myotis myotis*, *Myotis velifer*, *Myotis vivesi*, *Nyctalus lasiopterus*, *Antrozous pallidus*, *Eptesicus serotinus*, *Otonycteris hemprichi*, *Lasiurus cinereus*, *Lasiurus borealis* (23% of vespertilionid genera), *Cheiromeles torquatus*, *Eumops perotis*, *Eumops underwoodi*, *Otomops martiensseni*, *Tadarida brasiliensis*, *Molossus molossus* (50% of molossid genera), *Noctilio leporinus*, *Noctilio albiventris* (100% of noctilionid genera), *Mormoops megalophylla* and *Pteronotus parnellii* (100% of mormoopid genera). Phyllostomids found in this insectivorous space are: *Macrotus californicus*, *Micronycteris megalotis*, *Lonchorhina aurita*, *Mimon bennettii*, *Phylloderma stenops*, *Phyllostomus hastatus*, *Phyllostomus elongatus*, *Phyllostomus discolor* and *Tonatia silvicola*. *Carollia perspicillata* and *Uroderma bilobatum*, both known frugivores, and *Glossophaga soricina*, a known nectarivore, are also found in this space. The carnivorous non-phylostomids are: *Macroderma gigas*, *Megaderma lyra*, *Cardioderma cor* (100% of megadermatid genera) and *Nycteris grandis* (100% of nycterid genera). The carnivorous phyllostomids are: *Vampyrum spectrum*, *Chrotopterus auritus* and *Trachops cirrhosus*. The nectarivorous phyllostomids are: *Phyllonycteris poeyi*, *Erophylla sezekorni*, *Glossophaga longirostris*, *Monophyllus plethodon*, *Monophyllus redmani*, *Lichonycteris obscura*, *Leptonycteris curasoae*, *Anoura caudifer*, *Anoura geoffroyi*, *Hylonycteris underwoodi*, *Choeroniscus godmani*, *Choeroniscus intermedium*, *Choeroniscus mexicana*, *Musonycteris harrisoni*, *Lonchophylla thomasi*, *Lonchophylla handleyi* and *Lionycteris spurrelli*. The frugivorous phyllostomids are: *Artibeus jamaicensis*, *Artibeus lituratus*, *Dermanura phaeotis*, *Dermanura toltecus*, *Chiroderma villosum*, *Ametrida centurio*, *Centurio senex*, *Ectophylla alba*, *Pygoderma bilabiatum*, *Sphaeronycteris toxophyllum*, *Sturnira lilium*, *Brachyphylla nana* and *Brachyphylla cavernarum*. The sanguinivorous phyllostomids in the study but not in this figure are *Diphylla ecaudata* and *Desmodus rotundus*.

