

MORPHOMETRIC ANALYSIS OF THE CHIROPTERAN SKULL WITH REGARD TO MODE OF ECHOLOCATION

SCOTT C. PEDERSEN

*School of Biological Sciences and University of Nebraska State Museum,
University of Nebraska, Lincoln, NE 68588-0548*

I compared simple morphometric data with cephalometric data on the angular arrangements of the facial and neural components of the skull of bats. The morphological dichotomy between oral and nasal emission of the echolocation pulse in the Microchiroptera is presumably under strong selective pressure to provide an acoustical horn for efficient emission of the echolocative call. Cephalometric and morphometric data compliment each other in the distinction between oral and nasal *baupläne*. However, fine taxonomic resolution provided by morphometric data is subject to the otherwise plastic functional matrix of the head conforming to the acoustical axis of the skull.

Key words: skull, bats, echolocation, morphometrics

Functional morphology of the mammalian rostrum and pharynx is influenced by several factors: respiratory tidal airflow (Solow and Greve, 1979), forces of tooth eruption and autoclusal mechanisms (Lakars and Herring, 1980), tissue pressures from lips and tongue (Proffit, 1978), organization and coordination of each muscle mass in proportion to complexity of dentition and associated dynamics of mastication (Herring, 1985), and phonation or echolocation (Hartley and Suthers, 1988; Roberts, 1972, 1973; Suthers et al., 1988). Although the present study focuses primarily on proportions of adult skull, the *bauplan* and much of the functional integration among components are the direct result of strong selective forces that act on packaging of and spatial competition between adjacent tissues and organ systems during embryogenesis and fetal development (Bosma, 1976; Haines, 1940; Hanken, 1983; Silver, 1962). Herein, I use the term *bauplan* in a general context to describe an idealized structural plan (sensu Simpson, 1961) composed of developmentally connected suites of traits (Mitchell, 1992) and do not infer a systematic hierarchy (sensu Mayr, 1982).

Evolution of the microchiropteran phar-

ynx is firmly constrained by demands imposed by emission of ultrasonic vocalizations—echolocation. Accordingly, there is a fundamental dichotomy in the form of the microchiropteran skull corresponding with emission of echolocative calls through either the oropharynx or nasopharynx (Freeman, 1984; Mohl, 1971; Pedersen, 1993, 1995; Starck, 1952). Orofacial and neurocranial components are aligned in a tandem fashion in heads of oral-emitting bats. This construct is similar to that of most terrestrial quadrupeds in which the foramen magnum faces caudally and the plane of lateral semicircular canals remains relatively parallel with that of the cranial base. Conversely, rostra of skulls of nasal-emitting taxa are rotated ventrally below the braincase to align the nasal cavity, rather than the oral cavity, with the direction of flight. Additionally, the foramen magnum is moved antero-inferiorly and the inner ear rotated posteriorly to compensate for the general rotation of the skull ventrally about the cranio-cervical axis (Pedersen, 1993, 1995). This morphological dichotomy represents either upward or downward deflection of the hard palate; intermediate positions of the hard palate are poorly suited, biome-

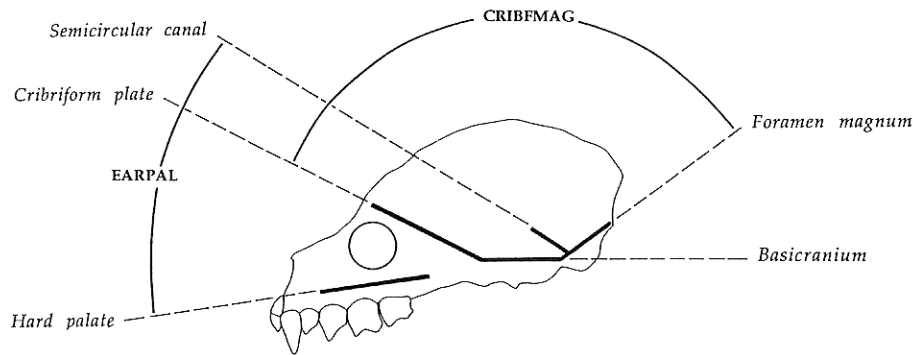


FIG. 1.—Cephalometric angles (after Pedersen, 1993) as seen on *Artibeus* (New World nasal-emitter): 1) angle between a plane encompassing both of the lateral semicircular canals and the plane of the hard palate—the ear-palate angle (EARPAL); and 2) angle between a plane determined by the cribriform plate of the ethmoid and a plane encompassing the foramen magnum—the cribriform-foramen magnum angle (CRIBFMAG).

chanically, for echolocation as the call would be directed either above or below the direction of flight.

Because cephalometric variation in skull *baupläne* reflects use of the microchiropteran head as an acoustical horn (Pedersen, 1993), there should be only minor modifications in osteological counterparts of the pharynx and oral cavity in oral-emitting forms, commonly held to be the primitive state among echolocating bats (Valdivieso, et al., 1979; Van Valen, 1979; Vaughan, 1972). Conversely, in taxa that echolocate through the confines of the nasal passages, one could expect to find a suite of predictable modifications to the choanae, external nares, hard palate, and soft palate that accommodate the echolocative call without undue distortion of its acoustical signature.

I investigated the nature of these modifications by integrating a traditional morphological analysis of osteological landmarks with previous cephalometric findings (Pedersen, 1993, 1995). Specifically, I had three expectations: 1) clarity of the taxonomic “signal” (i.e., ability to distinguish between oral-emitting and nasal-emitting taxa) derived from morphometric (landmark) data would not differ from that derived from cephalometric (angular) data; 2) nasal-emitting groups from the New and

Old World that are similar cephalometrically (Pedersen, 1993, 1995) would differ morphometrically in keeping with the established taxonomy (Koopman, 1984); and 3) morphometric data for megachiropteran skulls should clarify their “intermediate” (Pedersen, 1993) position between the two echolocating *baupläne*.

