

## Cephalometric Correlates of Echolocation in the Chiroptera: II. Fetal Development

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**ABSTRACT** Cephalometry was used to detect patterns of cranial growth in fetal bats that were stained differentially for bone and cartilage. Three developmental features distinguish embryos of taxa that echolocate nasally from embryos of taxa that echolocate orally: 1) the basicranium is retained ventral to the cervical axis, 2) the rostrum is retained below the basicranial axis, and 3) the lateral semicircular canals are rotated caudally. Together, the first two actions align the fetal nasal cavity with what will be the long axis of the adult body in flight. The third action aligns the lateral semicircular canals with the horizontal. In contrast, skulls of oral-emitting taxa are constructed such that the oral cavity is aligned with the long axis of the body in flight. The evolution of head posture and skull form in microchiropteran bats has been constrained by the demands of vocalization, i.e., ultrasonic echolocation. Accordingly, the ontogeny of the microchiropteran skull has been canalized along two distinct developmental paths—oral-emitting and nasal-emitting *Baupläne*. © 1995 Wiley-Liss, Inc.

The fundamental construct of the vertebrate head is strongly influenced by the growth of the brain and the underlying pharynx early in development. Differential growth of these structures determines the shape of the chondrocranium and eventually distorts the overlying membranous bones that compose the desmo- and viscerocrania (Hanken and Thorogood, '93; Klima, '87; Ranly, '80; Sperber, '89). Within the confines of the fetal head, further volumetric changes among the brain, brainstem, eyes, pharynx, tongue, and musculature affect subsequent bone growth via forces transmitted through the dura and periosteum to developing suture systems and synchondroses (Blechs Schmidt, '76a,b). The ensuing spatial competition among the various components effects further changes in the overall conformation of the skull (Haines, '40; Hanken, '83, '84; Solow and Greve, '79). As these components compete for space, orientation, and position throughout development, they 1) effect changes to the three-dimensional construct of the developing head (Bosma, '76; Haines, '40; Hanken, '83; Silver, '62); 2) affect the early migration of neural crest cells and development of neural crest-derived structures (Couly et al., '93; Noden, '80, '86; Stein, '80; Thorogood, '88);

and 3) may effect spatial or mechanical constraints within the growing skull (Hanken, '83; Herring and Lakars, '81; Herring, '85)—skull growth is the effect, not the cause, of cephalic growth (Moss, '60, '75, '76).

Within this dynamic environment, spatial constraints are accommodated by the inherent morphogenetic plasticity of the affected compartments (Alberch, '82). This plasticity is the result of self-regulating growth rates, and/or the gross translation or distortion of these compartments driven by morphogenetic events in adjacent structures, i.e., pharynx, braincase, and otic and optic capsules (Moss, '76; Müller, '90; Raff et al., '90). Subsequent ossification reduces this plasticity; ossification of the cranial base early in development effects a range of morphogenetic changes to the midface (rodents: Moss, '76; bats: Sperry, '72; cattle: Julian et al., '57; humans: Moore, '83; Sperber, '89; Thilander and Ingervall, '73). In summary, cranial growth and form are for the most part "soft tissue" phenomena that are affected only secondarily by osteological development

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(Bosma, '76; Haines, '40; Hanken, '83, '84; Moss, '72b; Silver, '62; Starck, '89).

Early in development, the mammalian head is tucked firmly against the thorax. From there the braincase rotates dorsad about the cervical axis while the rostrum rotates dorsad about the skull base into alignment with the basicranial axis (Schachner, '89). Microchiroptera that emit echolocation calls (biological sonar) through the mouth exhibit this basic, orthogonal skull plan (*Bauplan*) and are generally considered phylogenetically primitive (Vaughan, '72; Van Valen, '79: Emballonuridae, Craseonycteridae, Rhinopomatidae, Thyropteridae, Myzopodidae, Furipteridae, Natalidae, Mystacinidae, Molossidae, Vespertilionidae, but also Mormoopidae and Noctilionidae).

Despite tremendous differences in the external morphology of their skulls, Old World rhinolophoid and New World phyllostomid bats emit their echolocative calls through the nostrils. Accordingly, these phylogenetically distant groups share a cranial infrastructure in which the rostrum is located ventral to the basicranial axis where the nasal cavities, rather than the oral cavity, are aligned with the direction of flight (Freeman, '84; Mohl, '71; Pedersen, '93a; Starck, '52)—the nasal-emitting *Bauplan*.

Here, I evaluate previous taxonomic generalizations concerning the form of the adult skull (Pedersen, '93a) from a developmental perspective. Using chiropteran fetal material, I documented ontogenetic changes in the angular relationships among various anatomical planes that partition the skull into functionally distinct compartments. These angular relations reflect the differential growth and volumetric expansion of adjacent compartments or functional spaces.

The objectives of this study are threefold: 1) to verify that the dichotomy between oral- and nasal-emitting crania is a developmental

rather than a post-partum phenomenon; 2) to contrast the developmental patterns of a frugivorous New World nasal emitter and frugivorous non-echolocating megachiropteran to evaluate interactions of diet and vocalization with the form of the skull; and 3) to examine the developmental basis for the hypothesized phylogenetic convergence in form by the New World and Old World nasal-emitting Microchiroptera (Pedersen, '93a).

## MATERIALS AND METHODS

### *Specimens*

Longitudinal studies of pre-partum cranial development are not practical in mammals, particularly in small-bodied taxa such as bats. A primary assumption of this cross-sectional study is that I can construct a representative ontogenetic sequence for each species utilizing a series of closely related embryos of different ages (Table 1). "Complete" developmental series of bats are available, but I chose to analyze smaller series of bats collected at single localities to limit the potentially confounding effects of geographic variation on developmental variation.

To stage the fetal material and to ameliorate the differences in head sizes and shapes among taxa, I constructed an index (STAGE) to describe the extent to which a fetal skull has reached its full size. STAGE estimates the contribution of the fetal braincase to the entire fetal skull corrected to a percentage of the same proportion in an adult skull:

$$\text{STAGE} = \left[ \frac{(\text{square root of embryo brain case length} * \text{width})}{(\text{square root of embryo skull length} * \text{width})} \right] \text{divided by} \left[ \frac{(\text{square root of adult brain case length} * \text{width})}{(\text{square root of adult skull length} * \text{width})} \right] * 100.$$

TABLE 1. Chiropteran embryonic series were collected from the zoological collections at the University of Nebraska State Museum, American Museum of Natural History, and from the University of Kansas Natural History Museum

Emission type	Species	Embryos	Adults	Source
Oral emitters	<i>Eptesicus fuscus</i>	25	1	UNSM
	<i>Lasiurus borealis</i>	7	1	KU
	<i>Pteronotus parnellii</i>	23	1	KU
	<i>Taphozous georgianus</i>	11	1	AMNH
Old World nasal emitters	<i>Hipposideros armiger</i>	7	1	AMNH
	<i>Hipposideros galeritus</i>	21	1	AMNH
	<i>Rhinolophus affinis</i>	13	1	AMNH
New World nasal emitter	<i>Artibeus jamaicensis</i>	22	1	UNSM
Nonemitter	<i>Rousettus celebensis</i>	8	1	AMNH

*Cephalometry*

Camera lucida tracings were made of each fetal skull (left/lateral). When skulls became too heavily ossified to view intracranial features, they were radiographed at the University of Nebraska School of Dentistry using peri-apical X-ray film (Kodak #DF-58, shot at 80 KV, 10 mA). These larger, whole-mount embryos and representative adult skulls were held securely in a jig that positioned each 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 in which the right and left sides of the skull were perfectly registered were analyzed.

