NOSELEAF MORPHOLOGY AND ECOLOGICAL CORRELATES IN PHYLLOSTOMID BATS

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ABSTRACT.—Recent research has demonstrated that the noseleaves function in the echolocation system of phyllostomid bats. Species with different foraging habits would be expected to have different noseleaf morphology. Seven measurements of noseleaves of 46 species of phyllostomids were analyzed by use of multivariate techniques. Principal-components analysis separated desmodontines, brachyphyllines, glossophagines, and another group composed of the stenodermatines, carolliines, and phyllostomines. The first two principal components showed that noseleaf variables can be grouped by size of the horseshoe and size of the spear. Forearm length (a measure of body size) was correlated with general size of the noseleaf, spear size, and horseshoe size, but the correlation was strongest with the last feature, indicating that the spear is a more variable element that may depend on the ecology of the animal. A canonical discriminant analysis failed to separate stenodermatines from phyllostomines. However, it demonstrated an association between feeding habits and noseleaf morphology by creating a derived variable significantly correlated with feeding habits but not with body size among phyllostomines.

The faces of the Rhinopomatidae, Nycteridae, Rhinolophidae, Hipposideridae, Megadermatidae, and Phyllostomidae are ornamented by leaflike appendages that give these bats a bizarre appearance. Although these noseleaves are conspicuous structures, few investigators have analyzed their morphology, and almost nothing is known about their function, although it is believed that they play a role in the emission of the echolocation signals (Fenton, 1984, 1985; Novick, 1977).

Möhres (1953) suggested that the noseleaf of *Rhinolophus* could function as a parabolic horn for echolocation pulses. Early experimental studies failed to demonstrate the role of noseleaves in echolocation (Griffin and Novick, 1955; Grummon and Novick, 1963; Novick, 1958, 1977), but the noseleaf was demonstrated to provide a directional effect to the sounds of *Rhinolophus ferrumequinum* (Schnitzler and Grinnell, 1977), *Carollia perspicillata* (Hartley and Suthers, 1987), and probably *Megaderma lyra* (Möhres and Neuweiler, 1966).

New World bats of the family Phyllostomidae are characterized by the presence of a simple noseleaf that consists of a horseshoe-shaped structure surrounding the nostrils and a pointed "spear." There are no generalized names for the various parts of the noseleaf of phyllostomids, so terminology was established for use herein (Fig. 1). Considerable variation in size and shape of the noseleaf exists among phyllostomids. Some phyllostomines have elongated spears that project well beyond the top of the head, whereas those of vampires (Desmodontinae) are rudimentary. Among phyllostomids are species that feed on fruit, nectar and pollen, arthropods, vertebrates, or even blood (Gardner, 1977), so species within the group share a common phylogenetic history but presumably are adapted to different ecological constraints.

Comparative studies that take advantage of the great variation in ecological adaptations shown by phyllostomids face a possible lack of independence between feeding habits and phylogenetic history within the family. For example, the nectar-feeding specialists are grouped in the subfamily Glossophaginae, the strict frugivores belong to the Stenodermatinae and Carolliinae, and the hematophagous species constitute the Desmodontinae (Gardner, 1977). Brachyphyllines have a diet that includes mainly fruit and nectar, and among the Phyllostominae are insectivores, carnivores, and omnivores (Gardner, 1977; Humphrey et al., 1983). If the current taxonomic arrangement is accepted as reflecting the evolutionary history of the family, it is possible that species with similar feeding habits evolved through the same phylogenetic path, confounding the effects of diet and phylogenetic history on morphology.

Herein, I analyze variation in noseleaf shape and size within and between six subfamilies of

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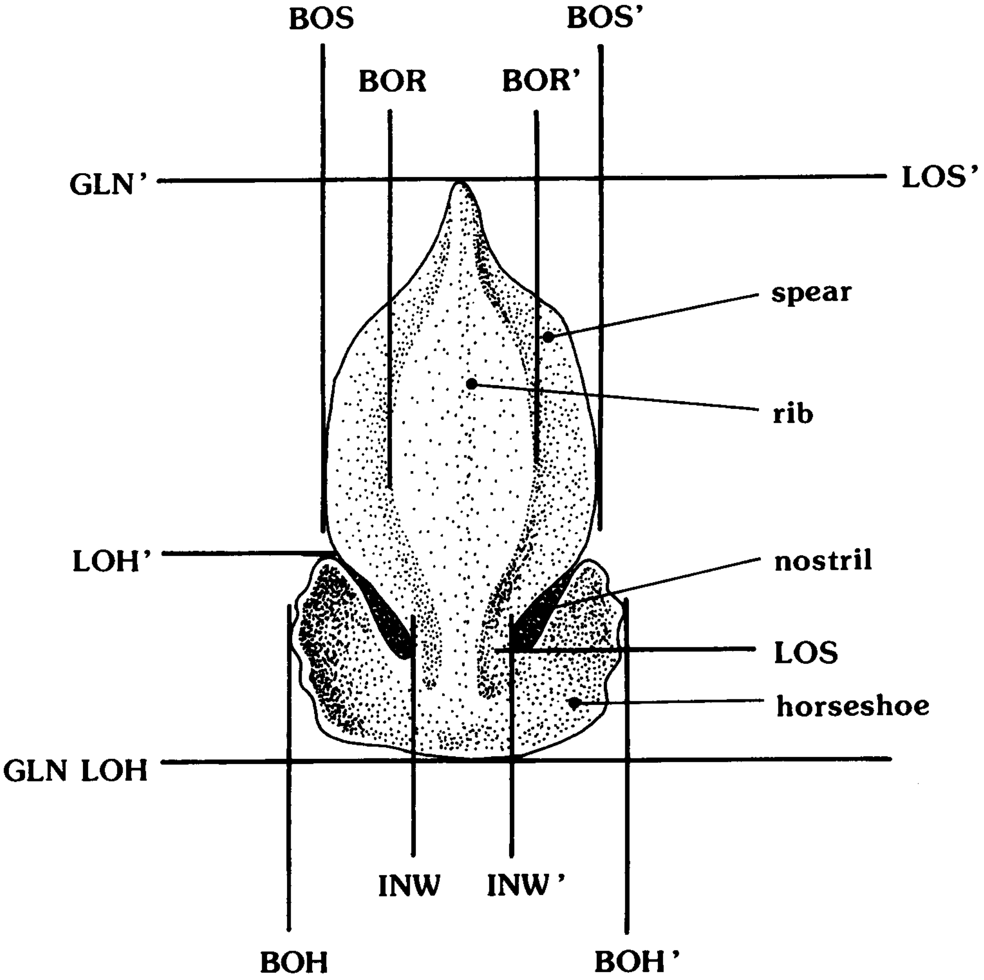

