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Echolocation, evo-devo and the evolution of bat crania

SCOTT C. PEDERSEN AND DOUGLAS W. TIMM

The geneticists are trying to make evolution fit the genes rather than to make the genes fit evolution. (Osborn, 1932)

14.1 Introduction

Despite all other cranio-dental adaptations (Covey and Greaves, 1994; Dumont and Herrel, 2003), the microchiropteran head must function as an efficient acoustical horn during echolocation. This becomes infinitely more interesting when one considers that echolocation 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 (Starck, 1954; Wimberger, 1991; Schneiderman, 1992), the advent of nasal emission is viewed as a complex morphological innovation that required a substantial redesign of the microchiropteran rostrum: the nasal passages must be reoriented and aligned with the direction of flight, and they must have dimensions that provide for the efficient transfer of sound (resonance) through the adult skull. Once the acoustical axis of the head is established, bats emit a remarkable array of echolocation calls that reflect a great deal of behavioral plasticity. In the following treatment, we draw examples from developmental studies and functional morphology to illustrate how evolution has solved this intriguing design problem associated with nasal emission of the echolocation call.

14.2 Terminology: operational definitions

The term echolocation has been broadly applied to the Microchiroptera and to some members of the Megachiroptera. Despite evidence that shows that *Rousettus aegyptiacus* is able to navigate quite well by tongue clicking (Waters and Vollratch, 2003), there is no clear neuroanatomical, dental, developmental or physiological data whatsoever suggesting that pteropodids ever

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had the capacity for laryngeal echolocation or were derived from bats that did echolocate. Herein, the term "echolocation" will refer only to ultrasound produced by the larynx. It is our opinion that to do otherwise will confuse the understanding of the evolution of chiropteran communication, navigational skills and neural processing, i.e., ultrasound and tongue clicking should be considered separately during taxonomic analyses.

There is some confusion in the recent literature concerning mode of echolocation and call design (Pedersen, 2000; Eick *et al.*, 2005; Jones and Teeling, 2006; Jones and Holderied, 2007). Pedersen used the phrase "mode of echolocation" to refer to oral or nasal emission of the echolocation call (Pedersen, 1993, 1995, 1996, 2000), but more recently, others have used the term "mode" to refer to duty-cycle and band-width of a call (e.g., Fenton *et al.*, 1998). Herein, we will follow the latter use of the term and will specify oral or nasal emission separately.

There is an interesting dichotomy that is either overlooked or ignored in the taxonomic literature – that is, narrow-band, high-duty-cycle (CF) calls emitted by oral-emitting bats are quite different from those emitted by rhinolophids and hipposiderids; such oral emitted calls emphasize the fundamental frequency of the call, whereas nasal emitted calls emphasize the second harmonic and significantly reduce the fundamental (see discussion below).

This is a conceptual chapter. We are not testing phylogenetic hypotheses. We follow the taxonomy proposed by Simmons and Geisler (1998) with regard to nasal-emitting bats: Rhinolophoidea – nycterids, megadermatids, rhinolophids and hipposiderids; Noctilionoidea – phyllostomids.

14.3 Packaging of the head

The dynamic nature of the developing skeletal system is all too frequently overlooked in phylogenetic reconstructions wherein the skull is presented as an immutable structure into which the brain, ears and eyes are stuffed during development. Rather, the converse is more accurate; head growth and form are soft tissue phenomena affected only secondarily by osteological development (Hanken, 1983). As such, there is a great need to critically re-evaluate morphological data sets to see if epigenetic characters (e.g., location of various foramina, muscular processes, joint surfaces, linear dimensions of various squama) might be replaced by more conservative characters driven by the growth of cavities and spatial relationships amongst the various components of the head. That is, some characters or processes that were considered independent may not be as independent as they first seemed (Kangas *et al.*, 2004).

Indeed, early in development, it is differential growth of the brain and pharynx that governs the shape of the chondrocranium. Later, differential volumetric changes (brain, brainstem, eyes, tongue, teeth and pharynx) together with the ensuing mechanical competition for space within the confines of the growing head effect a cascade of modifications (often distant) to the shape, position and orientation of other structures throughout the growing skull via forces transmitted through the dura and periosteum to adjacent bones and sutures. These packaging concerns are accommodated/restricted by the developmental plasticity of each system in proportion to tissue composition, material availability, compliance in growth rates, the gross translation-distortion of elements *in situ* and *in utero* neonatal function (Haines, 1940; Moss, 1958; Burdi, 1968; Hanken, 1983, 1984; Smit-Vis and Griffioen, 1987; Müller, 1990; Hanken and Thorogood, 1993; Ross and Ravosa, 1993; Pedersen, 1995; reviewed by Pedersen, 2000).

14.4 Cephalometry

14.4.1 Rotation of the rostrum

Radiographic study of the angular relationships among the various skull components provides a size-free description of the basic internal arrangement of the head using internal landmarks and anatomical planes that are otherwise unavailable for morphometric analysis during a developmental study (Figure 14.1). As is typical in mammals, bat heads begin growth tucked firmly against the chest wall from where they rotate dorsad about the cervical axis (Figure 14.2). Simultaneously, the facial component of the bat skull rotates dorsad about the braincase. Certainly, rotation of the rostrum is limited in rate and direction by the ability of adjacent structures to get out of each other's way (Starck, 1952; Gaunt, 1967; Radinsky, 1968; Spatz, 1968; Sperry, 1972; Thilander and Ingervall, 1973; Moss, 1976; Tejada-Flores and Shaw, 1984; Smit-Vis and Griffioen, 1987; Schachner, 1989; Pedersen, 1993; Ross and Ravosa, 1993; Ostyn *et al.*, 1995; reviewed by Pedersen, 2000).

The motive forces behind these rotations are complex, but the brain has been identified as the primary driving force in primate skulls (Sperry, 1972; Thilander and Ingervall, 1973; Moss, 1976). However, it would appear that brain volume in bats has not played a strong role in the craniofacial form; rather, the relative size and differential development of the chiropteran brain is associated with the occupation of specific aerial/feeding niches (Eisenberg and Wilson, 1978; Stephan *et al.*, 1981; Jolicoeur *et al.*, 1984, Pedersen, 1993, 2000; Reep and Bhatnagar, 2000; Hutcheon *et al.*, 2002; Safi and Dechmann, 2005; Dechmann and Safi, 2009) leaving us to search for other forcing elements such as the olfactory bulbs, eyes and larynx. Pedersen (2000) argued that there was only enough room in the bat rostrum to deploy (anatomically speaking) two of the three sensory modalities available to bats at any one time (visual, olfactory, echolocation).

