

## 6

## Skull growth and the acoustical axis of the head in bats

### INTRODUCTION

In this chapter, I place the extraordinary diversity in microchiropteran skull size and shape within a rather simplistic framework. That is, despite all other craniodental adaptations, the microchiropteran head must function as an efficient acoustical horn during echolocation. This truism becomes infinitely more interesting when one considers that echolocatory calls are either emitted directly from the open mouth (oral-emitters), or forced through the confines of the nasal passages (nasal-emitters). Given that oral-emission is the primitive state, the advent of nasal-emission is viewed as a complex morphological innovation that required a substantial redesign of the microchiropteran rostrum: 1) the nasal passages must be reoriented and aligned with the direction of flight, and 2) the nasal passages must exhibit dimensions that provide for the efficient transfer of sound (resonance) through the adult skull. In the following treatment, I draw examples from developmental studies and functional morphology to illustrate how evolution has solved this intriguing design problem.

### Spatial competition and the packaging of the fetal head

The dynamic nature of the developing skeletal system is all too frequently overlooked in the classroom where the skull is often presented as an immutable structure into which the brain, ears, and eyes are stuffed during development. Rather, the converse is a more accurate view; cranial growth and form are 'soft tissue' phenomena affected only secondarily by osteological development. Indeed, early in development, the differential growth of the brain and pharynx governs the shape of the chondrocranium and influences the forms of the embryonic neuro- and

viscerocrania (Ranly 1980; Klima 1987; Hanken & Thorogood 1993). Later, within the envelope of skin that confines the head, volumetric changes in the growing brain, brainstem, eyes, tongue, and pharynx affect bone growth via forces transmitted through the dura and periosteum to adjacent bones and sutures (Blechs Schmidt 1976*a, b*). The ensuing mechanical competition for space among the various cranial components effects a cascade of modifications throughout the growing skull in the shape, position, and orientation of distant components (Haines 1940; Silver 1962; Bosma 1976; Hanken 1983; Pedersen 1995). Evolutionarily, such patterns of differential growth among the braincase, trachea, and pharynx have been cited as driving forces behind gross morphogenetic changes in primate skulls (Baer & Nanda 1976; Blechs Schmidt 1976*a, b*; Enlow 1976; Moss 1976; Schön 1976; Schachner 1989). Such packaging constraints are accommodated by the developmental plasticity of each system (e.g., pharynx, braincase, otic capsules) in proportion to tissue composition, compliance in growth rates, the gross translation of elements or distortion of affected structures *in situ* (Müller 1990; Raff *et al.* 1990). When plastic mechanisms exceed their spatial or mechanical thresholds and fail, new morphogenetic paths may come into play that effect gross morphological changes in skull form (Herring & Lakars 1981; Hanken 1983; Herring 1985).

### Bone as a plastic entity

Throughout ontogeny, the changing size, shape, and orientation of each bony element reflect the dynamic interplay between the rate at which bone tissue responds by further mineralization and/or remodeling of existing bone surfaces and the volumetric expansion of underlying capsular spaces, such as the nasal capsules or brain (Sarnat & Shanedling 1979; Koskinen-Moffett *et al.* 1981; Choo & Covell 1996). Whereas the shape and orientation of each element is strongly influenced by the enclosed volume, the subsequent ossification of each element is independent of capsular growth. This independence permits epigenetic remodeling of the various skull elements to track developmental variation in the enclosed soft tissues (Haines 1940; Alberch & Alberch 1981; Hanken 1983, 1984; Griffioen & Smit-Vis 1985; Smit-Vis & Griffioen 1987; Starck 1989; Ross & Ravosa 1993; Ross & Henneberg 1995). A great deal of what we know about the reciprocity between bone growth and the shape of an enclosed space has come from studies of pathological suture formation (e.g., synostoses: Koskinen-Moffett & Moffett 1989; Pedersen & Anton 1998), instances of malformation of the

central nervous system (e.g., hydrocephaly, and anencephaly: Sperber 1989), and numerous studies concerning the experimental derangement of developing bone and sutures (Babler *et al.* 1987). I draw attention to such exaggerated examples to emphasize the epigenetic plasticity of bone and its ability to accommodate anatomical distortion, be it subtle accommodation of inter-individual variation, or gross alterations that accompany gross morphological innovation.

In addition to responding to general growth pressures, developing bone must also accommodate changes in the mechanical environment such as changes in the functional loading patterns attendant to shifts in behavior (e.g., the transition from suckling to mastication during weaning in mammals; Herring & Lakars 1981; Herring 1985). Examples of such directive interactions between muscle forces and bone development are found throughout the cranial vault. For example, the sutural complexity of the cranial vault and occiput decrease when masticatory and cervical muscles have been experimentally denervated or devascularized, and lacking appropriate muscular action, many bone features, such as the coronoid process, do not develop (Washburn 1947; Spyropoulos 1977; Von Schumacher *et al.* 1986, 1988; Byrd 1988; Kylamarkula 1988). Hoyte (1987) has suggested that masticatory muscles influence the shape of the cranial vault, and hence the shape and disposition of the brain itself. If true, the unique skulls of rhinolophid bats deserve further attention. Rhinolophid braincases are elongate and are distinctly 'compartmentalized,' with obvious strictures that partition the olfactory lobes from the cerebrum, and the cerebrum from the brainstem. Might this internal buttressing be a response to large, complex temporalis muscles or simply a developmental artifact of an elongate brain?

### Brain growth and skull form

Interactions between the developing brain and cranial base influence a wide range of morphogenetic changes to the midface throughout development (cattle: Julian *et al.* 1957; rodents: bats: Sperry 1972; Moss 1976; humans: Thilander & Ingervall 1973; Moore 1983; Sperber 1989). For example, in primates, the anterior and middle cranial fossae (olfactory bulbs and cerebrum) compete with the orbits for space, thereby influencing the shape, size, position, and orientation of the interorbital septum (Enlow & McNamara 1973). Clearly, brain development has a profound impact on vertebrate craniofacial development and evolution. However, it would appear that brain volume *per se* does not play a strong role in the craniofacial evolution of bats (Pedersen 1993). Rather, the relative size of

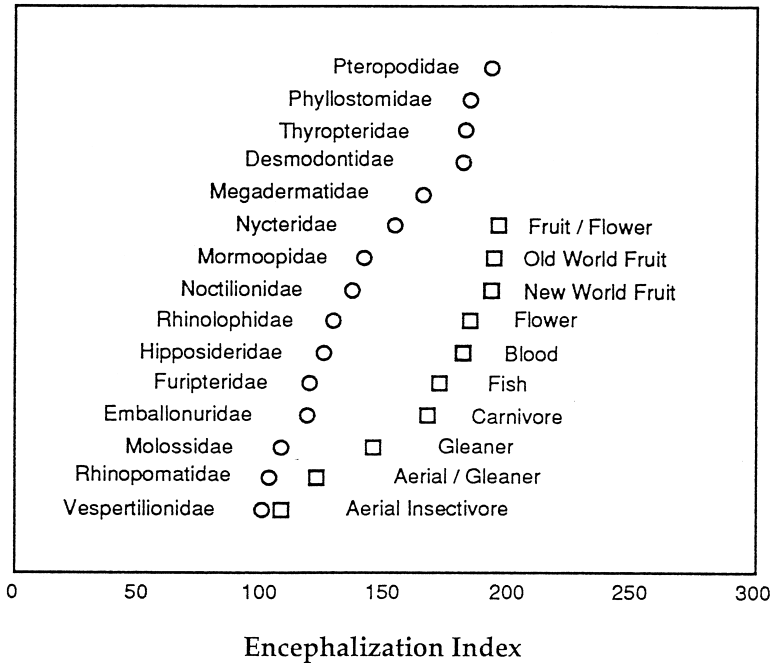


Figure 6.1 The encephalization index relates the average size of the brain in each family to the vespertilionid condition (index value of 100; after Stephan *et al.* 1981). Aerial insectivores have small brains and occupy the lower end of this index; frugivorous taxa possess larger brains and utilize more cluttered environments and dominate the upper end of the index. Brain size is closely associated with habitat use. Circles represent the average values of all known chiropteran families while squares represent the average values for foraging preference. (From Pedersen 1993.)

the adult chiropteran brain is associated with the occupation of a specific aerial niche (Eisenberg & Wilson 1978; Stephan *et al.* 1981; Jolicœur *et al.* 1984). Aerial insectivores and foliage gleaners are found in open habitats or along forest boundaries and possess relatively small brains (Fig. 6.1) Frugivorous and carnivorous taxa have relatively larger brains and forage in more complex, cluttered habitats (Eisenberg & Wilson 1978; Stephan *et al.* 1981; Jolicœur *et al.* 1984). Therefore, shape of the basicranium and cranial vault are affected by the gross morphology and organization of the brain rather than its size *per se* (Jolicœur *et al.* 1984). With respect to chiropteran evolution, brain anatomy and development are clearly fertile areas for future research that have only just been touched upon (Pirlot & Bernier 1991; see Reep & Bhatnagar, this volume).

## ONTOGENY OF THE CHIROPTERAN SKULL - CEPHALOMETRY

The study of the angular relationships among the various components of the skull (cephalometry) has been raised to a fine art in the dental profession where lateral head radiographs are an indispensable tool for planning dental treatment. Outside of the dental profession, cephalometry has gone relatively unappreciated. This is unfortunate because cephalometric analysis provides a rather unique method for evaluating functional morphology or for tracing evolutionary trends in cranial evolution. Specifically, cephalometry provides a size-free description of the basic internal arrangement of the head using internal landmarks and anatomical planes that are 1) otherwise unavailable for morphometric analysis (e.g., sella turcica, cribriform plate), and 2) relatively immune to developmental perturbations, such as malnutrition (Pucciarelli & Dressino 1996) and sexual dimorphism.