I identified six cephalometric "planes" on camera lucida tracings or lateral radiographs of each fetus (Fig. 1): 1) The plane described by the foramen magnum forms an important boundary between the occiput and the cervical axis (Baer and Nanda, '76; Schon, '76). This plane influences head posture and reflects the degree of flexibility in the cranio-cervical articulation (Fenton and Crerar, '84). 2) The basicranium lies between the brain and pharynx and extends from anterior lip of the foramen magnum to the anteroventral lip of the basioccipital synchondrosis (Radinsky, '84, '85). Its position reflects the differential growth between the brain and pharynx and influences position of the craniofacial complex (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 skull

(Ranly, '80). Its orientation is strongly influenced by the volumetric increase of the brain case during brain growth (Moss, '76; Young, '59). The orientation of 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 most dorsal and ventral extrema of the cribriform plate define the dimensions of this plane and are easily identified in all taxa. 4) Cephalometric studies of the semicircular canals of the inner ear are conspicuously absent from the more recent clinical and developmental literature despite the physiological connection between the lateral semicircular canals and head posture (Delattre and Fennart, '60; deBeer, '37). Because bats fly in the dark, the physiology of the inner ear is of critical importance. 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 a plane containing both lateral semicircular canals the tubular cross-sections of which are easily identified in all individuals. 5) The phonal axis of the head is aligned with the long axis of either the oral cavity or the nasal cavity. Because the hard palate separates these subdivisions of the pharynx, it is an important landmark. It is defined as a line drawn between the incisive foramen and the posterior palatine process.

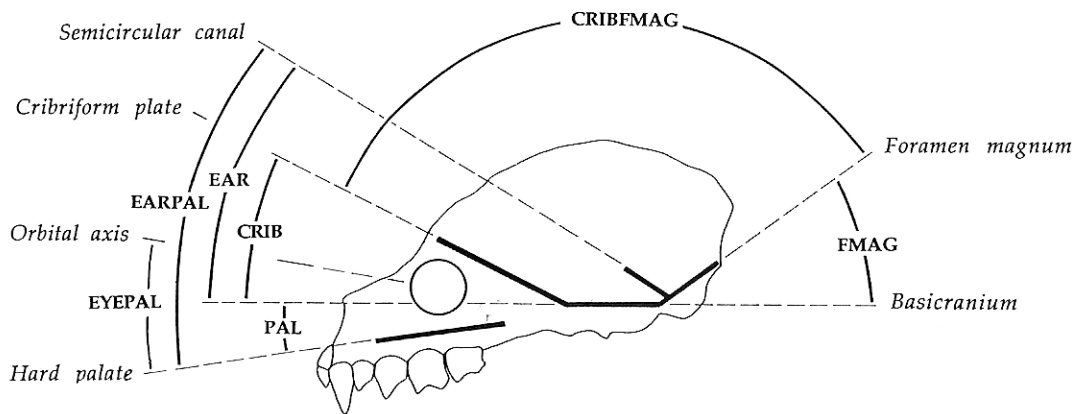


Fig. 1. Cephalometric angles used in study are shown superimposed on a tracing of an *Artibeus jamaicensis* skull. See text for description of each cephalometric angle and anatomical plane (after Pedersen, '93a).



6) The orbital axis of the eye is determined in lateral view by drawing a line from the center of the optic disk to the pupillary center (fetal material only).

I measured seven cephalometric angles (Fig. 1) to describe the relationships 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 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; 4) the angle between the orbital axis and the plane of the basicranium—EYE; 5) the angle between the plane of the foramen magnum and the plane of the basicranium—FMAG; 6) the angle between the cribriform plate and the foramen magnum—CRIBFMAG; 7) the angle between the lateral semicircular canals and the hard palate—EARPAL; and 8) the angle between the plane of the hard palate and the plane of the orbital axis—EYEPAL (Fig. 1). EYE and EYEPAL could be measured in fetal material only.

#### *Skeletal development*

I observed skeletal development in whole embryos by clearing tissues by maceration and staining differentially for bone and cartilage (Hanken and Wassersug, '81; Klymkowsky and Hanken, '91). This technique has been used to study skeletal development in many vertebrate species (Adams, '92; Condie and Capecchi, '93; Fritz, '75; Kaur et al., '92; Pedersen, '91, '93a; Reilly, '86; Trueb, '85; Wake and Hanken, '82; Wake et al., '83). Ossification sequences presented in this study are relative rather than absolute owing to the nature of the technique (Hanken and Hall, '88). In order to evaluate osteological development, I constructed an index to describe the proportion of cranial ossification foci present in each fetus relative to the number of foci (bones) expected in the adult skull.

$$\text{OSSSTAGE} = (\text{Fetal foci count} / \text{Adult foci count}) * 100$$

Bone foci include the dentary, maxilla, premaxilla, squamosal, parietal, frontal, nasal, jugal, palatine, pterygoid, basioccipital, prearticular, stylohyal, tympanic, basisphenoid, interparietal, vomer, supraoccipital, exoccipital, alisphenoid, prootic, orbitosphenoid, malleus, opisthotic, epiotic, lacrimal, incus, and stapes (Fig. 2). Because the jugal is absent in *Artibeus* and the lacrimal is absent in the three Old World nasal emitters, I

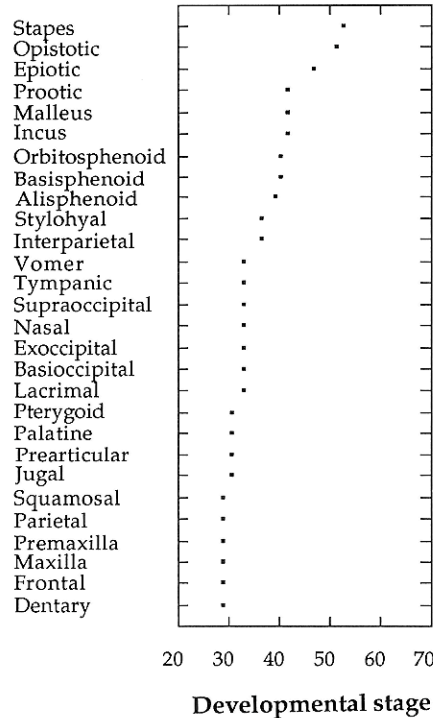


Fig. 2. Plot indicating first appearance of an ossification center of each bone vs. developmental stage (STAGE). All ossification foci (combined taxa) are present in the fetal skull by the time it has achieved two-thirds of its expected adult size.

recalculated OSSSTAGE as a percent of 27 rather than 28 bone foci in these four taxa.