MATERIALS AND METHODS

Adult specimens of male bats were selected without regard to dietary habit, geographic distribution, body size, or taxonomic affiliation. This sample represented 14 families, 39 genera, and 69 species including 30 oral-emitters, 28 nasal-emitters (9 Old World and 19 New World), and five megachiropterans that do not echolocate (Appendix I).

Each specimen was radiographed at the University of Nebraska School of Dentistry using periapical x-ray film. Two cephalometric angles were incorporated from the previous analysis to compare cephalometric interpretation of skull form with the present morphometric data: 1) ear-palate angle—angle between a plane encompassing the lateral semicircular canals and the plane of the hard palate 2) cribriform-foramen magnum angle—angle between a plane determined by the cribriform plate of the ethmoid and a plane encompassing the foramen magnum (Figs. 1 and 2).

I measured 39 cranial dimensions on each skull with dial calipers to the nearest 0.01 mm.

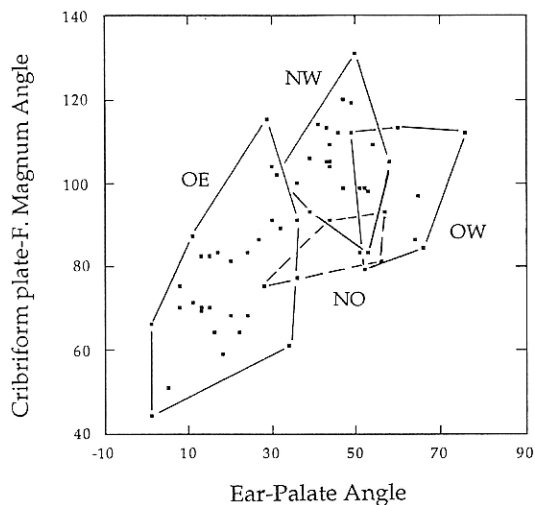


FIG. 2.—Ear-palate angle plotted against the cribriform-foramen magnum angle for all individuals in the study. Abbreviations: OE = oral-emitter, OW = Old World nasal-emitter, NW = New World nasal-emitter, and NO = non-emitter.

Using a subset of these measurements ($n = 12$), I derived 12 indices to evaluate the relationship among characters and quantify general proportions of these skulls (Appendix II). Interpretation of indices is complicated by uncertainty that the numerator or denominator may unduly influence the ratio (Marcus, 1990). As a precaution, I evaluated elements of each index separately with a regression against head size (cube root of the product of zygomatic width of skull, greatest length of skull, and midfacial depth). To summarize, individual variables were correlated highly with head size, but there was a near absence of multiple correlation (among the 12 indices) and head size—only one ($P < 0.001$) of 12 models tested were significant. That is, each ratio provide a usable measure of relationship that was not overtly influenced by overall head size. I imposed an angular transformation on each index to satisfy assumptions of the analysis of variance [*arcsine* (*square root* (*Index value* / *10*))]; a transformed index value of 0.32 radians represented a 1:1 relationship between the two quantities; Sokal and Rohlf, 1981].

I compared transformed indices among groups with one-way analyses of variance. This was done within a scheme of three separate taxonomic groupings: 1) Microchiroptera (two

groups)—comparison of oral- and nasal-emitting microchiropteran taxa, 2) Microchiroptera (three groups)—comparison among oral-emitting, New World nasal-emitting and Old World nasal-emitting microchiropteran taxa, and 3) Chiroptera (four groups)—comparison among megachiropteran taxa, oral-emitting, New World nasal-emitting and Old World nasal-emitting microchiropteran taxa.

In each scheme, I exercised caution during group-wide simultaneous comparisons of these measures by using the sequential Bonferroni method to reduce Type I error (Rice, 1989). There were 12 variates, hence the Bonferroni $P = 0.05/12 = 0.0042$. That conservative error rate ensured that groups were different from each other with regard to every variate in the analysis. In each scheme, I also tested for specific differences between groups with a posteriori pair-wise comparisons of group harmonic means using the Tukey HSD method at $P = 0.05$ (Wilkinson, 1990; Feldman et al., 1988).

RESULTS

Oral-emitting versus nasal-emitting Microchiroptera.—Of the many indices relating directly to the construction of the nasopharynx, only indices of choanal bore: pharyngeal length and choanal bore: narial bore exhibited significant differences between oral and nasal-emitting groups. The pterygoid width:TMJ (Temporo-mandibular joint, i.e., jaw joint) width index also differed significantly between groups albeit this index related to nasopharyngeal construction only indirectly (Fig. 3).

Subdivision of the Old and New World Microchiroptera.—With subdivision of nasal-emitting Microchiroptera into New and Old World taxa, 10 of the 12 indices exhibited differences among groups simultaneously. The two indices that did not differ between groups were pterygoid width:otic capsule separation and basioccipital: greatest skull length (Bonferroni $P = 0.0041$; Tables 1 and 2). Whereas oral-emitters differed from both Old and New World nasal-emitters (7 of 12 and 4 of 12 indices, respectively), Old and New World nasal-emitters differed significantly from each other in 8 of 12 between-group comparisons.