FIG. 1.—Seven dimensions of the noseleaf, shown in anterior view: GLN, greatest length of the noseleaf; LOS, length of the spear; LOH, length of the horseshoe; BOH, breadth of the horseshoe; BOS, breadth of the spear; BOR, breadth of the rib; INW, internostril width.

phyllostomid bats. This variation is compared with available data on feeding habits to determine if feeding ecology has affected noseleaf morphology.

MATERIALS AND METHODS

I examined 88 fluid-preserved specimens (Appendix 1) deposited in the mammal collections of the Florida Museum of Natural History, University of Florida and the National Museum of Natural History, Smithsonian Institution, Washington. The sample included 46 species and the six subfamilies of phyllostomid bats recognized by Hill and Smith (1984).

Noseleaf variables, measured to the nearest 0.01 mm with an electronic caliper, included (Fig. 1): greatest length of noseleaf from the inferior margin of the horseshoe to the tip of the spear; length of the spear from the lowermost margin of nostrils to the tip of the spear; length of the horseshoe from the inferior edge of the noseleaf to the superior border of the horseshoe; breadth of the horseshoe at its widest point; breadth of the spear at its widest point; breadth of the medial rib at its widest point; and internostril width measured between the proximal borders of the nostrils. Additionally, forearm length, a measure of body size in bats, was obtained for all specimens.

Statistical analyses were performed using the Statistical Analysis System (SAS), and the names of the

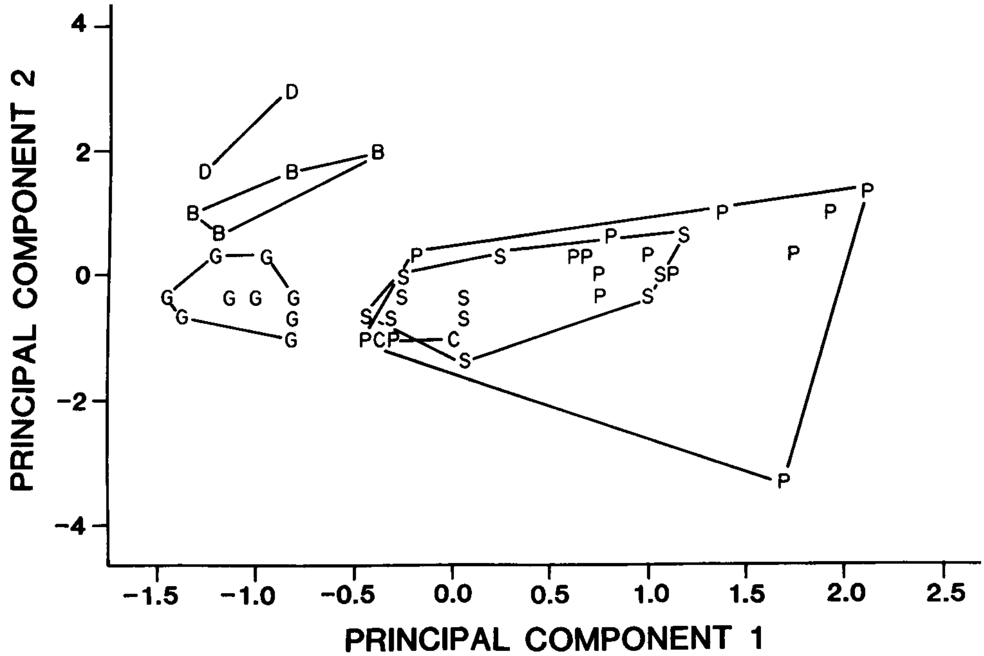

FIG. 2.—Projection of the bat species on the first two principal components derived from seven measurements of the noseleaf. P, Phyllostominae; G, Glossophaginae; C, Carolliinae; S, Stenodermatinae; B, Brachyphyllinae; D, Desmodontinae. The position of individual taxa on these axes is indicated in Appendix 2 (Table A).

routines refer to the procedures described by SAS Institute (1985). The position of the 46 species of phyllostomids in hyperspace defined by noseleaf measurements was assessed using principal-components analysis (PROC PRINCOMP). Principal components were extracted from the correlation matrix of the seven noseleaf variables, and the respective eigenvectors and eigenvalues were calculated to assess the relative contribution of each original measurement in explaining the variance among the observations.

