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Cephalometric Correlates of Echolocation in the Chiroptera

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ABSTRACT This study suggests that the evolution of head posture in bats is constrained by the demands of vocalization during echolocation. Nasal-emitting microchiropteran taxa are easily identified by their characteristic rotation of the basicranium ventrally about the cervical axis, the depression of the rostrum below the basicranial axis, and by the rotation of the lateral semicircular canals so as to maintain their horizontal orientation during flight. The converse is true for oral-emitting Microchiroptera. The general form of the microchiropteran skull has been canalized along two distinct evolutionary paths, respectively, towards oral-emitting or nasal-emitting forms.

Microchiroptera emit echolocation calls either through the mouth (oral-emitting bats) or through the nasal passages (nasal-emitting bats). Of the two possible forms, oral-emitters are generally considered the more primitive (Vaughan, '72; Van Valen, '79). Nasal-emitting taxa characteristically possess a fleshy, often elaborate, flap of skin projecting above the nose (the nose leaf) that is thought to help focus the echolocation call as it is emitted through the nostrils (Arita, '90; Hartley and Suthers, '87, '88, '90; Möhres, '66a,b; Pye, '88; Simmons and Stein, '80). Whereas the generalizations listed in Table 1 receive wide acceptance, the correlation between emission type and facial morphology has been quantified for only a limited number of taxa (Pollack and Casseday, '89).

The strong, positive correlation between relative brain size and the utilization of spatially complex foraging sites has dominated the evolution of the chiropteran brain (Eisenberg and Wilson, '78; Stephan et al., '81; Fig. 1). Although there is a large phylogenetic component to this correlation (Jolicoeur et al., '84), the evolution of the brain is strongly correlated with the occupation of a specific aerial niche. For example, aerial insectivores and foliage gleaners are found in open habitats or along forest boundaries and characteristically have relatively small brains. Conversely, frugivorous and animalivorous taxa have relatively larger brains and commonly forage in complex, cluttered habitats (Stephan et al., '81). This increase in brain volume is due to a larger neocortex that integrates the olfactory and visual stimuli that are necessary to live in such cluttered environments (Jolicoeur et al., '84).

The evolution of the brain and pharynx are not independent of other cranial structures. For example, the growth and position of the primate basicranium relative to the cervical axis is restricted by its contact with the pharynx (Blechschmidt, '76a). The accommodation of pharyngeal growth and stabilization of the pharyngeal functional space (tongue, larynx, and airway) influence both the rotation of the facial skull about the basicranium and the posture of the head and neck (Baer and Nanda, '76; Blechschmidt, '76a; Schön, '76; Solow and Greve, '79). Similarly, differential growth between the cerebrum and the midventral axis of the brain increases the flexure of the cranial base and influences the angle of the face and relationship between the face and mandible in humans (Baer and Nanda, '76; Enlow, '76; Moss, '76).

Such examples of morphological evolution require changes in the developmental program that force previously well-integrated systems to or beyond their spatial and temporal limits thus forming new morphogenetic interactions or dramatic phenotypic shifts (Alberch et al., '79; Alberch and Alberch, '81; Gould, '77; Müller, '90; Needham, '33). These emerging structural innovations may be "epigenetic amplifications" (Müller, '90) of selection upon other characters (Twitty, '32) and provide the impetus for great morphological changes with only minimal alterations of the genome. The underlying force behind epigenetic amplifications lies in the developmental plasticity of a system to either integrate or

TABLE I. Synopsis of the families of bats (after Koopman, 1984)

	Mode of echolocation[1]		
	None	Oral	Nasal
Order Chiroptera			
Suborder Megachiroptera			
Family Pteropodidae	AP	—	—
Suborder Microchiroptera			
(Infraorder Yinochiroptera)			
Superfamily Emballonuroidea			
Family Emballonuridae	—	AP*	—
Family Craseonycteridae	—	A	—
Family Rhinopomatidae	—	A	P
Superfamily Rhinolophoidea			
Family Nycteridae	—	—	AP*
Family Megadermatidae	—	—	AP*
Family Rhinolophidae	—	—	AP*
(includes Hipposideridae)	—	—	AP*
(Infraorder Yangochiroptera)			
Superfamily Phyllostomoidea			
Family Mormoopidae	—	AP	—
Family Noctilionidae	—	AP	—
Family Phyllostomidae	—	—	AP*
(includes Desmodontidae)	—	—	AP*
Superfamily Vespertilionoidea			
Family Thyropteridae	—	A	—
Family Myzopodidae	—	A	—
Family Furipteridae	—	A	—
Family Natalidae	—	AP	—
Family Mystacinidae	—	A	—
Family Molossidae	—	AP*	—
Family Vespertilionidae	—	AP*	—

[1]A, generally accepted; P, present study; *, Mohres, 1966b.

accommodate the morphological changes necessary for maintaining the functional relationships between affected structures, e.g., bone, cartilage, muscle, sense organs, air passages, and connective and nervous tissues. The summation of differential growth and functional interactions among components has been termed the "functional matrix" of the head (Moss, '60, '62, '72, '75, '76). Whereas Moss ('62) exaggerates the role of soft tissues by stating that "skull growth is secondary, compensatory and mechanically obligatory to cephalic growth," the role of soft tissues in skeletal morphogenesis is a recurring theme in studies concerning cranial evolution (Blechschmidt, '76a,b; Haines, '40; Hanken, '83). I will argue that the morphological dichotomy in nasal-emitting and oral-emitting forms of the microchiropteran skull provides indirect evidence of developmental constraint upon the relative position of the hard palate, and pharynx during echolocation.

The objectives of this study are three-fold: 1) verify and quantify the dichotomy in fundamental skull conformation between nasal-emitting and oral-emitting microchiropterans; 2) evaluate the correlation between skull shape, brain size, habitat selection, and mode of echolocation; and 3) examine the non-echolocating megachiropteran skull *bauplan* and determine whether it conforms to the same constructional rules that apply to the echolocating microchiropteran skull.

MATERIALS AND METHODS

Specimens

Perfect specimens of male bats were selected at random without regard to dietary habit, geographic distribution, body size, or taxonomic affiliation. My sample represents 14 families, 39 genera, and 69 species including 30 oral-emitters, 28 nasal-emitters (9 Old World and 19 New World), and 5 megachiropterans that do not utilize ultrasonic echolocation (Table 2). Each specimen was radiographed at the University of Nebraska School of Dentistry using periapical x-ray film (Kodak DF-58, shot at 80 kV, 10 mA). Each skull was held securely in a jig that positioned the skull against the film at the center of the x-ray beam so as to minimize parallax error and standardize skull orientation across taxa. Only films that exhibited perfect registry between right and left sides of the skull were utilized in the analysis. Population samples of both a nasal-emitting species, *Artibeus jamaicensis* (n = 20), and an oral-emitting species, *Eptesicus fuscus* (n = 25), were also radiographed.