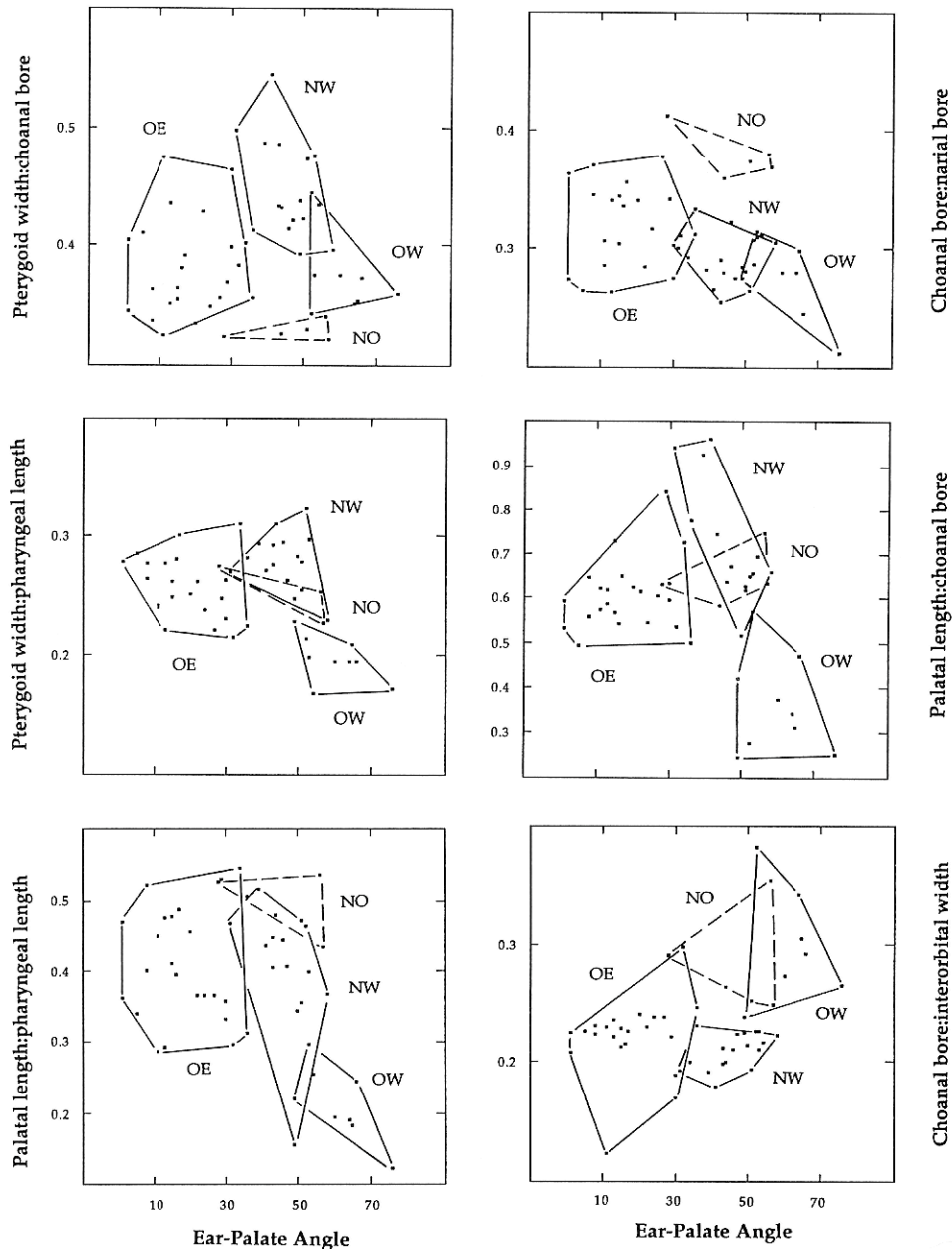


FIG. 3.—Six representative cranial indices plotted against ear-palate angle; abbreviations are the same as in Fig. 2.

This observation was of great interest because Old and New World nasal-emitters were predicted to have appeared more similar to each other, in keeping with cephalometric data (Fig. 3).

Megachiroptera versus Microchiroptera.

tera.—Inclusion of the non-echolocating megachiropteran taxa did not alter the basic conclusions presented above concerning Microchiroptera. Specific between-group comparisons were performed as in the previous section, albeit with the inclusion of

TABLE 1.—Analysis of variance for all Chiroptera.

Index	Emission type	\bar{X}	<i>SD</i>	<i>t</i>	<i>P</i> ^a
Pterygoid width : otic capsule separation	Oral ^b	0.43	0.091	5.845	0.0017
	OW—Nasal	0.46	0.122		
	NW—Nasal	0.36	0.027		
	None	0.32	0.017		
Pterygoid width : bi-TMJ width	Oral	0.19	0.017	10.484	<0.0001
	OW—Nasal	0.19	0.012		
	NW—Nasal	0.22	0.015		
	None	0.19	0.010		
Pterygoid width : choanal bore	Oral	0.38	0.040	17.458	<0.0001
	OW—Nasal	0.37	0.029		
	NW—Nasal	0.44	0.042		
	None	0.33	0.007		
Pterygoid width : pharyngeal length	Oral	0.25	0.026	11.885	<0.0001
	OW—Nasal	0.20	0.016		
	NW—Nasal	0.27	0.036		
	None	0.25	0.019		
Choanal bore : otic capsule separation	Oral	0.36	0.061	11.345	<0.0001
	OW—Nasal	0.41	0.128		
	NW—Nasal	0.26	0.020		
	None	0.31	0.019		
Choanal bore : pharyngeal length	Oral	0.22	0.029	8.673	0.0001
	OW—Nasal	0.17	0.014		
	NW—Nasal	0.20	0.028		
	None	0.24	0.019		
Choanal bore : narial bore	Oral	0.31	0.034	14.959	<0.0001
	OW—Nasal	0.27	0.034		
	NW—Nasal	0.29	0.022		
	None	0.38	0.019		
Choanal bore : interorbital width	Oral	0.22	0.031	15.638	<0.0001
	OW—Nasal	0.29	0.052		
	NW—Nasal	0.20	0.015		
	None	0.28	0.043		
Palatal length : choanal bore	Oral	0.60	0.079	12.874	<0.0001
	OW—Nasal	0.37	0.107		
	NW—Nasal	0.69	0.171		
	None	0.64	0.061		
Palatal length : pharyngeal length	Oral	0.40	0.080	16.943	<0.0001
	OW—Nasal	0.20	0.051		
	NW—Nasal	0.40	0.094		
	None	0.49	0.047		
Palatal length : toothrow length	Oral	0.32	0.026	29.024	<0.0001
	OW—Nasal	0.19	0.054		
	NW—Nasal	0.33	0.054		
	None	0.38	0.019		
Basioccipital length : greatest skull length	Oral	0.11	0.014	0.447	0.7202
	OW—Nasal	0.11	0.015		
	NW—Nasal	0.11	0.014		
	None	0.12	0.008		

^a Bonferroni *P* < 0.0041.