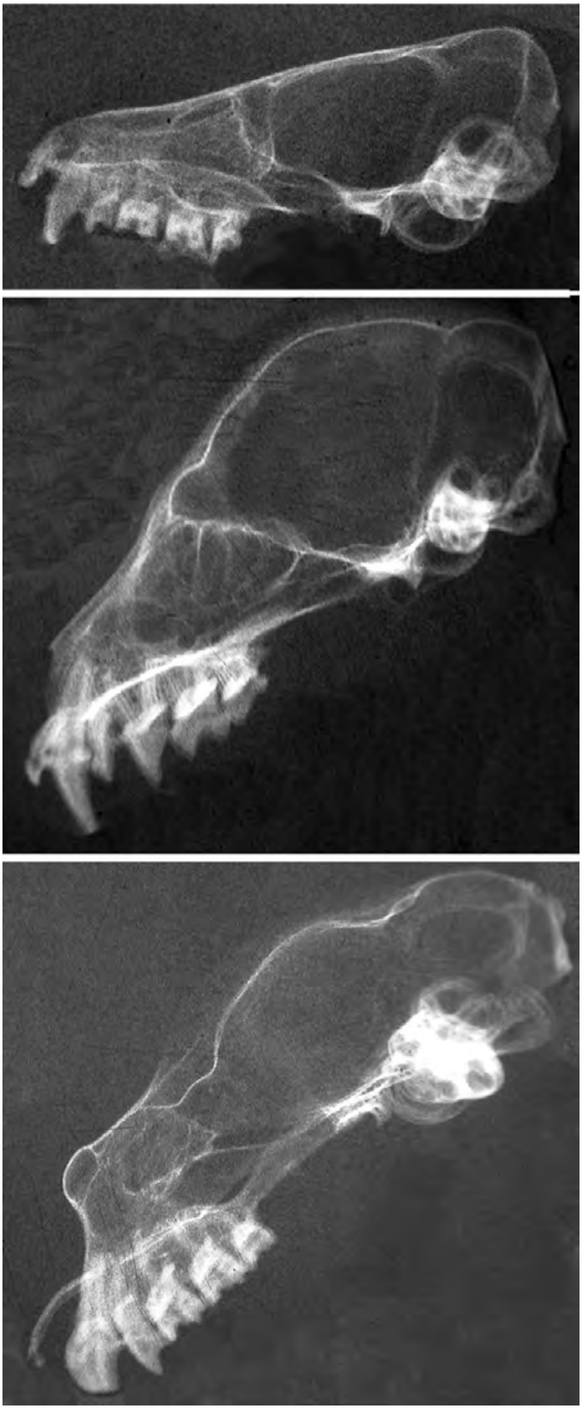

Figure 14.1 Representative skull radiographs (top to bottom): oral emitter (*Eptesicus*); phyllostomid nasal emitter (*Artibeus*); rhinolophid nasal emitter (*Rhinolophus*). Each skull is oriented such that the lateral semicircular canals share a similar orientation with the horizontal (approx. 15°).

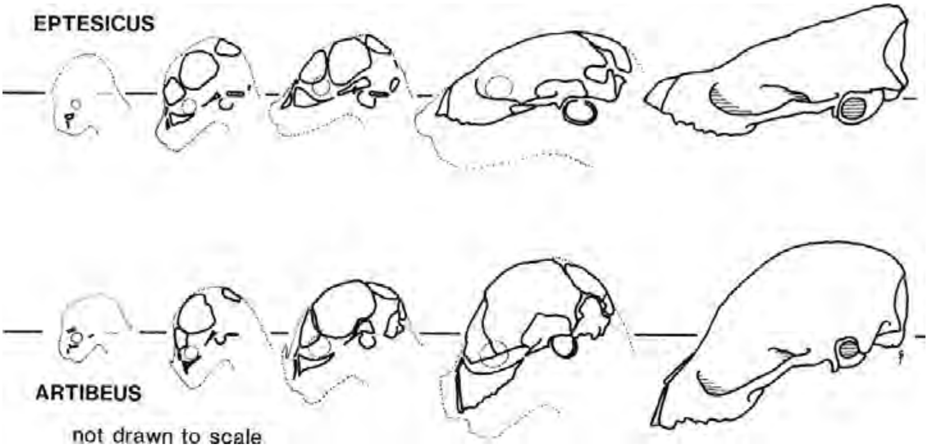

Figure 14.2 The distinctive dorsad rotation of the orofacial complex in oral emitters is illustrated by *Eptesicus*. The orofacial complex in nasal emitters as exemplified by *Artibeus* remains "tucked" throughout development (from Pedersen, 1993).

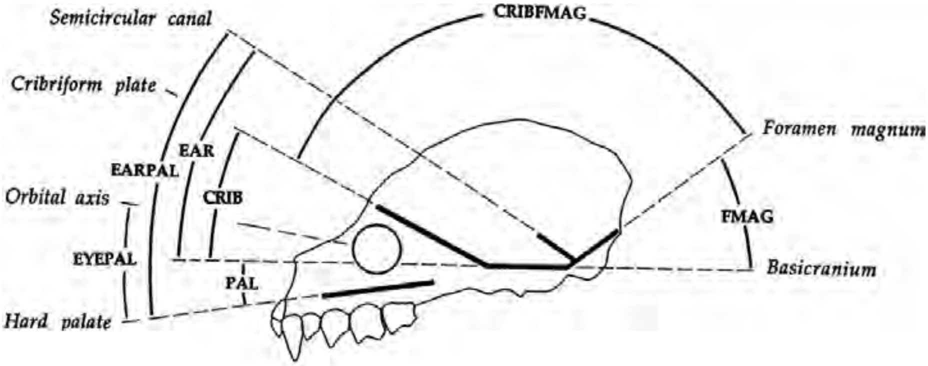

Figure 14.3 Anatomical planes and cephalometric angles are shown superimposed on a tracing of an *Artibeus jamaicensis* skull (from Pedersen, 1993).