**Rotation of the rostrum in fetal mammals**

One of the most obvious examples of the efficacy of cephalometry is demonstrated in studies concerning the elevation of the mammalian rostrum early in development. The mammalian head begins growth tucked firmly against the chest wall from where it rotates dorsad about the cervical axis. Simultaneously, the facial component of the skull rotates dorsad about the braincase. The motive forces behind these rotations are complex, as are the forces that ultimately determine the location and final orientation of the adult rostrum. Certainly, translocation of the rostrum is limited in rate and direction by the ability of adjacent bony structures to respond (i.e., their respective abilities to get out of each other's way). Such restrictions are clearly mediated by the adherent periosteum and sutural systems that envelop each bony element (McLain & Vig 1983; Muhl & Gedak 1986). In primates, it has been argued that spatial competition between the developing eyes and brain determines where the palate comes to rest in the adult skull (Radinsky 1968; Spatz 1968; Ross & Ravosa 1993). In other mammals, rotation has been attributed to elongation of the snout, growth of the cranial base, and tooth eruption (Starck 1952; Julian *et al.* 1957; Sperry 1972; Servoss 1973; Thilander & Ingervall 1973; Moss 1976; Gasson & Lavergne 1977; Moore 1983; Schachner 1989; Pedersen 1993). However, Microchiroptera interpret their environment acoustically and follow a different set of constructional rules based on the use of the facial skeleton as an acoustical horn. As such, the angular arrangement of the various skull components pro-

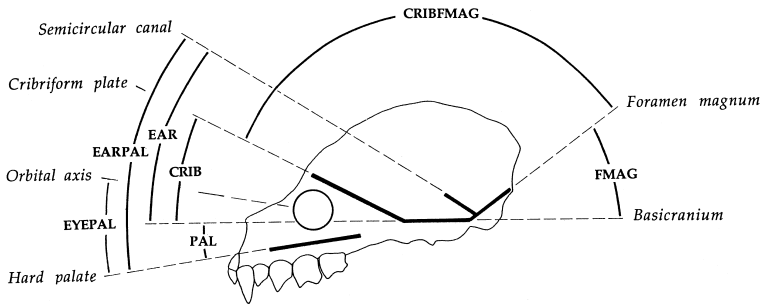


Figure 6.2. Anatomical planes and cephalometric angles are shown superimposed on a tracing of an *Artibeus jamaicensis* skull. See text for description of each cephalometric angle and anatomical plane. (From Pedersen 1993.)

vides a unique insight into the internal form and function of the microchiropteran head.

### Anatomical planes and cephalometric angles

Four anatomical planes are easily identified in the mammalian skull: lateral semicircular canals, palate, foramen magnum, and cribriform plate (Fig. 6.2). Here, they are used to delineate the inertial and acoustic axes of the head and relate the general organization of the braincase to the rest of the body. A brief explanation of each is in order.

#### *Inner ear*

The information concerning balance and orientation provided by the semicircular canals of the inner ear are of great importance to flying vertebrates, and absolutely critical to bats that often navigate through complex habitat without the aid of visual cues. Here, I use the orientation of the lateral semicircular canals to reflect the manner in which a bat holds its head during flight (de Beer 1937; Delattre & Fennart 1960).

#### *Hard palate*

The functional anatomy of the hard palate is multifaceted. It must support the dental battery and reinforce the rostrum during mastication, and it must accord sufficient space for tidal airflow across its superior surface. Because the phonal axis of the head must be aligned with the long axis of either the oral or the nasal cavities, the palate is an important landmark that lies just above, or just below this axis.

### *Foramen magnum*

The plane of the foramen magnum represents the boundary between the occiput and the cervical axis (Baer & Nanda 1976; Schön 1976). This plane influences head posture and reflects the degree of flexibility found in the cranio-cervical axis (Fenton & Crerar 1984). The maintenance of the airway also influences the cranio-cervical angulation of the head, which, in turn, influences the relative position and orientation of the stylohyoid chain and its attendant musculature (Bjork & Skieler 1972; Gaskell 1974; Solow & Greve 1979; Herring 1985; Tallgren & Solow 1987; Behlfelt *et al.* 1990). For example, the stylohyoid chain must increase in length to accommodate increases in pharyngeal and esophageal diameters and the bulk of the tongue and prevertebral musculature throughout ontogeny.

### *Cribriform plate*

The plane of the cribriform plate consists of a bony septum that lies between the nasopharynx and the brain and partitions the facial and neural components of the skull (Ranly 1980). Its relative position reflects the volumetric increase of the braincase during brain growth (Young 1959; Moss 1976), and is responsive to the structural mechanics of the midface, the volume of the olfactory lobes of the telencephalon (Frahm 1981; Jolicoeur *et al.* 1984; Pirlot & Bernier 1991), the development of the interorbital septum (Haines 1940), and the position of the rostrum relative to the anterior cranial base (Starck 1952).

Two cephalometric angles are useful in framing these four anatomical planes in a functional context (Pedersen 1993a, 1995). EARPAL relates the hard palate and middle ear, whereas CRIBFMAG relates the cribriform plate to the foramen magnum (Fig. 6.2). Here, and in subsequent sections, the discussion of fetal material and growth trajectories are based upon developmental (cross-sectional) series of nine species of Chiroptera (*Rousettus celebensis*, *Eptesicus fuscus*, *Lasiurus borealis*, *Pteronotus parnellii*, *Taphozous georgianus*, *Hipposideros armiger*, *H. galeritus*, *Rhinolophus affinis*, *Artibeus jamaicensis*; Pedersen 1995, 1998). All fetal material was cleared by maceration and differentially stained for bone and cartilage (Hanken & Wassersug 1981; Klymkowsky & Hanken 1991). Each fetus was staged using the index STAGE to describe the extent to which a fetal skull has reached its adult size, and to ameliorate the differences in head size and shape among species.

### Cephalometry of fetal bats

Though fetuses of oral-emitting and nasal-emitting species are grossly indistinguishable early in development, the internal arrangement of their heads is well established shortly thereafter, before the skull has begun to ossify, long before the approximation of the primary suture systems, and well before the forces of mastication begin to affect skull morphogenesis. Initially, the angular constructions of oral- and nasal-emitting fetal heads are very similar and share common values of EARPAL and CRIBFMAG ( $80^\circ$  and  $120^\circ$ , respectively). Species-specific skull morphology becomes increasingly more apparent, but always within the framework of either the nasal-emitting or oral-emitting cranial form. EARPAL of the four oral-emitters (*E. fuscus*, *L. borealis*, *P. parnellii* and *T. georgianus*) decreases dramatically throughout development, whereas EARPAL remains constant in the three Old World nasal-emitters (*H. armiger*, *H. galeritus* and *R. affinus*). The New World nasal-emitter and the non-emitter (*Rousettus celebensis* and *A. jamaicensis*, respectively) exhibit intermediate values of EARPAL. A similar pattern occurs in the braincase – CRIBFMAG (Fig. 6.3).

These changes show that the palate of oral-emitting fetuses rotates dorsad about the basicranium, as the occiput becomes more erect upon the floor of the braincase. Conversely, the relative positions of these anatomical planes remain fairly static throughout development in nasal-emitting taxa. The cartoon of *Eptesicus* (oral-emitter) and *Artibeus* (New World nasal-emitter) developmental series depicts this dichotomy (Fig. 6.4). As is the case with all oral-emitting taxa, the rostrum, hence hard palate, is aligned with or elevated above the basicranium (i.e., an airo-rhynchal skull type) and the echolocative call is forced directly out through the mouth. This basic skull form (*Bauplan*) is the plesiomorphic condition for mammals and clearly exemplified by emballonuroids and vespertilionoids. Conversely, palates of nasal-emitting bats are retained ventral to the basicranial axis, i.e., a klinorhynchal skull type (Starck 1952; Freeman 1984; Pedersen 1993a). In these derived forms, the echolocative call is forced out through the nostrils as exemplified by rhinolophoids and phyllostomids.

This dichotomy between oral-emitting and nasal-emitting *Baupläne* involves a change in head posture which has required a compensatory rotation of the otic capsules to keep the lateral semicircular canals aligned with the acoustical axis of the head. The orientation of the lateral semicircular canals differs dramatically between oral- (*Myotis* –  $0^\circ$  above the palate) and nasal-emitting taxa (*Nycteris* –  $75^\circ$  above the palate). As a