#### *Statistical analysis*

I used univariate and regression analyses to describe underlying patterns of cephalometric variation among taxa (Systat: Wilkinson, '89; Statview; Feldman et al., '88). I ran one-way analyses of variance (ANOVA) to test the differences among taxa with respect to three cephalometric angles that are of particular interest (EARPAL, EYEPAL, CRIBFMAG; Pedersen, '93a). Specific comparisons among group means (Table 2) were accomplished by the Tukey HSD method using Tukey-Kramer harmonic mean adjustments to accommodate the unequal cell sizes (Table 3). I regressed each of the eight cephalometric angles against developmental stage (STAGE). These linear regression lines represent a growth trajectory for each angle. The "multiple R" values listed in Table 4 are Pearson correlation coefficients for each angle



TABLE 2. Developmental data

Taxon	Angle	Mean	Minimum	Maximum
<i>Rousettus celebensis</i> (n = 10)	EARPAL	55.7	39.0	66.0
	EYEPAL	30.2	16.0	44.0
	CRIBFMAG	118.8	93.0	131.0
<i>Eptesicus fuscus</i> (n = 21)	EARPAL	35.2	10.0	53.0
	EYEPAL	9.7	-3.0	24.0
	CRIBFMAG	105.3	66.0	129.0
<i>Lasiurus borealis</i> (n = 11)	EARPAL	19.4	1.0	35.0
	EYEPAL	6.3	0.0	17.0
	CRIBFMAG	84.4	44.0	113.0
<i>Pteronotus parnelli</i> (n = 9)	EARPAL	30.8	15.0	40.0
	EYEPAL	13.1	-7.0	30.0
	CRIBFMAG	103.0	87.0	115.0
<i>Taphozous georgianus</i> (n = 10)	EARPAL	30.7	11.0	42.0
	EYEPAL	18.8	15.0	23.0
	CRIBFMAG	101.5	86.0	115.0
<i>Hipposideros armiger</i> (n = 9)	EARPAL	78.7	66.0	90.0
	EYEPAL	36.0	18.0	57.0
	CRIBFMAG	104.6	84.0	118.0
<i>Hipposideros galeritus</i> (n = 17)	EARPAL	72.2	53.0	81.0
	EYEPAL	38.7	29.0	53.0
	CRIBFMAG	118.2	110.0	125.0
<i>Rhinolophus affinus</i> (n = 15)	EARPAL	78.3	52.0	92.0
	EYEPAL	56.0	43.0	73.0
	CRIBFMAG	110.4	79.0	129.0
<i>Artibeus jamaicensis</i> (n = 19)	EARPAL	53.3	31.0	74.0
	EYEPAL	24.2	11.0	43.0
	CRIBFMAG	114.3	104.0	138.0

with STAGE (Bonferroni adjusted  $P = .0055$ ; Rice, '89). Given the serendipitous nature of embryo availability (hence non-normal distributions), all statistical analyses are to be interpreted as "suggestive" rather than predictive.

RESULTS  
Cephalometry

Ear-palate angles remain constant throughout development in the three Old World nasal emitters. This is evidenced by the insignificant correlations between ear-palate angle and STAGE, and the shallow positive slopes of all Old World nasal emitters. Conversely, the ear-palate angle decreases dramatically throughout development in the four oral emitters. The New World nasal emitter and the nonemitter (*Artibeus* and *Rousettus*, respectively) exhibit intermediate states (Tables 2, 4; Fig. 3). All trajectories diverge from a common ear-palate angle of 80°.

Growth trajectories of the cribriform plate-foramen magnum angle diverge from a common angle of 120°. Trajectories of the four oral emitters (*Eptesicus*, *Lasiurus*, *Pteronotus*, *Taphozous*) exhibit a greater change over time than do the trajectories of the New World nasal emitter (*Artibeus*) and the non-emitter (*Rousettus*, Tables 2, 4; Fig. 4).

Throughout development, growth trajectories of the eye-palate angle are poorly correlated with STAGE in all taxa except *Hipposideros armiger* (Table 4; Fig. 5). The orbital axis (EYE) rotates dorsally in all taxa and correlates best with the palatal angle in the four oral emitters (average multiple  $R = 0.771$ ) and correlates best with the lateral semicircular canals in the four nasal emitters (average multiple  $R = 0.536$ ).

I previously established a bivariate morphospace using the ear-palate and cribriform plate-foramen magnum angles for adults (Pedersen, '93a), and the same presently for fetal material (Fig. 6). The similarity between these cephalometric morphospaces is striking as the center of the nasal-emitting peaks in each morphospace lies at approximately 80° by 120°, EARPAL × CRIBFMAG, respectively.

Ossification

The general sequence of cranial ossification exhibited by the nine taxa investigated follow the common mammalian pattern (de Beer, '37). In each of the nine taxa (Table 1), every bony element appeared before the skull reached 66% of its expected adult size (Fig. 2). The auditory bullae and the ossicular chain are almost always the last series of bones to appear, and basicranial elements

TABLE 3. Tukey HSD comparisons

	Oral				Nasal				None
	EF	LB	PP	TG	HA	HG	RA	AJ	RC
EARPAL									
Oral									
<i>E. fuscus</i>									
<i>L. borealis</i>	*								
<i>P. parnelli</i>									
<i>T. georgianus</i>									
Nasal									
<i>H. armiger</i>	*	*	*	*					
<i>H. galeritus</i>	*	*	*	*					
<i>R. affinus</i>	*	*	*	*					
<i>A. jamaicensis</i>	*	*	*	*	*	*	*		
None									
<i>R. celebensis</i>	*	*	*	*	*	*	*		
EYEPAL									
Oral									
<i>E. fuscus</i>									
<i>L. borealis</i>									
<i>P. parnelli</i>									
<i>T. georgianus</i>									
Nasal									
<i>H. armiger</i>	*	*	*	*					
<i>H. galeritus</i>	*	*	*	*					
<i>R. affinus</i>	*	*	*	*	*	*			
<i>A. jamaicensis</i>	*	*				*	*		
None									
<i>R. celebensis</i>	*	*	*				*		
CRIBFMAG									
Oral									
<i>E. fuscus</i>									
<i>L. borealis</i>	*								
<i>P. parnelli</i>									
<i>T. georgianus</i>									
Nasal									
<i>H. armiger</i>		*							
<i>H. galeritus</i>		*							
<i>R. affinus</i>		*							
<i>A. jamaicensis</i>		*							
None									
<i>R. celebensis</i>		*							

\*Group means are significantly different,  $P = .05$ .

ossify in the correct posterior–anterior sequence typical of mammals (de Beer, '37). Lacrimal bones are absent in the three Old World nasal-emitting bats in my sample (*Hipposideros galeritus*, *Hipposideros armiger*, *Rhinolophus affinus*). Stylohyal elements of Old World nasal emitters ossify after the pterygoid processes, the reverse of which occurs in the other 6 taxa.

Oral-emitting and nasal-emitting forms are indistinguishable early in development before the skull has begun to ossify. As development continues, taxon-specific skull morphology becomes increasingly more apparent but always within the framework of either the nasal-emitting or oral-emitting Bauplan. The cartoon of *Eptesicus* (oral emitter) and *Artibeus* (New World nasal emitter) developmental series clearly depicts this dichotomy (Fig.

8). Fetal skulls acquire the appropriate phonal axis (ear–palate angle) before the skull has reached 60% of its adult size and before the fusion of any of the primary suture systems (Fig. 7). The fetal skull is about 80% of the expected adult size when parturition occurs.

#### DISCUSSION

##### *Brain and pharynx*

Oral-emitting and nasal-emitting skull forms are indistinguishable early in development but become apparent before the approximation of the primary suture systems and well before the forces of mastication begin to effect skull morphogenesis (Herring and Lakars, '81). Simply stated, the dichotomy between oral-emitting and nasal-emitting *Baupläne* is based upon the relative position

of the microchiropteran hard palate. Its position reflects the construction of the skull around either the oral or nasal cavity and the use of the facial skeleton as an acoustical horn. As a corollary, intermediate positions of the hard palate are poorly suited biomechanically for echolocation, as the call would be directed either above or below the mean flight path.

