

Scott C. Pedersen

Skull growth and the presence of auxiliary fontanels in rhinolophoid bats (*Microchiroptera*)

Accepted: 12 October 1996

Abstract Cephalometry was used to detect patterns of cranial growth in fetal bats that have been differentially stained for bone and cartilage. Rhinolophoid bats exhibit elaborate nasal cavities with coincidental distortions of the maxilla. The expansion of these cavities creates paired auxiliary fontanels among the nasal, maxillary, and frontal bones. This distortion of the rostrum is also associated with the loss of the lacrimal bones and the modification of the infraorbital foramen into a shallow canal. The use of the head as an acoustical horn is discussed with reference to the ontogeny of echolocation.

A. Introduction

Cranial growth and form are generally considered to be “soft tissue” phenomena that are affected only secondarily by osteological development (Bosma 1976; Moss 1972a, b; Silver 1962; Starck 1989). “Skull growth is the effect, not the cause of cephalic growth” (Moss 1960, 1975, 1976). Indeed, differential growth of the brain and pharynx governs the shape of the chondrocranium and influences the forms of the desmo- and viscerocrania in the embryo (Hanken and Thorogood 1993; Klima 1987; Ranly 1980; Sperber 1989). Within the confines of the 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 bones, sutures, and synchondroses (Blechschiidt 1976a, b). Ensuing spatial competition among the various components effects further changes in the overall conformation of the skull (Hanken 1984; Solow and Greve 1979) and in the relative shape, position, and orientation of each affected component (Bosma 1976; Haines 1940; Hanken 1983; Pedersen 1995; Silver 1962).

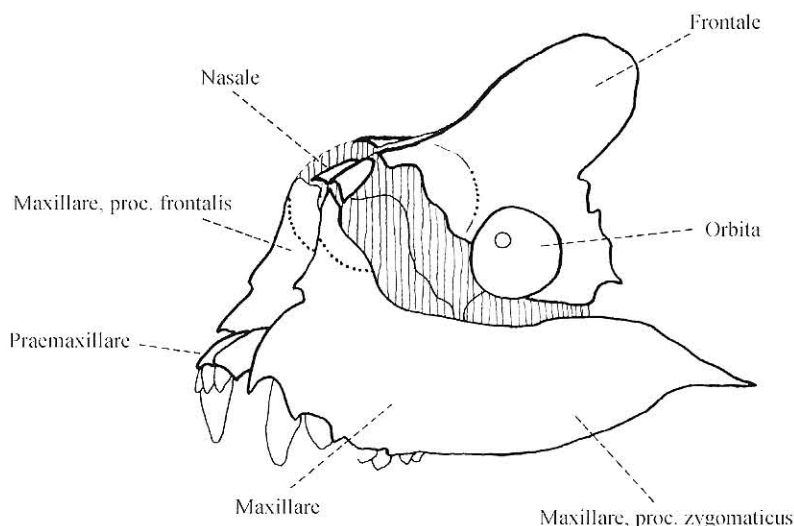
Spatial competition is accommodated by the inherent morphogenetic plasticity of the affected structures, e.g., pharynx, braincase, otic and optic capsules. This plasticity is in proportion to tissue composition, compliance in growth rates, the gross translation of elements, or distortion of affected structures in situ (Müller 1990; Raff et al. 1990). When such mechanisms fail, spatial or mechanical constraints come into play that can effect gross morphological changes in skull form (Hanken 1983; Herring 1985; Herring and Lakars 1981).

One of the most easily demonstrated examples of mechanical constraint is found at the interface between soft tissue and bone during the early stages of osteogenesis. For example, premature ossification of the cranial base effects a range of morphogenetic changes to the midface and cranial vault (rodents: Moss 1976; bats: Sperry 1972; cattle: Julian et al. 1957; humans: Moore 1983; Sperber 1989; Thilander and Ingervall 1973). Another example of mechanical constraint concerns the location and shape of fontanels which exist within the interface between bones within the capsular membrane. Their form reflects the dynamic interplay between capsular growth and the rate at which bone responds by further mineralization and remodeling of existing bone surfaces. The reciprocity between bone growth and the shape of an enclosed space is well represented in pathogenic studies where sutures are involved (synostoses: Koskinen-Moffet and Moffet 1989) and in instances of malformation of the central nervous system, e.g., hydrocephaly and anencephaly (Sperber 1989). Less well known are the dynamics of fontanels and their place in evolutionary patterns of skull evolution.

The mammalian head begins growth tucked firmly against the neck and chest from where it rotates dorsad about the cervical axis. Simultaneously, the rostrum rotates dorsad around the basicranium into alignment with the floor of the braincase (Schachner 1989). This basic skull organization and alignment (*Bauplan*) is the plesiomorphic condition for mammals (Van Valen 1979; Vaughan 1972: Emballonuroids, and Vespertilionoids).

S.C. Pedersen (✉)
School of Dentistry, Department of Orthodontics,
University of Washington, Seattle, WA 98195, USA;
Tel. 206 543 5788;
Fax 206 685 8163;
e-mail bathead@u.washington.edu

Fig. 1 Line drawing taken from photograph of the rostral fontanel in a fetal *Hipposideros galeritus*, AMNH no 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



With respect to microchiropteran evolution, the general organization of the rostrum reflects the construction of the microchiropteran skull around either the oral or nasal cavity and the use of the facial skeleton as an acoustical horn. As is the case with oral-emitting taxa, the rostrum, and hence the hard palate, is aligned with the basicranium and the echolocative call is forced directly out through the mouth. Conversely, palates of nasal-emitting bats are retained ventral to the basicranial axis (Freeman 1984; Pedersen 1993a; Starck 1952) and the echolocative call is forced directly out through the nostrils. Biomechanically, intermediate positions of the hard palate are poorly suited for echolocation as the call would be directed either above or below the mean flight trajectory.