^b Abbreviations are as follows: Oral = oral-emitter; OW—Nasal = Old World nasal-emitter; NW—Nasal = New World nasal-emitter; None = non-emitter, i.e., Megachiroptera.

TABLE 2.—Tukey HSD comparisons for all Chiroptera; asterisks indicate that group means are significantly different, $P < 0.05$. Abbreviation and indices as Table 1.

Index	Non-emitters versus oral emitters	Non-emitters versus OW—nasal emitters	Non-emitters versus NW—nasal emitters	Oral emitters versus OW—nasal emitters	Oral emitters versus NW—nasal emitters	OW—nasal emitters versus NW—nasal emitters
Pterygoid width:otic capsule separation	*	*				
Pterygoid width:bi-TMJ width			*		*	*
Pterygoid width:choanal bore	*		*		*	*
Pterygoid width:pharyngeal length		*		*		*
Choanal bore:otic capsule separation					*	*
Choanal bore:pharyngeal length		*	*	*		
Choanal bore:narial bore	*	*	*	*	*	
Choanal bore:interorbital width	*		*	*		*
Palatal length:choanal bore		*		*		*
Palatal length:pharyngeal length		*		*		*
Palatal length:toothrow length	*	*		*		*
Basioccipital length:greatest skull length						

the non-emitting Megachiroptera (Fig. 3, Tables 1 and 2). Megachiroptera appeared to be most consistently different from Old World nasal-emitters (7 of 12 indices) but different to a much lesser degree from the oral-emitters (5 of 12) and New World nasal-emitters (4 of 12).

DISCUSSION

Microchiroptera encompasses two broadly defined morpho-functional groups that relate to the most basic construction of the skull. The head of an oral emitting bat is constructed simply around the oral cavity that functions as an acoustical horn during echolocation. Bats that emit their echolocative calls from nostrils (nasal emitters) face a more difficult biomechanical problem. To emit sound efficiently and in the appropriate direction, the rostrum, midface, and nasal passages must be reconfigured as an acoustical horn. Accordingly, this fundamental dichotomy between oral- and nasal-emitting bats is clearly reflected in angular (cephalometric) relations of the hard palate to the neurocranium (Fig. 2; Pedersen, 1993, 1995).

In contrast, my analysis of landmark data describes a trichotomy composed of oral

emitters (open mouths), New World nasal-emitters (simple nasal passages), and Old World nasal-emitters (sophisticated resonance chambers within the nasal passages). Skull morphology of non-emitting megachiropterans is not so easily placed into this trichotomy because the form of the megachiropteran skull is not constrained by dynamics of ultrasonic echolocation and varies widely within the Family.

Cranial width-width relationships.—Four indices (pterygoid width:otic capsule separation, pterygoid width:choanal bore, choanal bore:otic capsule separation, choanal bore:narial bore) share the common feature that each component describes the lateral dimensions (osteological bounds) of the pharynx. Of these, the pterygoid width:choanal bore index demonstrates the best separation among emission groups (Tables 1 and 2, Fig. 3). Megachiroptera exhibit a relatively large choanal bore as a group. In contrast, New World nasal-emitting taxa are clustered apart from the rest because of their relatively large pterygoid widths.

The other three indices in that foursome distinguish among groups to a lesser extent (Tables 1 and 2, Fig. 3). However, the

choanal bore:narial bore index defines a form-function morphospace in which three distinct groups are clearly present: oral-emitting, nasal-emitting, and non-emitting. Non-emitting and oral-emitting groups exhibit high values of choanal bore:narial bore index while both Old and New World nasal-emitters are restricted to index values <0.33 , i.e., a simple ratio value of 1:1. Although choanal and narial diameters are absolutely larger in skulls of nasal-emitting bats than in skulls of oral-emitters, the nasal-emitting nasopharynx exhibits a relatively large narial bore. However, the narial bore is surrounded externally by the musculature and epithelium of the nostrils and nose-leaf. Since airflow out of the nasal cavity is restricted by the diameter of the nostrils rather than the narial bore (bone), the *in vivo* ratio should provide a better match between diameters. Further speculation concerning acoustic properties of the nasal cavity is beyond the scope of this analysis (Griffin, 1958; Hartley and Suthers, 1987, 1988, 1990; Roberts, 1972, 1973; Suthers et al., 1988). The significance of these relationships among nostril diameter, narial bore, and choanal bore deserves further investigation.

Laryngo-nasal junction.—The craniofacial component of the skull of Old World nasal-emitters is characterized by a short hard palate and relatively a long naso-laryngo-pharynx. This construction reflects the unique velopharyngeal junction that characterizes Old World nasal-emitters but is not found in New World nasal-emitting taxa (Hartley and Suthers, 1988; Matsu-mura, 1979). This junction is remarkable in its size and completeness of its seal, both of which have forced repositioning of all musculoskeletal elements associated with the soft palate and larynx, (pterygoid width, choanal bore, pharyngeal length, and otic-capsule separation).

Four indices concern the proportions of this complex space: pterygoid width:pharyngeal length, choanal bore:pharyngeal length, palatal length:choanal bore, palatal

length:pharyngeal length index. The unique pharynx of Old World nasal-emitting taxa influences values of each index, such that they are less than those exhibited by the other three comparison groups. Whereas the hard palate runs nearly the entire length of the maxilla in the Megachiroptera, New World nasal-emitters, and oral-emitters, the emarginate hard palate of the Old World nasal-emitters greatly decreases the value of the palatal length:toothrow length index (Tables 1 and 2; Fig. 3).

Basicranium, midface, and jaw.—Of the remaining three indices: pterygoid width: Temporomandibular joint (TMJ) width, basioccipital length:skull length, and choanal bore:interorbital width, only the latter two distinguish among groups (Tables 1 and 2). Dramatic differences among groups regarding the latter index are the result of variation in interorbital width. Dimensions of this restricted space are strongly influenced by the packaging of the olfactory fossae, contents of the orbit, and the choanae.