I used factor analysis (PROC FACTOR, ROTATE option) to rotate the axes of the principal components to find a set of derived variables (factors) such that the original seven measurements could be expressed as linear functions of these factors. After preliminary analyses, I retained only the first two factors because additional factors accounted for little variance and provided no better resolution. The separation of the variables after performing an orthogonal rotation (varimax) was not satisfactory, so an additional oblique rotation (promax) was performed. To get a clearer view of the differences between frugivorous, insectivorous, and omnivorous species, I subjected the data on stenodermatines and phyllostomines to a canonical discriminant analysis (PROC CANDISC) using subfamilial affiliation as an a priori criterion for grouping.

RESULTS

The first two principal components accounted for 82.4% of the total variance and clustered the bat species in clearly defined groups (Fig. 2). Desmodontines, brachyphyllines, and glossophagines were segregated readily from the other species, their clusters showing no overlap with other groups. Conversely, no clear separation could be demonstrated for clusters corresponding to phyllostomine, carolliine, and stenodermatine species.

The eigenvector of the first principal component has positive elements only (Fig. 3), indicating that the seven original variables are correlated positively with this parameter, so it can be considered as a measure of overall size of the noseleaf. The eigenvector of the second principal component has both positive and negative elements (Fig. 3), meaning that this component can be interpreted as a shape variable. The negative elements of the second eigenvector correspond

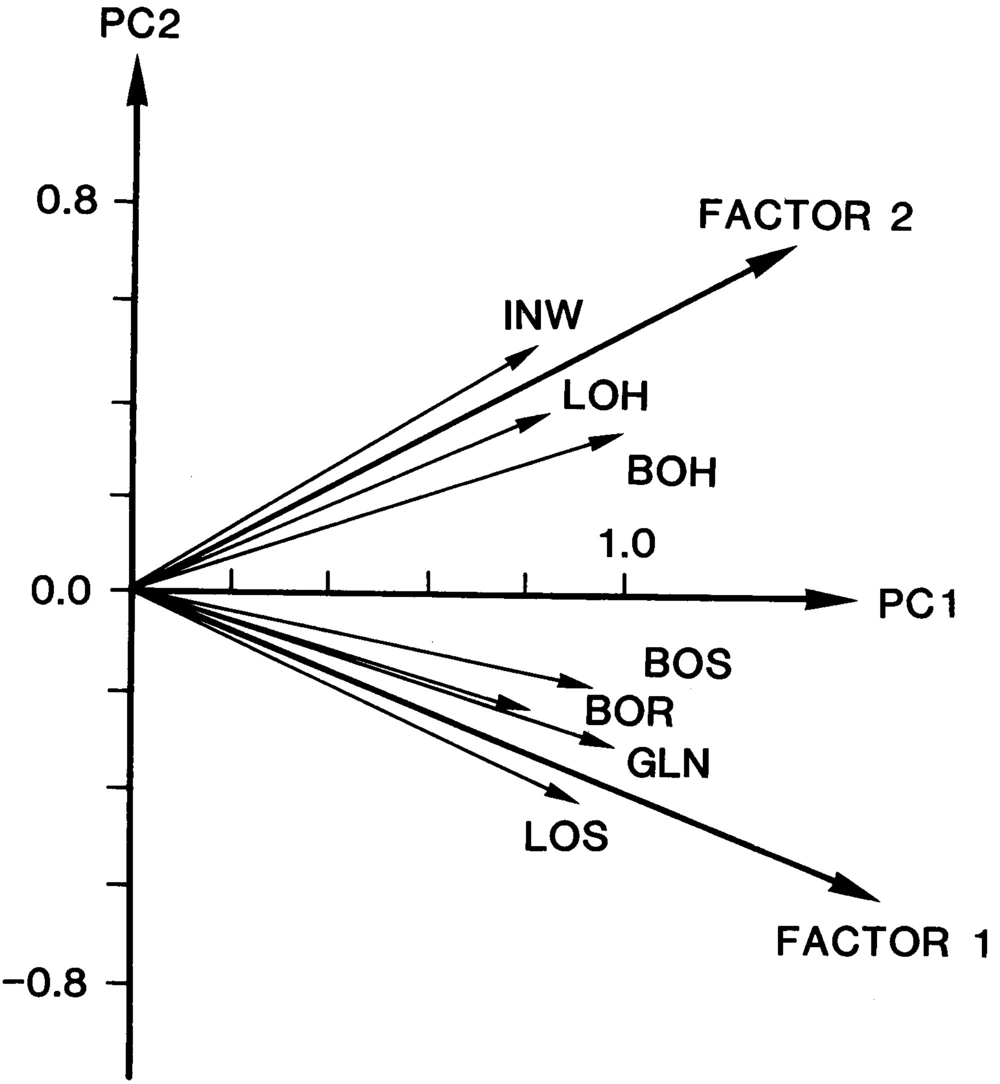

FIG. 3.—Projection of the factor pattern (the product of the eigenvectors of the correlation matrix and the square root of the respective eigenvalue) of the seven measurements of the noseleaf on the plane of the first two principal components (PC 1 and PC 2): GLN, greatest length of the noseleaf; LOS, length of the spear; LOH, length of the horseshoe; BOH, breadth of the horseshoe; BOS, breadth of the spear; BOR, breadth of the rib; INW, internostril width. The position of the arrows indicates the correlation with the principal components, and the length of the arrows are proportional to the amount of variance explained by the components. The projection of the two factors obtained by promax rotation of the principal components also is shown.

to the original variables that are measurements of the spear, whereas the positive elements correspond to the variables that are measurements of the horseshoe (Fig. 3).