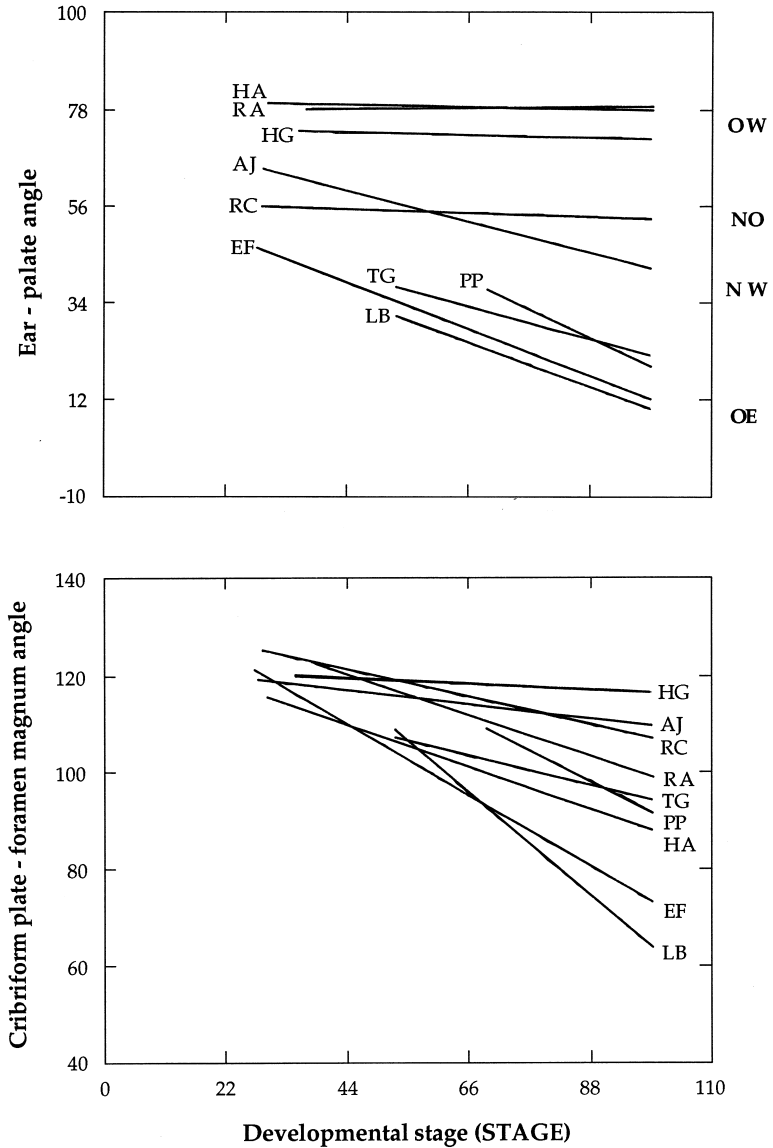


Figure 6.3. (Upper) EARPAL vs. developmental stage (STAGE) shows the clustering of all of the Old World nasal-emitting series together apart from all oral-emitting series. All trajectories diverge from an extrapolated common (primitive) angle between 60° and 80°. (Lower) CRIBFMAG vs. developmental stage (STAGE) trajectories decrease from a common angle of 130° (reflecting brain growth) and do not exhibit any emission-specific patterns.  $STAGE = \left[ \frac{\sqrt{(\text{embryo braincase length} \times \text{width})}}{\sqrt{(\text{embryo skull length} \times \text{width})}} \right] / \left[ \frac{\sqrt{(\text{adult braincase length} \times \text{width})}}{\sqrt{(\text{adult skull length} \times \text{width})}} \right] \times 100$ .

result of these otic and palatal rotations, oral-emitting fetuses 'migrate' (ontogenetically) away from the boundaries of a common 'fetal morphospace' towards various locations within the more broadly defined 'oral-emitting morphospace.' As discussed above, this migration (rostral rotation) is exhibited during the ontogeny of several non-echolocating mammals as well (e.g., rodents, rabbits, and primates: Schneiderman 1992) and reflects the primitive mammalian condition (Wimberger 1991). Of great interest, nasal-emitting fetuses remain within the 'fetal morphospace' throughout ontogeny as well as phylogeny (Fig. 6.5). This constraint, or 'morphostasis' is the derived condition in Microchiroptera and concerns only the angular arrangement of the skull and should not be confused with paedomorphic arguments.

Unlike microchiropterans, the form of non-echolocating megachiropteran skulls is not restricted by the demands of phonation. Mechanically, the relative position of the microchiropteran hard palate reflects the use of either the oral or nasal cavity as an acoustical horn. 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. Without constraints on the relative position of the hard palate, the non-echolocating megachiropteran skull appears as a morphological intermediate between the extreme oral-emitting forms and the Old World nasal-emitting forms (rhinolophids) in Figs. 6.6 and 6.7 (Pedersen 1993).

#### ONTOGENY OF THE CHIROPTERAN SKULL - ANATOMICAL LANDMARK DATA

The innovation and evolutionary potential of the nasal-emitting *Bauplan* have relied upon the morphogenetic plasticity of adjacent skeletal elements to accommodate changes throughout development and go on to function adequately in the adult. This balancing act is difficult given that the growth of the mammalian rostrum and pharynx are influenced by several factors: the respiratory tidal airflow (Solow & Greve

Figure 6.3 (cont.)

Taxonomic abbreviations are as follows: RC - *Rousettus celebensis*, EF - *Eptesicus fuscus*, LB - *Lasiurus borealis*, PP - *Pteronotus parnellii*, 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 - Non-emitter (Megachiroptera). (From Pedersen 1995.)

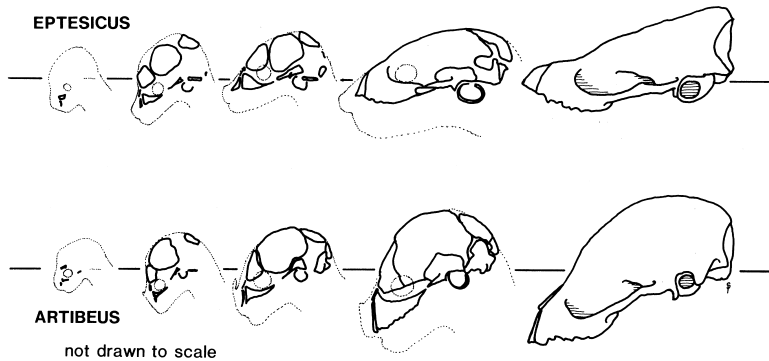


Figure 6.4. The distinctive dorsad rotation of the orofacial complex in oral-emitters is illustrated by *Eptesicus fuscus*. The orofacial complex in nasal-emitters remains 'tucked' throughout development (*Artibeus jamaicensis*). (From Pedersen 1995.)

1979), the forces of tooth eruption and auto-occlusal mechanisms (Lakars & Herring 1980), the tissue pressures from the lips and tongue (Proffit 1978), the organization and coordination of each muscle mass in proportion to the complexity of the dentition and associated dynamics of mastication (Herring 1985), and phonation/echolocation (Roberts 1972, 1973; Hartley & Suthers 1988; Suthers *et al.* 1988). Given this complex dynamic, it is of great interest that both rhinolophoids (Old World leaf-nosed bats) and phyllostomids (New World leaf-nosed bats) exhibit the anatomical requirements for the efficient emission of ultrasound through the nostrils (Hartley & Suthers 1987, 1988, 1990; Simmons 1980; Simmons & Stein 1980; Pye 1988). Though the cephalometric data suggest a classic example of convergent evolution, it is prudent to draw upon multivariate analyses of landmark data to investigate the developmental paths by which two taxonomically distinct clades of Microchiroptera (rhinolophoids and phyllostomids) arrived at their nasal-emitting *Baupläne*.

### Multivariate approach to growth trajectories

Cranial landmark data were taken from the same developmental series as described above (see Pedersen 1995 for detailed methods). These measurements (unpublished data) were grouped into distinct suites of variables according to function and/or anatomical relatedness. Each grouping was subjected to canonical analysis to identify covariance patterns among variables (~10) within each suite (jaw, ear, rostrum, cranial base, midface, temporomandibular joint). Bivariate plots of canonical

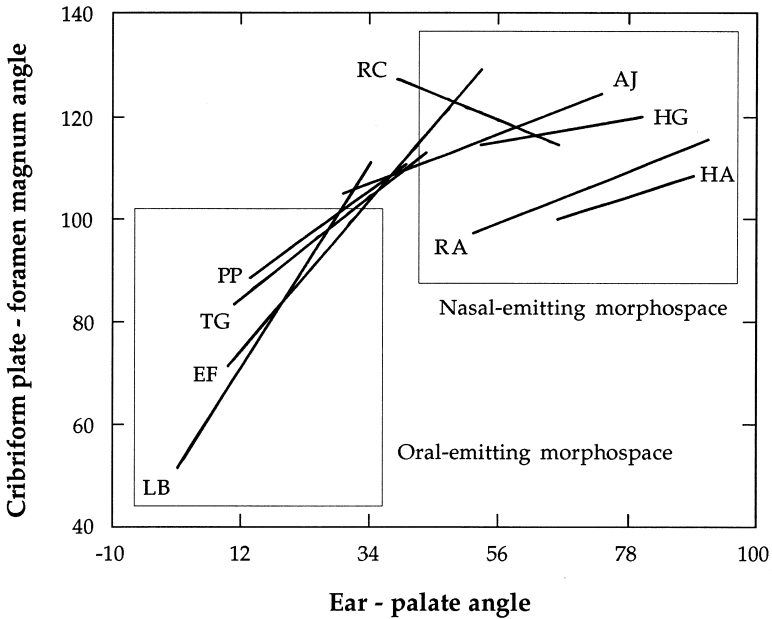


Figure 6.5. Bivariate plot of EARPAL vs. CRIBFMAG for fetuses and juveniles. Ontogenetic trajectories of oral-emitting and nasal-emitting developmental series are presented in this scatterplot. Each trajectory moves from right to left across the plot. Nasal-emitting taxa (*Hipposideros armiger*, *H. galeritus*, *Rhinolophus affinis*, *Artibeus jamaicensis*) are clustered together in the upper right-hand corner of the plot, whereas the trajectories of oral-emitting taxa (*Eptesicus fuscus*, *Lasiurus borealis*, *Pteronotus parnellii*, *Taphozous georgianus*) 'migrate' away from this nasal-emitting morphospace down towards the lower left-hand corner of the plot into an oral-emitting morphospace. (From Pedersen 1995.)