Cephalometry

Five cephalometric "planes" were identified in each lateral radiograph (Fig. 2): 1) The plane of the foramen magnum forms within the important boundary between the occiput and the cervical axis (Baer and Nanda, '76; Schön, '76). This plane influences head posture and reflects the degree of flexibility found in the cranio-cervical axis (Fenton and Crerar, '84). 2) The basicranium is sandwiched between the brain and pharynx and is limited by basion and the antero-ventral lip of the basioccipital synchondrosis. This axis is a foreshortened version of Radinsky's basicranial axis ('84, '85). In this position the basicranium reflects the differential growth between the brain and pharynx and has a direct influence on the position of the craniofacial complex of the skull (Laitman et al., '76). 3) The cribriform plate is the bony septum between the nasopharynx and the brain that partitions the facial and neural components of the

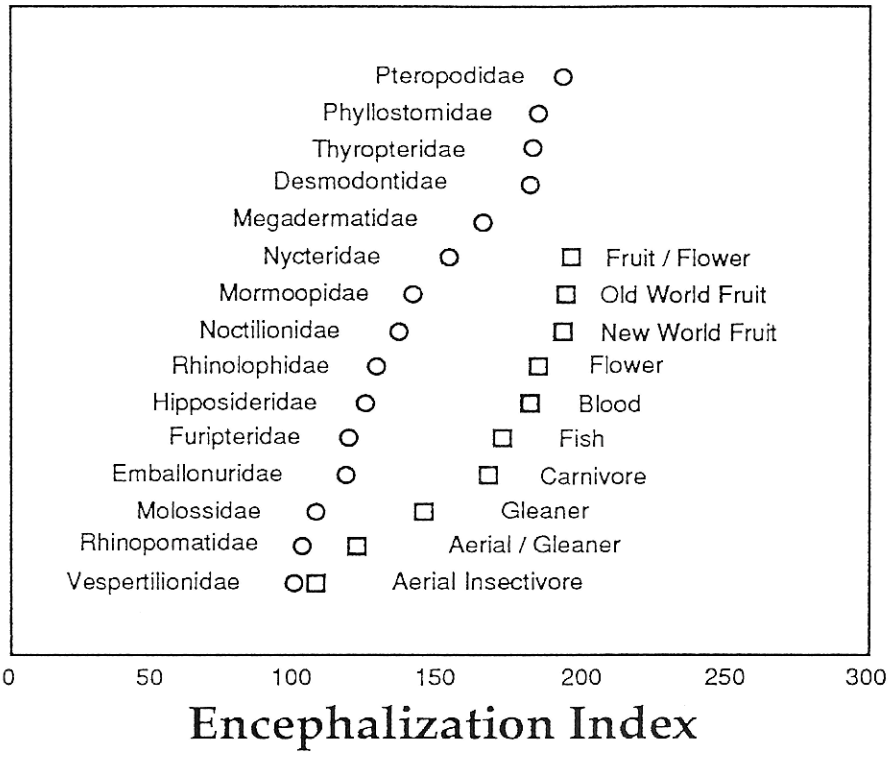

Fig. 1. Average encephalization indices of the Chiroptera by taxon and by food preference. The index is based upon distances from the vespertilionid regression: log brain weight = 1.655 + 0.684 × log body weight (after Stephan et al., '81). Note that aerial insectivores have small brains and occupy the lower end of this index, while frugivorous taxa possessing larger brains and utilizing more cluttered environments dominate the upper end, i.e., brain size is closely associated with habitat use.

skull (Ranly, '80). Its relative position reflects the volumetric increase of the brain case during brain growth (Moss, '76; Young, '59). The cribriform plate is also responsive to the structural mechanics of the midface, the volume of the olfactory lobes of the telencephalon (Frahm, '81; Jolicoeur, et al., '84; Pirlot and Bernier, '91), the development of the interorbital septum (Haines, '40), and the position of the rostrum relative to the anterior cranial base (Starck, '52). The dorsal and ventral most extrema of the cribriform plate define the dimensions of this plane and are easily identified in all taxa. 4) Despite the physiological connection between the lateral semicircular canals and head posture (Delattre and Fennart, '60; deBeer, '37), the more recent clinical and developmental literature conspicuously lacks cephalometric studies of the lateral semicircular canals. Because bats are nocturnal and fly in a three-dimensional environment, the physiology of the inner ear is important. Accordingly, the orientation of the lateral semicircular canals should reflect the manner in which a bat holds its head during flight. This landmark is defined by and limited to a plane containing both lateral semicircular canals of the inner ear. The tubular cross-section of the ossified canals are easily identified in all radiographs. 5) The phonal axis of the head is aligned with the long axis of either the oropharynx or the nasopharynx. Because the hard palate separates these two subdivisions of the pharynx, it is an important landmark. I define the hard palate as a line drawn between two consistent landmarks: the incisive foramen and the posterior palatine process.

I measured six cephalometric angles directly from camera lucida drawings made of each film to describe the relationship among the six anatomical planes: 1) the angle between the plane of the hard palate and the plane of the basicranium, PAL; 2) the angle