Phonation (echolocation) has been a primary factor in microchiropteran evolution, but the mechanism by which nasal emission evolved is speculative. However, nasal emission is most likely an exaptation (Gould and Vrba 1982) of selective forces acting upon the form and function of the larynx rather than the result of focused selection on head posture per se. But with respect to the form of the rostrum, rostra of rhinolophoid bats are dominated by large outpocketings of the nasal cavity, the dorsal nasal chambers. These chambers may act as resonators to amplify the echolocative call (Hartley and Suthers 1988; Roberts 1972, 1973; Suthers et al. 1988). Phyllostomids do not possess these resonant chambers so are incapable of amplifying the call. This feature led Griffin (1958) to label these New World nasal emitters as “whispering bats.” Despite tremendous differences in the external morphology 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). This convergence in form is an example of the independent evolution of: (1) a “nasal-emitting” fetal *Bauplan*, (2) a nasal-emitting adult skull form, and (3) a nose leaf.

Herein, relations between the nasal cavities and accessory fontanels (Fig. 1) in rhinolophoid bats are de-

scribed. In addition, I test the hypothesis that ontogenetic changes in the acoustical properties of the rhinolophoid rostrum precede and subordinate the maturation of the auditory system and the young animals subsequent ability to echolocate.

B. Materials and methods

1. Specimens

I observed skeletal development in cross-sectional series of whole embryos of the species *Hipposideros armiger*, *H. galeritus*, and *Rhinolophus affinis*¹. Fetuses were cleared by maceration and differentially stained for bone and cartilage (Hanken and Wassersug 1981; Klymkowsky and Hanken 1991). To stage the fetal material and to ameliorate the differences in head sizes and shapes among species, the index STAGE was used 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 final proportion in an adult skull:

$$\text{STAGE} = \left\{ \frac{\sqrt{(\text{embryo brain case length} \cdot \text{width})}}{\sqrt{(\text{embryo skull length} \cdot \text{width})}} \div \frac{\sqrt{(\text{adult brain case length} \cdot \text{width})}}{\sqrt{(\text{adult skull length} \cdot \text{width})}} \right\} \cdot 100 \quad (\text{Eq. 1})$$

In order to evaluate the degree to which each fetal skull had developed osteologically, a second index was used to describe the proportion of macroscopic bone foci present in each fetus relative to the number of bones expected in the adult skull:

$$\text{OSSSTAGE} = (\text{fetal foci count} / \text{adult bone count}) \cdot 100 \quad (\text{Eq. 2})$$

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).

¹ Specimens used in study: *Hipposideros armiger* Hodgson, 1835: AMNH 234113–117, 234120–121. *Hipposideros galeritus* Cantor, 1846: AMNH 104720, 152700, 152704–705, 158535, 158557, 158567–568, 158571–572, 158582, 158588, 158593, 158598, 158602, 158607. *Rhinolophus affinis* Horsfield, 1823: AMNH 216828, 216830, 216833, 216839, 216843, 234014, 234019, 234023, 234029, 247258, 247261, 247264, 247267

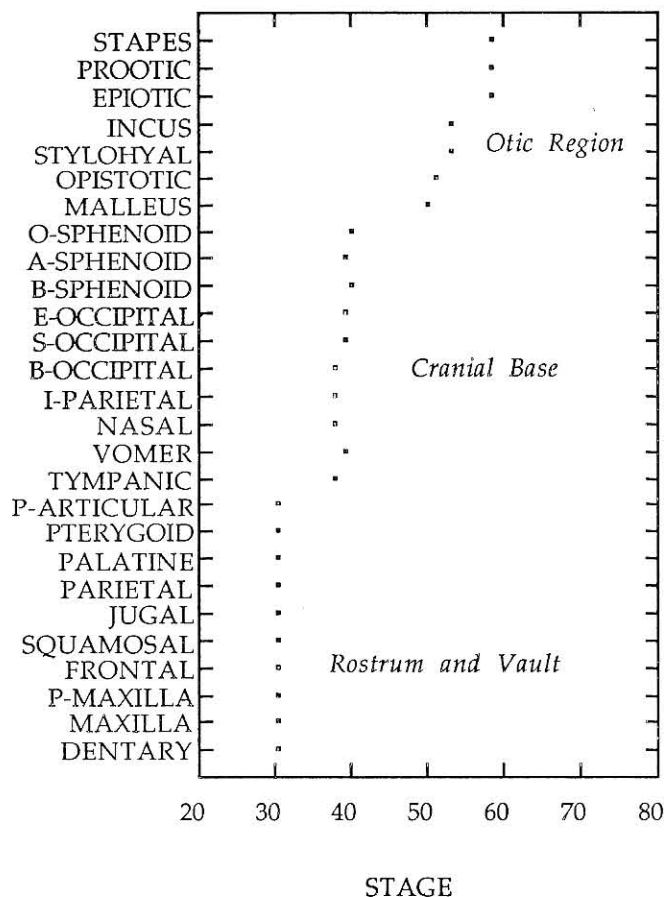


Fig. 2 Plot of cranial ossification sequences in three species of rhinolophoid bats: *H. armiger*, *H. galeritus*, and *Rhinolophus affinus*