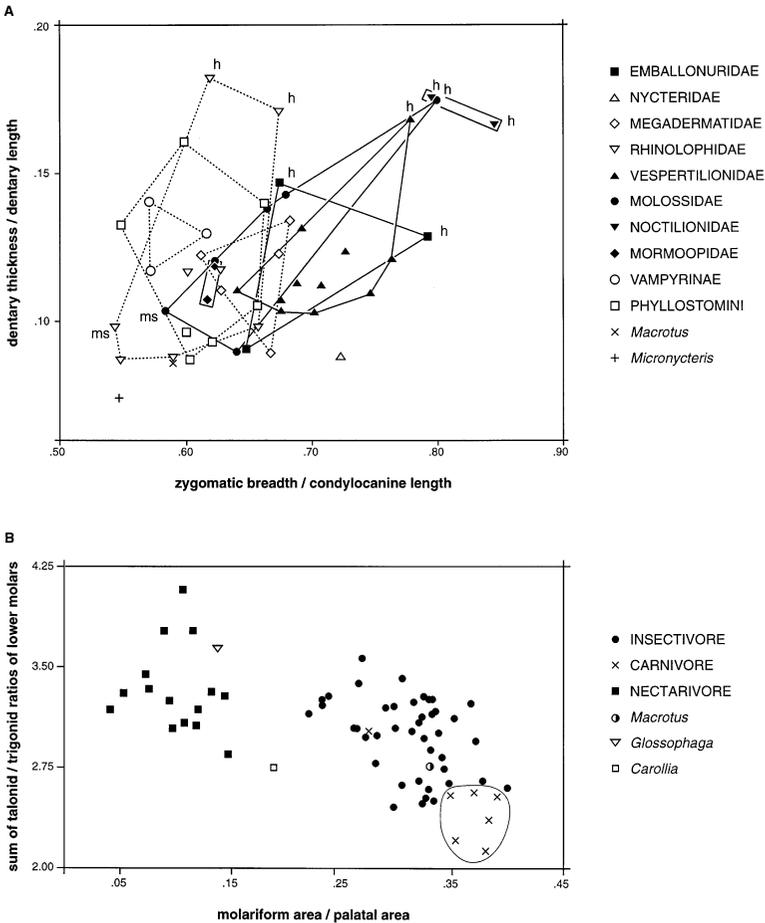


Fig. 3. (A) Non-phylostomid insectivorous families in a scattergram of relative dentary thickness versus relative width of skull. Although similar to the insectivore morphospace in Fig. 2A, durophagous (hard = h) and non-durophagus (as represented by moth specialists = ms) bats are more easily distinguished. Oral-emitting, durophagous species have short wide skulls; nasal-emitting species have vertically tall skulls including the vertical thickness of the dentaries (the rami of the mandibles are measured at the root of the first lower molar; Freeman, 1984). Non-durophagous species of both emission types overlap in the lower left. Also shown are the insectivorous and carnivorous phylostomids, here represented by *Macrotus*, *Micronycteris*, *Lonchorhina*, *Phyllostomus*, *Phylloderma*, *Mimon*, *Tonatia*, *Trachops*, *Chrotopterus* and *Vampyrum*. Although these bats traditionally have been put into the subfamily Phyllostominae (Miller, 1907; Koopman, 1994), there is now evidence that this group is paraphyletic (Baker *et al.*, 1989). Oral-emitters are represented by filled symbols and nasal emitters by open symbols. (B) Insectivorous and carnivorous species of bats are not easily differentiated (Freeman, 1984), and Savage (1977) found this to be true of fossil terrestrial carnivores and insectivores. The sum of the ratio, talonid/trigonid width, on the three lower molars plotted against the relative area that the upper molars occupy of the palate, groups six of the seven carnivores in this study (tooth diagram in Freeman, 1998). The ungrouped species is *Trachops*, a phylostomid that eats frogs and insects, and the circled group of six contain representatives of three unrelated families, Nycteridae (*Nycteris*), Megadermatidae (*Megaderma*, *Macroderma* and *Cardioderma*) and Phyllostomidae (*Chrotopterus* and *Vampyrum*), which may be more obligate carnivores.

expanded sagittal crest. Durophagous, oral-emitting bats tend to have robust skulls with short but wide faces that bring jaw muscles closer to the fulcrum of the jaw joint (Freeman, 1981b, 1984).

The opposites of durophagy, the species that specialize on soft-items such as moths, occur in both oral and nasal-emitting bats. In the Vespertilionids, plecotines such as *Euderma*, *Plecotus* and *Idionycteris* (Freeman, 1981b) are extreme moth specialists and have long thin jaws, gracile skulls with little or no cranial crest development, more but smaller teeth, and smaller canines. Gracile-skulled molossids with a similar morphology, such as *Otomops martiensseni* here, are known moth specialists (Rydell and Arlettaz, 1994; Rydell and Yalden, 1997). Non-durophagous, oral and nasal-emitting extremes are indistinguishable from each other and from carnivorous bats (Fig. 3A; Freeman, 1984). Freeman (1981b) ranked several rhinolophids as soft-item eaters. *Rhinolophus blasii*, a bat for which there is good diet information, is one of the non-durophagous rhinolophids in the lower left of Fig. 3A and is a known moth specialist (Whitaker and Black, 1976).

Carnivory evolved at least three times and includes the largest members of their respective families: *Nycteris grandis* in Nycteridae, *Macroderma gigas* in Megadermatidae, and *Vampyrum spectrum* in Phyllostomidae (Fig. 3B). These are nasal-emitting bats. Besides piscivory in noctilionids, there is no evidence for carnivory in oral-emitting bats. However, until recently, I could rarely distinguish non-durophagous bats from carnivorous bats. These have craniodental characteristics that are typically a continuum of subtle features (Freeman, 1984). More obligate carnivores have more robust protoconids, the principal cusp on the lower molars (Fig. 3B), which may aid mastication of endoskeletal items (soft outsides, hard insides). I have discussed differences in the nature of endo- and exoskeletal prey, and what it may take to eat them, elsewhere (Freeman, 1992, 1998).

The distribution of genera from the most speciose non-phyllostomid families (the Molossidae, Emballonuridae and Vespertilionidae) each span much of the range of insectivore eco-morphospace and overlap each other (Fig. 3A). Rhinolophidae is not as overlapping and for these characteristics and many others falls on the side of many insectivorous phyllostomids. Both are nasal-emitting echolocating families. If there were only nasal emission or only oral emission, there would be even more overlap than is present here.

PHYLLOSTOMIDS IN INSECTIVORE MORPHOSPACE

Insectivorous phyllostomids occur within insectivore eco-morphospace. If insectivorous forms were the only phyllostomids, they would simply be another family of bats fitting comfortably within the expected limits of the Microchiroptera. Sister families of phyllostomids are the mormoopids and the noctilionids (Smith, 1976; Griffiths, 1982; Baker *et al.*, 1989). Representatives of these families are also confined in this space (Fig. 3A). However, at least four clades of non-insectivorous phyllostomids have evolved out of the old eco-morphospace. Each group has adopted new diets and morphologies (Fig. 4).