TABLE 2. Taxonomic list

			FMAG	EAR	CRIB	PAL	EAR PAL	CRIB FMAG	VOL
Non-emitting taxa									
Epomophorus	Wahlbergi		62	20	43	8	28	75	2.10
Cynopterus	brachyotis		43	26	46	18	44	91	1.10
Pteropus	vampyrus		63	28	36	28	56	81	10.20
Rousettus	amplexicaudatus		60	31	37	20	51	83	1.45
Rousettus	celebensis		63	23	24	34	57	93	1.65
Oral-emitting taxa									
Natalus	stramineus	stramineus	45	20	20	9	29	115	0.21
Noctilio	leporinus	leporinus	55	31	64	3	34	61	1.20
Pteronotus	parnelli	mexicana	65	8	11	22	30	104	—
Rhinopoma	muscatellum		56	18	35	14	32	89	0.13
Diclidurus	virgo		64	29	25	1	30	91	0.35
Peropteryx	kappleri	kappleri	41	15	57	−2	13	82	0.17
Taphozous	georgianus		60	11	33	0	11	87	0.38
Eumops	perotis	perotis	65	18	56	0	18	59	—
Eumops	underwoodi	underwoodi	62	22	54	0	22	64	0.70
Molossus	molossus	molossus	47	27	42	9	36	91	0.25
Otomops	martiensseni	icatus	47	30	56	6	36	77	—
Tadarida	brasilensis	antillularum	49	24	45	3	27	86	0.17
Tadarida	brazilensis	mexicana	54	18	43	6	24	83	0.18
Antrozous	pallidus	bunkeri	48	18	51	2	20	81	0.30
Eptesicus	diminutus	fidelis	59	22	53	−2	20	68	—
Eptesicus	furinalis	furinalis	61	14	49	−1	13	70	—
Eptesicus	serotinus	horikawai	63	19	49	5	24	68	—
Lasionycteris	noctivagans		46	18	52	−3	15	82	0.18
Lasiurus	borealis	borealis	72	19	64	−18	1	44	0.17
Lasiurus	cinereus		62	30	67	−25	5	51	0.32
Myotis	keeni	septentrionalis	48	18	49	−1	17	83	0.13
Myotis	myotis	myotis	48	11	62	4	15	70	0.44
Myotis	velifer	incautus	55	10	50	−2	8	75	0.21
Myotis	vivesi		58	11	56	−10	1	66	0.42
Myotis	volans	interior	53	24	58	−11	13	69	0.13
Nyctecius	humeralis		55	13	61	3	16	64	0.11
Pipistrellus	subflavus	subflavus	54	11	56	−3	8	70	0.10
Scotophilus	nigrita	dinganii	59	22	50	−11	11	71	0.33
Nasal-emitting taxa									
Anoura	geoffroyi	lasiopyga	35	31	43	0	31	102	0.43
Artibeus	cinereus	cinereus	49	30	26	13	43	105	0.38
Artibeus	hirsutus		41	30	35	14	44	104	0.87
Artibeus	jamaicensis	yucatanicus	43	33	25	13	46	112	0.84
Artibeus	lituratus	palmarum	39	28	21	19	47	120	1.30
Artibeus	phaeotis	nanus	35	37	14	13	50	131	0.44
Brachyphylla	cavernarum	cavernarum	42	32	39	15	47	99	—
Centurio	senex		49	19	22	25	44	109	—
Glossophaga	longirostris	rostrata	46	29	28	10	39	106	0.41
Leptonycteris	yerbabueuae		47	34	33	2	36	100	0.58
Lonchorhina	aurita	aurita	42	42	55	11	53	83	0.34
Macrotus	waterhousii	californicus	39	27	28	16	43	113	0.37
Mimon	cozumelae		37	46	38	12	58	105	0.68
Monophyllus	plethodon	luciae	43	25	23	16	41	114	0.42
Phyllostomus	discolor	verrucosus	36	38	35	16	54	109	1.15
Phyllostomus	hastatus	hastatus	35	41	46	11	52	99	1.50
Stenoderma	rufum		49	24	12	25	49	119	0.61
Sturnira	lilium		43	37	38	14	51	99	0.58
Vampyrum	spectrum		52	26	35	13	39	93	—
Desmodus	rotundus	murinus	46	46	29	−2	44	105	—
Rhinolophus	affinis	affinis	47	33	54	19	52	79	0.31
Rhinolophus	euryale	euryale	37	44	46	21	65	97	0.21
Rhinolophus	ferrumequinum	ferrumequinum	40	42	54	22	64	86	0.29
Hipposideros	armiger	armiger	57	43	39	23	55	84	0.72
Hipposideros	caffer		45	31	23	18	49	112	0.21
Hipposideros	galeritus		29	52	38	8	60	113	0.20
Megaderma	spasma		47	42	35	11	53	98	1.04
Nycteris			41	56	27	20	76	112	0.29

TABLE 2. Taxonomic list (continued)

			FMAG	EAR	CRIB	PAL	EAR PAL	CRIB FMAG	VOL
Eptesicus	fuscus	fuscus	47	17	46	−6	11	87	—
Eptesicus	fuscus	fuscus	51	11	59	−7	4	70	—
Eptesicus	fuscus	fuscus	52	21	69	−8	13	59	—
Eptesicus	fuscus	fuscus	53	20	72	−6	14	55	—
Eptesicus	fuscus	fuscus	53	21	69	−6	15	58	—
Eptesicus	fuscus	fuscus	54	13	58	−3	10	68	0.21
Eptesicus	fuscus	fuscus	54	18	61	−5	13	65	—
Eptesicus	fuscus	fuscus	54	26	58	−6	20	68	—
Eptesicus	fuscus	fuscus	56	5	61	0	5	63	—
Eptesicus	fuscus	fuscus	57	10	62	−3	7	61	—
Eptesicus	fuscus	fuscus	57	17	56	−1	16	67	—
Eptesicus	fuscus	fuscus	57	18	60	2	20	63	—
Eptesicus	fuscus	fuscus	57	18	66	−2	16	57	—
Eptesicus	fuscus	fuscus	57	26	58	−5	21	65	—
Eptesicus	fuscus	fuscus	58	11	65	0	11	57	—
Eptesicus	fuscus	fuscus	58	14	69	−8	6	53	—
Eptesicus	fuscus	fuscus	58	16	67	−10	6	55	—
Eptesicus	fuscus	fuscus	58	20	45	2	22	77	—
Eptesicus	fuscus	fuscus	58	23	61	−1	22	61	—
Eptesicus	fuscus	fuscus	59	19	67	9	28	54	—
Eptesicus	fuscus	fuscus	60	17	53	−5	12	67	—
Eptesicus	fuscus	fuscus	61	21	68	−8	13	51	—
Eptesicus	fuscus	fuscus	62	13	66	−9	4	52	—
Eptesicus	fuscus	fuscus	67	7	64	0	7	49	—
Eptesicus	fuscus	fuscus	67	22	64	2	24	49	—
Artibeus	jamaicensis	jamaicensis	44	22	23	15	37	113	0.84
Artibeus	jamaicensis	jamaicensis	35	27	28	17	44	117	—
Artibeus	jamaicensis	jamaicensis	35	31	31	12	43	114	—
Artibeus	jamaicensis	jamaicensis	35	39	28	12	51	117	1.10
Artibeus	jamaicensis	jamaicensis	37	27	24	10	37	119	—
Artibeus	jamaicensis	jamaicensis	38	20	26	10	30	116	—
Artibeus	jamaicensis	jamaicensis	38	25	26	16	41	116	—
Artibeus	jamaicensis	jamaicensis	38	27	19	15	42	123	—
Artibeus	jamaicensis	jamaicensis	38	33	22	14	47	120	—
Artibeus	jamaicensis	jamaicensis	39	29	17	16	45	124	—
Artibeus	jamaicensis	jamaicensis	40	25	21	16	41	119	—
Artibeus	jamaicensis	jamaicensis	40	28	31	11	39	109	—
Artibeus	jamaicensis	jamaicensis	40	29	23	15	44	117	—
Artibeus	jamaicensis	jamaicensis	40	32	29	11	43	111	—
Artibeus	jamaicensis	jamaicensis	41	28	23	19	47	116	—
Artibeus	jamaicensis	jamaicensis	41	32	27	17	49	112	—
Artibeus	jamaicensis	jamaicensis	43	23	26	18	41	111	—
Artibeus	jamaicensis	jamaicensis	44	26	25	14	40	111	—
Artibeus	jamaicensis	jamaicensis	45	29	23	15	44	112	—
Artibeus	jamaicensis	jamaicensis	48	32	17	16	48	115	—