2. Cephalometry

General protocol followed that used by Pedersen (1995). Camera lucida tracings were made of each cleared and stained fetal skull (left/lateral). Older specimens 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). Dimensions of adult skulls were measured directly from radiographs of each specimen with dial calipers (0.01 mm). Identical measurements were taken on the whole-mount fetal material with the aid of a calibrated optical micrometer mounted in a dissection microscope. There are several measurements of immediate interest. Firstly, the length of the right dorsal nasal chamber (DCI) approximates the diameter of one of the paired "resonators" in the rhinolophoid rostrum; one-half of this length approximates the radius (DCr) of each spherical chamber (Hartley and Suthers 1988). Secondly, in the nasal passages, the distance between the sphenoccipital synchondrosis and the posterior nasal spine represents the combined lengths of the nasopharynx (NPI) and the pharyngeal bursae (PBI). The tip of the epiglottis contacts the posterior edge of the soft palate at a point halfway between the aforementioned landmarks. Thirdly, the choanal bore, the internal diameter of both nasal passages together, affects airflow through the nasal cavities. One-quarter of this repeatable measurement approximates the radius of a single nasal passage (NPr). Lastly, the length of the maxillary portion of the hard palate, the distance between the posterior nasal spine and the premaxillary-maxillary suture, defines the contribution to the hard palate by the maxilla (MXI). This distance approximates the orifice diameter leading up into the dorsal and lateral nasal chambers. The allometric relations between these variables and STAGE are presented in Fig. 3 for each species.

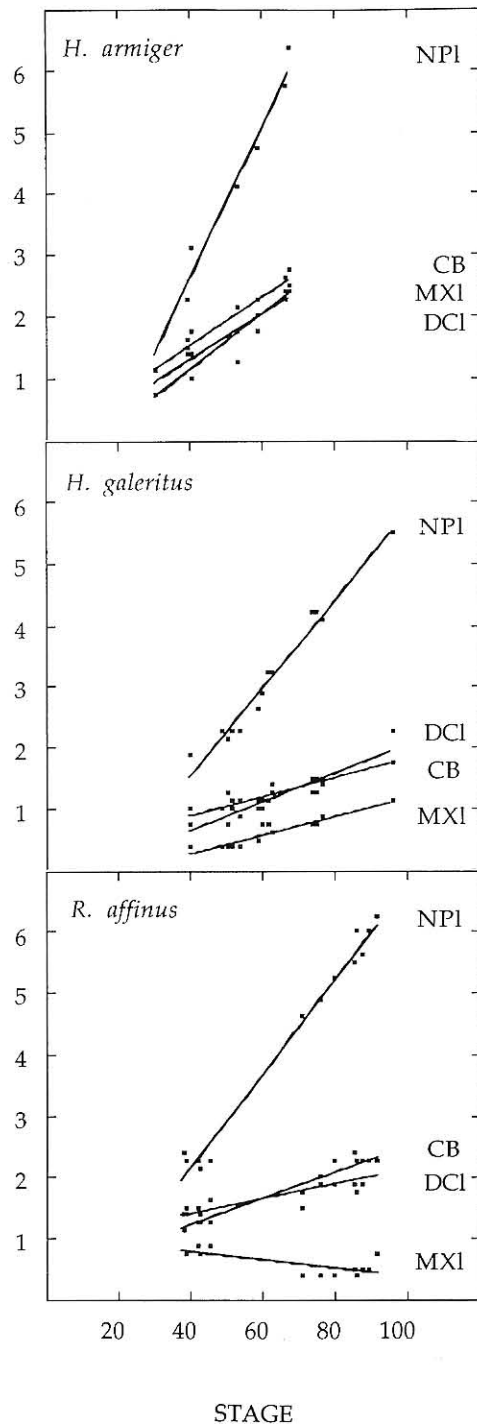


Fig. 3 Scatterplots showing lengths (mm) of the nasopharynx (NPI), dorsal nasal chamber (DCI), maxillary palate (MXI), and the choanal bore (CB) plotted against developmental stage (STAGE) in *H. armiger* ($n=7$), *H. galeritus* ($n=16$), and *R. affinus* ($n=13$)

3. Acoustic relationships

The sound emitted by the larynx consists of a fundamental frequency (f_1) that may be accompanied by several overtones, or harmonics. The rhinolophoid echolocative call passes through the nasal cavities and is commonly dominated by the second harmonic (Hartley and Suthers 1988). If this sound (f_2) is to pass with mini-