During his analyses, Pedersen identified four anatomical planes that were readily located in radiographs of bat skulls: lateral semicircular canals, palate, foramen magnum and cribriform plate. Two angles relate these four anatomical planes in a functional context (EARPAL and CRIBFMAG; Figure 14.3; Pedersen, 1993, 1995, 2000), delineate the inertial and acoustic axes of the head and relate the general organization of the braincase to the rest of the body. These data clearly show that microchiropteran skulls follow a unique set of constructional rules based on the use of either the oral cavity or the facial skeleton as an acoustical horn. However, the fetal heads of oral-emitting and nasal-emitting taxa are grossly indistinguishable early in development. Species-specific skull morphology becomes increasingly

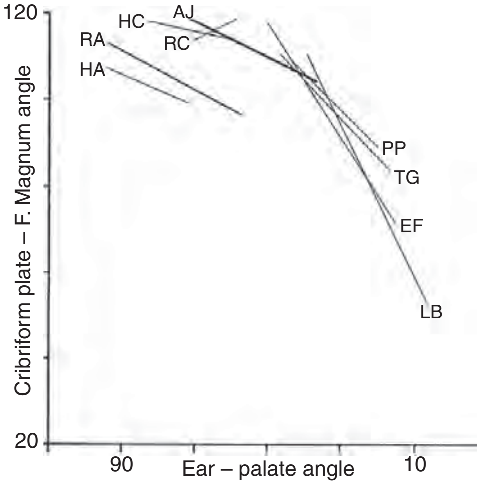

Figure 14.4 Bivariate plot of EARPAL vs. CRIBFMAG for fetuses and juveniles – ontogenetic trajectories of oral-emitting and nasal-emitting developmental series are presented in this scatterplot. Each trajectory moves from left to right across the plot. Nasal-emitting taxa (*Hipposideros armiger, Hipposideros galeritus, Rhinolophus affinus, Artibeus jamaicensis)* are clustered together in the upper left-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 right-hand corner into an oral-emitting morphospace (from Pedersen, 1993).

more apparent, but always within the framework of either the nasal-emitting or oral-emitting cranial form (Figures 14.3–14.4). Remarkably, the internal dichotomous arrangement of the two "kinds" of head is well established before the skull has begun to ossify and well before the forces of mastication begin to affect skull morphogenesis. In all oral-emitting taxa, the hard palate rotates dorsally until it is aligned with or elevated above the basicranium and the echolocation call is forced directly out through the mouth. This skull form is the plesiomorphic condition for mammals (Starck, 1954; Wimberger, 1991; Schneiderman, 1992) and is clearly exemplified by mormoopids, emballonurids and vespertilionids.

Conversely, palates of nasal-emitting bats are retained ventral to the basicranial axis (Starck, 1952; Freeman, 1984; Pedersen, 1993). This dichotomy between oral- and nasal-emitting baupläne has imposed dramatic changes in general head posture and compensatory rotation of the otic capsules to align them with the inertial axis of the head. As a result, fetuses of oral-emitting species follow a very different developmental trajectory than do fetuses of nasal-emitting species. Skulls of nasal-emitting taxa remain within a well-defined morphospace through both ontogeny and phylogeny (Figure 14.4).

The innovation and evolutionary potential of the nasal-emitting baupläne have relied upon the morphogenetic plasticity of adjacent skeletal elements to accommodate changes throughout development and then function adequately in the adult. This balancing act is difficult because the growth of the mammalian rostrum and pharynx are influenced by many factors including: (1) tooth eruption (Lakars and Herring, 1980); (2) the tissue pressures from the muscles, lips and tongue (Proffit, 1978); (3) the organization and coordination of each muscle mass in proportion to the complexity of the dentition and associated dynamics of mastication (Herring, 1985); (5) the respiratory tidal airflow (Solow and Greve, 1979); and (6) phonation/echolocation (Roberts, 1972, 1973; Hartley and Suthers, 1988; Suthers *et al.*, 1988).

Given this dynamic, it is of great interest that at least two evolutionary lineages (Rhinolophoidea – nycterids, megadermatids, rhinolophids, hipposiderids and Noctilionoidea – phyllostomids; *sensu* Simmons and Geisler, 1998) exhibit the anatomical requirements for the emission of calls through the nostrils (Simmons, 1980; Simmons and Stein, 1980; Hartley and Suthers, 1987, 1988, 1990; Pye, 1988). The developmental and the cephalometric data both suggest a classic example of convergent evolution on nasal-emitting baupläne driven by a developmental shift involving the rotation of the rostrum and inner ear. However, it is naïve to think that this can translate into a simple character state (see below).

Taken in isolation, nasal-emitting baupläne have evolved at least twice by retention of a developmental construct reminiscent of the fetal shapes of oral-emitting taxa (neoteny rather than hypo-morphosis). Because of the precise anatomical and physiological requirements needed for the efficient emission of ultrasound (Simmons and Stein, 1980; Pye, 1988; Suthers *et al.*, 1988), intermediate states would be quickly weeded out, suggesting that the shift from oral emission to nasal emission must have occurred swiftly, both in developmental and evolutionary terms (Lewin, 1986; Price *et al.*, 1993). Certainly, the divergence between oral- and nasal-emitting forms is an exaptation (Gould and Vrba, 1982) resulting from selective forces acting upon echolocation rather than the result of selection on cranial shape or head posture per se.