between the plane of the cribriform plate and the plane of the basicranium, CRIB; 3) the angle between the plane of the lateral semicircular canals and the plane of the basicranium, EAR; and 4) the angle between the plane of the foramen magnum and the plane of the basicranium, FMAG; 5) CRIB-FMAG, angle between the cribriform plate and the foramen magnum; and 6) EAR-PAL, angle between the lateral semicircular canals and the hard palate.

Brain and head size

Brain volume was approximated by filling the braincase of each specimen with dust shot (1.1 mm diameter) and then measuring the shot volume in a graduated cylinder (0.01 cc). The size of the head was estimated by taking the cubed root of the product of three skull measurements: zygomatic width, greatest length of skull, and midface depth (after Freeman, '84). The LOG (base 10) of both brain volume and head size, LOG(VOL) and LOG(SIZE), will be reported in subsequent analyses.

Statistical analyses

I used univariate and multivariate analyses to focus upon underlying patterns of variation among taxa and between the two emission types with respect to the cephalometric angles, brain volume, and habitat type (SYSTAT:

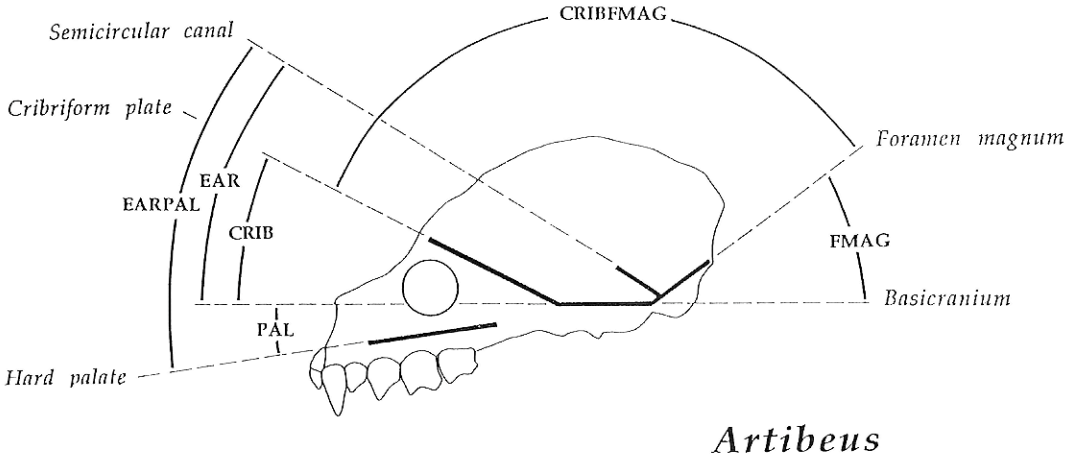

Fig. 2. Cephalometric angles used in study. See text for description of each cephalometric angle and anatomical plane.

Wilkinson, '90; STATVIEW: Feldman et al., '88). I ran sequential one-way analyses of variance to test the differences between groups with respect to each of the six cephalometric angles. I exercised caution during the group wide, simultaneous comparisons of these angles by employing the sequential Bonferroni method (Rice, '89). I investigated the correlations among head size, brain volume, and the six cephalometric angles in adult bats simultaneously with a Pearson correlation analysis.

Discriminant analysis (DA; Systat; Wilkinson, '90) "discriminates" between group centroid (multivariate) means based on patterns of covariance within their pooled covariance matrix. The Likelihood ratio test of homogeneity of covariance matrices showed a significant difference between group matrices. Under conditions of covariance heterogeneity, small sample size, and small number of variables, a linear discriminant function based on the pooled covariance matrix outperforms a quadratic function based on separate matrices (Dillon and Goldstein, '84). Therefore, the pooled covariance matrix was utilized in both Discriminant analyses.

The canonical coefficients were standardized by the within groups, standard deviations. From these standardized coefficients, factor scores were calculated that allow graphic representation of each case in discriminant, multivariate space. Using the Maximum-likelihood approach, Mahalonobis distances were calculated between each case and the multivariate centroid of each group. Group affiliation was assigned according to the posterior probability method.

Discriminant analysis I (DA-I)

I derived a Fischer's Discriminant function (linear) based upon populations of a nasal-emitting species, *Artibeus jamaicensis* (n = 20), and of an oral-emitting species, *Eptesicus fuscus* (n = 25). Using a cross-validation approach, I applied this same function to a group of 58 "unknown" microchiropteran taxa to test the original classification scheme (oral-emitting: n = 30 vs. nasal-emitting: n = 28). Not unlike the jackknife approach, the cross-validation method avoids the self-fulfilling under-estimation of misclassification encountered when classifying observations with a Discriminant function derived from the very same set of observations.

Discriminant analysis II (DA-II)

This second analysis was performed on the same 58 "unknown" microchiropteran taxa utilized in DA-I with the inclusion of five megachiropteran taxa to evaluate their relative position among oral-emitting and nasal-emitting microchiropteran skull forms within the same multivariate space.