Fossil evidence is too meagre to be useful in determining the ecomorphology of the early phyllostomids. However, cladistical analysis of the family can narrow our image of the ancestral phyllostomid considerably. Traditionally, phyllostomids that ate insects, other vertebrates and some fruit were placed in the subfamily Phyllostominae, the most primitive subfamily of phyllostomids, because of similarity in craniodental and external morphology (Miller, 1907; Simpson, 1945; Koopman, 1994). Bats in this subfamily were characterized by having a distinctive W-shaped ectoloph on their molars and broad dietary habits that

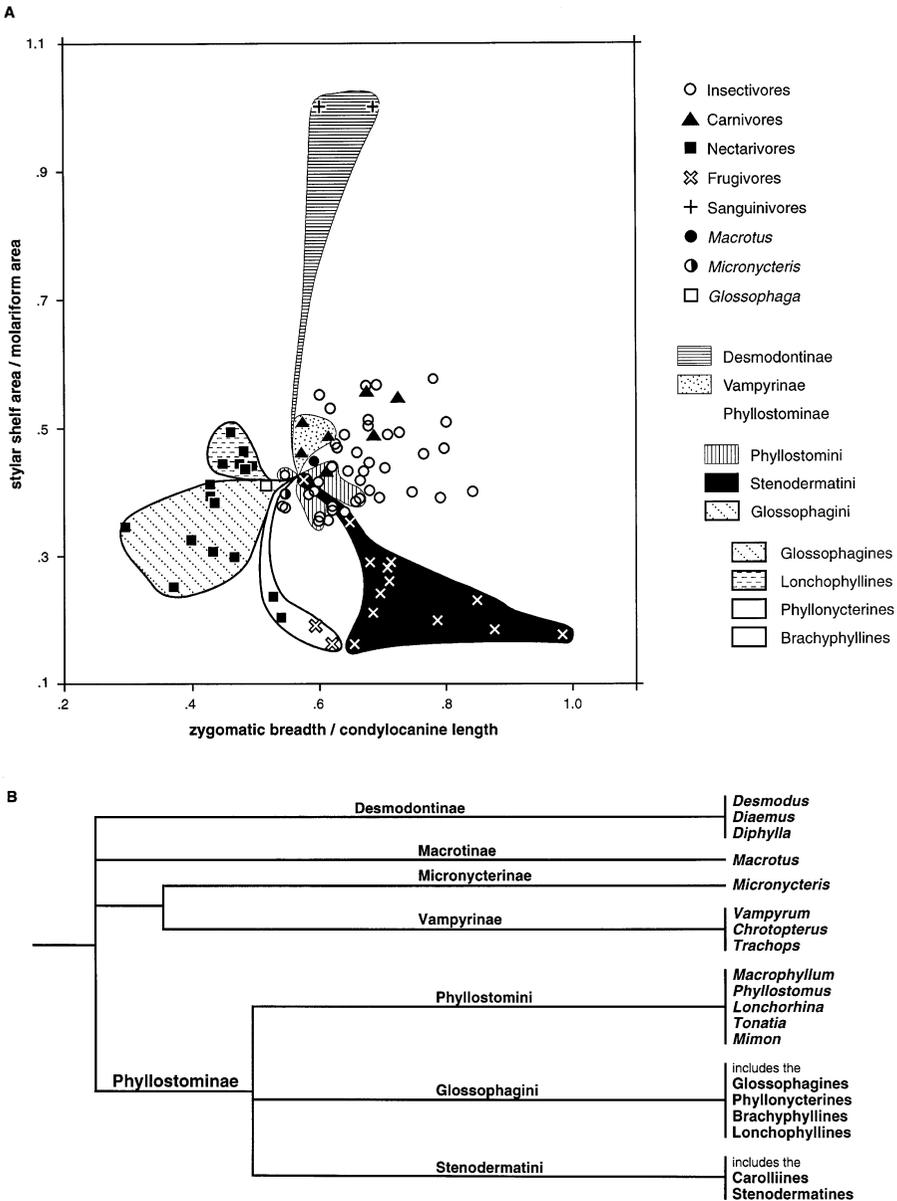


Fig. 4. All families of microchiropterans across eco-morphological space (A) with the phylogeny (B) of the Phyllostomidae (Baker *et al.*, 1989; Van Den Bussche, 1992). The higher phylogenetic categories, represented by different black-and-white patterns, are superimposed on the ecomorphological scattergram in (A). Axes in (A) are the same as in Fig. 2A. *Micronycteris*, *Macrotus*, *Glossophaga* and *Carollia* (the most central frugivore) all occupy a central position. *Musonycteris* is the most extreme nectarivore on the left and *Centurio* the most extreme frugivore on the right. The brachyphyllines are ecologically convergent frugivores that are not as closely related to the Stenodermatini as once thought (Miller, 1907). The blood-feeders, *Desmodus* and *Diphylla*, are at the top.