Clearly, adult phonation (echolocation) has been under strong selective pressures throughout microchiropteran evolution, but the underlying morphogenetic dynamics that led to the divergence between oral- and nasal-emitting *Baupläne* are unclear. Certainly, anatomical planes such as the cribriform plate are responsive to the differential expansion and distortion of adjacent structures such as the brain and pharynx (Baer and Nanda, '76; Blechschmidt, '76a,b; Enlow, '76; Moss, '76; Schon, '76; Schachner, '89). However, microchiropteran brain size is only poorly correlated with the cephalometry of the cranial base in adults (Pedersen, '93a). Rather, brain size is associated with the occupation of a specific aerial niche regardless of taxonomy. Generally, aerial insectivores and foliage gleaners are found in open habitats or along forest boundaries and possess relatively small brains. Frugivorous and carnivorous taxa have relatively larger brains and forage in more complex, cluttered habitats (Eisenberg and Wilson, '78; Jolicoeur et al., '84; Stephan et al., '81). Perhaps, the form of the cranial base is influenced by the gross morphology of the brain rather than its size.

The divergence between oral- and nasal-emitting forms of the skull has primarily affected those components immediately adjacent to the vocal tract. Therefore, nasal emission is most likely an exaptation (Gould and Vrba, '82) of selective forces acting upon the form and function of the pharynx and larynx during echolocation rather than the result of focused selection on cranial form or head posture per se.

Such shifts in the morphology of the pharynx and surrounding structures must be integrated functionally with the rest of the head (Moss, '60, '62, '72a, '75, '76). For example, the maintenance of the airway is of utmost importance and is affected by head posture, which in turn influences the relative position and orientation of the tongue, stylohyoid chain, and their attendant musculature (Behlfelt et al., '90; Bjork and Skieller, '72; Gaskell, '74; Herring, '85; Solow and Greve,

'79; Tallgren and Solow, '87). Further, Old World nasal emitters exhibit a unique coupling of the glottis and soft palate that is remarkable in the completeness of its seal (Hartley and Suthers, '88; Matsumura, '79). This coupling affects the ossification of the stylohyoid chain in Old World nasal emitters, i.e., the ossification of all chain elements are delayed until *after* the pterygoid processes are ossified. This pharyngeal coupling is not found in New World nasal-emitting bats that consequently exhibit the more generic sequence in which the chain is ossified before the pterygoid processes (de Beer, '37). These dynamics clearly deserve further investigation.

Unlike microchiropterans which utilize ultrasonic echolocation as a means to locate prey items, the form of the non-echolocating megachiropteran skull is not restricted by the demands of phonation. Without constraints on the relative position of the hard palate, the megachiropteran skull appears most frequently as a morphological intermediate between the extreme oral-emitting forms and nasal-emitting forms from the Old World (Pedersen, '93a). I have argued that the demands of nasal emission have exacted a strong influence (constraint) on the evolution and conformation of rostra of nasal-emitting bats from the New World. However, the similarity between the Megachiroptera and the New World nasal emitters (Miller, '07) strongly suggests that echolocation is only one of many possible factors that influence the form of the skull. Such intermediate shapes of the skull are found in taxa that emphasize visual and olfactory cues in contrast to the more extreme skull forms found in taxa that rely on acoustical orientation.

#### *Nasal cavity and Orbit*

The nasal cavities of Old World nasal emitters (Rhinolophoidea) are radically modified into "resonators" (Hartley and Suthers, '88; Roberts, '72, '73; Suthers et al., '88) which amplify the echolocative call (Roberts, '72, '73; Hartley and Suthers, '88; Suthers et al., '88). These chambers are absent in the skulls of New World nasal emitters, whose rostra exhibit large olfactory fossae and extensive turbinate development instead. Without resonating chambers, the power output during echolocation is so reduced that Griffin ('58) labeled the New World nasal emitters "whispering bats." Given the spatial restrictions of the midface, it seems unlikely that the skull of a nasal emitter could exhibit both