RESULTS

Anova

Statistical comparison of oral-emitting and nasal-emitting taxa yielded significant differences between groups for all six variables (FMAG, EAR, CRIB, PAL, EAR-PAL, and CRIB-FMAG; Table 3). I re-ran this analysis using log(VOL) as a covariate to investigate the influence of brain volume on each angle. The results are similar except that EAR and

TABLE 3. Chiropteran skulls. Analysis of variance: oral-emitting vs. nasal-emitting taxa[1]

Variable	SS	df	MS	F	P
ANOVA					
FMAG	2,314.28	1	2,314.28	49.32	0.000*
error	2,533.64	54	49.61		
EAR	3,894.44	1	3,894.44	64.08	0.000*
error	3,281.39	54	60.76		
CRIB	3,255.87	1	3,255.87	21.09	0.000*
error	8,336.10	54	154.37		
PAL	2,857.14	1	2,857.14	43.55	0.000*
error	3,542.57	54	65.60		
EARPAL	13,423.01	1	13,423.01	132.07	0.000*
error	5,488.10	54	101.63		
CRIBFMAG	11,060.16	1	11,060.16	59.64	0.000*
error	10,012.67	54	185.42		
ANCOVA					
FMAG	630.27	1	630.27	13.86	0.001*
error	1,909.79	42	45.47		
EAR	271.34	1	271.34	4.88	0.033
error	2,334.71	42	55.58		
CRIB	1,070.27	1	1,070.27	6.94	0.012
error	6,473.15	42	154.12		
PAL	649.29	1	649.29	10.67	0.002*
error	2,554.58	42	60.82		
EARPAL	1,760.10	1	1,760.10	16.16	0.000*
error	4,732.22	42	108.88		
CRIBFMAG	3,343.19	1	33.43	16.76	0.000*
error	8,377.49	42	199.46		

[1]FMAG, angle of the foramen magnum; EAR, angle of the lateral semicircular canals; CRIB, angle of the cribriform plate; PAL, angle of the hard palate; EARPAL, angle between the EAR and PAL; CRIBFMAG, angle between CRIB and FMAG. *Bonferroni $P = 0.0083$. Log (VOL) is the covariate.

CRIB were no longer statistically different (Table 3). Neither brain volume nor head size are significantly correlated with any of the six cephalometric angles (Table 4).

Discriminant analysis I (DA-I)

The single discriminant function easily distinguished between samples of the oral-emitting *Eptesicus fuscus* and the nasal-emitting *Artibeus jamaicensis* (Table 5). The multivariate distributions of *E. fuscus* and *A. jamaicensis* did not overlap and the probability of their misclassification was 0.00%. High positive loadings along the discriminant axis (Fig. 3) are characteristic of the nasal-emitting taxa while high negative loadings characterize the oral-emitting taxa.

Using a cross-validation approach, this analysis classified the 58 "unknown" taxa according to the discriminant function derived from the samples of *Eptesicus fuscus* and *Artibeus jamaicensis* as either oral-emitting or nasal-emitting (Table 5). The analysis assigned specimens to the correct group in 54 of 58 cases (93%). Four of the fifty-eight taxa were misclassified: *Rhinopoma muscatellum, Natalus stramineus, Molossus molossus,* and *Pteronotus parnelli.*

Statistical comparison of the oral-emitting, nasal-emitting, and non-emitting taxa yielded significant differences among groups for all six angles (Table 6). A posteriori comparisons between pairs of group means, using the Tukey HSD method, show that oral-emitting and nasal-emitting groups are significantly different for all six angles (Table 6).

Discriminant analysis II (DA-II)

The second discriminant analysis incorporated the non-emitting Megachiroptera and subdivided the nasal-emitting group into New and Old World taxa: 5 Megachiroptera (non-emitters), 30 oral-emitters, 9 Old World nasal-emitters, and 19 New World nasal-emitters. The first discriminant axis clearly discriminates between oral-emitting and nasal-emitting forms of the skull. High positive loadings characterize nasal-emitting taxa while

TABLE 4. Chiropteran skulls. Pearson correlation matrices

(n = 56)	FMAG	EAR	CRIB	PAL	EAR PAL	CRIB FMAG
Nasal- and oral-emitting taxa (*Bonferroni $P = 0.0033$).						
FMAG	1.000					
EAR	−0.610*	1.000				
CRIB	0.309	−0.223	1.000			
PAL	−0.497*	0.394*	−0.641*	1.000		
EAR-PAL	−0.665*	0.845*	−0.510*	0.824*	1.000	
CRIB-FMAG	−0.709*	0.458*	−0.890*	0.714*	0.698*	1.000
Nasal- and oral-emitting taxa (*Bonferroni $P = 0.0017$).						
Log (VOL)	−0.231	0.388	−0.269	0.354	0.424	0.303
Log (SIZE)	−0.210	0.425	−0.160	0.434	0.490*	0.213
Nasal-, oral, and non-emitting taxa (*Bonferroni $P = 0.0033$).						
FMAG	1.000					
EAR	−0.582	1.000				
CRIB	0.242	−0.215	1.000			
PAL	−0.315	0.347	−0.631*	1.000		
EAR-PAL	−0.544*	0.814*	−0.519*	0.827*	1.000	
CRIB-FMAG	−0.689*	0.456*	−0.870*	0.631*	0.664*	1.000

TABLE 5. Chiropteran skulls. Discriminant analysis (DA-I): oral-emitting vs. nasal-emitting taxa

	Canonical loadings	Group classification coefficients (Fishers' discriminant function)		
		Oral	Nasal	
FMAG	−0.452	3.807	2.439	
EAR	0.244	1.080	1.466	
CRIB	−0.701	1.585	0.737	
PAL	0.511	−0.950	0.545	
		−168.879	−83.026	Constants

Classification matrix

		Predicted				
		Eptesicus	*Artibeus*	Oral	Nasal	Total
Observed	*Eptesicus*	25	0			25
	Artibeus	0	20			20
	Oral			26	4	30
	Nasal			0	28	28
		25	20	26	32	99/103

Oral, oral-emitting microchiroptera; Nasal, nasal-emitting microchiroptera; Multivariate test: Wilks' Lambda = 0.043; F = 222.048, df = 4, 40, $P = 0.000$, Residual Root test $\chi^2 = 311.291$, df = 4, $P = 0.000$, Canonical correlation = 0.978.

high negative loadings characterize oral-emitting taxa (Fig. 4). The second discriminant axis reflects variation in head posture about the cervical axis. High negative values characterize the morphology of the occiput of nasal-emitting bats in which the foramen magnum is rotated inferiorly (Table 7).

Eleven of sixty-three taxa are misclassified (17.5%). Six of these misclassifications are instances where Old World nasal-emitting forms could not be distinguished from New World nasal-emitting forms. Therefore if this misclassification rate is re-evaluated in terms of function, rather than taxonomy, the rate is only 8% (Table 8).

Discriminant analysis was necessary to provide a statistical basis for group classification (Tables 5, 6, 8). However, sample variation in skull shape is most easily interpreted in a simple bivariate plot of EAR-PAL against CRIB-FMAG (Fig. 5) and is further illustrated in Figure 6.