This pattern suggests that overall variation in noseleaf morphology results from variation in size of the spear and variation in size of the horseshoe. Results of factor analysis are consistent with this interpretation. Factor 1 can be interpreted as a measure of size of the spear because it is highly correlated with the four original spear variables, whereas factor 2 is a measure of

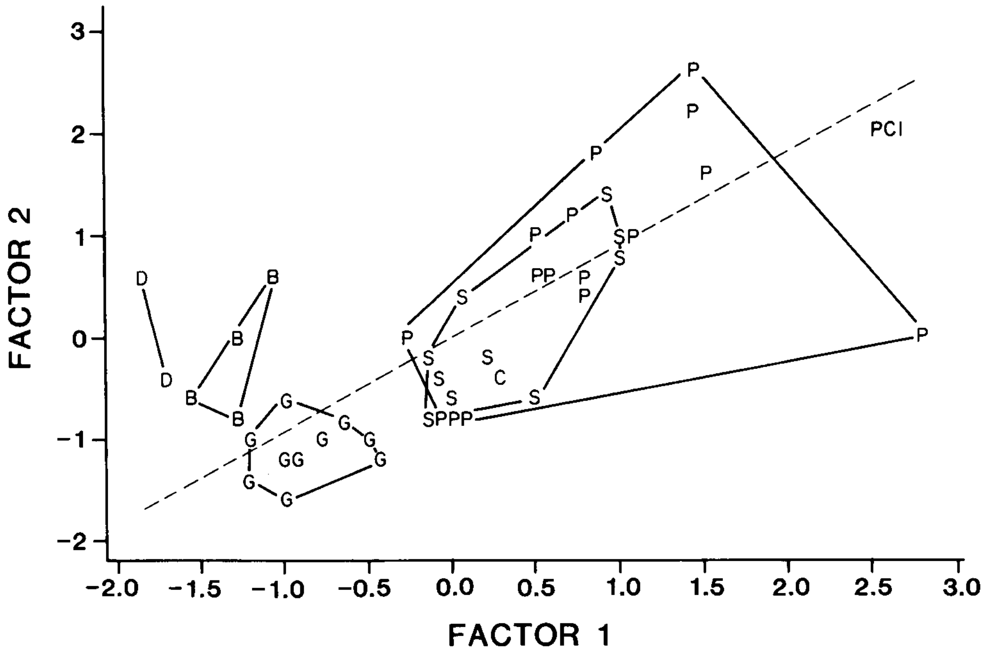

FIG. 4.—Projection of the bat species on the plane of the factors extracted from the seven measurements of the noseleaf. Factor 1 corresponds to size of spear, factor 2 to size of horseshoe, and PC 1 to general size of the noseleaf. The position of individual taxa on these axes is indicated in Appendix 2 (Table A).

size of the horseshoe because it is correlated with the three original horseshoe measurements (Fig. 3).

The noseleaves of brachyphyllines and desmodontines are distinctive because they have proportionally smaller spears than the rest of the phyllostomids, falling above principal component 1 (Fig. 4). Conversely, glossophagines cluster apart from phyllostomines and stenodermatines, but they lie around principal component 1, so their noseleaves are small but have the same proportions as those of the other groups. *Lonchorhina aurita* is clearly an outlier, and its extremely elongated noseleaf is unique among phyllostomids.

The correlation coefficients of the derived noseleaf variables with forearm length were all positive (Fig. 5). The correlation was higher for factor 2 ($r = 0.83$) than for either factor 1 ($r = 0.42$) or principal component 1 ($r = 0.66$). Thus, sizes of both the horseshoe and the spear are determined by an allometric relation with body size, but there is more variation in spear size than in horseshoe size. Brachyphyllines and desmodontines, which have rudimentary spears and cluster apart (Figs. 5a and 5b), have horseshoes of the "correct" size as predicted from their body size (Fig. 5c). In contrast, glossophagines have noseleaves with smaller horseshoes and spears than expected on the basis of overall body size.

The discriminant analysis showed no significant difference between the centroids of the phyllostomines and stenodermatines ($P > 0.25$, Wilk's lambda test). Stenodermatines had low values on the canonical variable, but among the phyllostomines the variation was greater (Fig. 6).