included insectivory, frugivory and carnivory. In his classic overview of the food habits of phyllostomids, Gardner (1977b) considered omnivory to be a hallmark of this subfamily. The genera included were *Micronycteris*, *Macrotus*, *Lonchorhina*, *Macrophyllum*, *Tonatia*, *Mimon*, *Phyllostomus*, *Phylloderma*, *Trachops*, *Chrotopterus* and *Vampyrum*, in that order. Order was critical in these classifications with the result that *Micronycteris* and *Macrotus* were seen as primitive and *Trachops*, *Chrotopterus* and *Vampyrum* as derived.

Several authors had problems with monophyly of the Phyllostominae (Baker, 1967, 1973; Walton and Walton, 1968; Smith, 1972, 1976; Gardner, 1977a; Honeycutt and Sarich, 1987). Finally, Baker *et al.* (1989) proposed a phylogeny of the entire family, Phyllostomidae, grounded in a broad array of non-craniodental characteristics for a broad array of genera (Baker *et al.*, 1989). These authors maintain that *Macrotus* and *Micronycteris* have masqueraded as close relatives to other insectivorous and carnivorous phyllostomids based on a host of plesiomorphic characteristics (Fig. 4). Walton and Walton (1968) and Smith (1972, 1976) had found problems in post-cranial morphology that upset the primitive-derived order of the traditional classifications. Baker (1967, 1973) and Gardner (1977a) suggested that *Macrotus* and *Micronycteris* were unlike and distant from other phyllostomines based on karyology. Honeycutt and Sarich (1987) also found that inclusion of *Macrotus* in the Phyllostominae was contraindicated based on albumin immunology.

Evidence from Baker *et al.* (1989) and Van Den Bussche (1991, 1992) suggested that, even though they have similar teeth and diet, *Micronycteris* and *Macrotus* are both distantly related to each other and to all other phyllostomids. Indeed, it is not entirely clear how closely the nine or ten species within *Micronycteris* are related (Baker, 1973; Simmons, 1996). Both genera have a clear W-shaped ectoloph on the molars and both eat insects and some fruit. As it turns out, *Micronycteris* and *Macrotus* have retained ancestral characteristics for teeth, reproductive histomorphology, chromosomes, post-cranial anatomy, and ribosomal DNA (Walton and Walton, 1968; Patton and Baker, 1978; Hood and Smith, 1982; Van Den Bussche, 1991, 1992). Van Den Bussche (1992) proposed that, since these two genera were as distant to each other and to other phyllostomids as the vampire bats (Desmodontinae), they should each be in their own subfamilies, Macrotinae and *Micronycterinae* respectively (Fig. 4). And although Van Den Bussche found some association of *Micronycteris* with *Vampyrinae*, it is not a close association. Given the large phylogenetic distance between *Micronycteris* and *Macrotus* and their similar morphology and diet, it is most parsimonious to assume that their common ancestor was also similar to them in diet and morphology. I think this hypothetical ancestor is an excellent model for the common ancestor of all phyllostomids.

Phyllostomids had origins at least 25–38 million years ago, at a time when frugivorous vertebrates increased in number (Fleming, 1991). I suspect the ancestral phyllostomid, like *Micronycteris* and *Macrotus*, was primarily insectivorous but also ate some fruit. Evidence from other bat groups suggests that bats can undergo remarkable stasis. Even with a meagre fossil record, the current genera of Microchiroptera (e.g. *Myotis*, *Tadarida*, *Mormopterus*, *Rhinolophus*, *Hipposideros*, *Taphozous*) are found in the fossil record 25 million years ago (Dawson and Krishtalka, 1984; Hand, 1990; Czaplewski, 1997).

What was unusual about a *Micronycteris/Macrotus*-like ancestral species that might have been a pre-adaptation for the remarkable phyllostomid adaptive radiation? Liem (1973) suggested that a morphological novelty in jaw mechanics was critical in the radiation of cichlid fishes. A similar thing could have happened in bats: a minor change in jaw mechanics could have major implications at the tooth–food interface. Indeed, Griffiths (1978, 1994)

and Griffiths *et al.* (1992) dissected the hyoid region in several families of bats and noted that there is a unique 'free-floating' hyoid shared by phyllostomids, noctilionids, moroopids and mystacinids that would make for an adaptable tongue. The tongue is an important organ for feeding in phyllostomid nectarivores, frugivores and sanguivores (Freeman, 1995, 1998). However, the common ancestor of phyllostomids was ecologically unusual for an insectivorous bat, especially if it ate at least some fruit. Or, put another way, frugivory may be the dietary synapomorphy of the Phyllostomidae. In other words, during the explosion in frugivorous vertebrates 25–38 million years ago, nearly all microchiropteran bats ignored fruit except the phyllostomids. Without obvious dental or cranial adaptations, ancestral phyllostomids began to experiment with frugivory. This change in ecology set the stage for further change in diet and great morphological diversification.