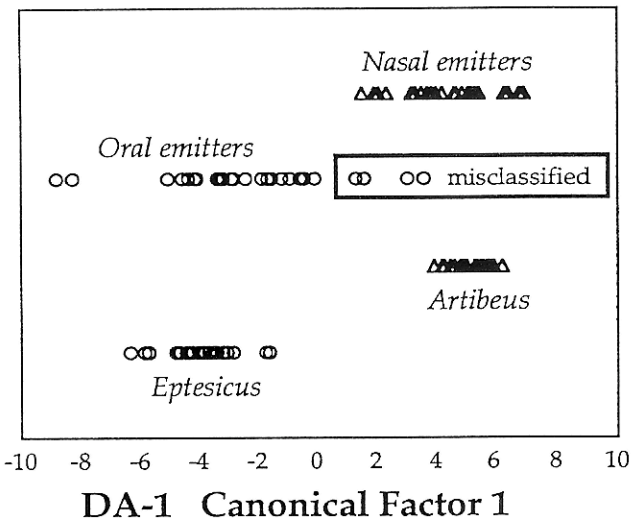

Fig. 3. Discriminant analysis I (DA-I): Results of the first discriminant function analysis. Adult crania were classified as either oral-emitting or nasal-emitting using a cross-validation approach based upon a linear discriminant function drawn from populations of adult *Eptesicus* (oral-emitter) and *Artibeus* (nasal-emitter). See text for a description of the four misclassified taxa.

TABLE 6. Chiropteran skulls. Analysis of variance: oral-emitting, nasal-emitting, and non-emitting taxa

	ANOVA				
Variable	SS	df	MS	F	p
FMAG	2,705.81	2	1,352.90	27.47	0.000*
error	2,828.44	58	48.76		
EAR	3,907.76	2	1,953.88	33.78	0.000*
error	3,354.59	58	57.83		
CRIB	3,330.50	2	1,665.25	11.20	0.000*
error	8,622.90	58	148.67		
PAL	3,826.03	2	1,913.01	28.17	0.000*
error	3,937.77	58	67.89		
EAR-PAL	14,178.01	2	7,089.00	67.90	0.000*
error	6,054.90	58	104.39		
CRIB-FMAG	11,184.44	2	5,592.22	31.69	0.000*
error	10,231.87	58	176.41		

	Tukey HSD group comparisons		
	Nasal vs. oral	Nasal vs. none	None vs. oral
FMAG	**	**	
EAR	**	**	
CRIB	**		
PAL	**		**
EAR-PAL	**		**
CRIB-FMAG	**	**	

*Bonferroni $P = 0.0083$.
**Group means are significantly different, $P = 0.05$.

TABLE 7. Chiropteran skulls. Discriminant analysis (DA-II)

	Canonical loadings		
	Factor 1	Factor 2	Factor 3
FMAG	−0.455	0.599	−0.222
EAR	0.650	−0.079	0.711
CRIB	−0.301	0.227	0.807
PAL	0.508	0.411	−0.713

Group classification coefficients[1]				
NONE	ORAL	NWNE	OWNE	
1.493	1.365	1.309	1.179	
1.059	0.771	1.281	1.074	
0.648	0.598	0.585	0.476	
1.072	0.639	1.016	0.814	
−82.023	−61.481	−76.526	−56.475	Constants

Residual roots test				
	Chi-square	df	*P*	Canonical correlation
1	209.496	12	0.000	0.877
2	58.737	6	0.000	0.615
3	9.757	6	0.008	0.301

[1]Multivariate test: Wilks' Lambda = 0.131, F = 14.314, df = 12, 148, $P = 0.000$. NONE, Megachiroptera, NWNE, New World nasal-emitting Microchiroptera; ORAL, oral-emitting Microchiroptera; OWNE, Old World nasal-emitting Microchiroptera.

DISCUSSION

The present study shows that the dichotomy in the fundamental form of the microchiropteran skull corresponds with the emission of the echolocation call through either the mouth or through the nose and is directly related to the relative position of the hard palate. This observation is not original (Freeman, '84; Mohl, '71; Starck, '52), yet the present study is the first statistical test of the hypothesis. In contrast to oral-emitting

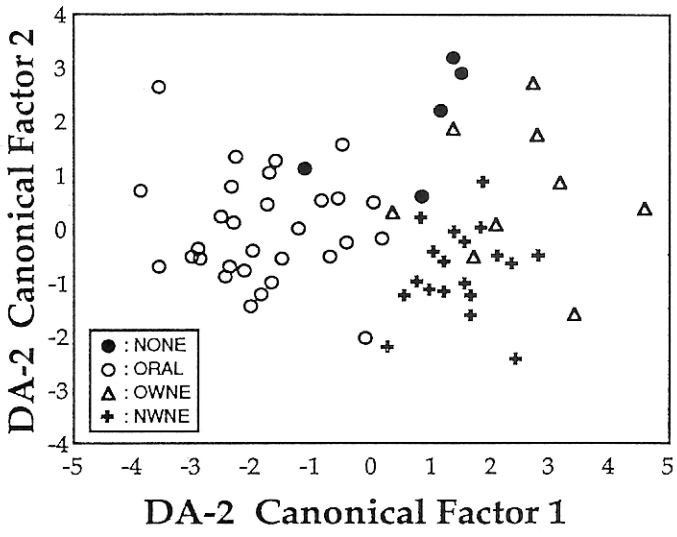

Fig. 4. Discriminant analysis II (DA-II): Scatterplot of the first and second canonical factors in the second discriminant function analysis. Note: a) the intermediate position of the megachiropteran taxa (NONE) between the oral-emitting and nasal-emitting (OWNE, NWNE) on the first canonical factor, and b) the overlapping distributions of the Old and New World nasal-emitting taxa (OWNE, NWNE) along both axes.

TABLE 8. Chiropteran skulls. Discriminant analysis (DA-II)

Classification matrix[1]

		Predicted				
		NONE	ORAL	NWNE	OWNE	Total
Observed	NONE	4	1	0	0	5
	ORAL	1	27	0	2	30
	NWNE	1	0	6	2	9
	OWNE	0	0	4	15	19
		6	28	10	19	52/63

[1]NONE, Megachiroptera; NWNE, New World nasal-emitting Microchiroptera; ORAL, oral-emitting Microchiroptera; OWNE, Old World nasal-emitting Microchiroptera.

skulls, the general organization of the nasal-emitting skull is distinctive: 1) the nasal-emitting rostrum is rotated ventrally to align the nasopharynx with the direction of flight, 2) the foramen magnum is moved inferiorly, and 3) the inner ear rotates posteriorly to compensate for the general rotation of the skull ventrally about the cranio-cervical axis. This complex reorganization of the nasal-emitting skull gives the general impression that the skull has been bent into an "angular" shape. The skulls of oral-emitting bats exhibit a form in which the orofacial, midfacial, and neurocranial components are aligned in a more linear fashion giving the skull a somewhat "blocky" appearance. Specifically, 1) the oral-emitting rostrum is elevated dorsally above the basicranium, 2) the foramen magnum faces posteriorly, and 3) the plane of the lateral semicircular canals remains relatively parallel with that of the cranial base (Fig. 6).