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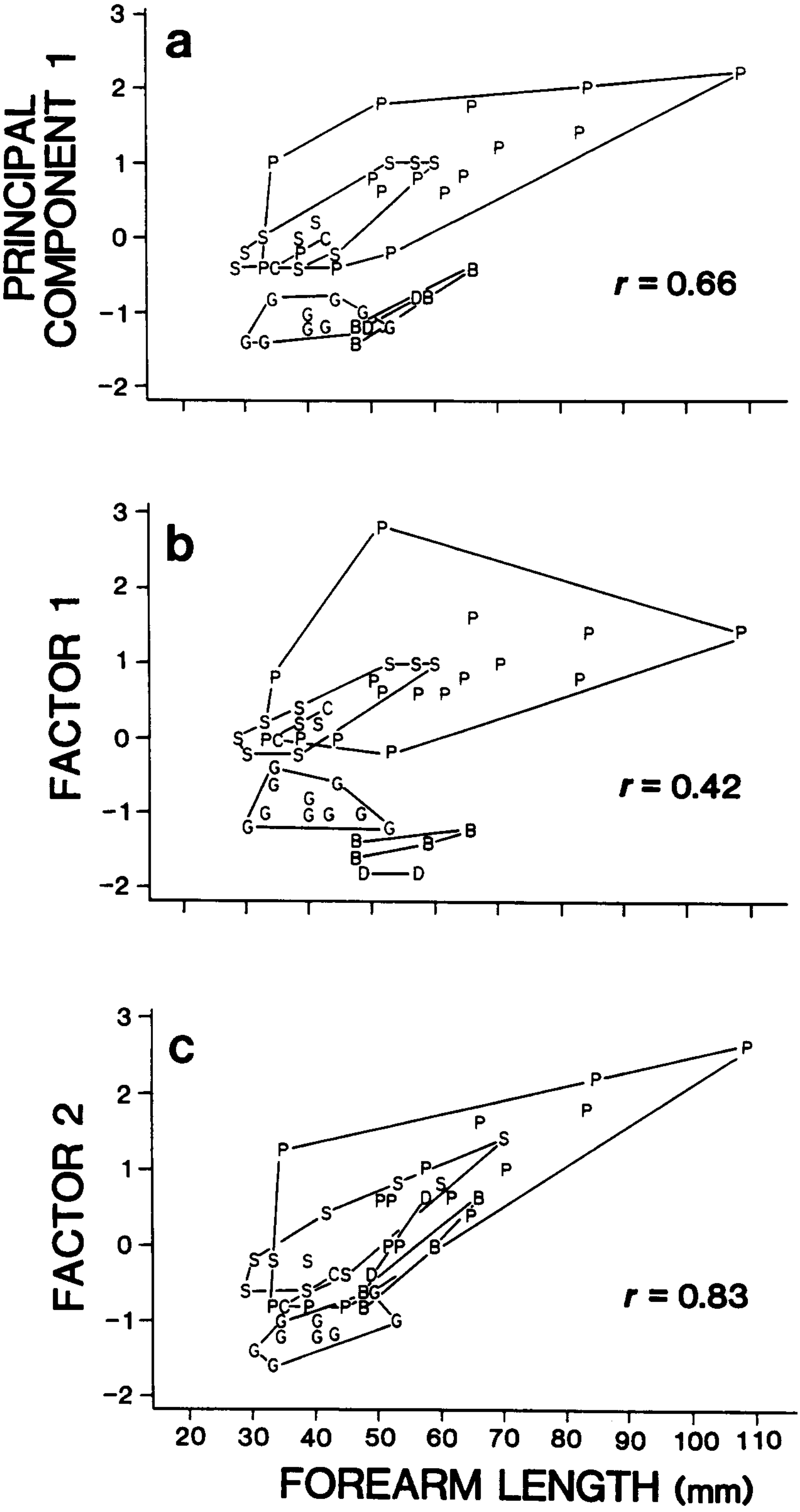
FIG. 5.—Correlations between forearm length (a measure of body size) and three variables derived from the noseleaf: a, principal component 1 (general size); b, factor 1 (size of the spear); and c, factor 2 (size of the horseshoe). The position of individual taxa on these axes is indicated in Appendix 2 (Table A).


a
PRINCIPAL COMPONENT 1
3
2
1
0
−1
−2
r = 0.66
b
FACTOR 1
3
2
1
0
−1
−2
r = 0.42
c
FACTOR 2
3
2
1
0
−1
−2
r = 0.83
20
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40
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80
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FOREARM LENGTH (mm)
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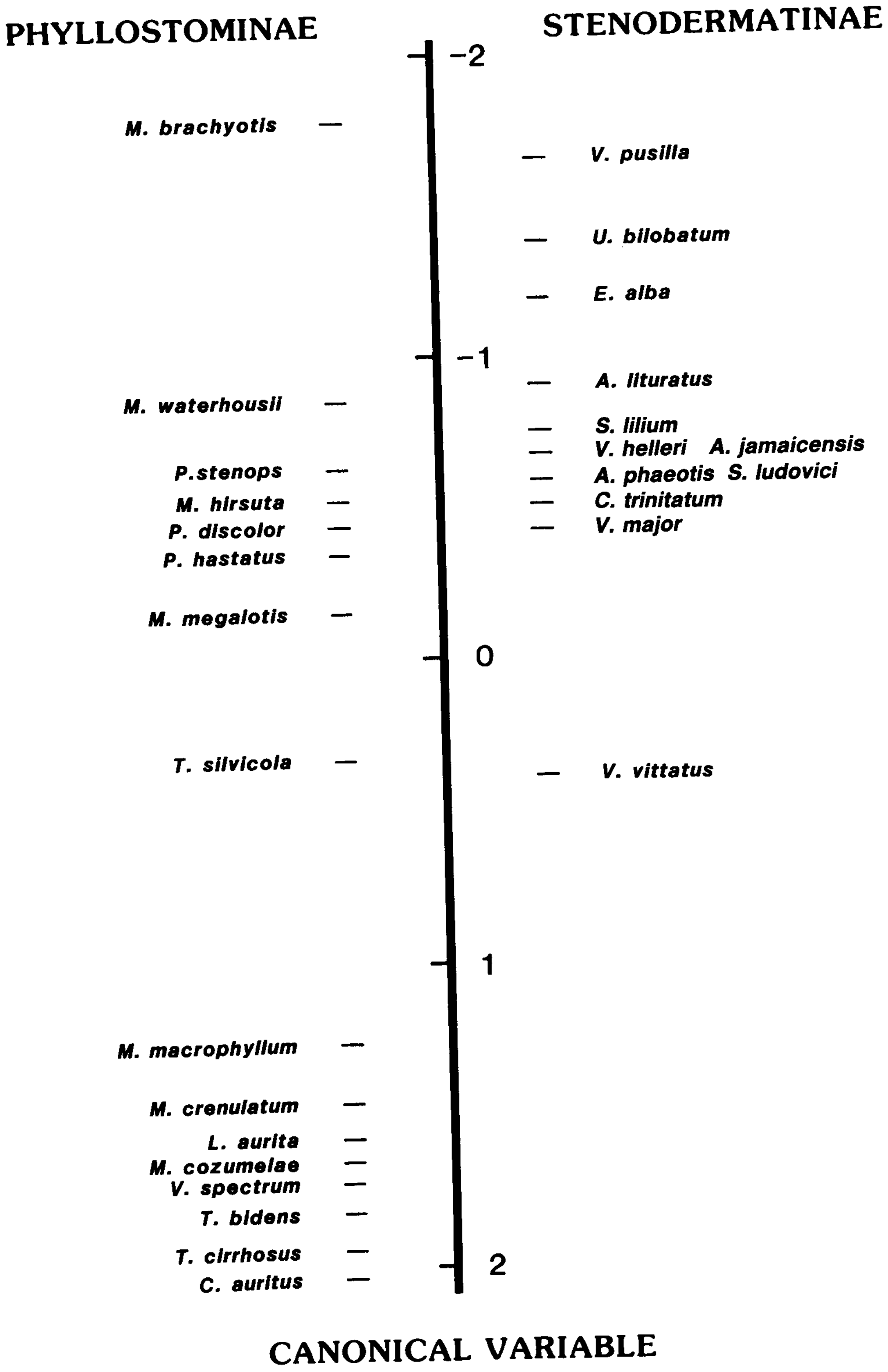