PHYLLOSTOMID NOVELTIES

From an ancestor resembling *Micronycteris/Macrotus*, four major eco-morphological novelties evolved (Fig. 4). The first group, the Vampyrinae, evolved a carnivorous diet. This shift resulted in a subtle but quantifiable change in tooth morphology (Fig. 3B). The premier cusp on the lower toothrow, the protoconid, is enlarged and borne on the anterior portion (trigonid) of each lower molar. Carnivorous bats have trigonids that are larger than talonids (the posterior heels of the lower molars; Freeman, 1998). Furthermore, teeth are large relative to the size of the palate (Freeman, 1984, 1995, 1998). This change in diet also allowed larger body masses with *Vampyrum*, the largest microchiropteran, reaching weights of 200 g or 20 times the mass of *Micronycteris/Macrotus*. Indeed, the independently derived Old World carnivorous bat, *Macroderma* (Megadermatidae), evolved a similar large mass, similar tooth shape and similar large teeth relative to the palate. Thus, the phyllostomid, *Vampyrum*, escaped the morphospace of the insectivorous Microchiroptera by a common evolutionary mechanism: it became a giant (Fig. 1).

Nectarivores are in the tribe Glossophagini (Baker *et al.*, 1989) (Fig. 4). Much of the diversification within this group occurred by lengthening the snout or rostrum and reducing the size of the teeth on the palate in conjunction with evolution of a specialized nectar-feeding tongue (Freeman, 1995, 1998). Change in rostral length is a malleable evolutionary phenomenon in mammals. Slaughter (1970) called the early trend towards short and wide skulls in bats 'brachycephaly'. Indeed, under intensive selection of domestication, large changes in rostral length have been achieved in the domestic dog in a short period of time (borzoi to bulldog). Under natural selection, there is also change in rostral length across families of carnivores that is correlated with the generalized diet of Canidae and the specialized diet of Felidae. Part of the lengthening in bats, at least 50%, occurred in parallel in two separate clades (glossophagine and lonchophylline; Griffiths, 1978, 1982; Baker *et al.*, 1989). Although lengthening of the rostrum and tooth diminution proceeded in parallel, the specifics of tongue modification and hyoid musculature did not (Griffiths, 1978, 1982). Another clade within the Glossophagini, containing the brachyphyllines and phyllonycterines, took a third path (Fig. 4). Cladistical analysis by Griffiths led him to conclude that the most parsimonious ancestor of the brachyphylline–phyllonycterine clade was similar to *Glossophaga* (Griffiths, 1982). The brachyphyllines show evolution towards increasing specialization for frugivory (Freeman, 1995, 1998). The culmination is *Brachyphylla* with massive teeth, which are no longer dilambdodont, and its unspecialized tongue (Griffiths, 1982). Convergence with the main fruit-eating group (stenodermatines)

was so great that *Brachyphylla* was classified as a member of that group (Miller, 1907; Griffiths, 1985) for many years (Fig. 4).

To summarize the Glossophagini, there was a macroevolutionary event to move out of the insectivore eco-morphospace. By macroevolutionary event, I simply mean a major evolutionary shift; that is, changes that warrant at least the naming of a new genus (Lemen and Freeman, 1984). No good model of this bat is extant today. We can infer that it was similar to *Glossophaga*, but with a more ancestral tongue and hyoid (Griffiths, 1982) and karyotype (Baker and Bass, 1979; Haiduk and Baker, 1982). Another macroevolutionary event occurred in the brachyphylline line with movement away from specialized nectarivory to more generalized feeding and frugivory (Freeman, 1995, 1998).

