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(Reptilia: Ornithischia)**

David B. Weishampel

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Acoustic analyses of potential vocalization in lambeosaurine dinosaurs (Reptilia: Ornithischia)

David B. Weishampel

Abstract.—Lambeosaurine dinosaur crests are judged to have been conducive to resonance on the basis of an acoustic analysis of the structure of the nasal cavity. Size and shape of the nasal cavity suggest low vocal frequencies in adults, as does information on potential auditory acuity in these animals. Lateral diverticula (present in all but juvenile specimens) acted to suppress portions of the vocal spectrum. Juveniles vocalized at higher frequencies than adults and potential auditory sensitivity at high frequencies in adults suggests a high degree of parent-offspring vocal communication. Sexual variation and causes of selection for low frequency vocalization are also examined.

David B. Weishampel. Department of Geology, University of Pennsylvania, Philadelphia, Pennsylvania 19104

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Introduction

During the Late Cretaceous, hadrosaurs were the most abundant and diverse group of large terrestrial vertebrates of the Northern Hemisphere (Fig. 1). These bipedal herbivores were most distinctive in the shapes of their skulls. The family Hadrosauridae is divisible into the subfamily Hadrosaurinae (individuals possessing a solid crest or lacking a crest altogether) and the subfamily Lambeosaurinae (forms that bear hollow crests containing portions of the nasal cavity). Proposed functions for the lambeosaurine crest have been studied from many perspectives, including underwater feeding (Romer 1933, 1945; Wilfarth 1939, 1947; Colbert 1951; Russell 1946; Sternberg 1935), olfaction (Ostrom 1961, 1962), thermoregulation (Wheeler 1978), sodium secretion (Maryanska and Osmolska 1979), and sociosexual functions (Abel 1924; Wiman 1931; Nopcsa 1929; Davitashvili 1961; Hopson 1975). Yet few of these ideas are based on the detailed relationships between internal and external form and the shape of the nasal cavity itself. Ostrom (1961, 1962) suggested that the enlarged nasal cavity allowed for extensive olfactory epithelium and thus increased olfactory acuity, while Wheeler (1978) hypothesized that these spaces permitted increased cooling of the central nervous system. Hopson (1975) pointed out that selection for increased olfactory acuity in living animals does not yield the extreme variability in cranial struc-

tures seen in lambeosaurines (the same is true for thermoregulation), and hypothesized that lambeosaurine crests functioned as acoustic resonators (following Wiman 1931) and visual display structures (following Davitashvili 1961) for intraspecific social behavior. Recently, Maryanska and Osmolska (1979) contested Hopson's hypothesis, suggesting instead that portions of the nasal cavity in hadrosaurids housed prominent, rigid salt glands, thus discounting the possibility of acoustic signaling.

Since the acoustic properties of lambeosaurine crests form an important feature of Hopson's (1975) interpretations of the evolution of vocal display in lambeosaurines, it is desirable to analyze lambeosaurine crests as potential acoustic resonators. Is the nasal cavity within lambeosaurine crests conducive to resonance? If not, then selection for distinctive vocalization could not have played a part in the evolution of lambeosaurine crests. However, if resonance could occur within the crest, the probability of vocal display occurring in lambeosaurines is high. Vocalization will be analyzed by means of resonance modeling to determine potential vocal frequency ranges for species of *Parasaurolophus*, *Corythosaurus*, *Lambeosaurus*, and *Hypacrosaurus*. These vocal frequency ranges, in turn, will then be compared with potential ranges of auditory acuity in each species to judge whether or not the two ranges overlap.