The olfactory fossae and vomeronasal complex are relatively large in the New World nasal-emitting group but quite small in the Old World nasal-emitters (Bhatnagar, 1980; Bhatnagar and Kallen, 1974*a,b*; Cooper and Bhatnagar, 1976; Suthers et al., 1988). In contrast, rostra of Old World nasal-emitting taxa are dominated by large outpocketings of the nasal cavity (dorsal nasal chambers) that are absent in skulls of oral-emitting, New World nasal-emitting, and megachiropteran bats. Although the entire supra-glottal vocal tract of an Old World nasal emitter is tuned such that the echolocation call may pass through the rostrum with little decrement, the dorsal-nasal chambers are highly derived structures that serve as both notch filters and as resonators during echolocation (Hartley and Suthers, 1988; Roberts, 1972, 1973; Suthers et al., 1988). Because New World nasal-emitters possess neither chambers nor a "tuned" rostrum, the call is relatively muffled by the

nasal passages; as such, Griffin (1958) termed these animals "whispering bats."

Given the spatial restrictions of the mid-face (Haines, 1940; Hanken, 1984; Hoyte, 1987), it seems unlikely that the skull of a nasal-emitting bat could exhibit both a large olfactory complex and a resonating chamber in the rostrum. It would appear that the anatomical correlates of olfaction and echolocation have worked at cross-purposes during cranial evolution of Old World nasal-emitters.

Index summary.—The taxonomic "signal" from the present morphometric data matches previous morphology-based taxonomies that distinguish between oral- and nasal-emitting taxa, and between New and Old World nasal-emitting taxa (Koopman, 1984). This finding meets the first two expectations of the study. Despite gross differences in the external appearance of their skulls, it is of interest that New and Old World nasal-emitting taxa have converged on the same cephalometric *bauplan* as demanded by the acoustics of nasal emission.

With respect to the third expectation of this study, these data do not improve taxonomic resolution regarding the intermediate position of megachiropteran skulls (Pedersen, 1993). Neither dimensions nor organization of the unspecialized megachiropteran rostrum are constrained by ultrasonic vocalization leaving the Megachiroptera as morphological intermediates between the two echolocating *baupläne*.

Evolutionary concerns.—The present system is of interest because the nasal-emitting *bauplan* has arisen twice in apparent isolation (Carroll, 1988; Jepsen, 1966; Novacek, 1985; Pettigrew, 1991; Smith, 1972, 1976; Van Valen, 1979); rhinolophoid and phyllostomid bats have derived independently the anatomical requirements for efficient nasal-emission of ultrasound (Hartley and Suthers, 1987, 1988, 1990; Pye, 1988; Simmons, 1980; Simmons and Stein, 1980). In the balance, phyllostomids have retained olfaction at

the cost of loudness of the call, but rhinolophoids have emphasized loudness of the call at the expense of olfaction. This latter hypothesis is necessarily simplistic and deserves further investigation.

Anatomical correlates of nasal-emission provide a dramatic structural signal that is pervasive throughout the rostrum of nasal-emitting bats. This fundamental reorganization of the cranial *bauplan* required the re-routing of presumptive nasal-emitters from an ancestral developmental path onto a new morphogenetic trajectory. Such branching events have been termed "key innovations" (Cracraft, 1990; Frazzetta, 1975; Müller, 1990; Raff et al., 1990). That early morphogenesis has dramatic and far reaching effects on evolutionary mechanics is not a new concept (Alberch, 1982; Blechschmidt, 1976; Devillers, 1965; Gans, 1988; Herring, 1985; Hoyte, 1987; Klima, 1987; Müller et al., 1989; Ranfjord and Ash, 1966; Thorogood, 1988).

Paleochiroptera may have used echolocation (Novacek, 1985; Pettigrew 1988), although their skulls exhibited neither cochlear nor whole-skull morphologies suggestive of advanced echolocative ability (Habersetzer and Storch, 1987, 1992; Smith, 1976). Strong selective pressures on the relative position of the hard palate partitioned early unspecialized Microchiroptera into oral- and nasal-emitting forms. I argue that elevation of the palate in oral-emitting forms is as much a derived character as the depression of the palate in nasal-emitting forms. Without the selective pressures of echolocation, skulls of megachiropterans appear to have retained the unspecialized, and in this case, "intermediate" form of the chiropteran skull.

ACKNOWLEDGMENTS

I thank S. Swartz, P. Freeman, R. Adams, and several anonymous reviewers for providing valuable commentary throughout the project and on preliminary drafts of the manuscript. I also thank the curators and staff of the University of Nebraska State Museum, the University of Kan-

sas Museum of Natural History, and the American Museum of Natural History. I also am grateful to L. C. Williams, scientific illustrator at the University of Nebraska State Museum, for preparing Fig. 1.