variates map each taxon's developmental path through multivariate space. Taxa that share similar covariance schemes (i.e., similar developmental patterns) co-occupy regions in multivariate space. An important capability of canonical analysis is the *post-hoc* identification of individuals. That is, known fetuses may be drawn out of the pool at random and re-identified to test the precision of the model. Suites of variables that concern the jaw, temporomandibular joint, cranial base, or ear capsule distinguish poorly among taxa. For example, fetal material was classified to the correct taxon only 52% of the time, and to the correct emission-form in only 68% of the cases using 'jaw' characters (Table 6.1). On the other hand, suites of variables concerning the rostrum or midface clearly distinguish among taxa (i.e., fetuses were correctly identified to both the

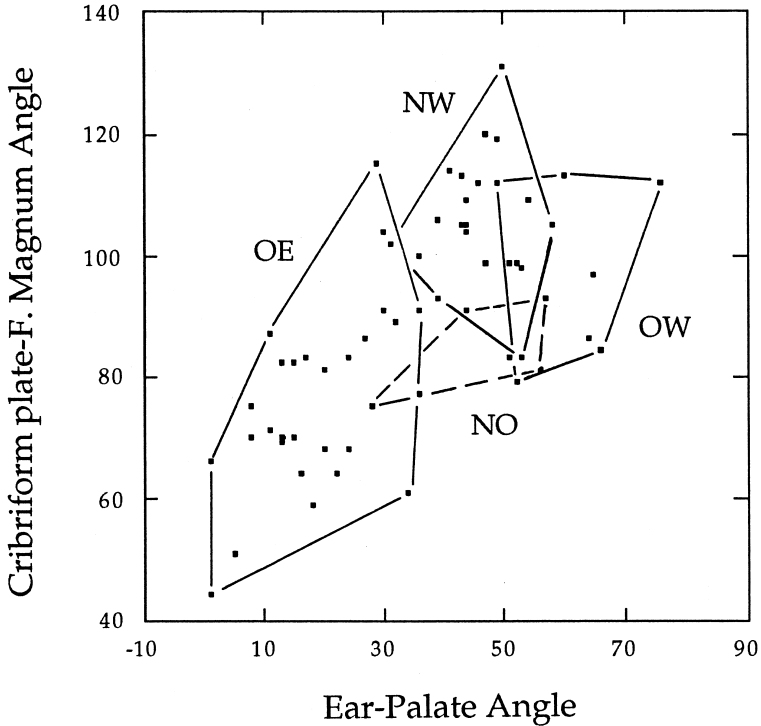


Figure 6.6. Bivariate plot of EARPAL vs. CRIBFMAG for adults. Non-emitters (Megachiroptera) are intermediate between the oral-emitting and the two nasal-emitting groups. The scatter of the Old and New World nasal-emitting taxa overlaps along both axes. OW – Old World nasal-emitter, NW – New World nasal-emitter, OE – oral-emitter, NO – Megachiroptera. (From Pedersen 1998.)

correct taxon and emission form 97% of the time; Figs. 6.8, 6.9). Of interest, nasal-emitting and oral-emitting fetuses are rarely mistaken for each other, however, individual fetuses are frequently misclassified within the same emission type.

The clarity of these separations lies in the fact that the skull of Old World nasal-emitting bats is characterized by a short hard palate, large-bore choanae, and a relatively long naso-laryngo-pharynx (estimated by the distance between the posterior nasal spine and the spheno-occipital synchondrosis). This construction is related to the unique, laryngo-nasal junction between the soft palate and the cartilages of the larynx found in the Old World nasal-emitters (Matsumura 1979; Hartley & Suthers 1988). The anatomical coupling of this junction is remarkable in the completeness of its seal and presumably requires a repositioning of all musculos-

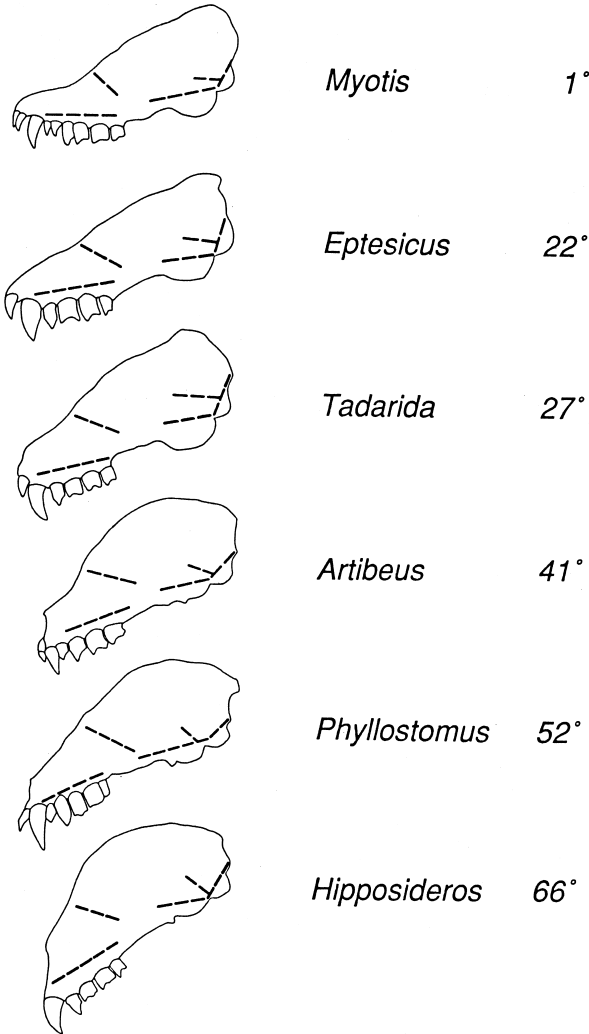


Figure 6.7. Cartoon depicting the wide range of rostral rotation (EARPAL values) within the suborder Microchiroptera. *Myotis*, *Eptesicus*, and *Tadarida* are oral-emitting taxa, while *Artibeus*, *Phyllostomus*, and *Hipposideros* are nasal-emitting taxa. (From Pedersen 1993.)

keletal elements associated with the soft palate and larynx (i.e., pterygoid width, choanal bore, pharyngeal length, and otic capsule separation) and is responsible for the clustering of the Old World nasal-emitting taxa in multivariate space. The Megachiroptera are clustered apart from the other developmental series because of their relatively large, albeit unspecialized, choanae and pterygoid complexes.

**Table 6.1. Canonical analysis post-hoc identification of individuals taken from the same developmental series using cranial landmark data. Distinct suites of variables were bundled to identify covariance patterns among variables (jaw, ear, rostrum, cranial base, midface, temporomandibular joint). For demonstration purposes, only the Jaw and Rostral groupings are presented. Tabular values are the number of individual fetuses identified for each actual-predicted (row-column) couplet. Abbreviations: EF – E. fuscus; LB – L. borealis; PP – P. parnellii; TG – T. georgianus; HG – H. galeritus; HC – H. cervinus; RA – R. affinis; AJ – A. jamaicensis; RC – R. celebensis; UNK – unidentified individuals**

	EF	LB	PP	TG	HG	HC	RA	AJ	RC	UNK	Total	Classification
<i>Jaw structures</i>												
Oral Emitters	6	4	4	1	1	2				14	21	52% Correct by Taxon
	4			1	1		2				11	
		13					2			2	17	
		1	5	2	2			1		1	9	
Nasal Emitters		1	2	2	2			1		1	8	68% Correct by Emission
		1	3	3	1	6	1			1	16	
		2		3	3	3	3	1		1	14	
		1	3				6	2		6	18	
No Echo						1		4		4	9	
Total	12	8	21	10	10	12	6	8	6	30	123	
<i>Rostral structures</i>												
Oral Emitters	8									13	21	97% Correct by Taxon
		11									11	
			12							5	17	
				8						1	9	

Nasal Emitters	<i>H. galeritus</i>	<i>H. cervinus</i>	<i>R. affinis</i>	<i>A. jamaicensis</i>	<i>R. celebensis</i>					97% Correct by Emission
			7							8
		14								16
				11						14
					10					18
No Echo						1			7	9
Total	9	11	12	9	1	7	14	11	10	123



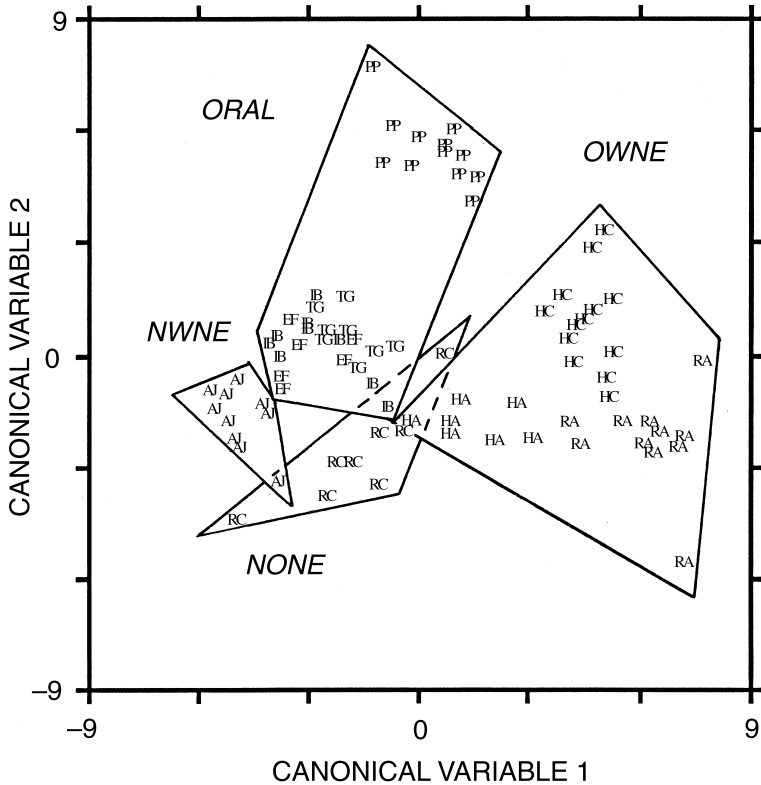


Figure 6.8. Scatterplot of the first and second canonical axes derived from the canonical analysis of the following rostral characters: canine width, palate width, external narial width, choanal diameter, temporomandibular joint width, pterygoid width, hard palate length, pharynx length, interorbital width, infraorbital foramen width, and toothrow length. Taxonomic abbreviations are as follows: OWNE – Old World nasal-emitter, NWNE – New World nasal-emitter, ORAL – oral-emitter, NONE – Megachiroptera, RC – *Rousettus celebensis*, EF – *Eptesicus fuscus*, LB – *Lasiurus borealis*, PP – *Pteronotus parnellii*, TG – *Taphozous georgianus*, HA – *Hipposideros galeritus*, HC – *H. cervinus*, RA – *Rhinolophus affinus*, AJ – *Artibeus jamaicensis*.