TABLE 4. Regression analysis<sup>1</sup>

	Mean	Standard deviation	Regression coefficient	Intercept	T value	P value	Multiple R	Bonferroni P value
Eye								
<i>R. celebensis</i>	21.33	5.83	0.167	13.824	2.151	.068	0.420	.2610
<i>E. fuscus</i>	15.85	11.37	-0.421	36.460	6.588	.000*	0.683	.0009**
<i>L. borealis</i>	8.30	13.03	-0.610	54.485	5.313	.000*	0.853	.0017**
<i>P. parnelli</i>	14.56	12.91	-0.507	50.334	2.254	.040*	0.397	.1280
<i>T. georgianus</i>	11.00	4.00	-0.062	15.095	1.647	.160	0.199	.6686
<i>H. armiger</i>	12.57	7.21	-0.232	24.435	2.167	.082	0.438	.3261
<i>H. galeritus</i>	10.92	11.28	0.106	4.313	0.309	.762	0.145	.6354
<i>R. affinus</i>	-4.38	8.31	-0.086	1.423	0.181	.858	0.228	.4530
<i>A. jamaicensis</i>	13.18	14.28	-0.463	40.105	4.764	.000*	0.690	.0044**
Ear								
<i>R. celebensis</i>	4.00	4.12	-0.096	8.333	1.772	.119	0.342	.3671
<i>E. fuscus</i>	10.90	7.97	0.155	3.280	0.661	.516	0.360	.1187
<i>L. borealis</i>	6.70	6.12	0.059	2.192	0.241	.815	0.177	.6245
<i>P. parnelli</i>	12.06	7.31	-0.492	47.268	3.982	.001*	0.638	.0104
<i>T. georgianus</i>	6.50	3.77	0.166	-4.971	-0.976	.366	0.685	.0609
<i>H. armiger</i>	32.00	10.29	-0.244	44.454	2.832	.036	0.345	.4492
<i>H. galeritus</i>	23.46	10.66	0.195	11.381	0.890	.392	0.281	.3518
<i>R. affinus</i>	29.58	7.31	0.021	28.072	3.628	.004*	0.064	.8425
<i>A. jamaicensis</i>	17.06	9.74	0.245	2.999	0.452	.658	0.539	.0379
PAL								
<i>R. celebensis</i>	51.00	6.98	-0.063	53.863	6.413	.000*	0.134	.7318
<i>E. fuscus</i>	25.55	13.73	-0.600	54.932	0.001	.000*	0.807	.0000**
<i>L. borealis</i>	14.60	10.02	-0.451	48.796	5.666	.000*	0.821	.0035**
<i>P. parnelli</i>	32.31	9.65	-0.617	75.802	5.452	.000*	0.645	.0069
<i>T. georgianus</i>	26.12	11.26	-0.406	54.192	3.143	.019*	0.562	.1471
<i>H. armiger</i>	48.57	14.30	0.689	13.453	0.810	.454	0.699	.0804
<i>H. galeritus</i>	49.69	10.90	-0.062	53.554	3.950	.002*	0.088	.7750
<i>R. affinus</i>	51.61	7.17	0.094	45.253	6.818	.000*	0.290	.3366
<i>A. jamaicensis</i>	37.56	16.16	-0.593	71.887	8.790	.000*	0.782	.0005**
CRIB								
<i>R. celebensis</i>	-10.22	5.93	-0.117	-4.926	-0.715	.497	0.291	.4477
<i>E. fuscus</i>	6.95	16.68	-0.676	-26.124	-3.541	.002*	0.748	.0001**
<i>L. borealis</i>	17.30	14.22	0.651	-31.963	-2.700	.027*	0.834	.0027**
<i>P. parnelli</i>	5.50	9.70	0.555	-33.624	-2.251	.040*	0.577	.0192
<i>T. georgianus</i>	3.50	13.11	0.439	-26.832	-1.296	.242	0.522	.1846
<i>H. armiger</i>	4.57	7.20	-0.026	5.904	0.505	.634	0.053	.9107
<i>H. galeritus</i>	-5.84	10.38	0.388	-29.860	-2.815	.016	0.574	.0400
<i>R. affinus</i>	7.92	12.20	0.457	-22.842	-3.409	.005*	0.823	.0005**
<i>A. jamaicensis</i>	0.62	13.53	0.465	-25.603	-3.789	.002*	0.766	.0008
FMAG								
<i>R. celebensis</i>	67.66	4.92	-0.071	70.886	0.001	.000*	0.213	.5822
<i>E. fuscus</i>	65.85	4.82	-0.077	69.628	0.002	.000*	0.295	.2062
<i>L. borealis</i>	74.20	6.69	0.160	62.056	6.838	.000*	0.437	.2070
<i>P. parnelli</i>	65.56	8.61	-0.199	79.626	5.045	.000*	0.234	.3834
<i>T. georgianus</i>	73.00	7.32	-0.307	94.240	9.190	.000*	0.654	.0786
<i>H. armiger</i>	67.85	6.84	0.286	53.242	6.037	.001*	0.608	.1471
<i>H. galeritus</i>	67.23	7.99	-0.380	90.737	0.001	.000*	0.731	.0045**
<i>R. affinus</i>	59.23	7.51	-0.188	71.916	0.001	.000*	0.551	.0507
<i>A. jamaicensis</i>	63.87	11.91	-0.265	79.694	9.352	.000*	0.474	.0741
EARPAL								
<i>R. celebensis</i>	55.00	10.38	-0.160	32.196	5.067	.001*	0.226	.5590
<i>E. fuscus</i>	36.45	9.91	-0.444	58.212	0.001	.000*	0.828	.0000**
<i>L. borealis</i>	21.30	8.13	-0.392	50.988	8.702	.000*	0.878	.0008**
<i>P. parnelli</i>	43.13	12.42	-0.990	113.931	6.640	.000*	0.756	.0011**
<i>T. georgianus</i>	32.62	9.56	-0.240	49.221	3.025	.023*	0.392	.3373
<i>H. armiger</i>	80.57	6.58	0.445	57.908	0.001	.000*	0.942	.0015**
<i>H. galeritus</i>	73.15	7.49	0.133	64.936	7.216	.000*	0.272	.3679
<i>R. affinus</i>	80.58	7.06	0.167	68.967	0.001	.000*	0.512	.0887
<i>A. jamaicensis</i>	54.62	11.39	-0.347	74.886	0.001	.000*	0.646	.0092
EYEPAL								
<i>R. celebensis</i>	29.66	9.19	-0.231	40.039	3.858	.006*	0.368	.3304
<i>E. fuscus</i>	9.70	7.56	-0.179	18.471	4.080	.000*	0.438	.0536
<i>L. borealis</i>	6.30	5.14	0.158	-5.689	-0.887	.400	0.561	.0913
<i>P. parnelli</i>	17.75	10.80	-0.109	25.467	1.258	.228	0.102	.7061
<i>T. georgianus</i>	18.85	2.96	0.127	10.546	1.812	.129	0.544	.2063
<i>H. armiger</i>	36.00	14.28	0.922	-10.981	-1.353	.233	0.937	.0018**

TABLE 4. (continued)

	Mean	Standard deviation	Regression coefficient	Intercept	T value	P value	Multiple R	Bonferroni P value
<i>H. galeritus</i>	38.76	8.03	-0.169	49.241	5.191	.000*	0.324	.2804
<i>R. affinus</i>	56.00	9.61	0.181	43.830	5.178	.000*	0.414	.1601
<i>A. jamaicensis</i>	24.37	8.62	-0.129	31.781	4.782	.000*	0.319	.2466
CRIBFMAG								
<i>R. celebensis</i>	122.55	8.03	0.189	114.039	0.001	.000*	0.345	.3627
<i>E. fuscus</i>	107.20	17.07	-0.599	136.496	0.001	.000*	0.647	.0020**
<i>L. borealis</i>	88.50	17.92	-0.811	149.907	9.817	.000*	0.825	.0033**
<i>P. parnelli</i>	108.93	7.85	-0.355	133.997	0.001	.000*	0.457	.0750
<i>T. georgianus</i>	103.50	9.31	-0.131	112.591	6.696	.000*	0.220	.6004
<i>H. armiger</i>	107.57	8.40	-0.260	120.853	9.917	.000*	0.450	.3108
<i>H. galeritus</i>	118.61	4.85	-0.008	119.123	0.002	.000*	0.026	.9329
<i>R. affinus</i>	112.84	7.66	-0.269	130.926	0.002	.000*	0.770	.0020**
<i>A. jamaicensis</i>	115.50	10.93	-0.199	125.909	0.001	.000*	0.440	.1007
EYE vs. PAL								
<i>R. celebensis</i>	21.33	5.83	-0.017	22.248	1.371	.212	0.021	.9562
<i>E. fuscus</i>	15.85	11.37	0.691	-1.819	-0.587	.564	0.835	.0000**
<i>L. borealis</i>	8.30	13.03	1.124	-9.428	-3.282	.011*	0.934	.0000**
<i>P. parnelli</i>	14.56	12.91	0.768	-10.263	-1.043	.314	0.575	.0199
<i>T. georgianus</i>	11.00	4.00	0.698	-9.845	-1.163	.296	0.743	.0554
<i>H. armiger</i>	12.57	7.21	0.147	5.421	0.463	.662	0.273	.5540
<i>H. galeritus</i>	10.92	11.28	0.764	-27.064	-2.532	.027*	0.738	.0039**
<i>R. affinus</i>	-4.38	8.31	0.272	-18.443	-1.042	.139	0.235	.4396
<i>A. jamaicensis</i>	13.18	14.28	0.748	-14.911	-2.915	.011*	0.847	.0000**
EYE vs. EAR								
<i>R. celebensis</i>			-0.492	23.303	8.338	.000*	0.348	.3582
<i>E. fuscus</i>			-0.876	24.403	7.154	.000*	0.615	.0039**
<i>L. borealis</i>			-0.967	14.782	2.487	.037	0.455	.1866
<i>P. parnelli</i>			0.147	10.888	1.907	.078	0.100	.7240
<i>T. georgianus</i>			-0.403	13.362	4.259	.008*	0.361	.4264
<i>H. armiger</i>			-0.386	24.948	2.600	.048*	0.516	.2360
<i>H. galeritus</i>			-0.702	27.395	4.482	.000*	0.663	.0134
<i>R. affinus</i>			-0.277	2.125	0.293	.774	0.346	.2706
<i>A. jamaicensis</i>			-0.907	28.672	4.781	.000*	0.619	.0105

<sup>1</sup>Independent variable = STAGE except where noted.