LITERATURE CITED

- ALBERCH, P. 1982. Developmental constraints in evolutionary processes. *Evolution and development*. Pp. 313–332, in Dahlem Konferenzen, 1982 (J. T. Bonner and I. Dawid, eds.). Springer-Verlag, Berlin, Germany, 356 pp.
- BHATNAGAR, K. 1980. The chiropteran vomernasal organ: its relevance to the phylogeny of bats. Proceedings of the Fifth International Bat Research Conference, Texas Tech Press, 5:282–315.
- BHATNAGAR, K., AND F. KALLEN. 1974a. Morphology of the nasal cavities and associated structures in *Arctibeus jamaicensis* and *Myotis lucifugus*. *American Journal of Anatomy*, 139:167–190.
- . 1974b. Cribriform plate of ethmoid, olfactory bulb and olfactory acuity in forty species of bats. *Journal of Morphology*, 142:71–90.
- BLECHSCHMIDT, M. 1976. Biokinetics of the developing basicranium. Pp. 44–53, in *Development of the basicranium*. United States Department of Health, Education, and Welfare Publication, 76-989:1–700.
- BOSMA, J. F. 1976. Introduction to the symposium. Pp. 3–28, in *Development of the basicranium*. United States Department of Health, Education, and Welfare Publication, 76-989:1–700.
- CARROLL, R. 1988. *Vertebrate paleontology and evolution*. W. H. Freeman and Company, New York, 698 pp.
- COOPER, J., AND K. BHATNAGAR. 1976. Comparative anatomy of the vomernasal organ complex in bats. *Journal of Anatomy*, 122:571–601.
- CRACRAFT, J. 1990. The origin of evolutionary novelties: patterns and process at different hierarchical levels. Pp. 21–44, in *Evolutionary innovations* (M. H. Nitecki, ed.). The University of Chicago Press, Chicago, Illinois, 304 pp.
- DEVILLERS, C. 1965. The role of morphogenesis in the origin of higher levels of organization. *Systematic Zoology*, 14:259–271.
- FELDMAN, D., J. GAGNON, R. HOFMAN, AND J. SIMSON. 1988. Statview, the solution for data analysis and presentation graphics. Abacus Concepts, Berkeley, California, 1.03:1–278.
- FRAZZETTA, T. 1975. Complex adaptations in evolving populations. Sinauer Associates Inc., Publishers, Sunderland, Massachusetts, 267 pp.
- FREEMAN, P. W. 1984. Functional analysis of large animalivorous bats (Microchiroptera). *Biological Journal of Linnean Society*, 21:387–408.
- GANS, C. 1988. Craniofacial growth, evolutionary questions. *Development (supplement)*, 103:3–15.
- GRIFFIN, D. 1958. *Listening in the dark*. Yale University Press, New Haven, Connecticut, 413 pp.
- HABERSETZER, J., AND G. STORCH. 1987. Ecology and echolocation of the Eocene Messel bats. *European Bat Research*, 1987:213–233.
- . 1992. Cochlea size in extant Chiroptera and middle Eocene microchiropterans from Messel. *Naturwissenschaften*, 79:462–466.
- HAINES, W. 1940. The interorbital septum in mammals. *Journal of the Linnean Society, London*, 41:585–607.
- HANKEN, J. 1983. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae): II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. *Journal of Morphology*, 177:255–268.
- . 1984. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia: Plethodontidae). I. Osteological variation. *Biological Journal of the Linnean Society*, 23:55–75.
- HARTLEY, D., AND R. SUTHERS. 1987. The sound emission pattern and the acoustical role of the noseleaf in the echolocating bat, *Carollia perspicillata*. *Journal of Acoustical Society of America*, 82:1892–1900.
- . 1988. The acoustics of the vocal tract in the horseshoe bat, *Rhinolophus hildebrandti*. *Journal of Acoustical Society of America*, 84:1201–1213.
- . 1990. Sonar pulse radiation and filtering in the mustached bat, *Pteronotus parnellii rubiginosus*. *Journal of Acoustical Society of America*, 87:2756–2772.
- HERRING, S. W. 1985. The ontogeny of mammalian mastication. *American Zoologist*, 25:339–349.
- HOYTE, D. A. N. 1987. Muscles and cranial form. Pp. 123–144, in *Mammalia depicta: morphogenesis of the mammalian skull* (H. Kuhn and U. Zeller, eds.). Verlag Paul Parey, Hamburg, Germany, 144 pp.
- JEPSSEN, G. 1966. Early Eocene bat from Wyoming. *Science*, 154:1333–1339.
- KLIMA, M. 1987. Morphogenesis of the nasal structures of the skull in toothed whales (Odontoceti). Pp. 105–121, in *Mammalia depicta: morphogenesis of the mammalian skull* (H. Kuhn and U. Zeller, eds.). Verlag Paul Parey, Hamburg, Germany, 144 pp.
- KOOPMAN, K. 1984. A synopsis of the families of bats—Part VII. *Bat Research News*, 25:25–27.
- LAKARS, T., AND S. HERRING. 1980. Ontogeny and oral function in hamsters (*Mesocricetus auratus*). *Journal of Morphology*, 165:237–254.
- MARCUS, L. 1990. Traditional morphometrics. Pp. 77–122, in *Proceedings of the Michigan morphometrics workshop* (F. Rohlf and F. Bookstein, eds.). Special Publication, University of Michigan Museum of Zoology, 2:1–380.
- MATSUMURA, S. 1979. Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): development of vocalization. *Journal of Mammalogy*, 60:76–84.
- MAYR, E. 1982. *The growth of biological thought*. The Belknap Press of Harvard University, Cambridge, Massachusetts, 974 pp.
- MITCHELL, S. D. 1992. On pluralism and competition in evolutionary explanations. *American Zoologist*, 32:135–144.
- MOHL, N. 1971. Craniofacial relationships and adaptations in bats. Ph.D. dissertation, State University of New York, Buffalo, 341 pp.
- MÜLLER, G. B. 1990. Developmental mechanisms: a