### Regression analyses and growth trajectories

Whereas a multivariate approach is useful in identifying patterns among large numbers of variables, several individual characters were analyzed more carefully using regression analyses. In general, all features increase in size throughout development (Fig. 6.10), the notable exception being the minimal growth in the length of the hard palate in the Old

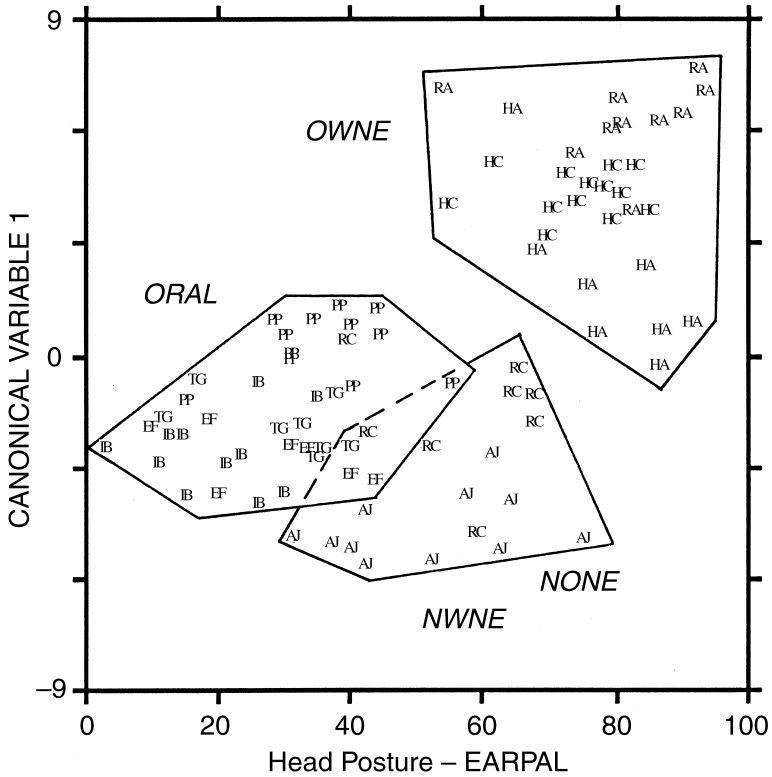


Figure 6.9. Scatterplot of the first canonical axis (previous figure) plotted against EARPAL. Note the clean separation of the OWNE and the overlay of the NWNE and NONE. Taxonomic abbreviations as for Fig. 6.8.

World nasal-emitter *Rhinolophus*. Individual structures exhibit a fair degree of variation early in development, though this variability tends to decrease after interaction and integration into other functional units in the head (Kay 1986; Zelditch & Carmichael 1989). Old World nasal-emitting taxa share a cohesive developmental trajectory. Oral-emitters are equally cohesive amongst themselves, but the trajectories of the New World nasal-emitter (*Artibeus*) and the megachiropteran (*Rousettus*) exhibit an unpredicted similarity with each other. This resemblance is most likely related to the fact that both *Rousettus* and *Artibeus* exhibit well-developed visual and olfactory acuities.

The simplistic dichotomy between oral- and nasal-emitting skulls must therefore be revised to include the observation that there are two distinct developmental paths that lead to the nasal-emitting construct. Subsequently, there are, in fact, three fundamental evolutionary programs

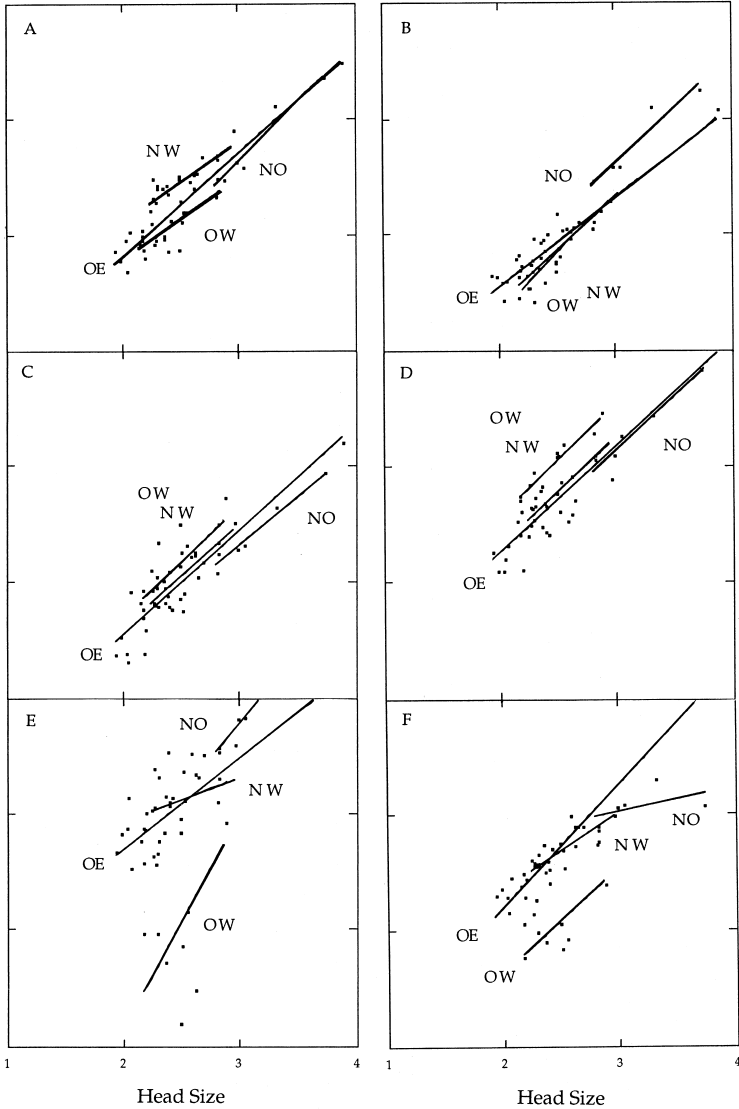


Figure 6.10. Growth trajectories of A) pterygoid width, B) choanal bore, C) narial width, D) pharyngeal length, E) palatal length, and F) interorbital width plotted against log head size (the cube root of the greatest length of skull  $\times$  zygomatic breadth  $\times$  midfacial depth). Taxonomic abbreviations are as follows: OW – Old World nasal-emitter, NW – New World nasal-emitter, OE – oral-emitter, NO – non-emitter (Megachiroptera).

for the microchiropteran skull: 1) relatively unmodified skulls (oral-emitters), 2) highly derived forms built around expansive nasal cavities (Old World nasal-emitters; see below), and 3) forms in which olfactory and visual (rather than acoustic) factors dominate the form-function of the facial component of the skull (i.e., New World nasal-emitting taxa).

#### OSSIFICATION OF THE CRANIUM

Given that developing cranial bone is a plastic entity, responsive to *in utero* and neonatal function (Lanyon 1980; Herring 1993), material availability (Müller & Streicher 1989; Presley 1989), brain development (Smith 1997), and spatial constraints (Haines 1940; Sarnat & Shanedling 1979), has the gross redesign of the microchiropteran skull altered the number of ossification centers or their sequence of appearance in any systematic pattern?

Fortunately, skeletal development is easily observed by clearing and differentially staining in whole-mount embryos. The presence of Alizarin red S stain in a skeletal element is evidence of the first macroscopic appearance of calcification. Yet this macroscopic calcification is a proliferation of pre-existing microscopic bone foci that may have appeared several developmental stages earlier (Hanken & Hall 1988). This time-lag between bone differentiation and bone proliferation means that the ossification sequences presented in this study are relative rather than absolute in nature. To register the degree to which each fetal skull had developed osteologically, 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. Observed 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. The jugal is absent in *Artibeus* and the lacrimal was absent in the three Old World nasal-emitters, therefore, the ossification index was recalculated as a percent of 27 rather than 28 bone foci in these four taxa.

The general sequence of cranial ossification exhibited by the nine taxa follow the common mammalian pattern (de Beer 1937; Smith 1997). The basicranial elements ossify in the correct posterior-anterior sequence typical of mammals while the auditory bullae and the ossicular chain are almost always the last series of bones to appear (de Beer 1937). In each taxa, every bony element had appeared before the skull reached 66% of its expected adult size (Fig. 6.11).