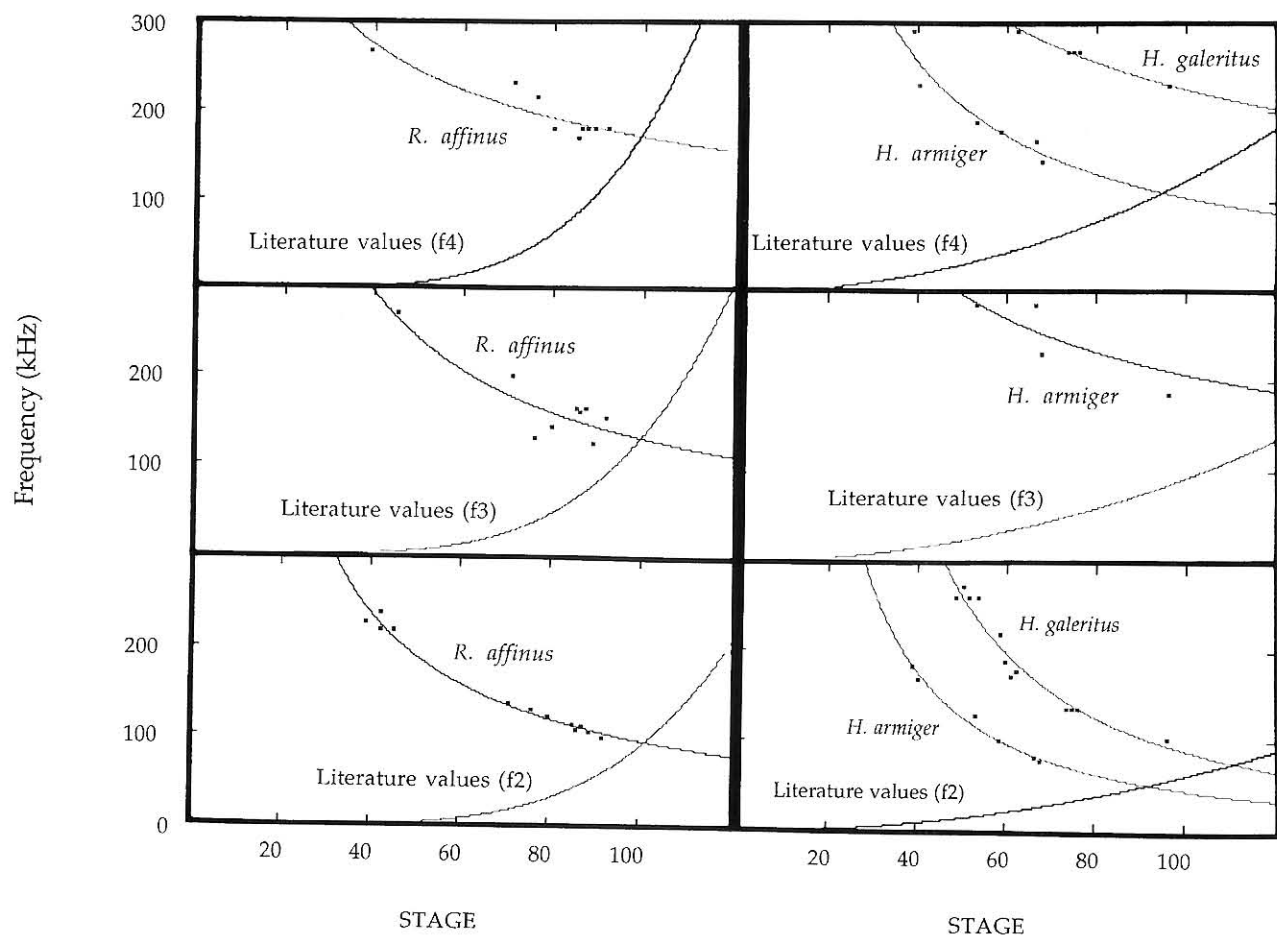


Fig. 4 Scatterplots showing hypothetical length-frequency curves for the nasal cavities ($NCI - f_2$), the dorsal nasal chambers ($HR - f_3$) and KA (f_4) filtering. Literature values (congeneries, Table 1) for the fourth, third and second harmonics (top to bottom) are included in successive plots. Plots of *Rhinolophus* are on the left and those of *Hipposideros* are on the right. Note: (1) hypothetical (fetal) and actual (literature) values for the second harmonic (f_2) do not intersect until pups have reached adult or near-adult size, (2) dimensions of the dorsal nasal chambers could accommodate HR (f_3) suppression in *R. affinis*, and (3) KA filtering is capable of removing the fourth harmonic (f_4) from adult calls in all three species

mal impedance through the nasal cavity (NPI), there is a fixed relationship between the length of the cavity and the frequency, i.e., resonance (velocity of sound = 343 m/s):

$$f_2 \cdot NPI = 343 \text{ m/s} \quad (\text{Eq. 3})$$

The relationship (KA) between pipe diameter and wavelength affects how sound passes through a pipe as well (Kinsler and Frey 1962):

$$KA = (2 \cdot \pi \cdot f_n \cdot \text{radius of pipe}) / 343 \text{ m/s} \quad (\text{Eq. 4})$$

Values of KA above 1.85 but below 2.5 are effectively filtered out in proportion to dimensions of the nasopharynx and the maturation of the vocal cords. That is, there exists an anatomical "filter window" for each frequency-pipe relationship (Crocker 1987; Hartley and Suthers 1988). If the radius of the pipe (NPr) is taken as one-quarter of the choanal bore (CB), and the resonant frequency (f_R) is estimated from the pipe length (NPI, see above) then the ratio of the pipe diameter to usable wavelengths can be refigured as:

$$KA = [\pi \cdot f_R \cdot (CB/2)] / 343 \text{ m/s} \quad (\text{Eq. 5})$$

If each spherical dorsal nasal chamber functions as a Helmholtz resonator (Suthers et al. 1988), there will be a direct relationship

between the dimensions of the Helmholtz chamber and the frequency that is removed from the call structure by this filter:

$$f_{HR} \approx (343 \text{ m/s}) \cdot \sqrt{S / (L \cdot V)}, \quad (\text{Eq. 6})$$

where,

$$V = \text{chamber volume} = 4/3 \cdot \pi \cdot (DCI/2)^3 \quad (\text{Eq. 7})$$

$$S = \text{orifice area} = \pi \cdot (MXI/2)^2 \quad (\text{Eq. 8})$$

$$L = \text{orifice length} = (MXI/2) \quad (\text{Eq. 9})$$

Approximations of orifice area and length are based on histological material presented by Grosser (1902). Length-frequency curves that represent the *theoretical* f_2 resonant within the fetal nasopharynx and the *theoretical* f_{HR} captured by fetal dorsal nasal chambers for each fetus in the study are presented in Fig. 4. Literature values of f_2 produced by rhinolophoid neonates and adults are presented in Table 1 and included in Fig. 4.