FIG. 6.—Projection of the phyllostomine and stenodermatine species on the canonical variable derived from seven measurements of the noseleaf, with subfamilial affiliation as an a priori-grouping criterion.

Among phyllostomines, the score on the canonical variable was correlated with a rank value assigned to each species on the basis of degree of frugivory, based on data from the literature (Gardner, 1977; Humphrey et al., 1983; Kendall's rank correlation coefficient, $t = 0.58$, $P < 0.001$), showing an association between food habits and morphology of the noseleaf. In contrast, scores on the canonical variable were not correlated with forearm length ($t = 0.03$, $P > 0.9$), supporting the association between food habits and noseleaf morphology independent of body size.

DISCUSSION

The principal-components analysis of the seven measurements of the noseleaf suggests an association between feeding habits and noseleaf morphology, but the results are not conclusive. Hematophagous (Desmodontinae), nectarivorous (Glossophaginae), and some omnivorous (Brachyphyllinae) bats have distinctive noseleaves, but the noseleaves of frugivores (Stenodermatinae and Carolliinae) are similar to that of the Phyllostominae, which include insectivores, carnivores, and omnivores.

Factor analysis demonstrated that horseshoe size and spear size explain most of the variation in noseleaf morphology among phyllostomids. The functional significance of these noseleaf elements has been demonstrated by Hartley and Suthers (1987), who showed that the position of nostrils and associated elements can modulate the frequency and intensity of the echolocation sound, directing it in the horizontal dimension; the spear seems to be responsible for the directionality of sounds in the vertical direction. Separation of original variables into two factors, one related to the horseshoe and the other to the spear, indicates ranges of adaptation in these character complexes. The size of the nostrils and associated structures (horseshoe) seems to be determined by their function in modulating the sound, whereas the size of the spear is more variable and depends on the need by bats to direct the echolocation signals.

Species that depend on olfaction or sight to locate food nevertheless use echolocation to avoid obstacles, but they do not require high directionality. Such bats might have evolved emitting structures (horseshoes), but they have relatively small directing devices (spears). This is the case with vampire bats (Desmodontinae) and brachyphyllines. However, this is not true in the case of nectarivorous species (Glossophaginae), in which both the spear and the horseshoe are reduced, or with frugivores (most stenodermatines and some phyllostomines) that have noseleaves of size comparable to those of the insectivorous species.

The differences between the noseleaves of frugivores and those of insectivores and carnivores are subtle, as shown by the lack of statistical significance when comparing the centroids of phyllostomines and stenodermatines. However, correlation between degree of insectivory and carnivory, and the score on the canonical variable among phyllostomines, indicates that inconspicuous differences in noseleaf morphology may be related to the feeding ecology of these bats.

The ultimate cause of the correlation between trophic ecology, noseleaf morphology, and echolocation ability most likely is related with foraging behavior and habitat (Belwood, in press; Neuweiler, 1984). Different hunting strategies have been demonstrated for phyllostomids, even among species with similar diets. Large carnivorous bats, such as *Vampyrum spectrum* and possibly *Chrotopterus auritus*, are able to locate their prey by scent (Medellín, 1988; Vehrencamp et al., 1977). Similarly, *Tonatia silvicola*, *Trachops cirrhosus*, and *C. auritus* use auditory cues to locate prey. These species seem to rely little on echolocation to locate food (Belwood and Morris, 1987; Medellín, 1988; Tuttle and Ryan, 1981), and they tend to have well-developed horseshoes but comparatively small spears. Conversely, species such as *Mimon cozumelae*, *Mimon crenulatum*, and *Lonchorhina aurita* possess large spears. Unfortunately, little is known about the foraging behavior of these species, but on the basis of the data presented herein, I predict that they depend on echolocation to find their prey. The huge spear of *L. aurita* could be an adaptation to locate prey undetectable by means other than echolocation, such as highly mobile species. The ecological correlates of noseleaf morphology will be better understood when more information on the foraging behavior and the characteristics of the echolocation signals of phyllostomids are available. Different strategies for locating the prey are predicted from the differences in morphology of the noseleaf.