14.4.2 Anatomical landmark data

Multivariate analyses of landmark data allowed identification of developmental paths by which these taxonomically distinct clades arrived at their nasal-emitting baupläne. Cranial landmark data were taken from developmental series of bats (see Pedersen, 1995, 2000 for details; Figure 14.5) and these measurements were grouped into distinct suites of variables

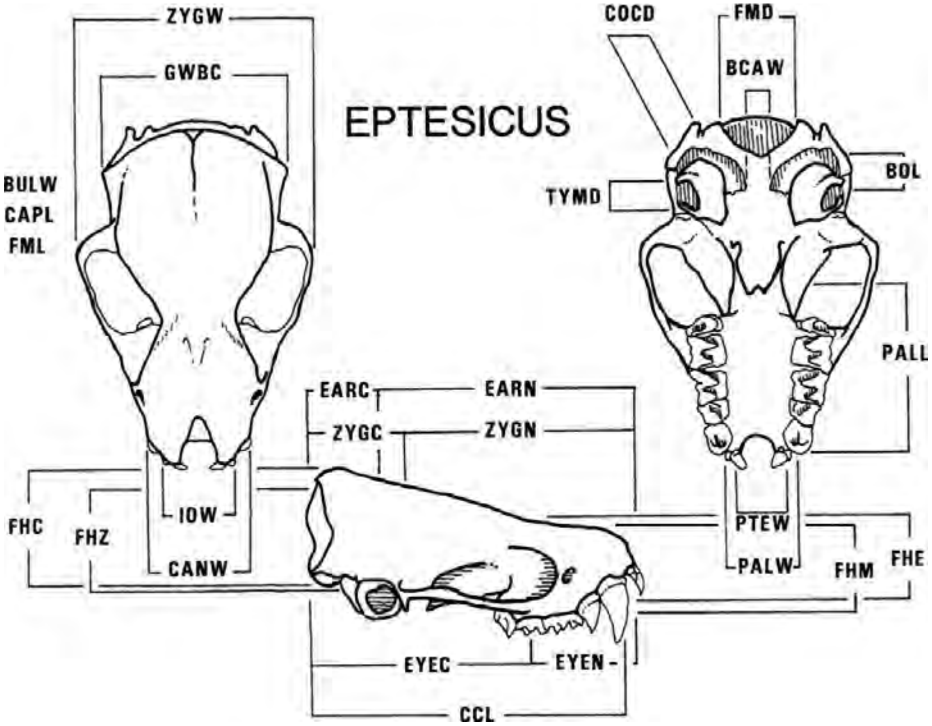

Figure 14.5 Anatomical measurements used in the canonical function analysis are shown on a tracing of an *Eptesicus fuscus* skull (from Pedersen, 1993).

according to function and/or anatomical relatedness. Each grouping was subjected to canonical analysis to identify covariance patterns among variables (Figure 14.6). In post-hoc identification of individuals, nasal-emitting and oral-emitting fetuses were rarely mistaken for each other and although early fetuses were frequently misclassified to the incorrect species, they were always assigned to the correct oral- or nasal-emitting types. For the most part, the clarity of these groupings can be attributed to the functional integration within each of the two major skull components (neuro- and viscerocrania).

Some unique features deserve discussion. Megachiroptera are clustered apart from the other developmental series because of their relatively large, albeit unspecialized, choanae and pterygoid complexes. Oral emitters are equally cohesive. The skull of rhinolophid bats, however, is characterized by a short, hard palate, large-bore choanae and a relatively long nasopharynx. Therein, the unique laryngo-nasal junction between the soft palate and the cartilages of the larynx (Matsumura, 1979; Hartley and Suthers, 1988) has forced a repositioning

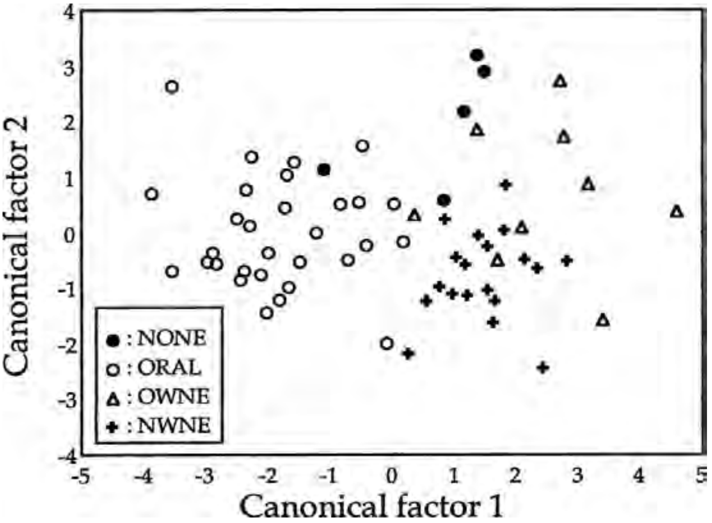

Figure 14.6 Scatterplot of the first and second axes derived from the canonical analysis of the following rostral characters: canine width, palate width, external narial width, choanal diameter, TMJ width, pterygoid width, hard palate length, pharynx length, interorbital width, infraorbital foramen width and toothrow length. Taxonomic abbreviations are as follows: OWNE = Old World nasal emitter, NWNE = New World nasal emitter, ORAL = oral emitter, NONE = Megachiroptera.

of all musculoskeletal elements associated with the soft palate and larynx (i.e., pterygoid width, choanal bore, pharyngeal length and otic capsule separation). Phyllostomids cluster near other nasal emitters, but exhibit some affinity for the megachiropteran morphospace most likely due to the fact that they both have well-developed visual and olfactory acuities. Given the diversity in phyllostomid dentition and diet, it would be very interesting to re-evaluate the packaging of the rostrum in this diverse group.

Therefore, the simplistic dichotomy between oral- and nasal-emitting skulls was revised to include the observation that there are at least two distinct developmental paths that generate a nasal-emitting skull and there are four fundamental assembly plans for the chiropteran head in general: (1) skulls relatively unmodified from the basic mammalian plan (oral emitters); (2) highly derived nasal-emitting forms built around expansive nasal cavities (rhinolophids, see discussion below); (3) nasal-emitting forms in which olfactory/visual modalities dominate the facial component of the skull (i.e., phyllostomids); and (4) skulls of non-echolocating megachiropterans that exhibit a wide range of skull shapes not restricted by the demands of ultrasonic echolocation.

14.4.3 Ossification rates and skull design

Have these gross reformulations of the bat skull altered the number of ossification centers or their sequence of appearance in any systematic pattern? We know that the shape and orientation of each element is strongly influenced by the enclosed volume, but ossification is usually independent of capsular growth. This permits epigenetic remodeling of the skull to accommodate developmental variation in the enclosed soft tissues and changing directive interactions in the mechanical environment, e.g., functional loading patterns during weaning (Haines, 1940; Washburn, 1947; Spyropoulos, 1977; Buckland-Wright, 1978; Alberch and Alberch, 1981; Herring and Lakars, 1981; Hanken, 1983, 1984; Griffioen and Smit-Vis, 1985; Herring, 1985; Von Schumacher *et al.*, 1986, 1988; Hoyte, 1987; Smit-Vis and Griffioen, 1987; Starck, 1989; Byrd, 1988; Kylamarkula, 1988; Ross and Ravosa, 1993; Ross and Henneberg, 1995).