Intermediate positions of the palate have not been tolerated by microchiropteran evolution. This dichotomy in skull form is established in utero when skull shape, skull posture, and the orientation of each osteological, functional unit are more responsive to the shape and rate of growth of the underlying brain, paired sensory capsules, and the pharynx (Bosma, '76; Hanken, '83, '84; Silver, '62; Sperber, '89; Zelditch and Carmichael, '89a,b; Zelditch et al., '90) than to the strictly mechanical forces that will come to play a predominant role in skull morphogenesis with the advent of suckling and mastication (Herring and Lakars, '81; Herring, '85). Changes in the morphogenesis of one structure, i.e., the pharynx, cascade throughout other systems leaving the remainder of cranial development to accommodate these newly imposed spatial requirements and functional demands (Devillers, '65; Thompson, '66). The observations of present study are the indirect result of similar ontogenetic shifts in the spatial accommodation of the orofacial construct around either the nasopharynx or the oropharynx.

Emission behavior was correctly identified in nearly every case by DA-I on the basis of

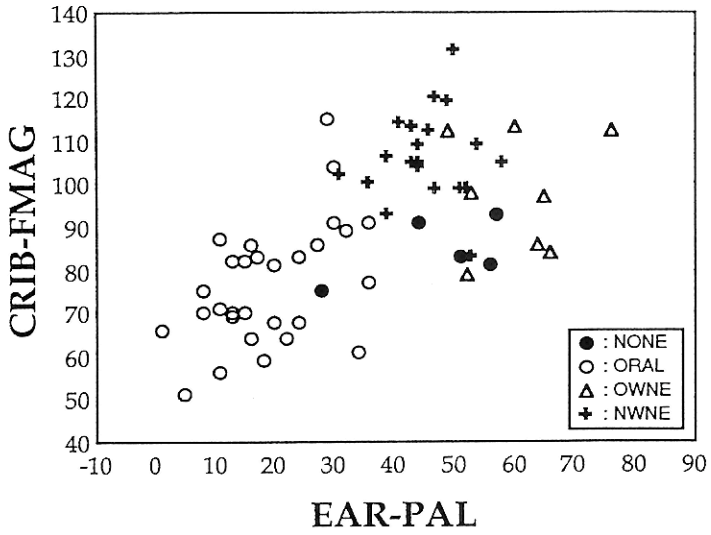

Fig. 5. Scatterplot of CRIB-FMAG against EAR-PAL. Note again: a) the intermediate position of the megachiropteran taxa (NONE) between the oral-emitting and nasal-emitting groups (OWNE, NWNE), and b) the overlapping distributions of the Old and New World nasal-emitting taxa (OWNE, NWNE) along both axes.

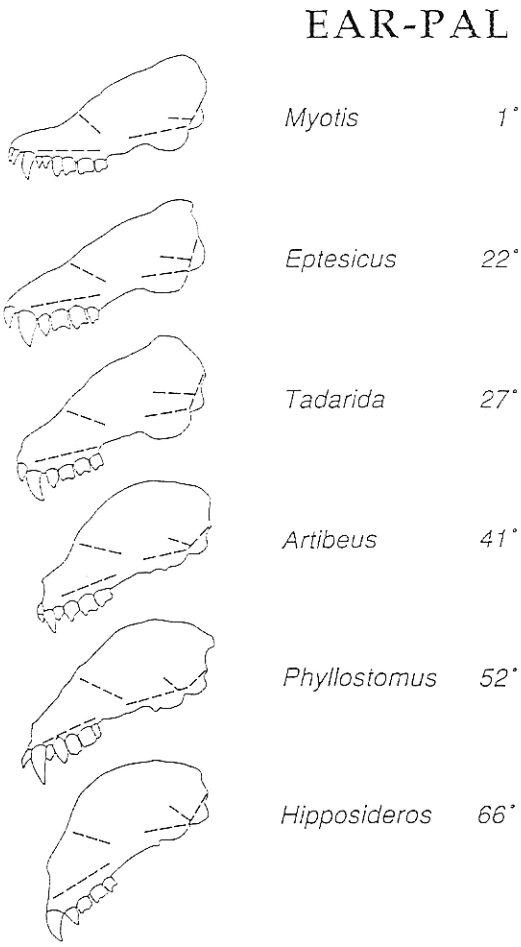

Fig. 6. Representative cephalograms of six microchiropteran taxa demonstrating the wide range of rostral rotation (EAR-PAL) within the order. *Myotis, Eptesicus,* and *Tadarida* are oral-emitting taxa, whereas *Artibeus, Phyllostomus,* and *Hipposideros* are nasal-emitting taxa.

the fundamental organization of the cranium. The four misclassifications consisted of an "oral" taxon being misclassified as a "nasal" taxon. Historically, *Rhinopoma* has been generally regarded as primitive on the basis of its post-cranial osteology (Miller, '07; Simmons, '80; Van Valen, '79, but see Smith, '76). Accordingly, I coded *Rhinopoma* as an oral-emitter because oral-emitters are generally considered primitive to the nasal-emitters. However, *Rhinopoma muscatellum* possesses a rudimentary nose-leaf, an inflated rostrum, and complicated basisphenoidal pits; it has been classified as a nasal-emitting form by this analysis. These data suggest that *Rhinopoma* is a nasal-emitter and that my initial classification of the taxon as an oral-emitter was incorrect. *Molossus molossus, Natalus stramineus,* and *Pteronotus parnelli* are known oral-emitting taxa yet were misclassified as nasal-emitting taxa because of gross distortions of the cribriform plate. Apparently, spatial competition between the elevated rostrum and the relatively large brain in these three taxa (Stephan et al., '81) flattens the cranial base and cribriform plate into a construct resembling a nasal-emitting skull.

It could be argued that DA-I discriminates between Vespertilionids (*Eptesicus*) and Stenodermines (*Artibeus*) rather than between oral-emitting and nasal-emitting forms of the skull. However, this dichotomy in *baupläne* is independent of diet, dentition, body size, and biogeography of the Microchiroptera. It might also be argued that brain growth influences the position of the orofacial complex and that skull shape may be an allometric artifact of brain volume in bats. However, neither brain volume nor head size are significantly correlated with any of the six cephalometric angles in this sample. This lack of correlation suggests that evolutionary increases in chiropteran brain volume have had little or no influence on the mode of echolocation but may reflect the pressures of habitat selection instead (Stephan et al., '81).