Present knowledge of the phylogeny of phyllostomids does not allow a conclusive assessment of the effects of phylogenetic inertia on noseleaf morphology. For example, it is impossible to separate ecology from phylogeny in hematophagous (Desmodontinae) and frugivorous (Stenodermatinae) bats, because both subfamilies seem to be monophyletic (Owen, 1987; Smith, 1976). A polyphyletic origin for nectarivorous bats (Glossophaginae) has been proposed (Griffiths, 1982, 1983), but an alternative scheme that suggests a common origin for all glossophagines has been discussed by Haiduk and Baker (1982), Hood and Smith (1982), and Smith and Hood (1984). If the phylogenetic tree proposed by Griffiths (1982) is correct, then my results show convergent evolution in noseleaf morphology in the two main lines of nectarivorous phyllostomids (Glossophaginae and Lonchophyllinae in Griffiths' [1982] classification). Conversely, if glossophagines are monophyletic as proposed by Haiduk and Baker (1982), then it would be difficult to interpret my results independently of phylogenetic constraints. Both Griffiths' (1982) and Haiduk and Baker's (1982) explanations include brachyphyllines within the glossophagines. If this is correct, then noseleaves of brachyphyllines represent a deviation from the general trend within the Glossophaginae-Brachyphyllinae complex.

Although the subfamily Phyllostominae appears to be paraphyletic, there is little agreement on the correct arrangement of genera within the group (Baker, 1967; Honeycutt and Sarich, 1987; Patton and Baker, 1978; Smith, 1976). Because the arrangement of phyllostomine species on the basis of noseleaf variables (Fig. 6) cannot be explained by any of the proposed phylogenies for the subfamily, I tentatively conclude that the association between diet and noseleaf morphology in the Phyllostominae does not reflect phylogenetic history, but rather adaptations to different feeding strategies.

RESUMEN.—Investigaciones recientes han demostrado el papel que juega la hoja nasal de los murciélagos filostómidos en su sistema de localización por eco. Como consecuencia, sería de esperar que especies con diferentes hábitos ecológicos difieran en la morfología de sus hojas nasales. Técnicas de análisis multivariado se emplearon para estudiar siete medidas tomadas de las hojas nasales de 46 especies de filostómidos. El análisis por componentes principales separó cuatro grupos: desmodontinos, braquifilinos, glosofaginos y un grupo formado por los estenodermatinos, carolinos y filostominos. El análisis de factores indicó que las medidas tomadas de las hojas nasales pueden ser clasificadas en dos factores: tamaño de la herradura y tamaño de la lanceta. El largo del antebrazo (una medida del tamaño del animal) está correlacionado con el tamaño de la hoja nasal, el tamaño de la herradura y el tamaño de la lanceta. Sin embargo, la correlación es mayor con el tamaño de la herradura, lo que sugiere que la lanceta es una estructura más variable que dependería de los rasgos ecológicos del animal. El análisis canónico discriminante fue incapaz de separar estenodermatinos y filostominos, pero indicó una asociación entre los hábitos de alimentación y la morfología de la hoja nasal al crear una variable derivada que está altamente correlacionada con el tipo de alimentación de los filostominos pero que es independiente del tamaño del animal.

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Appendix 1

Specimens examined.—Museum acronyms are as follows: Florida Museum of Natural History, University of Florida, Gainesville (UF); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

PHYLLOSTOMINAE: *Micronycteris hirsuta*, UF 9815; *Micronycteris megalotis*, UF 10167, UF 13851; *Micronycteris brachyotis*, UF 13853; *Macrotus waterhousii*, UF 13767, UF 13770; *Lonchorhina aurita*, USNM 346266, USNM 491180, USNM 491182; *Macrophyllum macrophyllum*, USNM 476547, USNM 476548;

Tonatia bidens, UF 13843; *Tonatia silvicola*, UF 13844; *Mimon cozumelae*, UF 9733, UF 20480; *Mimon crenulatum*, USNM 521580, USNM 534241, USNM 534242; *Phyllostomus discolor*, UF 9819, UF 9821; *Phyllostomus hastatus*, UF 13382, UF 13383; *Phylloderma stenops*, USNM 491318, USNM 555814; *Trachops cirrhosus*, UF 9734, UF 10157, UF 13846; *Chrotopterus auritus*, UF 9142, UF 9143, UF 1944; *Vampyrum spectrum*, USNM 346265, USNM 346266. GLOSSOPHAGINAE: *Glossophaga soricina*, UF 5536, UF 5537, UF 9816; *Glossophaga commissarissi*, UF 9895, UF 9896; *Monophyllus redmani*, UF 22366, UF 22368; *Leptonycteris curasoae*, UF 10042, UF 13668, USNM 52351; *Lonchophylla concava*, UF 13854; *Anoura geoffroyi*, UF 9899, UF 9900; *Lichonycteris obscura*, UF 7911; *Platalina genovensium*, USNM 268765, USNM 268766; *Choeroniscus intermedius*, UF 19057; *Choeronycteris mexicana*, USNM 80713, USNM 96492. CAROLLIINAE: *Carollia perspicillata*, UF 5458, UF 9263; *Rhinophylla fischerae*, UF 9274. STENODERMATINAE: *Sturnira lilium*, UF 9887, UF 9889; *Sturnira ludovici*, UF 9892, UF 9893; *Uroderma bilobatum*, UF 5532, UF 5533; *Vampyrops vittatus*, UF 9262; *Vampyrops helleri*, UF 13848, UF 13849; *Vampyrodes caraccioloi*, UF 9885, UF 13850; *Vampyressa pusilla*, UF 9820, UF 10163; *Chiroderma trinitatum*, UF 13852; *Ectophylla alba*, USNM 336259, USNM 336262; *Artibeus lituratus*, UF 9918, UF 9919; *Artibeus jamaicensis*, UF 10160, UF 10161; *Artibeus phaeotis*, UF 14730, UF 14731. BRACHYPHYLLINAE: *Brachyphylla cavernarum*, UF 5522, UF 5524; *Brachyphylla nana*, UF 23273; *Erophylla bombifrons*, UF 9432, UF 9433; *Phyllonycteris poeyi*, UF 22377. DESMODONTINAE: *Desmodus rotundus*, UF 10158, UF 14733; *Desmodus youngi*, USNM 347071, USNM 347077.