Previous work suggested that bat ossification patterns follow the common mammalian pattern (de Beer, 1937; Pedersen, 1996, 2000): basicranial elements ossify in the correct posterior–anterior sequence, the auditory bullae and the ossicular chain are almost always the last series of bones to appear, and every bony element appears before skulls reach two-thirds of their expected adult size. Exceptions of note are related to the unique pharynx of rhinolophid/hipposiderid bats. The great expansion of their nasal passages has led to a local derangement of tissues, including the presence of a large fontanel between the nasal, maxillary and frontal bones that persists until well after birth. Such elemental translations and/or distortions to the midface are not uncommon in either developmental or evolutionary terms (Haines, 1940; Presley and Steel, 1976; Presley, 1981; Hanken, 1983, 1984; Pedersen, 1996, 2000). However, the unique coupling and suspension of the larynx and soft palate in rhinolophids manifests itself in a characteristic shift in the ossification sequence of the stylohyoid chain. These features do not appear to be shared with the phyllostomids, which exhibit a more generic ossification sequence (Pedersen, 1996).

14.4.4 Skull mechanics

Within each skull form, bat crania exhibit a stunning range of morphological diversity reflecting their diverse dietary specializations. The opposing jaws, teeth and muscles of mastication exist as a well-integrated functional unit, regardless of their relative position on the braincase (Starck, 1952; Czarnecki and Kallen, 1980; Freeman, 1984; Pedersen, 1993). Despite this generalization, does the dichotomy in skull form partition skull mechanics in any predictable manner?

During mastication, the rostrum and zygomatic arches brace the palate against the braincase posteriorly, which then transfers these forces to the occiput, cervical spine and thorax. The distribution of bone mass in the strongly ventro-flexed skulls of many rhinolophids/hipposiderids suggests a skull poorly designed to resist torsional/bending forces; the zygoma are relatively weak and the midface is attenuated dorsally – together leaving the pterygoid complex to be the primary reinforcement of the palate (Starck, 1952; Czarnecki and Kallen, 1980). As such, occlusal dynamics should help avoid structural failure in what can only be described as a flimsy rostrum, i.e., muscle, ligament and tendons must play a far more important role therein than do self-limiting features of the skeleton. In contrast, a generic nasal-emitting phyllostomid skull is more robust, exhibiting a solid midface and zygoma in all but the most extreme forms (e.g., glossophagines). Only the phyllostomines, wherein insects and vertebrates comprise the bulk of the diet, have retained tuberculosectorial teeth. It would be interesting to compare phyllostomine feeding mechanics with those of rhinolophids. Bat skulls that are strongly dorsi-flexed are typically constructed so 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.

One might predict that bats with extremely klinorhynchal (ventro-flexed) or aryrhynchal (dorsi-flexed) skulls cannot generate robust masticatory forces (Starck, 1952; Czarnecki and Kallen, 1980), rather, durophages must exhibit more moderate skull angulations within their oral- or nasal-emitting construct (*Cheiromeles* and *Vampyrum*, respectively; see Freeman, 1984). The inner dimensions of the nasal passages and the composition of the nasal septum are strangely absent from discussions concerning the evolution of echolocation or of skull mechanics in bats. 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 midface. In the balance, phyllostomids may have retained olfaction at the cost of loudness of the call, while rhinolophids may have emphasized loudness of the call at the expense of olfaction and robust mastication (Pedersen, 1996, 2000).

14.4.5 Ultrasonic vocalization

The echolocation pulses emitted by the larynx in microchiropterans consist of a fundamental frequency ($f1$) 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. Filtering (removal of harmonics) is affected by changes in the length and diameter of the vocal tract and discontinuities in the pharyngeal wall. Ultrasound produced by the larynx is subsequently emitted from either the mouth or the nostrils.

Regardless of the orifice, ultrasonic calls show striking variation in terms of emitted power and frequency structure (broad band, low-duty-cycle, frequency-modulated (FM) multiharmonic calls; narrow band, high-duty-cycle, "single" harmonic calls and everything in between). Depending on prey type, foraging strategy and habitat complexity, many species of bats will shift between broad- and narrow-band types of calls (e.g., *Eptesicus fuscus*; Surlykke and Moss, 2000), or modulate where they put energy into each type of call. Consequently, there is no fixed relationship/constraint between call structure and taxonomy, except perhaps in the rhinolophids and hipposiderids, where tuned nasal cavities impose significant restrictions on the emitted sound (Pedersen, 2000).

Call design has been mapped onto various molecular and morphological phylogenies (Eick *et al.*, 2005; Jones and Teeling, 2006; Jones and Holderied, 2007) and Jones and Teeling (2006) state explicitly that "Overall, our perspective on the evolution of echolocation is clouded by the diversity and plasticity of signals that we see in extant bats, suggesting that the animal's habitat is often more important in shaping its call design than is its evolutionary history." However, this particular statement neglects a body of work showing that the evolution of nasal-emitting heads has imposed significant mechanical restrictions on echolocation (Roberts, 1972, 1973; Hartley and Suthers, 1988; Suthers *et al.*, 1988; Pedersen, 1996). More specifically, the echolocation calls of oral-emitting bats vary from narrow-band calls without harmonics to broad-band calls with harmonics, and may combine the two. Some oral-emitting bats may employ narrow-band (CF)-type calls (emballonurids, molossids, mormoopids), but typically oral emitters produce multiharmonic, broad-band calls.