C. Results

I. Gross observations

The sequence of cranial ossification follows the general mammalian pattern (de Beer 1937), with the exception that the lacrimal bone was not observed macroscopically in any of the three taxa (Fig. 2). The lacrimals may very well exist histologically, but were not grossly visible with the present technique. Initially, intact infraorbital foramina are present, but are eventually transformed into infraorbital canals located superficially on the lateral sur-

Table 1 Second harmonic frequencies of some Old World nasal-emitting bats. All values are taken directly from the literature or approximated from figures

| | Neonate f_2 | Adult f_2 | Source |
|---|---------------|-------------|---|
| <i>Asellia tridens</i> (Geoffroy, 1812) | — | 111, 120 | Obrist et al. 1993, Pye 1972; Roberts 1972 |
| <i>Hipposideros caffer</i> (Sundervall, 1846) | — | 138, 150 | Obrist et al. 1993, Pye 1972; Roberts 1972 |
| <i>H. clivus</i> | — | 70 | Obrist et al. 1993 |
| <i>H. commersoni</i> (Geoffroy, 1813) | — | 56, 69 | Pye 1972; Roberts 1972 |
| <i>H. diadema</i> | 40 | 58, 63 | Brown and Grinnell 1980; Roberts 1972 |
| <i>H. lankadiva</i> | — | 70 | Obrist et al. 1993 |
| <i>Rhinolophus alcyon</i> Temminck, 1852 | — | 90 | Roberts 1972 |
| <i>R. eloquens</i> | — | 80 | Obrist et al. 1993 |
| <i>R. euryale</i> Blasius, 1853 | — | 104 | Pye 1972 |
| <i>R. ferrumequinum</i> Schreber, 1775 | 40 | 82, 86 | Konstantinov 1973, 1987; Pye 1972; Roberts 1972, 1973 |
| <i>R. f. nippon</i> | 48 | 72 | Brown and Grinnell 1980; Matsumura 1979, 1981 |
| <i>R. f. ferrumequinum</i> | 25 | 83 | Brown and Grinnell 1980 |
| <i>R. fumigatus</i> | — | 45 | Roberts 1972 |
| <i>R. hildebrandti</i> Peters, 1878 | — | 46 | Hartley and Suthers 1988, Suthers et al. 1988 |
| <i>R. hipposideros</i> Bechstein, 1801 | 50 | 110, 114 | Konstantinov 1978; Pye 1972; Roberts 1972 |
| <i>R. landeri</i> Martin, 1837 | — | 121 | Roberts 1972 |
| <i>R. luctus</i> | — | 42, 45 | Roberts 1972, 1973 |
| <i>R. rouxii</i> | 20 | 72, 78 | Obrist et al. 1993; Rübsamen 1987, 1988 |
| <i>Trionops afer</i> | — | 79 | Roberts 1972 |

face of the maxillary corpus. Paired fontanels bounded by the frontal, nasal, and maxillary bones were present in all specimens examined (Fig. 1). These fontanels are centered over each of the paired dorsal nasal chambers, they expand in kind with volumetric changes in the underlying cavities, and they remain open until 2–3 weeks post-partum.

II. Tuning of the head

The space between the adult glottis and the laryngo-nasal junction is one quarter of a wavelength (f_1) in length (*Rhinolophus*), and is shaped like an expansion chamber. The elongate nasopharynx is one wavelength (f_2) long, beginning at the laryngo-nasal junction and terminating anteriorly at the orifices of the dorsal nasal chambers and choanae. The dimensions of the dorsal, nasal chambers (*Rhinolophus*) are insufficient to contribute Helmholtz resonance of the third harmonic (f_3) until late in the juvenile period. Neither of the hipposiderid species exhibit a dorsal nasal chamber with dimensions capable of effecting any sort of f_3 filtering at any point in development. The dimensions of the nasopharynx suggest that a KA filter for the fourth harmonic (f_4) exists in all three species (Fig. 4).

D. Discussion

I. Fontanels

Adult rhinolophoid bats emit their echolocative calls through a nasopharynx that has been extensively modified to act as an acoustical horn. One correlate of this modification is the gross distortion of the nasal passages to form "dorsal nasal chambers", the expanse of which

maintain large fontanels between the nasal, maxillary, and frontal bones throughout the juvenile period and into early adulthood (Fig. 1). The dilation of the nasal chambers and the appearance of these supernumerary fontanels are matched by the gross posterolateral distortion of the maxillary corpus. Further consequences of this dilation include: (1) the apparent loss of the lacrimal bone as a separate ossification center, (2) the transformation of the infraorbital foramen into a superficial infraorbital canal, and (3) 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).

Such elemental losses, fusions, and distortions are not uncommon to the midface in either developmental or evolutionary terms (Haines 1940; Hanken 1983, 1984; Pedersen 1991, 1993a, b; Presley 1981, 1989; Presley and Steel 1976). These modifications are examples of how morphogenetic changes in one structure effect a cascade of changes in the structural integrity or spatial representation of adjacent elements (Bleichschmidt 1976b; Devillers 1965; Hanken 1983, 1984; Hanken and Hall 1988; Herring 1985; Hoyte 1987; Kay 1986; Klima 1987; Müller et al. 1989; Ranfjord and Ash 1966; Straney 1984; Thorogood 1988; Zelditch and Carmichael 1989). The influence of these chambers on the construction of the midface is also a clear example of how capsular growth is independent of the growth of adjacent or overlying bone(s) early in development (Hanken 1983; Pedersen 1991, 1993a, b; Presley 1981; Presley and Steel 1976). Similar observations have been reported in frogs (Hanken 1984), artiodactyls, lagomorphs, rodents (Hoyte 1987), marsupials, carnivores, and primates (Haines 1940). But with respect to chiropteran evolution, the construction and relative position of the hard palate are taxonomically relevant features that distinguish rhinolophoids from all other chiropteran taxa (Pedersen 1993a, 1995).