\*P = .05 is a test for Y-intercept = 0.0.

\*\*Bonferroni P = .0055 is a test for the significance of correlation between X and Y.

large olfactory fossae and resonating chambers. The anatomical correlates of olfaction and echolocation have apparently worked at cross-purposes during the morphogenesis and evolution of the nasal-emitting rostrum.

The expansion of the resonating chambers effect large fontanels between the nasal, maxillary, and frontal bones in Old World nasal emitters. These "rostral fontanels" have gone unreported to the author's knowledge. In addition, the sutural system of the orbital walls is disturbed such that the lacrimal bones are lost. They may exist histologically, but they are not visible grossly with the present technique. Such elemental losses (or distortions) are not uncommon to the midface in either developmental or evolutionary terms (Haines, '40; Hanken, '83, '84; Pedersen, '91, '93a,b; Presley and Steel, '76; Presley, '81). Unlike other Old World nasal emitters, the resonating chambers of the Nycteridae are found outside of the bony nasal cavity. It would be interesting to know what, if any,

osteological involvement within the rostrum is shared with other rhinolophoids.

The characteristic dorsad rotation of the rostrum in oral-emitting bats carries the orbital axis dorsally as well. Conversely, rostra of nasal emitters are more stationary throughout development and do not affect the orbital axis. As a result, the eyeballs of oral-emitting bats are directed above both the phonal axis of the head and the direction of flight, whereas both orbital and phonal axes are aligned with the direction of flight in nasal-emitting bats. The physiological consequences of this pattern are beyond the scope of this project but deserve further investigation.

*Nasal emission—a "Key innovation"?*

To visualize morphological evolution, taxa have been pictured as migrating through an adaptive landscape representing different morphological constructs (Simpson, '44, '53). Highly cohesive and adaptive morphological constructs appear as mounds or peaks spot-

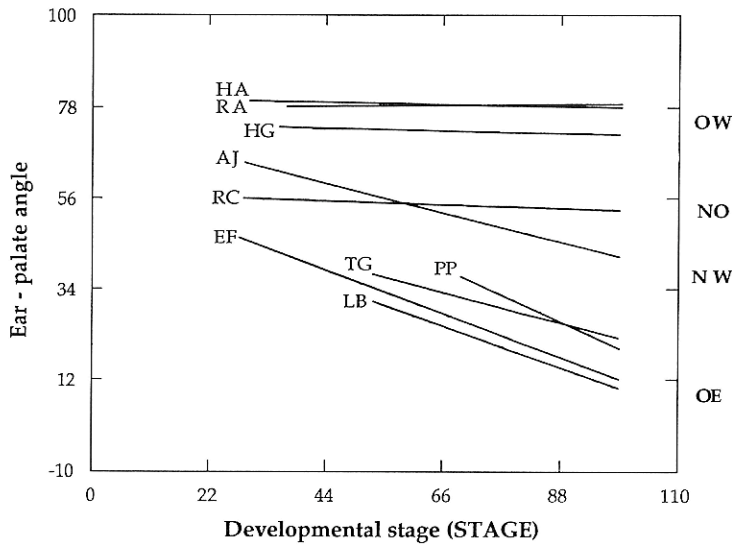


Fig. 3. Scatterplot: Angle between the ear and the palate vs. developmental stage (STAGE). This plot clearly shows the clustering of all of the Old World nasal-emitting series together apart from all oral-emitting series. All trajectories diverge from a common (primitive) angle of about 80°. Taxonomic abbreviations are as follows: RC = *Rousettus celebensis*; EF = *Eptesicus fuscus*;

LB = *Lasiurus borealis*; PP = *Pteronotus parnelli*; TG = *Taphozous georgianus*; HA = *Hipposideros armiger*; HG = *Hipposideros galeritus*; RA = *Rhinolophus affinis*; AJ = *Artibeus jamaicensis*; OW = Old World nasal emitter; NW = New World nasal emitter; OE = oral emitter; NO = nonemitter (Megachiroptera).

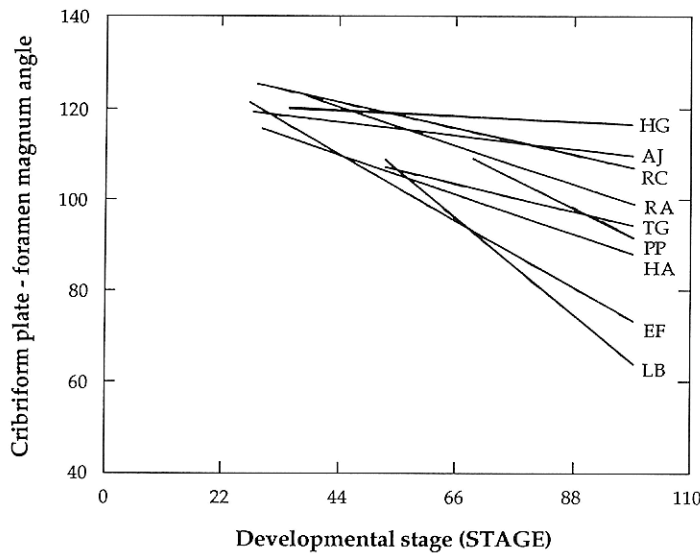


Fig. 4. Scatterplot: Cribriform plate–foramen magnum angle vs. developmental stage (STAGE). All trajectories diverge from a common angle of 130° and do not exhibit any emission-specific patterns. Abbreviations as in Figure 3.



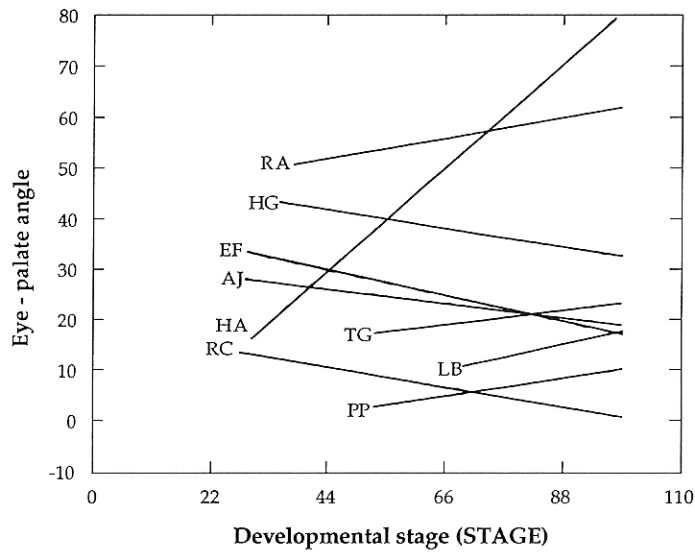


Fig. 5. Scatterplot: Angle between the eye and the palate vs. developmental stage (STAGE). The trajectories of all oral-emitting taxa are similar to each other in that the eye-palate angle begins and remains small throughout development. Abbreviations as in Figure 3.