Conversely, nasal-emitting bats are faced with the problem of projecting sound through the restrictive nasal passages (Pedersen, 1993, 1995, 2000). Therefore, nycterids, megadermatids and most phyllostomid bats generate low-intensity multiharmonic calls of varying structure due primarily to the restrictions of the nasal cavity. The low-intensity calls of phyllostomid bats led Griffin (1958) to refer to them as "whispering bats," though recent work has shown these bats to be much louder than previously believed (Brinkløv *et al.*, 2009). Conversely, the nasal cavities of rhinolophid and hipposiderid bats are tuned to dramatically reduce the general impedance of the cavity (Roberts, 1972, 1973; Hartley and Suthers, 1988; Suthers *et al.*, 1988). These bats typically emit loud high-duty-cycle (CF) calls comparable to those of oral-emitting bats, but with one very important difference. The acoustic limitations imposed by the dimensions of the nasal passages in these rhinolophid and hipposiderid bats emphasize the second harmonic ($f2$) while reducing or removing the remaining overtones, including the fundamental ($f1$) (Roberts, 1972; Matsumura, 1979; Hartley and Suthers, 1988; Suthers *et al.*, 1988).

In rhinolophids, neither the nasal passages nor the pinnae exhibit dimensions capable of sending or receiving the dominant spectral component of the adult call ($f2$) until well after birth (Matsumura, 1979; Konstantinov, 1989; Obrist *et al.*, 1993; Pedersen, 1996). Infants must literally grow into their second harmonic – the use of $f2$ does not lie in some unique feature of the frequency itself, but rather that it is the only frequency permitted by the anatomical constraints imposed by the supra-glottal vocal tract in these bats (Roberts, 1973; Matsumura, 1979; Hartley and Suthers, 1987; Pedersen, 1996, 2000). Once established, the tuning of these systems is exquisite (Leonard *et al.*, 2004; Zhuang and Müller, 2006, 2007).

Call structure does not correlate well with brain size, dentition or taxonomic diversity (Pedersen, 2000) and may be best seen as a behavioral response to clutter and selection of prey-type (Surlykke and Moss, 2000). So, what if any advantage comes from being a nasal-emitting bat? Could it be something so simple as how these animals use their mouths? After all, an echolocating predator would have difficulty flying and orienting simultaneously if it's mouth is full, or the food item requires a great deal of on-the-wing processing. Therein, the majority of carnivorous/durophagous microchiropterans are perch-hunting nasal-emitters (e.g., *Nycteris*, *Chrotopterus* etc.) that can echolocate with their mouths full; or are nasal-emitting nocturnal frugivores (e.g., *Artibeus*, *Sturnira* etc.) or are oral-emitting bats that must forage in open air well away from clutter whilst processing food items (e.g., *Lasiurus*, *Molossus* etc.).

14.4.6 Facial ornamentation: nose leaves

All nasal-emitting forms exhibit at least two taxonomically related features: reorganization of the skull about the nasal passages and flaps of skin projecting around the nostrils. Earlier in this chapter, we postulated that the carrying of food/prey items in the mouth by a primitive oral-emitting bat might suffice to favor the evolution of bats that emitted their calls from their nasal passages either primarily or secondarily.

The evolution of facial ornamentation may be a predictable response to nasal emission of the call, but this ornamentation is at least as varied as the differential packaging of the rostrum in the various nasal-emitting taxa.

Are mammalian nasal cartilages and facial musculature predisposed/preadapted to generate a nose leaf (Göbbel, 2000, 2002)? This elaborate flap of skin is the final element of a bat's vocal tract and it reduces back pressure in the nasal cavity and may also help focus the call as it is emitted through the nostrils (Möhres, 1966a, 1966b; Simmons and Stein, 1980; Hartley and Suthers, 1987, 1988, 1990; Pye, 1988; Arita, 1990; Ghose, 2006; Zhuang and Müller, 2007). Such immediate physiological benefits would be sufficient to drive a standard issue mammalian nose into a rudimentary nose leaf or into something far more elaborate (Arita, 1990; Göbbel, 2000, 2002a, 2002b). Significantly, nose-leaf primordia appear before eyes and external ears are visible, indicating that such ornamentation is related to developmental timing and construction of the face, and not simply the product of ecological niche specialization (Göbbel, 2000, 2002a, 2002b; Yokoyama and Uchida, 2000; Chen *et al.*, 2005; Cretekos *et al.*, 2005, 2007; Giannini *et al.*, 2006; Wyant and Adams, 2007; Nolte *et al.*, 2008).

The homology of nose leaves is still debated (Yokoyama and Uchida, 2000; Springer *et al.*, 2001a; Göbbel, 2002a, 2002b). What are we to make of nasal-emitting taxa that reduce the size and complexity of their nose leaves (brachyphyllines) or those oral-emitting taxa that exhibit incipient nose leaves (plecotines, *Antrozous*, *Craseonycteris* or *Rhinopoma*)? Certainly, the facial cleft of nycterids is unique, if not bizarre, leaving Pedersen (1995) to muse that the unique length/depth relationship in the facial cleft of nycterid bats might be a "resonating chamber outside the bony nasal cavity." Recently, our lab has worked out the anatomy of this cleft and its articulated muscular palps, leaving no question that these structures are: (1) homologous (though reduced in complexity) with the nose leaves of rhinolophids and (2) constructed so as to modify the nasally emitted call in these unique slit-faced bats.

It is naïve to think that nuclear or mitochondrial gene sequences will provide answers to these questions; however, there are several regulatory genes (*Sumo*, *Irf*, *Bmp*, *Msx*, *Shox*, *Gabrb*) associated with the integration and development of the frontonasal process/palate that might provide a better place to start looking at the evolution of these remarkable facial ornaments.

14.5 Beyond the genetic code: evolutionary developmental biology

The last decade has witnessed giant steps in the field of developmental genetics insofar as to exhaust the coding sequence as the impetus for morphological evolution (Hanken and Thorogood, 1993; Carroll 2005; Chai and

Maxson, 2006; Radlanski and Renz, 2006; Young and Badyaev, 2007). Indeed, the key to understanding evolutionary change has now shifted focus to the study of regulatory gene function and the function of regulatory gene networks (Beddington and Robertson, 1989; Hanken and Thorogood, 1993; Keranen *et al.*, 1998, 1999; Acampora *et al.*, 1999; Merlo *et al.*, 2000; Trainor and Krumlauf, 2000; Alappat *et al.*, 2003; Trainor *et al.*, 2003; Blechschmidt, 2004; Meulemans and Bronner-Fraser, 2004; Carroll, 2005; Chai and Maxson, 2006; Evans and Noden, 2006; Radlanski and Renz, 2006; Hoekstra and Coyne, 2007; Young and Badyaev, 2007).