DA-II and the new and old world nasal-emitters

Nasal-emitting taxa are geographically and morphologically distinct. The Old World families include the Nycteridae, Megadermatidae, Rhinolophidae, and perhaps Rhinopomatidae, whereas the Phyllostomatidae exist as the only, albeit diverse, New World family (Koopman, '84). Although the skulls of Old World and New World nasal-emitting bats differ from each other externally, discriminant analysis could not consistently distinguish between the fundamental structure of the skull in these two taxonomic groups. Based upon this convergence of the basic form of the skull in these two groups, I believe that phonation is a primary determinant of skull form in the nasal-emitting Microchiroptera.

DA-II and the megachiroptera

The Megachiroptera possess large eyes, large highly complex brains, and a wide range of rostral deflections (e.g., Macroglossinae; Andersen, '12) but have never evolved the

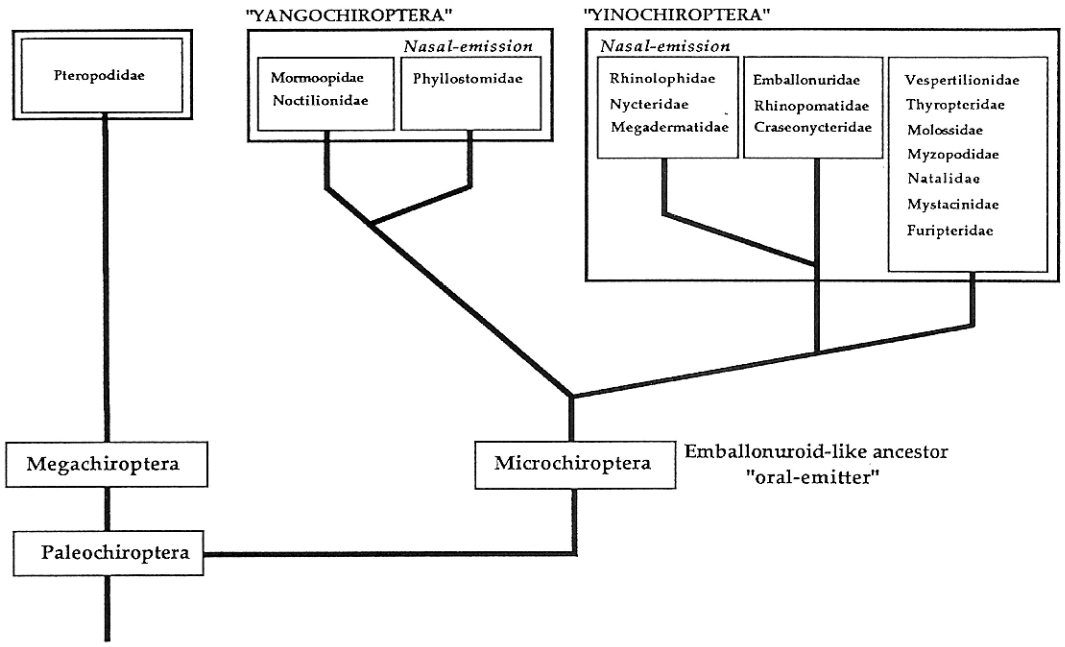

Fig. 7. Hypothesized dendrogram of the Chiroptera (after Koopman, '84).

ability to echolocate ultrasonically. It should be noted that *Rousettus* is considered to "echolocate" using tongue clicking but *Rousettus* is incapable of the highly derived ultrasonics exhibited by the Microchiroptera (Roberts, '75). It is of particular interest that the Megachiroptera lie in an intermediate position relative to the oral-emitting and nasal-emitting Microchiropterans (Figs. 4, 5). This is certainly due to the fact that the megachiropteran palate is not constrained by the demands of echolocation, i.e., the megachiropteran palate does not have to be elevated above, or depressed below the axis of the emitted echolocative call. Hence, the general underlying form of the megachiropteran skull is free, in both developmental and evolutionary terms, to accommodate a very different suite of morphogenetic forces that are not shared with the Microchiroptera. This suggests that the phenomenon of facial deflection in the Chiroptera, as a whole, is influenced by several different morphogenetic factors, only one of which being related to the relative position of the hard palate with respect to the emission of the echolocative call.

Systematic significance

Microchiroptera evolved from a primitive emballonuroid-like paleochiropteran stock that was distributed world-wide by the early Eocene (Jepsen, '66). Paleochiroptera were capable oral-emitters (Novacek, '85; Pettigrew, '88) albeit equipped with poorly developed cochlea (Habersetzer and Storch, '87, '92; Smith, '76). In the most comprehensive recent attempt to organize the 888 extant species of Chiroptera, Koopman ('84) chose to separate the microchiropteran lineages into two infraorders based upon the mobility of the premaxillae: the Yinochiroptera (premaxillae free from the maxillae) and the Yangochiroptera (premaxillae fused to the maxillae). The Old World nasal-emitters belong to the Yinochiroptera which radiated primarily within the Old World, while New World nasal-emitters (Yangochiroptera) are restricted to the New World (Smith, '76). Though distinct in terms of premaxillary mobility, each infraorder contains both nasal-emitting and oral-emitting forms (Fig. 7).

Old World nasal-emitters evolved directly from the paleochiropteran stock but it is uncertain if the New World nasal-emitters radiated from the Paleochiroptera as well or if they evolved from an emballonuroid-like migrant from the Old World (Pettigrew, '91; Smith, '72, '76). In either case, Paleochiroptera were present in the New World from the early Eocene until the early Oligocene with-

out any evidence of nasal-emitting taxa (Carroll, '88); the common ancestor to both the New World and Old World nasal-emitters would not have possessed a nose-leaf (Van Valen, '79).

Current phylogenetic analyses infer the independent and convergent evolution of nasal-emission by the New and Old World nasal-emitting Microchiroptera but never state this specific hypothesis in a systematic context (Pettigrew, '91). Accordingly, I believe that the independent coevolution of nasal-emission, nose-leaves, and the reorganization of the skull around the nasal cavity is an example of convergent morphological evolution in the Old World and the New World nasal-emitting taxa. Although based on a relatively small sample, this study opens a series of testable hypotheses concerning the ontogeny and phylogeny of the basic construct of the chiropteran skull.

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