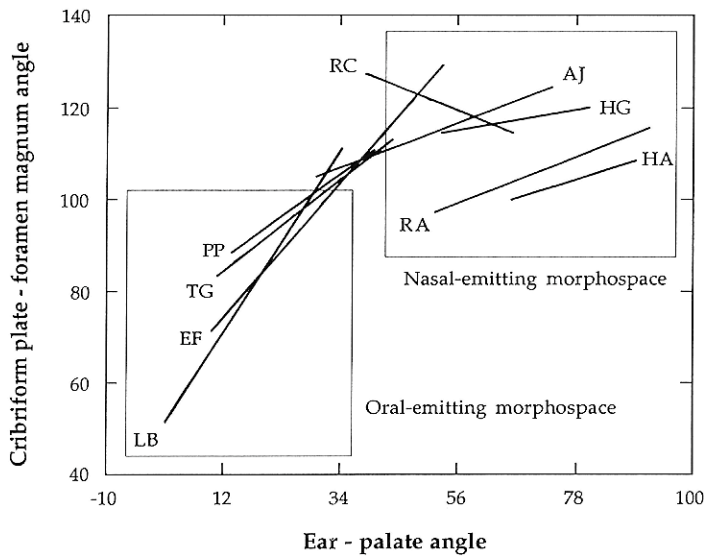


Fig. 6. Scatterplot: Cribriform plate-foramen magnum angle vs. the ear-palate angle. The difference between oral-emitting and nasal-emitting ontogenies is evident in this scatterplot. Trajectories of nasal-emitting taxa (*Hipposideros armiger*, *Hipposideros galeritus*, *Rhinolophus affinus*, *Artibeus jamaicensis*) are clustered together in the upper right-hand corner of the plot.

Trajectories of oral-emitting taxa (*Eptesicus fuscus*, *Lasius borealis*, *Pteronotus parnelli*, *Taphozous georgianus*) initiate their development in the same corner yet "migrate" away from this nasal-emitting morphospace down toward the lower left-hand corner of the plot into an oral-emitting morphospace. Abbreviations as in Figure 3.

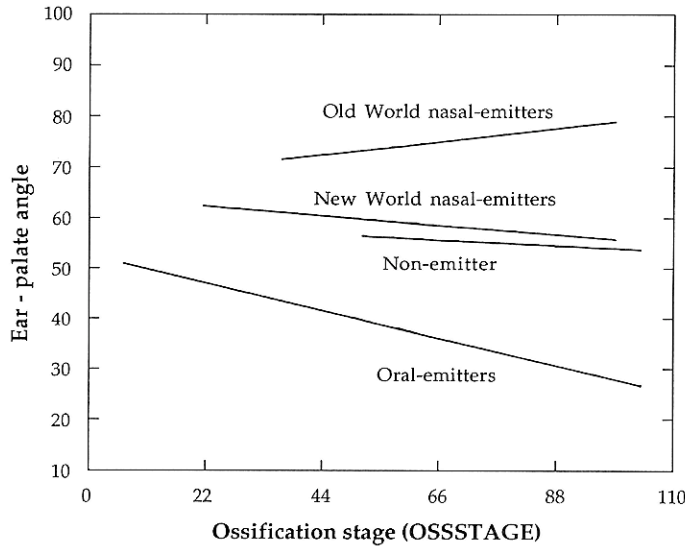


Fig. 7. Scatterplot: Ear-palate angle vs. ossification stage (OSSSTAGE). The fundamental conformation of the chiropteran skull is established before the skull begins to ossify.

ted throughout this landscape. Developmentally, taxa migrate through a morphogenetic landscape as well. While the spaces between peaks in the adult landscape are often considered “non-adaptive” (Simpson, '44), inter-peak regions in the developmental landscape must be traversed or transiently occupied by individuals sufficiently integrated to survive gestation (Cheverud, '82, '89). This selection in utero is based upon mechanical feasibility

and compatible histogenesis within the ontogenetic milieu (Alberch, '82; Katz et al., '81; Katz, '82; Müller, '90), i.e., structural accommodation throughout development may be more important than Darwinian selection after parturition (Bonner, '88; Kuhn, '87; Maier, '89; Presley, '89; Schmalhausen, '49).

The adaptive landscapes in Figure 9 each exhibit two peaks representing the oral-emitting and nasal-emitting *Baupläne*, re-

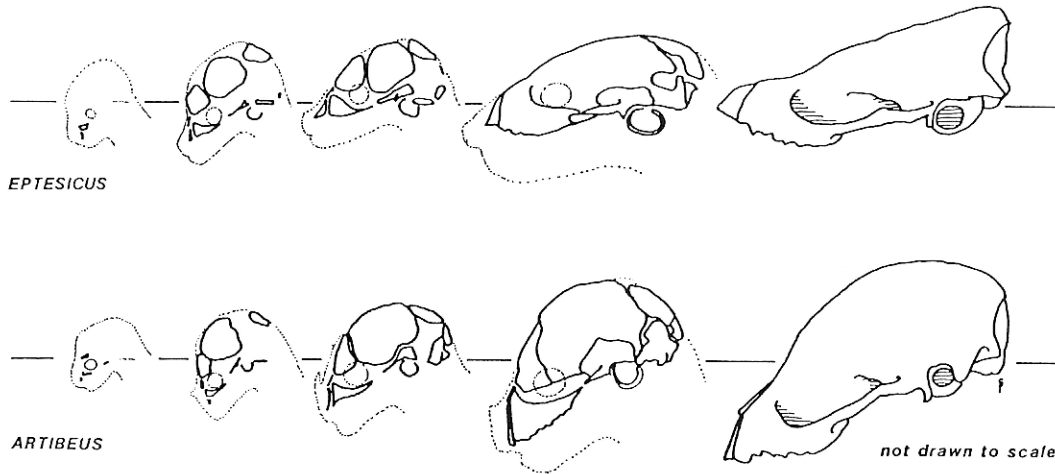


Fig. 8. *Eptesicus fuscus* and *Artibeus jamaicensis* development. The distinctive dorsad rotation of the orofacial complex in *E. fuscus* is clearly visible in this illustration. The orofacial complex in *A. jamaicensis* remains “tucked” throughout development.

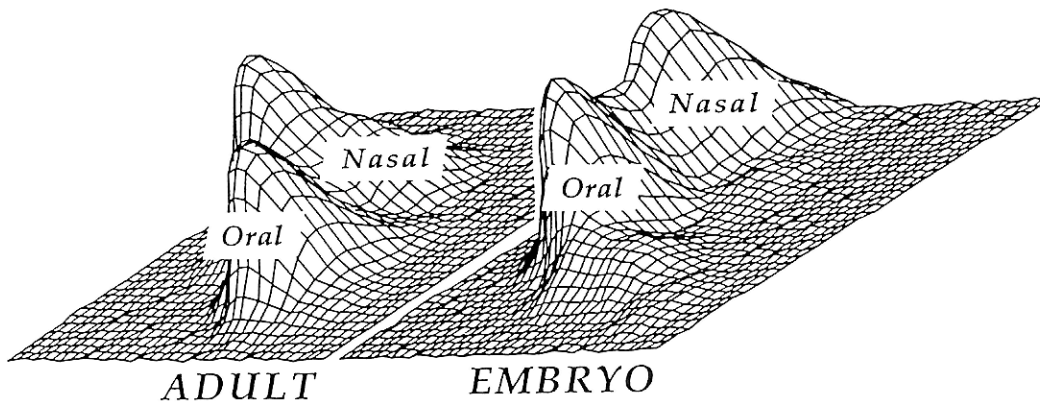


Fig. 9. Adaptive landscape. This figure is a three-dimensional reinterpretation of Figure 6, which plotted the ear-palate angle against the angle between the cribriform plate and the foramen magnum. Both the adult and developmental landscapes illustrate the two basic forms

of the chiropteran skull. The shallow saddle between peaks is formed by second-trimester oral-emitting embryos as they migrate away from the rudimentary, nasal-emitting morphospace toward the oral-emitting morphospace.

spectively (Fig. 9 is a three-dimensional reconstruction of Fig. 6). Both nasal- and oral-emitting forms begin their ontogeny on the "nasal-emitting peak" (i.e., the nasal-emitting morphospace of Fig. 6), but "oral-emitting" fetuses subsequently migrate away from this region toward the "oral-emitting peak" (i.e., the oral-emitting morphospace of Fig. 6). This migration reflects the cephalometric changes that occur within the growing skull of most non-echolocating mammals (e.g., rodents, rabbits, and primates; Schneiderman, '92) and represents the primitive mammalian pattern (Wimberger, '91).