It is instructive to step back and remember that the vertebrate head is in itself a novelty and its genes, tissues and form are often cannibalized from old postcranial material (Gans and Northcutt, 1983). Events associated with the innovation of the vertebrate head include, but are not limited to, signaling cascades that effect pattern organogenesis, the establishment of tissue boundaries and tissue–tissue induction, and site-specific induction (Beddington and Robertson, 1989; Acampora *et al.*, 1999; Blechschmidt, 2004; Radlanski and Renz, 2006; Hoekstra and Coyne, 2007). Studies regarding cranial neural crest cell migration and *Hox* gene regulation have dramatically improved our understanding of morphogenetic plasticity and evolutionary novelty (Couly *et al.*, 1993; Keränen *et al.*, 1998, 1999; Acampora *et al.*, 1999; Merlo *et al.*, 2000; Trainor and Krumlauf, 2000; Brault *et al.*, 2001; Alapatt *et al.*, 2003; Trainor *et al.*, 2003; Meulemans and Bronner-Fraser, 2004; Wilson and Tucker, 2004; Gross and Hanken, 2005; Chai and Maxson, 2006; Evans and Noden, 2006). Additional studies of craniofacial development continue to evaluate this exceedingly complex network of mechanisms that contribute to morphological form (Hanken and Thorogood, 1993; Carroll, 2005; Creuzet *et al.*, 2005; Chai and Maxson, 2006; Radlanski and Renz, 2006; Young and Badyaev, 2007). Arguably, selection *in utero* (Katz *et al.*, 1981; Alberch, 1982; Katz, 1982; Müller, 1990) may well be more important than natural selection after parturition (Schmalhausen, 1949; Kuhn, 1987; Bonner, 1988; Maier, 1989).

Therefore, it seems apparent that the driving force behind morphological novelty will not be found in some mitochondrial gene sequence or in some nuclear gene with a limited/unknown connection with organogenesis; but rather from an understanding of developmental timing, regulatory genes and the ability of various anatomical structures to accommodate change (Lauder, 1982; Alberch, 1989; Klingenberg, 1998; Carroll, 2000; Chase *et al.*, 2002; Hilliard *et al.*, 2005; Peaston and Whitlaw, 2006; Radlanski and Renz, 2006; Hallgrimsson *et al.*, 2007, 2008; Salazar-Ciudad, 2007; Young and Badyaev, 2007).

14.6 Bat phylogeny: molecules, morphology and developmental mechanisms

Molecules have become the apparent gold standard of many recent reconstructions of bat phylogeny and several studies have sequenced a rather impressive collection of genes from a wide variety of locations within the genome (Hutcheon *et al.*, 1998; Springer *et al.*, 2001b; Teeling *et al.*, 2002; Eick *et al.*, 2005; Lim and Dunlop, 2008). This remains despite the fact that genes do not provide equally valid phylogenetic signals and the addition of more genes does not necessarily clarify the situation and may generate anomalous trees (Wiens and Hollingsworth, 2000; Wiens, 2004; Willa and Rubinoff, 2004; Degnan and Rosenberg, 2006; Rodriquez-Ezpeleta *et al.*, 2007; Belfiore *et al.*, 2008).

Regardless, the molecular lobby postulates that the evolution of echolocation must be far more complex than previously thought (Jones and Teeling, 2006). If they are correct, the evolution of echolocation is actually quite messy, with nasal emission having evolved independently four different times (Rhinolophidae + Hipposideridae; Megadermatidae; Nycteridae and Phyllostomidae; Figure 14.7).

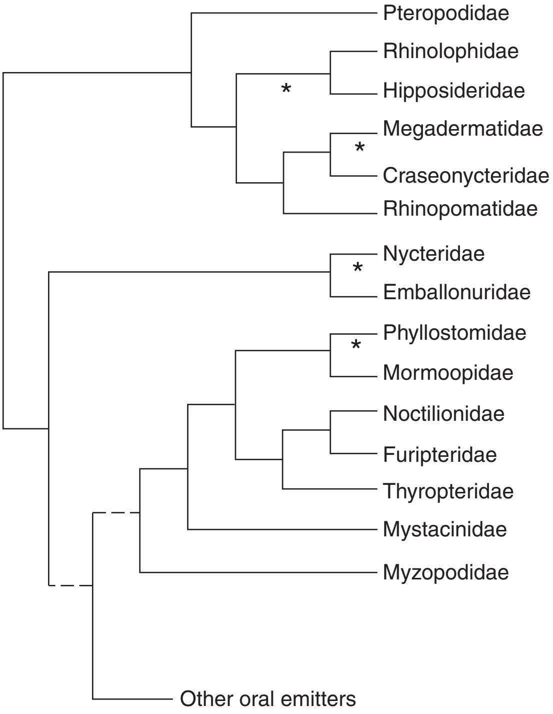

Figure 14.7 Molecular tree (after Teeling *et al.*, 2005). Asterisks indicate nose-leafed, nasal-emitting bats.

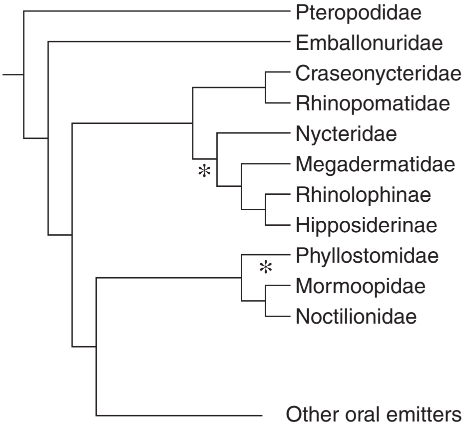

Figure 14.8 Morphology tree (after Simmons and Geisler, 1998). Asterisks indicate nose-leafed, nasal-emitting bats.