II. Tuning of the head

Vocalizations of nasal-emitting bats 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 orifices. Adult 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.

The acoustical dynamics of the vocal tract in a young bat are constantly changing in proportion to the changes in the growing larynx, pharynx, and rostrum. As juveniles shift from orally emitted isolation calls to their first nasally emitted calls, several harmonics remain, each of which is at a frequency much lower than the adult equivalents. It is not until the juvenile has been flying for about a week that adult frequencies and adult-type resonant filters are present leaving and second harmonic to dominate the CF call structure (Konstantinov 1987; Matsumura 1979; Rübsamen 1988).

Suppression of the f_1 may have more to do with the shape of the vocal tract itself than with any specific diverticulum or bursa (Hartley and Suthers 1988; Roberts 1972; Suthers et al. 1988). For example, the space between the glottis and the laryngo-nasal junction is one-quarter of a wavelength (f_1) in length (*Rhinolopus*) and shaped like an expansion chamber resonator. Such chambers specifically absorb quarter wavelengths (Kinsler and Frey 1962), making this the most likely location at which the fundamental is suppressed in the supraglottal vocal tract.

The rhinolophoid rostrum is incapable of resonating at its second harmonic until well after birth, sometime in the third or fourth week postpartum. However, this coincides nicely with the timing of the first appearance of a near-adult f_2 s noted in several other studies (Fig. 4, Table 1). It would appear that a juvenile must "grow into" its second harmonic and that there exists a point at which the sounds produced by the larynx come to match those sustained by the resonant qualities of the supraglottal vocal tract, one wavelength long (f_2). The usage of the second harmonic by nasal emitting CF bats may not lie in some unique feature of a second harmonic per se (Hartley and Suthers 1987; Roberts 1973), but rather that f_2 is what remains of the vocalization after it passes through the rostrum. Though Hartley and Suthers (1988) stated that the dorsal nasal chambers sit one full wavelength (f_2) above the glottis, it is more likely that the orifices of these chambers are positioned one wavelength (f_2) above the unique laryngo-nasal constriction (epiglottis).

Because the sub- and supraglottal portions of the vocal tract are acoustically isolated (Suthers et al. 1988), the presence of an f_3 in rhinolophid juveniles and its absence in adults indicates an additional filter must develop elsewhere in the nasal passages. The dorsal nasal chambers have been hypothesized to function as Helmholtz resonators (Suthers et al. 1988), however, there is little

support for the suppression of f_3 by Helmholtz resonance in the current study. The calculated Helmholtz suppression of the third harmonic (Eq. 6) matches the f_3 produced by *R. affinis* pups around the third week postpartum (Fig. 4, STAGE 90). However, this suppression does not appear to be a consideration for either of the hippo-siderids as the dorsal nasal chambers in these two species never achieve the necessary dimensions. In deference to Hartley and Suthers' (1988) rejection of Helmholtz suppression of f_3 in *R. hildebrandti*, the present data are suggestive enough to warrant further investigation of *R. affinis*.

An alternative interpretation of the function of the dorsal nasal chambers would be that they may function as spacing elements within the maxillary corpus. Their dimensions influence the location of the posterior edge of the nasal septum (choanae) and the anterior wall of the standing wave chamber (f_2). The characteristic bossing of the maxillary bone above and anterior to the dorsal nasal chambers may also help support the adjacent noseleaf.

The present data show that the fundamental, f_2 , and f_3 are not affected by KA filtering, whereas the fourth harmonic is removed by a KA filter in all three species (Hartley and Suthers 1988). It will be of great interest to test the uniformity of these results throughout the Rhinolophidae (see Novacek 1991).

III. A question of timing

The physiological integration of vocalization with audition is a gradual process that first appears around the time that pups begin to emit vocalizations nasally and make their first attempts at flight. This integration is primarily dependent on the maturation of the head in 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 to the brain can be measured (Brown and Grinnel 1980; Konstantinov 1973; 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 upward into the higher frequencies used by adults (Konstantinov 1973; Rübsamen 1987, 1988).

Although Rübsamen (1987, 1988) puts forth the excellent argument that maturation of neurological processing and cochlear function are the dominant processes during the ontogeny of echolocation in rhinolophids (*Rhinolophus rouxi* Temminck, 1835), I argue that neurological development must lag behind the maturation and tuning of the head. Indeed, it is difficult to conceive of a control mechanism that regulates cranial growth such that the pharynx grows to match cochlear dynamics.

Rather, a more parsimonious explanation is that, as the rostrum grows, cochlear dynamics track those sounds that are produced by the larynx and "permitted" by the supraglottal vocal tract.

Acknowledgements I wish to thank Drs. Patricia Freeman, Betty Sindelar, Rick Adams, Susan Herring, and several unknown reviewers for critical evaluation of this manuscript. I wish to thank the curators and staff of the zoological collections of the University of Nebraska State Museum and the American Museum of Natural History.