In contrast, fetuses of both New World and Old World nasal-emitting taxa remain on a "nasal-emitting peak" throughout their ontogeny. The restrictive occupation of the nasal-emitting peak required the re-routing of an ancestral developmental path (oral emission) onto a new morphogenetic trajectory (nasal emission)—a "key innovation" (Craft, '90; Frazzetta, '75; Müller, '90; Raff et al., '90; Fig. 9). Such changes to one system during morphogenesis can effect a cascade of changes in the structural integrity or spatial representation of adjacent elements throughout the remainder of development (Bleichschmidt, '76b; Devillers, '65; Hanken, '83, '84; Hanken and Hall, '88; Herring, '85; Hoyte, '87; Kay, '86; Klima, '87; Müller et al., '89; Ranfjord and Ash, '66; Thorogood, '88; Zelditch and Carmichael, '89). This sorting-out and re-integration of form and function after such an innovative event provide raw material for phylogenetic radiation (Alberch

et al., '79; Alberch and Alberch, '81; Gould, '77; Müller, '90; Needham, '33).

The present data base is mute with respect to the specific mechanism by which this key innovation was made although it presumably entails retrograde selection on the morphogenesis and function of the pharynx. Because this dichotomy is clearly associated with the use of the head as an acoustical horn in adults, intermediate states would be quickly weeded out because of the precise anatomical and physiological requirements for the efficient emission of ultrasonic echolocation (Pye, '88; Suthers et al., '88; Simmons and Stein, '80). The strictness of this retrograde selection leads to the conclusion that if strong selective forces are indeed associated with faster rates of morphological evolution (Simpson, '44, '53), the shift from oral emission to nasal emission must have occurred quickly both in developmental and evolutionary terms (Lewin, '86; Price et al., '93).

#### *Phylogenetic significance*

Extant Microchiroptera are separated 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; Koopman, '84). Each infraorder contains both oral-emitting and nasal-emitting forms. Old World nasal emitters belong to the Yinochiroptera, whereas New World nasal emitters belong to the Yangochiroptera. New and Old World nasal-emitting groups have been separate since the early Eocene (Carroll, '88; Pet-



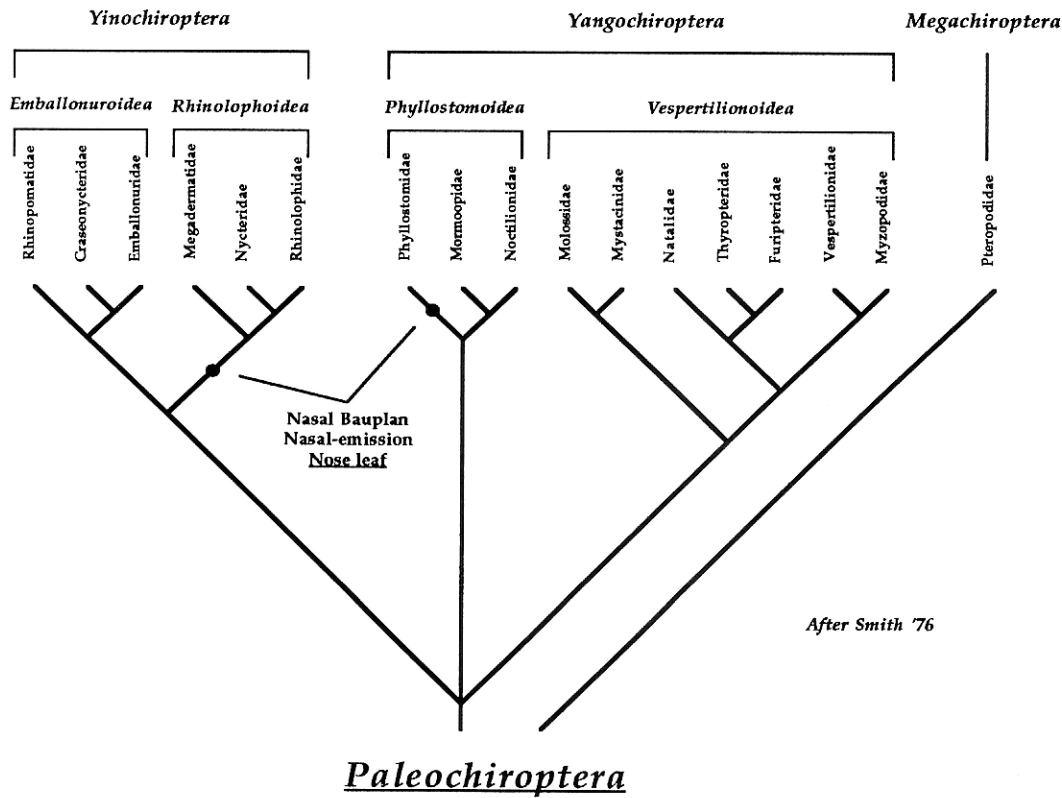


Fig. 10. Convergent evolution of nasal-emitting forms in the Microchiroptera. Extant Microchiroptera are separated into two infraorders based upon the mobility of the premaxillae: the Yinochiroptera (premaxillae free from the maxillae) and the Yangochiroptera (premaxillae fused

to the maxillae; Koopman, '84). Nasal-emitting groups have evolved three unique features independently: 1) nasal emission of the echolocative call, 2) rearrangement of the skull about the nasal cavity, and 3) possession of a nose leaf.

tigrew, '91; Smith, '72, '76) but have evolved three unique features independently: 1) nasal emission of the echolocative call, 2) rearrangement of the skull about the nasal cavity (present study, and Pedersen, '93a), and 3) possession of a fleshy flap of skin that projects from the nose (nose leaf) that focuses the echolocative 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). Because the basal members of each infraorder neither have nose leaves nor emit their echolocative calls nasally, I consider nasal emission to be a convergent apomorphic character and propose that the advent of nasal emission was the "key innovation" for all subsequent radiation in both Old and New World Microchiroptera (Fig. 10).

In summation, the microchiropteran skull has been canalized into three distinct evolu-

tionary paths (Fig. 10): 1) primitive state—oral-emitting forms (Emballonuroidea and Vespertilionoidea), 2) simple nasal-emitting forms (New World nasal emitters: Phyllostomidae), and 3) derived nasal-emitting forms (resonator equipped Old World nasal emitters: Rhinolophoidea).

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