- side-effect hypothesis. Pp. 99–130, *in* Evolutionary innovations (M. H. Nitecki, ed.). The University of Chicago Press, Chicago, Illinois, 304 pp.
- MÜLLER, G., G. WAGNER, AND B. HALL. 1989. Experimental vertebrate morphology and the study of evolution: report of a workshop. *Trends in Vertebrate Morphology*, 35:299–303.
- NOVACEK, M. 1985. Evidence for echolocation in the oldest known bats. *Nature*, 315:140–141.
- PEDERSEN, S. 1993. Cephalometric correlates of echolocation in the Chiroptera. *Journal of Morphology*, 218:85–98.
- . 1995. Cephalometric correlates of echolocation in the Chiroptera: II. fetal development. *Journal of Morphology*, 225:107–123.
- PETTIGREW, J. 1988. Microbat vision and echolocation in an evolutionary context. Pp. 645–650, *in* Animal sonar—processes and performance (P. E. Nachtigall and P. W. B. Moore, eds.). Proceedings NATO Advanced study institute on animal sonar systems. Plenum Press, New York, 862 pp.
- . 1991. A fruitful, wrong hypothesis? Response to Baker, Novacek, and Simmons. *Systematic Zoology*, 40:231–239.
- PROFFIT, W. 1978. Equilibrium theory revisited: factors influencing position of the teeth. *Angle Orthodontist*, 48:175–186.
- PYE, J. 1988. Noseleaves and bat pulses. Pp. 791–796, *in* Animal sonar—processes and performance (P. E. Nachtigall and P. W. B. Moore, eds.). Proceedings NATO Advanced study institute on animal sonar systems. Plenum Press, New York, 862 pp.
- RAFF, R., B. PARR, A. PARKS, AND G. WRAY. 1990. Heterochrony and other mechanisms of radical evolutionary change in early development. Pp. 71–98, *in* Evolutionary innovations (M. H. Nitecki, ed.). The University of Chicago Press, Chicago, Illinois, 304 pp.
- RANFJORD, S., AND M. ASH. 1966. Occlusion. W. B. Saunders Company, Philadelphia, Pennsylvania, 396 pp.
- RICE, W. 1989. Analyzing tables of statistical significance. *Evolution*, 43:223–225.
- ROBERTS, L. 1972. Variable resonance in constant frequency bats. *Journal of Zoology (London)*, 166:337–348.
- . 1973. Cavity resonances in the production of orientation cries. *Periodicum Biologorum*, 75:27–32.
- SILVER, P. A. S. 1962. *In ovo* experiments concerning the eye, the orbit and certain juxta-orbital structures in the chick embryo. *Journal of Embryology and Experimental Morphology*, 10:423–450.
- SIMMONS, J. 1980. Phylogenetic adaptations and the evolution of echolocation in bats. Proceedings of the Fifth International Bat Research Conference, Texas Tech Press, 5:267–278.
- SIMMONS, J., AND R. STEIN. 1980. Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. *Journal of Comparative Physiology A. Sensory, Neural, and Behavioral Physiology*, 135:61–84.
- SIMPSON, G. G. 1961. Principles of animal taxonomy. Columbia University Press, New York, 247 pp.
- SMITH, J. 1972. Systematics of the chiropteran family Mormoopidae. Miscellaneous Publications, Museum of Natural History, University of Kansas, 56:1–132.
- . 1976. Chiropteran evolution. Special Publications, The Museum, Texas Tech University, 10:49–70.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry: the principles and practice of statistics in biological research. Second ed. W. H. Freeman and Company, New York, 859 pp.
- SOLOW, B., AND E. GREVE. 1979. Craniocervical angulation and nasal respiratory resistance. Pp. 87–119, *in* Naso-respiratory function and craniofacial growth. Craniofacial Growth Series, University of Michigan, Monograph 9:1–332.
- STARCK, D. 1952. Form und Formbildung der Schädelbasis bei Chiropteren. *Ergänzungsheft zum 99 Band; Ver. Anat. Ges., 50th Versammlung Marburg. Anatomischer Anzeiger*, 99:114–121.
- SUTHERS, R., D. HARTLEY, AND J. WENSTRUP. 1988. The acoustical role of tracheal chambers and nasal cavities in the production of sonar pulses by the horseshoe bat, *Rhinolophus hildebrandti*. *Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology*, 162:799–813.
- THOROGOOD, P. 1988. The developmental specification of the vertebrate skull. *Development (supplement)*, 103:141–153.
- VALDIVIESO, D., R. PETERSON, AND J. TAMSITT. 1979. Morphology of the basisphenoid pits and related structures of the bat *Otomops martiensseni* (Chiroptera: Molossidae). *Royal Ontario Museum, Life Sciences Contributions*, 119:1–19.
- VAN VALEN, L. 1979. The evolution of bats. *Evolutionary Theory*, 4:103–121.
- VAUGHAN, T. A. 1972. *Mammalogy*. Second ed. W. B. Saunders Company, Philadelphia, Pennsylvania, 522 pp.
- WILKINSON, L. 1990. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois, 724 pp.

Submitted 27 April 1996. Accepted 1 May 1997.

Associate Editor was James R. Purdue.

APPENDIX I.

Taxonomic list of specimens examined annotated with emission type: no ultrasonic echolocation (); oral emission of ultrasonic call (**); nasal emission of ultrasonic call (***). Taxonomy after Koopman (1984).*

Suborder Megachiroptera	<i>Centurio senex</i>
Family Pteropodidae*	<i>Stenoderma rufum</i>
<i>Cynopterus brachyotis</i>	<i>Sturnira lilium</i>
<i>Epomophorus wahlbergi</i>	<i>Lonchorhina a. aurita</i>
<i>Pteropus vampyrus</i>	<i>Macrotus waterhousii californicus</i>
<i>Rousettus amplexicaudatus</i>	<i>Mimon cozumelae</i>
<i>Rousettus celebensis</i>	<i>Phyllostomus discolor verrucosus</i>
	<i>Phyllostomus h. hastatus</i>
Suborder Microchiroptera	<i>Vampyrum spectrum</i>
Infraorder Yinochiroptera	<i>Brachyphylla c. cavernarum</i>
Superfamily Emballonuroidea	<i>Desmodus rotundus murinus</i>
Family Emballonuridae**	
<i>Diclidurus virgo</i>	Suborder Microchiroptera
<i>Peropteryx k. kappleri</i>	Infraorder Yangochiroptera
<i>Taphozous georgianus</i>	Superfamily Vespertilionoidea
Family Craseonycteridae**	Family Thyropteridae**
Family Rhinopomatidae**	Family Myzopodidae**
<i>Rhinopoma muscatellum</i>	Family Furipteridae**
Superfamily Rhinolophoidea	Family Natalidae**
Family Nycteridae***	<i>Natalus s. stramineus</i>
<i>Nycteris spp.</i>	Family Mystacinidae**
Family Megadermatidae***	Family Molossidae**
<i>Megaderma spasma</i>	<i>Eumops p. perotis</i>
Family Rhinolophidae***	<i>Eumops u. underwoodi</i>
<i>Hipposideros a. armiger</i>	<i>Molossus m. molossus</i>
<i>Hipposideros caffer</i>	<i>Otopomops martiensseni icatus</i>
<i>Hipposideros galeritus</i>	<i>Tadarida brasiliensis antillarum</i>
<i>Rhinolophus a. affinis</i>	<i>Tadarida brasiliensis mexicana</i>
<i>Rhinolophus e. euryale</i>	Family Vespertilionidae**
<i>Rhinolophus f. ferrumequinum</i>	<i>Antrozous pallidus bunkeri</i>
Suborder Microchiroptera	<i>Eptesicus diminutus fidelis</i>
Infraorder Yangochiroptera	<i>Eptesicus f. furinalis</i>
Superfamily Phyllostomoidea	<i>Eptesicus serotinus horikawai</i>
Family Mormoopidae**	<i>Lasionycteris noctivagans</i>
<i>Pteronotus parnelli mexicana</i>	<i>Lasiurus b. borealis</i>
Family Noctilionidae**	<i>Lasiurus cinereus</i>
<i>Noctilio l. leporinus</i>	<i>Myotis keeni septentrionalis</i>
Family Phyllostomidae***	<i>Myotis m. myotis</i>
<i>Anoura geoffroyi lasiopyga</i>	<i>Myotis velifer incautus</i>
<i>Glossophaga longirostris rostrata</i>	<i>Myotis vivesi</i>
<i>Leptonycteris yerbabueuae</i>	<i>Myotis volans interior</i>
<i>Monophyllus plethodon luciae</i>	<i>Nyctecius humeralis</i>
<i>Artibeus c. cinereus</i>	<i>Pipistrellus s. subflavus</i>
<i>Artibeus hirsutus</i>	<i>Scotophilus nigrata dinganii</i>
<i>Artibeus jamaicensis yucatanicus</i>	
<i>Artibeus lituratus palmarum</i>	
<i>Artibeus phaeotis nanus</i>	