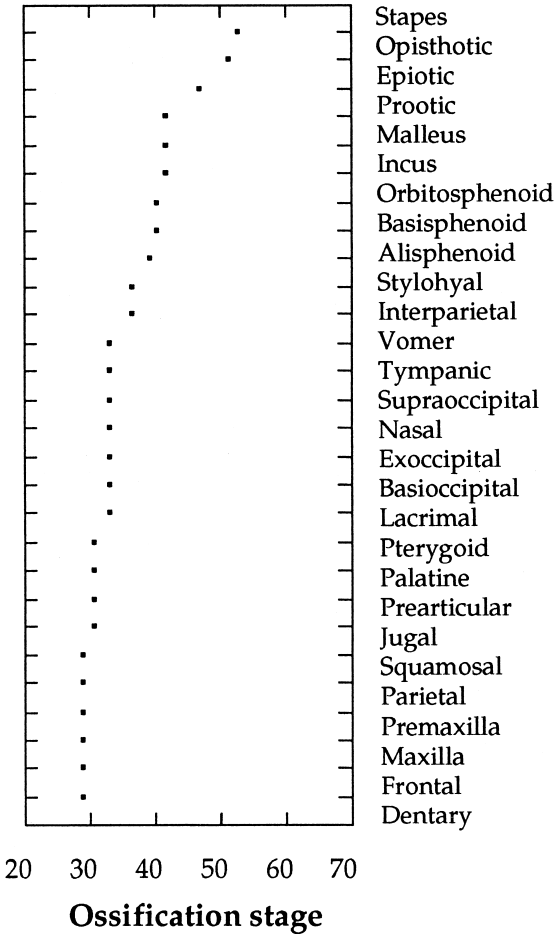


Figure 6.11. Plot indicating first appearance of an ossification center of each bone vs. developmental stage. All ossification foci (combined taxa) are present in the fetal skull by the time it has achieved two-thirds of its expected adult size. (After Pedersen 1995.)

Exceptions of note are related to the unique pharynx of rhinolophid bats (Simmons & Stein 1980; Hartley & Suthers 1987, 1988, 1990; Pye 1988; Pedersen 1993a, 1995, 1996). I will return to this in a later section, but the rhinolophid rostrum has been extensively modified to function as a 'resonator' for the echolocative call (Roberts 1972, 1973; Hartley & Suthers 1988; Suthers *et al.* 1988; Pedersen 1996). The great expansion of the nasal passages has led to a local derangement of tissues including: 1) the presence of a large fontanel between the nasal, maxillary, and frontal

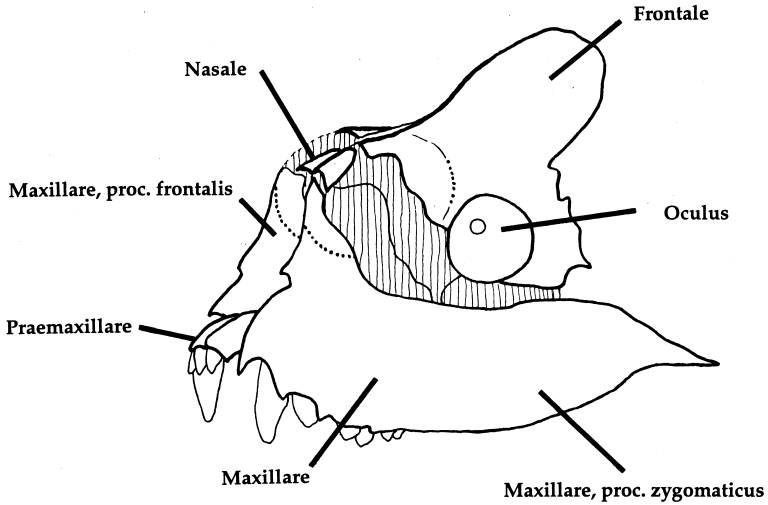


Figure 6.12. Line drawing taken from photograph of the rostral fontanel in a fetal *Hipposideros galeritus*, AMNH #152700; greatest length of skull = 12.38 mm, preserved body mass = 1.30 g, forearm length = 12.00 mm. Dotted lines represent the extent of the dorsal nasal chambers. Shaded regions represent the membranous median wall of the orbit and the rostral fontanel. (From Pedersen 1996.)

bones that persists until well after birth (Fig. 6.12), 2) the apparent loss of the lacrimal bone (as observed with the present technique), and 3) a reduction in the size of the nasal bones. Such elemental losses, translations, and/or distortions are not uncommon to the midface in either developmental or evolutionary terms (Haines 1940; Presley & Steel 1976; Presley 1981; Hanken 1983, 1984; Pedersen 1996). However, the unique coupling and suspension of the larynx and soft palate in rhinolophids manifests itself in characteristic shift in the ossification sequence of the stylohyoid chain, i.e., the ossification of all stylohyal elements is delayed until *after* the pterygoid processes are ossified. These features do not appear to be shared with the phyllostomids which exhibit the more generic sequence in which the chain ossifies before the pterygoid processes (de Beer 1937).

As an aside, the deciduous (milk) teeth of *Hipposideros caffer* are either resorbed or shed before parturition and the pups are born with a full battery of adult teeth ready to cut through the gums. This interesting feature is found in many chiropteran lineages (see Phillips, this volume). Here, however, it is important to note that the overall appearance of the perinatal skull of *Hipposideros* (and *Rhinolophus*) are exceedingly bizarre to

say the least. Lateral to the nasal passages, the maxillary corpus is dominated by dental crypts to the extent that it has the appearance of a thin-walled, elongate bag, stuffed with ball-bearings (Fig. 6.12). The appearance of the mandible is similar. Presently, work is being done to describe this unique relationship between maxillofacial growth and odontogenesis in rhinolophids.

#### THE ACOUSTICAL AXIS AND SKULL MECHANICS

Despite the wealth of information concerning the mechanics of the mammalian skull, there have been relatively few investigations of the biomechanics of bat skulls (Marshall & Butler 1966; Freeman 1979, 1984, 1988, 1992; Czarnecki & Kallen 1980). Apart from some experimental work concerning mastication (*Myotis*: Kallen & Gans 1972; *Pteropus*: de Guedre & de Vree 1984, 1988), most research in this area has either gone unpublished (Mohl 1971; Sperry 1972), is incidental to other studies (Matsumura 1979), or can be sampled in the present volume (see chapters by Pedersen, Phillips, and Vater, this volume). Bat crania exhibit a stunning range of morphological diversity that reflects their diverse dietary specializations. However, the orofacial component of the skull is exceedingly well integrated *regardless* of its relative position on the braincase (Starck 1952; Czarnecki & Kallen 1980; Freeman 1984; Pedersen 1993a). Despite this, does the dichotomy in skull form affect general skull mechanics in any predictable manner?

#### Mechanics of the midface

During mastication, the rostrum and zygomatic arches brace the palate against the braincase posteriorly, which then transfers these forces to the occiput and cervical spine. Strongly klinorhynchal skulls are thought to transfer forces from the palate to the basicranium ventrally with little involvement of the interorbital midface (e.g., *Daubentonia*: Cartmill 1977; Ross 1996). The distribution of bony mass in the strongly ventro-flexed skulls of many rhinolophids suggests a skull poorly reinforced to resist torsional forces; the rhinolophid zygoma is relatively weak, while the rostrum is extremely narrow dorsally. The bulk of the bony midface is distributed lateral to the choanae (pterygoid complex) where it may convey some degree of reinforcement to the palate akin to what is seen in other extremely klinorhynchal skulls (above). Conversely, bat skulls that are strongly aryrhynchal (dorsi-flexed rostra) are constructed such that forces are passed directly from the rostrum to the braincase via

the frontal bones (i.e., *Mormoops*) through a rather broad, robust interorbital midface. Little work has been done along these lines, but one might predict that bat species with extremely klinorhynchal or aiorrhynchal skulls will not exhibit robust masticatory forces. Rather, durophages (species that eat hard-bodied food items) should exhibit more moderate skull angulations (i.e., EARPAL) within their oral- or nasal-emitting construct (*Cheiromeles* and *Vampyrum* respectively; see also Freeman 1984).

### Nasal septum and the Old World nasal-emitters

The inner dimensions of the nasal passages and the composition and mass of the nasal septum (vomer, ethmoid, maxilla, vomeronasal cartilages, turbinates, etc.) are most often absent from discussions concerning bending and torsional forces within the rostrum. Extreme forms, such as Old World leaf-nosed bats (Rhinolophidae), exhibit unusual septa that are confounded by the adjacent dorsal nasal chambers and underlain by an abbreviated hard palate. Mechanically, this organization of the skull is not optimized for robust masticatory function. Among the many extraordinary features of this system is a kinetic premaxillary segment that is unique among mammals. Drs Bhatnagar and Wible have produced some intriguing evidence concerning a reinforced vomeronasal complex within the rhinolophoid nasal septum, possible sequelae of the kinetic premaxilla (personal communication). Furthermore, given the spatial restrictions of the midface (Haines 1940; Hanken 1984; Hoyte 1987), it seems unlikely that a nasal-emitting skull could exhibit both large olfactory fossae and resonating chambers within the interorbital septum. In the balance, phyllostomids may have retained olfaction at the cost of loudness of the call, while rhinolophoids may have emphasized loudness of the call at the expense of olfaction.