References

- Beer GR de (1937) Development of the vertebrate skull. Oxford University Press, Oxford (republished: University of Chicago Press, Chicago, 1985)
- Blechsmidt E (1976a) Principles of biodynamic differentiation. In: Bosma JF (ed) Development of the basicranium. DHEW publication no (NIH) 76-989, pp 54-76
- Blechsmidt M (1976b) Biokinetics of the developing basicranium. In: Bosma JF (ed) Development of the basicranium. DHEW publication no (NIH) 76-989, pp 44-53
- Bosma JF (1976) Introduction to the symposium. In: Bosma JF (ed) Development of the basicranium. DHEW publication no (NIH) 76-989, pp 3-28
- Brown PE, Grinnell AD (1980) Echolocation ontogeny in bats. Animal sonar systems. Plenum Press, New York, p 355-382
- Crocker M (1988) Acoustic noise. In: Parker SP (ed) Acoustics source book. McGraw-Hill Press, New York, pp 150-158
- Devillers C (1965) The role of morphogenesis in the origin of higher levels of organization. Syst Zool 14:259-271
- Freeman PW (1984) Functional analysis of large animalivorous bats (Microchiroptera). Biol J Linn Soc 21:387-408
- Gould SJ, Vrba ES (1982) Exaptation - A missing term in the science of form. Paleobiology 8:4-15
- Griffin D (1958) Listening in the dark. Yale University Press, New Haven, p 413
- Grosser O (1902) Zur Anatomie der Nasenhöhle und des Rachens der einheimischen Chiropteren. Gegenbaur Morphol Jahrb 29:1-77
- Haines W (1940) The interorbital septum in mammals. J Linn Soc London 41:585-607
- Hanken J (1983) Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae): II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. J Morphol 177:255-268
- Hanken J (1984) Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia: Plethodontidae). I. Osteological variation. Biol J Linn Soc 23:55-75
- Hanken J, Hall BK (1988) Skull development during anuran metamorphosis: I. Early development of the first three bones to form the exoccipital, the parasphenoid, and the frontoparietal. J Morphol 195:247-256
- Hanken J, Thorogood P (1993) Evolution and development of the vertebrate skull: The role of pattern formation. Trends Evol Ecol 8:9-15
- Hanken J, Wassersug R (1981) The visible skeleton. Funct Photog 4:22-26
- Hartley D, Suthers R (1987) The sound emission pattern and the acoustical role of the noseleaf in the echolocating bat, *Carollina perspicillata*. J Acoust Soc Am 82:1892-1900
- Hartley D, Suthers R (1988) The acoustics of the vocal tract in the horseshoe bat, *Rhinolophus hildebrandti*. J Acoust Soc Am 84:1201-1213
- Herring SW (1985) The ontogeny of mammalian mastication. Am Zool 25:339-349
- Herring SW, Lakars TC (1981) Craniofacial development in the absence of muscle contraction. J Craniofac Gen Dev Biol 1:341-357
- Hoyte DAN (1987) Muscles and cranial form. In: Kuhn HJ, Zeller U (eds) Mammalia depicta: morphogenesis of the mammalian skull. Paul Parey, Hamburg, pp 123-144
- Julian L, Tyler W, Hage T, Gregory P (1957) Premature closure of the spheno-occipital synchondrosis in the Horned Hereford Dwarf of the "short-headed" variety. Am J Anat 100:269-287
- Kay E (1986) The phenotypic interdependence of the musculo-skeletal characters of the mandibular arch in mice. J Embryol Exp Morphol 98:123-136
- Kinsler L, Frey A (1962) Fundamentals of acoustics. John Wiley, New York, pp 186-216
- Klima M (1987) Morphogenesis of the nasal structures of the skull in toothed whales (Odontoceti). In: Kuhn HJ, Zeller U (eds) Morphogenesis of the mammalian skull. Paul Parey, Hamburg, pp 105-121
- Klymkowsky M, Hanken J (1991) Whole-mount staining of *Xenopus* and other vertebrates. Methods Cell Biol 36:419-441
- Konstantinov A (1973) Development of echolocation in bats in postnatal ontogenesis. Period Biol 75:13-19
- Konstantinov A (1987) The ontogeny of echolocation functions in Horseshoe bats. In: Hanák V, Horáček I, Gaisler J (eds) European bat research 1987. Charles University Press, Praha, pp 271-280
- Koopman K (1984) A synopsis of the families of bats - Part VII. Bat Res News 25:25-27
- Koskinen-Moffet L, Moffet B (1989) Sutures and intrauterine deformation. In: Persing JA et al (eds) Scientific foundations and surgical treatment for craniosynostosis. Williams and Wilkins, Baltimore, pp 96-106
- Matsumura S (1979) Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): Development of vocalization. J Mammal 60:76-84
- Matsumura S (1981) Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): Vocal communication in three-week-old infants. J Mammal 62:20-28
- Moore KL (1983) Before we are born. 2nd edn. WB Saunders Co, Philadelphia
- Moss M (1960) Functional analysis of human mandibular growth. J Prosthet Dent 10:1149-1159
- Moss M (1972a) Functional cranial analysis and the functional matrix. In: Schumacher GH (ed) Morphology of the maxilla-mandibular apparatus. Symp Proc IX Int Cong Anat 1970. VEB Georg Thieme, Leipzig, pp 160-165
- Moss M (1972b) The regulation of skeletal growth. In: Goss RJ (ed) Regulation of organ and tissue growth. Academic Press, New York, pp 127-142
- Moss M (1975) Functional anatomy of cranial synostosis. Child's Brain 1:22-33
- Moss M (1976) Experimental alteration of basisynchondrosal cartilage growth in rat and mouse. In: Bosma JF (ed) Development of the basicranium. DHEW publication no (NIH) 76-989, pp 541-569
- Müller GB (1990) Developmental mechanisms: a side-effect hypothesis. In: Nitecki MH (ed) Evolutionary innovations. Chicago Press, Chicago, pp 99-130
- Müller G, Wagner G, Hall B (1989) Experimental vertebrate morphology and the study of evolution. Report of a workshop. Trends Vert Morphol 35:299-303
- Novacek MJ (1991) Aspects of the morphology of the cochlea in microchiropteran bats: An investigation of character transformation. Bull Am Mus Nat Hist 206:84-100
- Obrist M, Fenton MB, Eger J, Schlegel P (1993) What ears do for bats: a comparative study of pinna sound pressure transformation in Chiroptera. J Exp Biol 180:119-1552
- Pedersen S (1991) Dental morphology of the cannibal morph in the tiger salamander, *Ambystoma tigrinum*. Amphib-Rept 12: 1-14
- Pedersen S (1993a) Cephalometric correlates of echolocation in the Chiroptera. J Morphol 218:85-98