APPENDIX II

Description of morphometric characters and indices used in study

Length of palate.—Distance along the intermaxillary suture from the posterior nasal spine to a line connecting the posterior-most margin of the incisive foramen. Because the posterior margin of the hard palate is the demarcation between the nasal cavity and the nasopharynx, this measurement also describes the length of the nasal cavity-palatal length.

Length of tooththrow.—Length of the upper tooththrow from the anterior-most surface of the upper canine to the posterior-most surface of the last cheek tooth along the mean alveolar line. The mean alveolar line is drawn between the anterior margin of the alveolus of the first cheek tooth (PM3) to the posterior margin of the alveolus of the last cheek tooth (M3) along the labial surface of the maxillary dental arcade. This line crosses the labial margin of the alveoli of each cheek tooth and is similar to that used by Freeman (1984).

Interorbital width.—Minimum width of the skull between orbits.

Bore of external nares.—Maximum internal diameter of the external nares-narial bore.

Greatest length of skull.—Greatest length of the skull excluding teeth.

Distance between pterygoid processes.—Maximum distance between the posterior extrema of the pterygoid processes. I estimated this distance if one of the fragile extrema was broken away-ptyergoid width.

Bore of choanae.—Maximum inner diameter of the paired choanae measured laterally between the perpendicular plates of the palatine bone-choanal bore.

Width of skull at zygoma.—Maximum width of skull across the zygoma-zygomatic width.

Length of pharynx.—Distance between the center of the sphenoccipital synchondrosis to the posterior nasal spine-pharyngeal length. Transillumination of a skull was often necessary to locate these landmarks.

Length of basioccipital.—Length of the basioccipital bone along its median axis-basioccipital length. Transillumination of a skull is often necessary to locate the anterior landmark, the sphenoccipital synchondrosis.

Distance between otic capsules.—Minimum

distance between the auditory bullae viewed ventrally capsule separation.

Distance between temporomandibular joints (TMJ).—Distance between the centers of the condylar fossae. Because the shape of the temporal fossa varies considerable among genera, the center of the fossa was estimated in every case. However, this point coincides with the deepest portion of the fossa in most cases.

Depth of midface.—Distance from the center of the condylar fossa to nasion-midfacial depth.

Head size.—Estimated by taking the cube root of the product of the length, width and depth of the skull, i.e., zygomatic width, greatest length of skull, and midfacial depth.

Cranial Indices

Ratio of the width between the pterygoid processes to the distance between the otic capsules.—Approximates the relationship between the diameter of the nasopharynx and the diameter of the trachea. The distance between the otic capsules is determined by the tracheal diameter in many mammals-ptyergoid width : otic capsule separation.

Ratio of the width between the pterygoid processes to the width across the condylar fossae.—Relates the width of the nasopharynx to the width of the jaw-ptyergoid width : bi-TMJ width.

Ratio of the width between the pterygoid processes to the diameter of the choanae.—Approximates the relationship between the diameter of the nasopharynx and the diameter of the nasal cavity-ptyergoid width : choanal bore.

Ratio of the width between the pterygoid processes to the length of the pharynx.—Approximates the width and length of the entire oronasopharyngeal space-ptyergoid width : pharyngeal length.

Ratio of the choanal diameter to the distance between the otic capsules.—Approximates the relationship between the diameter of the nasal cavity and the diameter of the trachea-choanal bore : otic capsule separation.

Ratio of the choanal diameter to the length of the pharynx.—Approximates the width and length of the entire oro-nasopharyngeal space-choanal bore : pharyngeal length.

Ratio of the choanal diameter to the diameter of the external nares.—Relates two measurements of the diameter of the nasal cavity, i.e., narial and choanal diameters-choanal bore : narial bore.

Ratio of the choanal diameter to the interorbital width.—Relates the two major volumetric components of the midface, the width of the nasal cavity and the width of the skull between the orbits. This index reflects the relative packaging of the midface-choanal bore: interorbital width.

Ratio of the length of the hard palate to the choanal diameter.—Relates the length and width of the nasal cavity with each other-palatal length: choanal bore.

Ratio of the length of the hard palate to the length of the pharynx.—Describes the propor-

tion between the length of the nasal cavity and the rest of the pharynx-palatal length: pharyngeal length.

Ratio of the length of the hard palate to the length of the maxillary tooththrow.—Describes the degree of emargination of the hard palate-palatal length: tooththrow length.

Ratio of the length of the basioccipital to the greatest length of the skull.—Describes the relative contribution of the basioccipital to the overall length of the skull-Basioccipital length: greatest skull length.