The stenodermatine frugivores in the tribe Stenodermatini (Baker *et al.*, 1989) (Fig. 4) shifted out of insectivorous eco-space to form the most speciose group of phyllostomids (about 49% of Recent phyllostomid species including the carollines; Koopman, 1993, 1994). These bats are largely frugivorous and can have very shortened rostra (Fig. 1). Furthermore, most have lost the dilambdodont pattern, and the morphologies of their teeth vary widely (Freeman, 1988, 1995, 1998). The most ancestral and least specialized taxon is *Carollia*. It is not clear if *Carollia* represents a model for the ancestral stenodermatine in the same way that *Macrotus* or *Micronycteris* does for Phyllostomidae and *Glossophaga* does for the Glossophagini. Like those species, *Carollia* is plesiomorphic for tooth morphology and ribosomal DNA (Van Den Bussche, 1992); however, its karyology has undergone a radical reorganization (Baker *et al.*, 1989). Phillips *et al.* (1984) and Tandler *et al.* (1988) considered the gastric mucosa and parotid salivary gland ultrastructure, respectively, in *Carollia* to be intermediate between insect-eating phyllostomines and frugivorous stenodermatines. Whether *Carollia* is a gracile offshoot of a line that leads to the rest of the stenodermatines or closely similar to the ancestral form is uncertain. It is a fruit bat that has not fallen far from the tree because it retains dilambdodont teeth and is not far from *Macrotus* and *Micronycteris* in eco-morphological space (Figs 3, 4). The skull proportions of *Carollia* are like those of insectivorous bats. But although the dilambdodont pattern is measurable, the inner arms of the W-shape are weakened (Slaughter, 1970). Ecologically, most researchers consider *Carollia* a frugivore (Wilson, 1973; Gardner, 1977b; Fleming, 1988; Charles-Dominique, 1991; Willig *et al.*, 1993). Most of the rest of the stenodermatines have lost dilambdodonty and have evolved teeth specialized for processing fruit (Freeman, 1988, 1995, 1998). It could be argued there is more diversity in tooth morphology within the stenodermatines than in all other Microchiroptera combined. I have suggested elsewhere that some of these differences in teeth may reflect differences in the types of fruit eaten (Freeman, 1988, 1992). If true, this would make frugivores much like the Cenozoic ungulate folivores, in which differences in diet (for example, browsers *vs* grazers) make for predictable differences in teeth (Jernvall *et al.*, 1996).

There is no fossil evidence to suggest how Megachiroptera evolved from a supposed insectivorous chiropteran ancestor, and cusps on the molars cannot be homologized with those in microchiropterans (Koopman and MacIntyre, 1980). I find this lack of homology unsurprising because dilambdodonty had to have been lost early on, and the pattern of a basin surrounded by a simple rim is common in frugivorous mammals (megachiropterans and primates are good examples). Stenodermatine phyllostomids have sacrificed dilambdodonty for their frugivorous diet as well, and I am not sure that one should expect to find homologous cusps across every phyllostomid frugivore experiment. Once the W-shape pattern is lost on the molars, it may be too hard to recover. That is, it may be

unlikely for the W-shape to be secondarily evolved once it has disappeared in becoming the simple rim and basin pattern seen in frugivorous mammals. Losing all trace of the W-shape pattern is probably why the relationships of the island form, *Brachyphylla* (a glossophagine), have been so confusing (Griffiths, 1985; Freeman, 1998).

The last clade is the Desmodontinae (Fig. 4). It contains the highly specialized blood-feeding bats. Vampire bats have molars abbreviated to only a cutting edge and incisors and canines enlarged to occupy 80% of total tooth area (Freeman, 1998). How these bats evolved this dental configuration is not evident in the fossil record, nor are there any clues from living bats. No known Pleistocene (Arroyo-Cabrales, 1992) or extant intermediate forms link these bats to the ancestral insectivore or to any other group of phyllostomids (Baker *et al.*, 1989). All fossil forms are placed in the genus *Desmodus*, one of the three extant genera.

ECOLOGICAL IMPACT OF PHYLLOSTOMID DIVERSITY

What impact have these escapes from insectivorous eco-morphological space had on phyllostomids? There are several measures of impact. In Neotropical forests such as La Selva in Costa Rica and Barro Colorado in Panama, non-insectivorous species represent 40% of all bat species but 86–89% of all bat biomass (LaVal and Fitch, 1977; Bonaccorso, 1979; Timm *et al.*, 1989). A different calculation of impact is to tally the number of museum records for the number of specimens collected for each genus in the family Phyllostomidae. Field Museum of Natural History, the University of Kansas Museum and the Smithsonian all collected specimens in approximately the same way and in approximately the same habitats during this time period (late 1800s to about 1978). Prior to the early 1950s, bats were shot with shotguns or found in roosts in cracks, crevices and caves. Dalquest (1954) introduced the idea of using mist nets to capture bats, which soon became the sampling method of choice everywhere. Only recently have high canopy sampling with nets, use of radio transmitters and ultrasonic sampling impacted bat collecting. Furthermore, more effort is being made to collect in primary forest and other less inhabited areas and not just over streams or close to camp (R.J. Baker and H.G. Genoways, personal communication; Willig *et al.*, 1993; Medellín *et al.*, in press). Vespertilionids and certainly molossids are under-represented in mist net captures, particularly in primary and secondary forests, because of where they fly. Molossids are fast flyers and fly in more open spaces (savanna or caatinga) or above forest canopy (Freeman, 1981a). From these three museums, 69,463 phyllostomids were collected. Of those individuals, 90% are represented by nectarivorous (17%), frugivorous (68%) and sanguivorous (5%) species.