- Pedersen S (1993b) Skull growth in cannibalistic Tiger Salamanders, *Ambystoma tigrinum*. Southwest Nat 38:316-324
- Pedersen S (1995) Cephalometric correlates of echolocation in the Chiroptera II: Fetal development. J Morphol 225:107-123
- Presley R (1981) Alisphenoid equivalents in placentals, marsupials, monotremes and fossils. Nature 294:668-670
- Presley R (1989) Ala temporalis: function or phylogenetic memory. Trends Vert Morphol 35:392-395
- Presley R, Steel F (1976) On the homology of the alisphenoid. J Anat 121:441-459
- Pye J (1972) Bimodal distribution of constant frequencies in some hipposiderid bats (Mammalia: Hipposideridae). J Zool London 166:323-335
- Raff R, Parr B, Parks A, Wray G (1990) Heterochrony and other mechanisms of radical evolutionary change in early development. In: Nitecki MH (ed) Evolutionary innovations. University of Chicago Press, Chicago, pp 71-98
- Ranfjord S, Ash M (1966) Occlusion. W.B. Saunders Co, Philadelphia, pp 1-396
- Ranly D (1980) A synopsis of craniofacial growth. Appleton Century Crofts, Norwalk
- Roberts L (1972) Variable resonance in constant frequency bats. J Zool London 166:337-348
- Roberts L (1973) Cavity resonances in the production of orientation cries. Period Biol 75:27-32
- Rübsamen R (1987) Ontogenesis of the echolocation system in the rufous horseshoe bat, *Rhinolophus rouxi* (Audition and vocalization in early postnatal development). J Comp Phys A 161:899-913
- Rübsamen R (1988) Ontogeny of the echolocation system in rhinolophoid CF-FM bats: Audition and vocalization in early postnatal development. In: Nachtigall PE, Moore PWB (eds) Animal sonar, processes and performance. Proceedings NATO advanced study institute on animal sonar systems. Plenum Press, New York, pp 335-340
- Schachner O (1989) Raising of the head and allometry: Morphometric study on the embryonic development of the mouse-skeleton. Trends Vert Morphol 35:291-298
- Silver PAS (1962) *In ovo* experiments concerning the eye, the orbit and certain juxta-orbital structures in the chick embryo. J Embryol Exp Morphol 10:423-450
- Solow B, Greve E (1979) Craniocervical angulation and nasal respiratory resistance. In: McNamara JA (ed) Naso-respiratory function and craniofacial growth. Craniofacial growth series, monograph no 9, University of Michigan, Ann Arbor, pp 87-119
- Sperber GH (1989) Craniofacial embryology, 4th edn. Wright Press, London
- Sperry T (1972) Development of the specialized craniofacial complex in the bats of the genera *Mormoops* and *Chilonycteris* (Family Mormoopidae). PhD dissertation, University of Illinois Medical Center
- Starck D (1952) Form und Formbildung der Schädelbasis bei Chiropteren. Ergänzungsheft zum 99 Band; Verh Anat Ges 50th Versammlung Marburg. Anat Anz 99:114-121
- Starck D (1989) Considerations on the nature of skeletal elements in the vertebrate skull, especially in mammals. Trends Vert Morphol 35:375-385
- Straney J (1984) The nasal bones of *Chiroderma* (Phyllostomidae). J Mammal 65:163-165
- Suthers R, Hartley D, Wenstrup J (1988) The acoustical role of tracheal chambers and nasal cavities in the production of sonar pulses by the horseshoe bat, *Rhinolophus hildebrandti*. J Comp Physiol A 162:799-813
- Thilander B, Ingervall B (1973) The human spheno-occipital synchondrosis II. A histological and microradiographic study of its growth. Acta Odontol Scand 31:323-336
- Thorogood P (1988) The developmental specification of the vertebrate skull. Development (suppl) 103:141-153
- Van Valen L (1979) The evolution of bats. Evol Theory 4:103-121
- Vater M (1988) Light microscopic observations on cochlear development in Horseshoe bats (*Rhinolophus rouxi*). In: Nachtigall PE, Moore PWB (eds) Animal sonar, processes and performance. Proceedings NATO advanced study institute on animal sonar systems. Plenum Press, New York, pp 341-345
- Vaughan TA (1972) Mammalogy, 2nd edn. WB Saunders Co, Philadelphia
- Zelditch M, Carmichael A (1989) Ontogenetic variation in patterns of developmental and functional integration in skulls of *Sigmodon fulviventer*. Evolution 43:814-824