#### RHINOLOPHOID SKULL DESIGN AND ACOUSTICS

Here, I will shift emphasis to focus upon the highly modified skulls of the Old World nasal-emitters. The rostra of rhinolophoid bats are dominated by large outpocketings of the nasal cavity, the dorsal nasal chambers. These chambers are thought to act as resonators to amplify the echolocative call (Roberts 1972, 1973; Hartley & Suthers 1988; Suthers *et al.* 1988). Phyllostomids do not possess these resonant chambers and are therefore incapable of such call amplification. This feature led Griffin (1958) to label these New World nasal-emitters as 'whispering bats.' Despite these tremendous differences in the external appearance of their



skulls, rhinolophoid (Infraorder: Yinochiroptera; Koopman 1984) and phyllostomid bats (Infraorder: Yangochiroptera) share the same cranial infrastructure in which the head is constructed around a ventrally deflected palate (Pedersen 1993a, 1995). However, both types of nasal-emitting bats are faced with the same problem of projecting sound through the restrictive nasal passages.

### Acoustical considerations

The sound emitted by the larynx consists of a fundamental frequency ( $f_1$ ) that may be accompanied by several overtones, or harmonics. Vocalizations are modified in the vocal tract by the differential filtering and amplification of various frequency combinations. This filtering is effected by abrupt changes in the diameter of the vocal tract and discontinuities in the pharyngeal wall (i.e., diverticular bursae and orifices). Adult Old World nasal-emitting bats that utilize constant-frequency (CF) calls typically emphasize the second harmonic ( $f_2$ ), eliminate the fundamental ( $f_1$ ), and de-emphasize the remaining overtones. In these animals, the acoustics of the vocal tract have been modeled with some success (Roberts 1972; Hartley & Suthers 1988; Suthers *et al.* 1988). Models of the vocal tract in non-adults are complicated by the constantly changing proportions of the growing larynx, pharynx, and rostrum. Nevertheless, the anatomical dimensions of fetal and juvenile vocal tracts (*R. affinus*, *H. armiger* and *H. galeritus*) were fitted to mathematical equations concerning acoustics theory (Pedersen 1996). In general, there is a mismatch between laryngeally produced sound and the acoustic properties of the developing rostrum in all three species until well after parturition (Fig. 6.13).

#### *Fundamental frequency*

As the rhinolophid juveniles shift from their multi-harmonic, orally-emitted, isolation calls to their first nasally emitted calls, several harmonics (including the fundamental) are lost from the call structure. The space between the adult glottis and the laryngo-nasal junction is one quarter of a wavelength ( $f_1$ ) in length (*Rhinolophus*), and shaped like an expansion chamber resonator. Such chambers specifically absorb quarter wavelengths making this the most likely location at which the fundamental is suppressed in the adult supraglottal vocal tract. The nasopharynx never reaches a length capable of supporting a resonant  $f_1$  at any age. As such, the apparent loss of  $f_1$  from echolocation calls may be a by-product of simply closing the mouth.

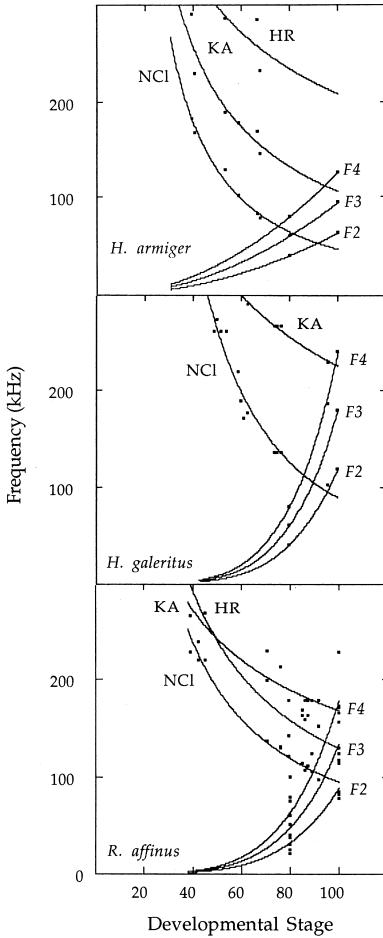


Figure 6.13. Hypothetical length-frequency curves. Based on the dimensions of the fetal nasal passages, hypothetical tuning/filter curves were calculated for the second (simple resonance equations), third (Helmholtz resonance within the dorsal nasal chambers), and fourth harmonics (KA filtering; see Kinsler & Frey 1962). Literature values for the second (Table 6.2), third, and fourth harmonics are included in successive plots for three rhinolophoid developmental series. Note: 1) hypothetical (calculated from measurements of fetal dimensions) and actual (literature) values for the second harmonic ( $F_2$ ) do not intersect until the pups have reached near-adult size, 2) dimensions of the dorsal nasal chambers in *R. affinis* are sufficient to suppress the third harmonic by way of Helmholtz resonance, and 3) KA filtering is capable of removing the fourth harmonic ( $F_4$ ) from adult calls in each of the three species.

### Second harmonic

If sound is to pass with minimal impedance (i.e., resonance) through the nasal cavity, there is a fixed relationship between the length of the cavity and the frequency (e.g., the second harmonic resonates when the length of the chamber is one wavelength). As the larynx grows, its sounds are not matched by the resonant properties of the nasal cavities until well after birth. It is only at this time that adult frequencies and adult-sized resonant filters match such that the second harmonic comes to dominate the CF call structure (Matsumura 1979; Konstantinov 1989). The results of this predictive model (Table 6.2, Fig. 6.13) coincide with the timing of the first appearance of adult  $f_2$ s noted by several other studies. It would appear that a juvenile must 'grow into' its second harmonic, and the dominance of the second harmonic in CF calls may not lie in some unique feature of a second harmonic *per se* (Roberts 1973; Hartley & Suthers 1987), but rather that it is the only frequency that is able to match the anatomical constraints imposed on echolocation by the nasal passages throughout the evolution of the rhinolophoid skull.

### Third harmonic

Adult rhinolophoid bats emit their echolocative calls through an extensively modified nasopharynx. One obvious modification is the gross distortion of the nasal passages to form 'dorsal nasal chambers.' The presence of an  $f_3$  in rhinolophid juveniles and its frequent absence in adults (e.g., *R. hildebrandti*) indicates an additional filter must develop elsewhere in the nasal passages, and it is the dorsal nasal chambers that have been hypothesized to remove the third harmonic from the vocalization by acting as Helmholtz resonators (Suthers *et al.* 1988). Hartley & Suthers (1988) rejected Helmholtz suppression of  $f_3$  in *R. hildebrandti*. However, dimensions of the dorsal nasal chambers in 3-week-old *R. affinus* pups were clearly capable of Helmholtz suppression of the third harmonic. Helmholtz suppression of  $f_3$  does not appear to be a consideration for *H. armiger* nor *H. caffer* as the dorsal nasal chambers in these two species never achieve the necessary dimensions (Fig. 6.13; Pedersen 1996).

### Anatomical correlates of the dorsal nasal chambers

Of great interest are the effects of the dilation of these chambers on craniofacial development and cranial evolution in rhinolophid bats. Developmental sequelae of the expansion of these chambers include:

Table 6.2. Second harmonic frequencies of some Old World nasal-emitting bats

	Neonate $f_2$	Adult $f_2$	Literature source
<i>Asellia tridens</i> (Geoffroy, 1812)	-	111, 120	Obrist <i>et al.</i> 1993; Pye 1972; Roberts 1972
<i>Hipposideros caffer</i> (Sundervall, 1846)	-	138, 150	Obrist <i>et al.</i> 1993; Pye 1972; Roberts 1972
<i>Hipposideros diavosus</i>	-	70	Obrist <i>et al.</i> 1993
<i>Hipposideros commersoni</i> (Geoffroy, 1813)	-	56, 69	Pye 1972; Roberts 1972
<i>Hipposideros diadema</i>	40	58, 63	Brown & Grinnel 1980; Roberts 1972
<i>Hipposideros lankadiva</i>	-	70	Obrist <i>et al.</i> 1993
<i>Rhinolophus alcyone</i> (Temminck, 1852)	-	90	Roberts 1972
<i>Rhinolophus eloquens</i>	-	80	Obrist <i>et al.</i> 1993
<i>Rhinolophus euryale</i> (Blasius, 1853)	-	104	Pye 1972
<i>Rhinolophus ferrumequinum</i> (Schreber, 1775)	40	82, 86	Konstantinov 1973, 1987; Pye 1972; Roberts 1972, 1973
<i>Rhinolophus f. nippon</i>	48	72	Brown & Grinnel 1980; Matsumura 1979, 1981
<i>Rhinolophus f. ferrumequinum</i>	25	83	Brown & Grinnel 1980
<i>Rhinolophus fumigatus</i>	-	45	Roberts 1972
<i>Rhinolophus hildebrandti</i> (Peters, 1878)	-	46	Hartley & Suthers 1988; Suthers <i>et al.</i> 1988
<i>Rhinolophus hipposideros</i> (Bechstein 1801)	50	110, 114	Konstantinov 1987; Pye 1972; Roberts 1972
<i>Rhinolophus landeri</i> (Martí 1837)	-	121	Roberts 1972
<i>Rhinolophus luctus</i>	-	42, 45	Roberts 1972, 1973
<i>Rhinolophus rouxii</i>	20	72, 78	Obrist <i>et al.</i> 1993; Rübtsamen 1987, 1988
<i>Trienops ajfer</i>	-	79	Roberts 1972

Note: All values are taken directly from the literature or approximated from figures. Neonate  $f_2$ s are typically 'isolation calls' emitted from the mouth.