How common the morphological extremes are emerges in a scattergram of the relative abundances of specimens in each genus arrayed on the same morphological axes as previous figures (Fig. 5). Abundant genera can be more than three orders of magnitude more common than rare genera. With the exception of *Desmodus*, a blood-feeder, there are no abundant or common genera that are morphological extremes, and it is probable that the abundance of *Desmodus* is a post-Columbian phenomenon resulting from a combination of the introduction of domestic livestock and habitat modification (Hill and Smith, 1984). Therefore, rare bats define the extremes in morphospace. Furthermore, the prognosis for rare morphological extremes lasting a long time evolutionarily is not good because many of these extremes are also restricted geographically (Hall, 1981). Jablonski (1991) thinks that widespread genera are more likely to survive mass extinctions, present-day perturbations and fragmentation better than geographically restricted genera. Also, there

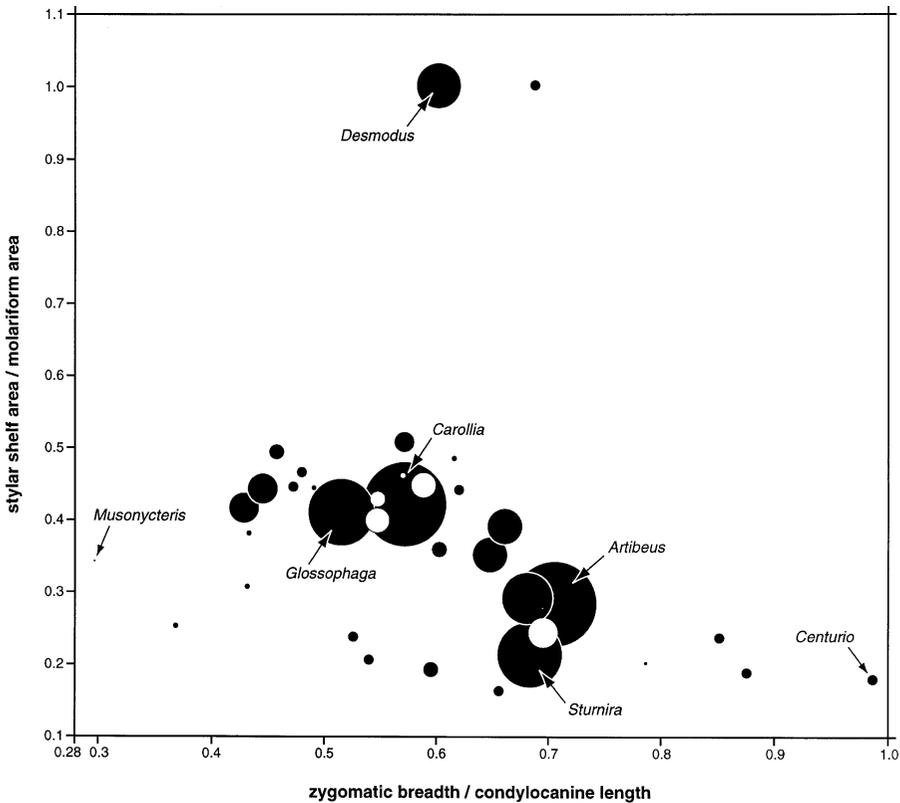


Fig. 5. The relative abundance of museum specimens in each phyllostomid genus from three museums totalling 64,011 specimens arrayed on the same axes as in Figs 2A and 4A. Diameters of each dot are directly related to their abundance in collections. The non-insectivorous phyllostomids *Carollia*, *Artibeus*, *Glossophaga* and *Sturnira* are most abundant and represent nearly 60% of the specimens in collections. The remaining 40% comprises 32 genera in this study. About 43 genera are possible. Many morphologically extreme genera are rare with the nectarivore, *Musonycteris*, on the far left and the frugivore, *Centurio*, on the far right. *Desmodus*, a blood-feeder, is morphologically extreme but is common. Medellín *et al.* (in press) found certain species typical of secondary growth (*Sturnira*, *Carollia* and *Artibeus*) and others, such as members of the former subfamily Phyllostomidae, rarer and more typical of non-secondary growth forests.

is evidence that tropical biotas are more sensitive to disturbance than temperate biotas (Jablonski, 1991). With the high number of rare genera of phyllostomids, which are restricted to the Neotropics, one wonders how often extreme phyllostomids wink in and out of existence.

MACROEVOLUTION

I draw several conclusions from this adaptive radiation in microchiropteran bats. First, there is parallel evolution with certain eco-morphotypes such as durophagous, non-durophagous and carnivorous bats evolving over and over again. This parallels the pattern seen in ungulate herbivores (Jernvall *et al.*, 1996).