The molecular sequence data also suggest that the non-echolocating pteropodids and the highly sophisticated nasal-emitting rhinolophids are closely related (Teeling *et al.*, 2000, 2002, 2005; Springer *et al.*, 2001b; Eick *et al.*, 2005; Hutcheon and Kirsch, 2006). But is it conceivable that megachiropterans are a sister group related to rhinolophid bats? After all, there is little or nothing about their brains, skulls, jaw suspension, dentition, cranial vasculature, neuroacoustic systems, flight musculature, thoracic compliance or even their reproductive biology that would support such a relationship (Roberts, 1972, 1973; Kallen, 1977; Czarnecki and Kallen, 1980; Hartley and Suthers, 1988; Suthers *et al.*, 1988; Pedersen, 1996, 2000; McNamara, 1997; Göbbel, 2000; Leonard *et al.*, 2004; Zhuang and Müller, 2006, 2007; DesRoche *et al.*, 2007; Pedersen *et al.*, 2009). This molecular scenario (Figure 14.7) also suggests that the oral-emitting Rhinopomatidae subsequently evolved from the highly derived nasal-emitting rhinolophids (a reversal of dramatic proportions), or that *Craseonycteris* and *Megaderma* are sister groups (a morphological absurdity: Simmons and Geisler, 1998).

The morphological data, however, suggest a less complicated scenario (Figure 14.8) and are largely supported by the fossil record – there were two separate and rather successful radiations of nasal-emitting forms, one in the Old World during the mid Eocene (rhinolophids+hipposiderids, nycterids, megadermatids), and another in the New World (phyllostomids) in the early-mid Oligocene (Wetterer *et al.*, 2000; Baker *et al.*, 2003). In each case, nasal-emitting bats are derived from more primitive oral-emitting stock, without any reversals in form. Examples of phylogenetic radiation coincident with morphological innovation such as this are relatively common (Needham, 1933; Alberch *et al.*, 1979; Alberch and Alberch, 1981; Müller, 1990).

The inclusion of developmental mechanisms into evolutionary theory, during the last decade, represents an important shift from studies that focus on adaptation to those that include *emergence* (Müller and Newman, 2005; Salazar-Ciudad, 2007). Towards this end, numerous studies have tied regulatory genes to the development of the palate (*Msx, Bapx, Gsc, Emx, Sox, Hox, Prx* – Kaur *et al.*, 1992; ten Berge *et al.*, 1998; Bianchi *et al.*, 2000; Scapoli *et al.*, 2002; López *et al.*, 2008; Ji *et al.*, 2009), the ear (*Prx, Otx, Six, Eya* – ten Berge *et al.*, 1998; Morsli *et al.*, 1999; Schlosser, 2007), the cranial base (*Papps, Kena* – Hallgrímsson and Lieberman, 2008), the cervical vertebra (*Hox* – Kaur *et al.*, 1992; Galis *et al.*, 2006) and skeletal development in general (Young and Badyaev, 2007).

It is of great interest that several papers have recently pursued regulatory genes or karyological data that may provide more appropriate insight into the emergence of morphological innovation in bats themselves (Volleth *et al.*, 2002; Sears *et al.*, 2006; Cretekos *et al.*, 2007, 2008; Hockman *et al.*, 2008; Veselka *et al.*, 2010), even if we disagree with their definition of echolocation or their acceptance of the yinpterochiroptera (Li *et al.*, 2007, 2008).

14.7 Closing comments and future directions

As we wrote this chapter, many of our colleagues argued that because molecular sequence data is more readily collected than morphological data, the sheer volume of data (weight of the evidence) somehow equates to a more complete, possibly more correct, phylogenetic signal. However, this "more is better" approach is under debate (Wiens and Hollingsworth, 2000; Wiens, 2004; Willa and Rubinoff, 2004; Degnan and Rosenberg, 2006; Rodriquez-Ezpeleta *et al.*, 2007; Belfiore *et al.*, 2008; McDonough *et al.*, 2008). The often impenetrable language of molecular systematics can further obfuscate why various gene sequences were chosen, or how they relate to bat evolution. Not surprisingly, when morphology conflicts with molecules, most of our colleagues found it easier to point to inadequate taxon sampling (Heath *et al.*, 2008), or to even dismiss poorly known chiropteran taxa, rather than challenge the nature of the data. As Osborn pointed out as far back as 1932, "The geneticists are trying to make evolution fit the genes rather than to make the genes fit evolution."

Because many aspects of cranial form and function are well integrated and auto-correlated (Atchley and Hall, 1991; Lieberman *et al.*, 2004; Bulygina *et al.*, 2006; Bruner and Ripani, 2008), many phylogenetic studies have tried to argue that nasal emission in bats is a simple, easily coded character state during phylogenetic analyses. However, as we gain greater understanding of the epigenome and developmental mechanics (Peaston and Whitelaw, 2006), it is now clearly a dangerous gamble to divorce an innovative suite of character states from their developmental history, and to do so would reflect a gross ignorance of vertebrate embryology and what we are now learning about developmental genetics (Willa and Rubinoff, 2004; Müller and Newman, 2005; Davidson, 2006; Degnan and Rosenberg, 2006; Salazar-Ciudad, 2007). In this light, the evolution of nose leaves and the myriad of changes required during the reformulation of the chiropteran head (discussed earlier in this chapter) provides a magnificent opportunity to take our field beyond the shop-worn molecules-vs.-morphology debate.

In a draft proposal for this symposium, the convenors (Gunnell, Simmons and Eiting) stated that, "Molecular studies based on different genes and taxon samples often produce somewhat incongruent results, and morphological trees often conflict with molecular trees. However, these conflicts may be more superficial than previously thought, and new analyses of larger data sets are quickly converging on a new consensus of the pattern, if not the *process*, of bat evolution." . . . and there's the rub.

It is our opinion that without the inclusion of the developmental process, phylogenetic inferences based in either adult morphology or molecular data (or a combination thereof) may be misleading or even specious. Are the genes that are currently being sequenced simply the low-hanging fruit that are at best casually correlated with evolutionary change, or should we shift our focus to developmental events and regulatory gene activity that directly relate to structural innovation and the emergence of novelty in a more causal manner?

So let us commit blasphemy and walk away from any pretense of *objectivity* and ignore the *populist* notion that more is better, but instead actively pursue causal mechanisms of novelty during phylogeny – the *cause célèbre* in the burgeoning field of developmental genetics. We argue that our field must refocus our efforts on epigenetic mechanisms that act throughout ontogeny as a way to better understand the evolution of bats – because it would seem that we can no longer see the forest for all the gene trees.

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