APPENDIX 2

TABLE A.—*Sample size, forearm length, score on the first two principal components, and score on the two factors derived from seven measurements of the noseleaf for the 46 phyllostomid species studied.*

Subfamily and species	*n*	Forearm length	Principal component		Factor	
			1	2	1	2
Phyllostominae						
Micronycteris hirsuta	1	44.13	−0.42	−1.09	0.01	−0.89
Micronycteris megalotis	2	33.41	−0.43	−0.91	−0.06	−0.82
Micronycteris brachyotis	1	38.75	−0.28	−0.95	0.08	−0.71
Macrotus waterhousii	2	52.29	−0.19	0.24	−0.26	−0.04
Lonchorhina aurita	3	51.05	1.70	−3.20	2.76	−0.07
Macrophyllum macrophyllum	2	34.80	1.00	0.50	0.74	1.11
Tonatia bidens	1	61.45	0.63	0.17	0.53	0.64
Tonatia silvicola	1	50.76	0.69	0.18	0.57	0.69
Mimon cozumelae	2	65.20	1.73	0.22	1.53	1.62
Mimon crenulatum	3	49.71	0.78	−0.15	0.78	0.61
Phyllostomus discolor	2	64.53	0.72	−0.33	0.79	0.47
Phyllostomus hastatus	2	83.94	1.94	0.99	1.44	2.18
Phylloderma stenops	2	69.87	1.11	−0.06	1.05	0.94
Trachops cirrhosus	3	57.42	0.82	0.71	0.50	1.07
Chrotopterus auritus	3	82.56	1.38	1.09	0.88	1.74
Vampyrum spectrum	2	108.81	2.16	1.47	1.46	2.60
Glossophaginae						
Glossophaga soricina	3	34.78	−0.83	−0.67	−0.53	−1.05
Glossophaga commissarissi	2	34.75	−0.81	−0.85	−0.44	−1.12
Monophyllus redmani	2	39.88	−1.14	−0.26	−0.97	−1.13
Leptonycteris curasoae	3	52.60	−1.19	0.26	−1.21	−0.92
Lonchophylla concava	1	33.24	−1.37	−0.80	−0.98	−1.58
Anoura geoffroyi	2	43.20	−1.14	−0.35	−0.93	−1.16
Lichonycteris obscura	1	30.18	−1.46	−0.32	−1.24	−1.43
Platalina genovensium	2	47.93	−0.92	0.42	−1.01	−0.60
Choeroniscus intermedius	1	39.46	−0.98	−0.35	−0.78	−1.03
Choeronycteris mexicana	2	43.88	−0.81	−0.27	−0.65	−0.84

APPENDIX 2

TABLE A.—*Continued.*

Subfamily and species	*n*	Forearm length	Principal component		Factor	
			1	2	1	2
Carolliinae						
Carollia perspicillata	2	42.45	−0.02	−0.88	0.30	−0.45
Rhinophylla fischerae	1	34.18	−0.39	−0.93	−0.02	−0.79
Stenodermatinae						
Sturnira lilium	2	38.76	−0.46	−0.73	−0.16	−0.76
Sturnira ludovici	2	44.10	−0.26	−0.43	−0.08	−0.43
Uroderma bilobatum	2	42.07	0.23	0.30	0.11	0.35
Vampyrops vittatus	1	53.47	0.98	−0.18	0.98	0.77
Vampyrops helleri	2	38.55	0.04	−0.55	0.24	−0.23
Vampyrodes caraccioloi	2	57.46	1.10	0.08	0.99	1.00
Vampyressa pusilla	2	29.81	−0.23	−0.14	−0.16	−0.27
Chiroderma trinitatum	1	33.52	0.08	−0.41	0.23	−0.13
Ectophylla alba	2	29.28	−0.33	−0.74	−0.03	−0.65
Artibeus lituratus	2	69.48	1.21	0.53	0.93	1.32
Artibeus jamaicensis	2	60.69	1.07	−0.07	1.02	0.90
Artibeus phaeotis	2	39.11	0.03	−1.18	0.47	−0.55
Brachyphyllinae						
Brachyphylla cavernarum	2	66.23	−0.39	2.02	−1.10	0.64
Brachyphylla nana	1	58.26	−0.79	1.58	−1.32	0.08
Erophylla bombifrons	2	46.74	−1.16	0.63	−1.31	−0.70
Phyllonycteris poeyi	1	47.60	−1.32	1.02	−1.60	−0.65
Desmodontinae						
Desmodus rotundus	2	57.11	−0.83	2.89	−1.89	0.68
Desmodus youngi	2	49.12	−1.26	1.52	−1.73	−0.36