1) gross dorsolateral distortion of the maxillary corpus, 2) the apparent loss of the lacrimal bone as a separate ossification center (see above), 3) the transformation of the infraorbital foramen into an infraorbital canal, 4) the reduction in mass of the floor of the nasal cavity (e.g., the premaxillary segment is kinetic, and the maxillary contribution to the hard palate is very small), and 5) the appearance of supernumerary fontanels centered over each of the paired dorsal nasal chambers (see above, Fig. 6.12). These fontanels expand with volumetric changes in the underlying chambers and remain open until 2–3 weeks postpartum. Their influence on the construction of the midface is a clear example of how capsular growth is independent of the growth of adjacent or overlying bone(s) early in development (Presley & Steel 1976; Presley 1981; Hanken 1983; Pedersen 1991, 1993*a, b*). Similar observations have been reported in frogs (Hanken 1984), artiodactyls, lagomorphs, rodents (Hoyte 1987), marsupials, carnivores, and primates (Haines 1940).

Additional interpretations of the function of the dorsal nasal chambers include the possibility that they may act as spacing elements within the maxillary corpus and affect the relative position of the posterior nasal septum and choanae. In this manner, the chambers indirectly determine the dimensions of the resonant chamber and the length of the standing wave of the second harmonic. In addition, the characteristic bossing of the maxillae above and anterior to the dorsal nasal chambers may also help support the adjacent noseleaf.

### Physiological integration

The physiological integration of vocalization with audition is a gradual process that is primarily dependent on the maturation of the head and its function as an acoustical horn and receiver. Neither the rostrum nor the pinnae (Obrist *et al.* 1993) exhibit dimensions capable of adult acoustics (certainly not the dominant spectral component of the adult call –  $f_2$ ) until well after birth. Ironically, the dimensions of the cochlea and the basal membrane are established at birth before physiological responses from the brain can be measured (Konstantinov 1973; Brown & Grinnel 1980; Vater 1988). Eventually, a neural-auditory filter focused at the second harmonic appears, but only at those frequencies used by the young animals. Gradually, a progressive tuning of the auditory filter and the maturation of the larynx shift upwards into the higher frequencies used by adults (Konstantinov 1973; RübSamen 1987, 1988). Although RübSamen (1987, 1988) put forth the excellent argument that maturation of neurological processing and cochlear function are the **dominant processes during the ontogeny of echolocation in rhinolophids**

(i.e., *Rhinolophus rouxi*), it is clear that neurological development is secondary to the maturation and ‘tuning’ of the head. Indeed, it is difficult to conceive of a control mechanism that regulates cranial growth such that the skull grows to match cochlear dynamics. Rather, a more parsimonious explanation would suggest that as the rostrum grows, neurophysiology must adapt to those sounds produced by the larynx and ‘permitted’ by the supraglottal vocal tract (but see Vater, this volume).

## EVOLUTIONARY SYNTHESIS

### Distinct developmental paths

Echolocation has been a primary factor in microchiropteran evolution, but the developmental and evolutionary mechanisms by which nasal-emission evolved are speculative. The divergence between oral- and nasal-emitting forms of the adult skull is most likely an exaptation (Gould & Vrba 1982), resulting from selective forces acting upon the form and function of the pharynx during echolocation rather than the result of selection on cranial shape or head posture *per se*. Developmentally, the microchiropteran skull has been canalized into three distinct evolutionary paths: 1) oral-emitting forms (primitive state: Jepsen 1966; Smith 1976; Van Valen 1979; Habersetzer & Storch 1987, 1992), 2) simple nasal-emitting forms (New World nasal-emitters), and 3) derived nasal-emitting forms (resonator-equipped Old World nasal-emitters). The latter two provide a clear example of convergent evolution in that both nasal-emitting forms share three distinct (albeit functionally related) features: 1) behavior: the nasal-emission of the echolocative call, 2) soft-tissue: the fleshy, often elaborate, flap of skin projecting around the nostrils (nose-leaf) that helps focus the call as it is emitted through the nostrils (Möhres 1966a, b; Simmons & Stein 1980; Hartley & Suthers 1987, 1988, 1990; Pye 1988; Arita 1990), and 3) osteology: the reorganization of the skull about the nasal passages (Fig. 6.14; Pedersen 1993a). As such, the fine details of microchiropteran skull morphology could be perceived as simple epigenetic accommodations to the fundamental use of the head as an acoustical horn. Similar examples of taxonomic radiations coincident with developmental pattern shifts are not uncommon (Needham 1933; Gould 1977; Alberch *et al.* 1979; Alberch & Alberch 1981; Müller 1990).

### Adaptive landscapes

To visualize morphological evolution, taxa have been pictured as migrating through an adaptive landscape whose topology represents

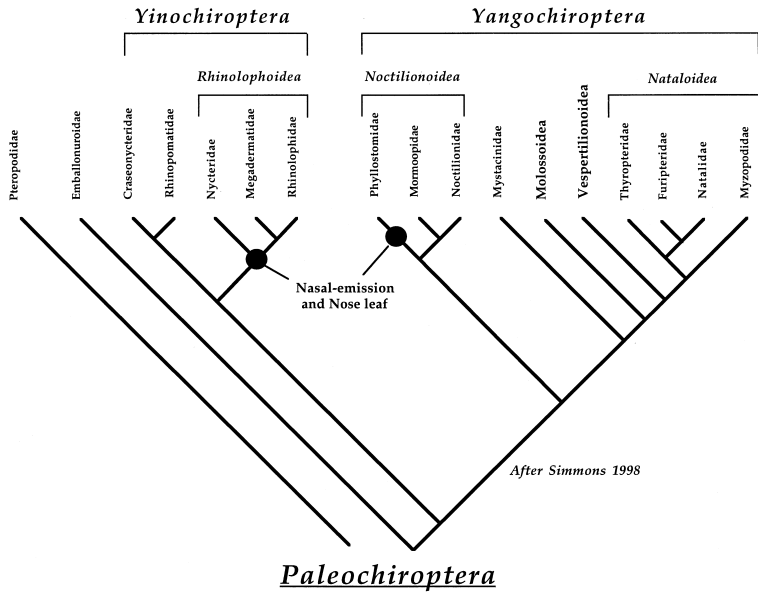


Figure 6.14. Convergent evolution of nasal-emitting forms in the Microchiroptera. Extant Microchiroptera are separated into two infraorders based upon the mobility of the premaxillae: the Yinochiroptera (premaxillae free from the maxillae) and the Yangochiroptera (premaxillae fused to the maxillae; Koopman 1984; see Simmons, this volume). Nasal-emitting groups have evolved three unique features independently: nasal-emission of the echolocative call, rearrangement of the skull about the nasal cavity, and possession of a noseleaf. (After Simmons 1998.)

different morphological constructs (Simpson 1944, 1953). Adaptive morphological constructs appear at the tops of peaks spotted throughout an evolutionary landscape. Accordingly, I reworked the bivariate representation of oral-emitting and nasal-emitting adult skull shapes (Fig. 6.6) as an adaptive landscape (Fig. 6.15) that clearly depicts two adaptive peaks representing the dichotomy between the nasal and oral phonal axes of the head.

Developmentally, taxa migrate through a morphogenetic landscape as well (Figs. 6.5, 6.15). Here, selection *in utero* is based upon mechanical feasibility and compatible histogenesis within the ontogenetic milieu (Katz *et al.* 1981; Alberch 1982; Katz 1982; Müller 1990) such that structural accommodation throughout development may be more important than Darwinian selection after parturition (Schmalhausen 1949; Kuhn 1987; Bonner 1988; Maier 1989; Presley 1989). While the spaces between peaks in the adult landscape are often considered 'non-adaptive' (Simpson 1944), inter-peak regions in the developmental landscape may

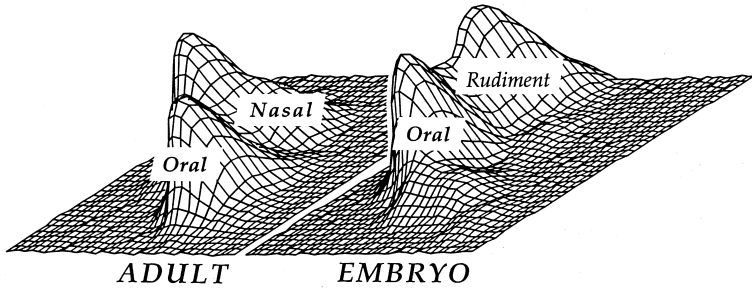


Figure 6.15. Adaptive landscapes. These landscapes are three-dimensional reconstructions of Figs. 6.5 and 6.6 designed to illustrate the two basic forms of the chiropteran skull (oral- and nasal-emitting peaks). The shallow saddle between peaks in the developmental landscape is occupied by oral-emitting fetuses as they migrate from the rudimentary morphospace toward the oral-emitting morphospace. (From Pedersen 1995.)

be traversed or transiently occupied by individuals sufficiently integrated to survive gestation (Cheverud 1982, 1989). Shifts from one peak to the other require the rerouting of an ancestral developmental path (oral axis) onto a new morphogenetic trajectory (nasal axis) – a ‘key innovation’ (Frazzetta 1975; Cracraft 1990; Müller 1990; Raff *et al.* 1990). This ‘new’ *Bauplan* is set in place before internal selective forces affect morphogenesis (mechanical integration of musculoskeletal elements surrounding the pharynx), and certainly before the first neonatal vocalizations.

Because this dichotomy is clearly associated with the co-opting of the nasopharynx as an acoustical horn in nasal-emitting species, intermediate states would be quickly weeded out early in the developmental program because of the precise anatomical and physiological requirements for the efficient emission of ultrasound by adult bats (Simmons & Stein 1980; Pye 1988; Suthers *et al.* 1988). The strictness of this selection suggests that the shift from oral-emission to nasal-emission must have occurred quickly both in developmental and evolutionary terms (Lewin 1986; Price *et al.* 1993). Continuing studies of this conjunction of developmental, behavioral, and morphological data provides a tremendous springboard from which to evaluate the genetic, paleontological, and biogeographical underpinnings of chiropteran evolution.

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