Second, the evolutionary history of insectivorous microchiropterans is dominated by constraint. These bats evolved from an insectivorous, dilambdodont ancestor. In 60 million years over a worldwide distribution through thousands if not tens of thousands of species, no insectivorous microchiropteran bat that has remained insectivorous has significantly altered that ancestral plan. Rather, they have used what might be called the 'cheap tricks' of mammal diversification: increase or decrease body size, lengthen or shorten the rostrum, or enlarge or diminish teeth. Some of these same developmental mechanisms have evolved in parallel in different families of bats over those millions of years. Microchiropteran bats are evidently on an adaptive peak that has proved quite successful but from which there is no escape as an insectivore. Over such a long time span, huge morphological changes could have evolved, but little change in ecology has resulted in little change in morphology in this group. There is no 'arms race' and there are no new 'technological breakthroughs' in cranial morphology here. Variations on limited themes evolve and go extinct and evolve again and go extinct again. New species of insectivorous bats, if discovered, will probably fall within the boundaries of the space just described.

Relative to other mammals, how constrained are microchiropteran bats? This insectivore space is not all that tiny and not all that constraining when viewed across terrestrial mammals. Variation in the shape of the face alone of aerial insectivorous bats is not unlike that variation between long, narrow-skulled predators like dogs on the one hand (Canidae, Order Carnivora) and short-faced cats on the other (Felidae, Order Carnivora; Freeman, 1984). Although the skull proportions of insectivorous bats are similar to those of dogs and cats, their dental characteristics are considerably more conservative. The W-shape ectoloph in cats, in particular, is lost and simplified into meat-cutting blades (Freeman, 1998).

There are a couple of lines of evidence to support the argument of constraint. First, several large families of insectivorous bats have diversified to occupy large areas of the eco-morphological space (Fig. 3A). These families largely overlap, especially along configurations that are related to oral or nasal echolocation, rather than exploring new morphological space. The overlap, I would argue, suggests insectivores are bounded within an eco-morphological space. Second, the bats that have not remained insectivorous have shifted out of the eco-morphological space of insectivory to a degree of unprecedented morphological diversity in the phyllostomids. The idea of constraint has a profound impact on how insectivorous microchiropteran evolution should be viewed. It is a mature system that has reached a dynamic equilibrium. Although constraint has been the one important theme within the insectivorous Microchiroptera, some bats have quite successfully escaped this adaptive peak, but not as insectivores. There were at least four escapes from the old eco-space within the Phyllostomidae, and in each case the escape was mediated by a change in diet. As an example, the ancestral frugivore did not have to improve on dilambdodonty; it was able to trade-off between frugivory and insectivory. *Macrotus* is estimated to be 90% insectivorous and 10% frugivorous. *Carollia* reverses that percentage, consuming mainly fruit (Wilson, 1973; Gardner, 1977b; Fleming, 1988; Charles-Dominique, 1991; Willig *et al.*, 1993). The change in morphology is not profound. The teeth are still dilambdodont and the skull has about the same shape. But at the same time, frugivorous adaptations are also present in gastric mucosa (Phillips *et al.*, 1984) and parotid salivary gland ultrastructure (Tandler *et al.*, 1988). *Carollia* is a good model for bridging the gap between frugivorous and insectivorous/carnivorous eco-morphological spaces. This transition has proved to be highly successful because *Carollia* is the second most abundant genus in the family (Fig. 5). Although *Carollia* is a good model as a transitional form for the more derived, but

closest relative, *Rhinophylla*, other frugivores have different cusp patterns that are difficult to relate to *Carollia* and to each other. There may have been a series of transitions to establish major tooth patterns found within the stenodermatines, particularly with the loss of the dilambdodont pattern.

Next, within the Phyllostomidae, I find both great stasis and great change within lineages. *Macrotus* and *Micronycteris* are almost unchanged, while *Desmodus*, *Centurio* and *Musonycteris* are greatly modified. Here, rates among lineages have been so diverse that no relationships between time and morphological change within the family are found (none were found biochemically, either; Haiduk and Baker, 1984).

Last, the evolutionary events that brought about great changes within the phyllostomids have humble beginnings. I hypothesize that the potential for this massive adaptive radiation is founded in the slight frugivory of the common ancestor. How a transition from insectivory to frugivory may have occurred was described by Gillette (1975). This change in diet was brought about with little or no morphological change. The first frugivores, perhaps much like *Carollia*, built upon this to become highly frugivorous but still with relatively little morphological change. Some of their descendants come down to the present relatively unchanged, like *Carollia* itself. Others have explored this new adaptive space and deviated significantly from their progenitors.

I believe combining phylogenetic analysis with eco-morphological data to reconstruct the course of an adaptive radiation is a productive exercise. However, much of my success here is based on the robust phylogeny by Baker *et al.* (1989) and the persistence of ancestral forms to the present (*Macrotus*, *Micronycteris*, *Glossophaga* and *Carollia*). Within the desmodontids, no ancestral forms have survived, and little can be said about the evolution of blood feeding.

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