The internal anatomy of the nasal cavity can

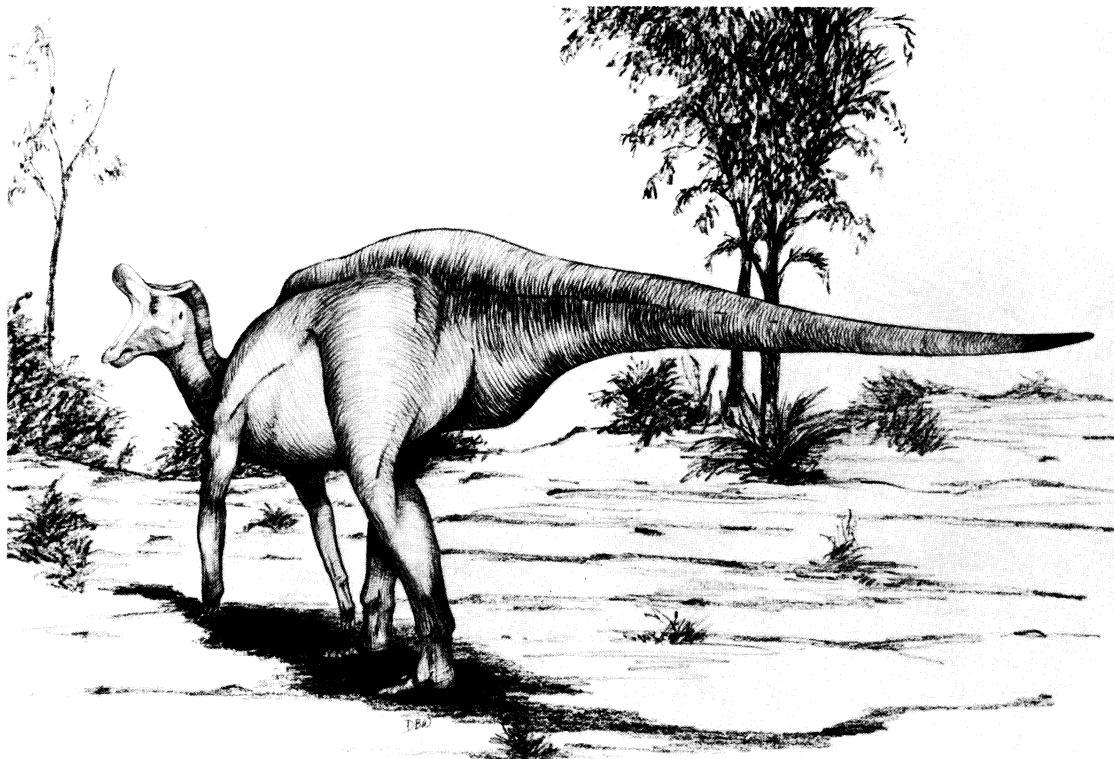


FIGURE 1. Reconstruction of *Lambeosaurus lambei*, based on ROM 1218.

be examined in only a few lambeosaurine specimens (Weishampel 1981). The nasal cavity is divisible into three regions (Fig. 2). The elongate vestibule is formed by paired tubes that extend from the external nares either to a common median chamber at the base of the crest, as in juveniles of *Lambeosaurus lambei* and *Corythosaurus casuarius*, and adults of *Parasaurolophus*, or to paired lateral diverticula adjacent to and communicating with the common median chamber, as in adult *C. casuarius*, *L. lambei*, and *H. altispinus*. In *C. casuarius*, *L. lambei*, and possibly *H. altispinus*, the vestibule forms S-shaped loops immediately rostral to the lateral diverticula. Comparable S-loops do not occur in species of *Parasaurolophus*, but the extremely elongated passages that make up the crest in this genus are considered homologous with the S-loops seen in the remaining lambeosaurines (Weishampel 1981). Lateral diverticula are present in species of *Parasaurolophus*, but they communicate with the common median chamber independently of the nasal vestibule. Subadult *C. casuarius* and *L. lambei* lack

lateral diverticula. Both lateral diverticula (when present) and the common median chamber make up the nasal cavity proper. From the common median chamber, the nasal cavity descends in a tubular fashion to the internal naris and this segment of the nasal cavity is considered homologous with the nasopharyngeal duct in modern reptiles; it then passes down to the pharyngeal region.

Abbreviations. AMNH: American Museum of Natural History, New York; FMNH: Field Museum of Natural History, Chicago; PIUU: Paleontologiska Institutionen, Uppsala, Sweden; ROM: Royal Ontario Museum, Toronto.

Resonance and the Nasal Cavity of *Parasaurolophus*

When considering the crest of *Parasaurolophus tubicen*, Wiman (1931) hypothesized that the elongated nasal passages acted as resonators and drew analogy between this crest and a Fenoscandian musical instrument known as a krumlur or krumhorne (Fig. 3a). He further compared the crest with the tracheal loops with-

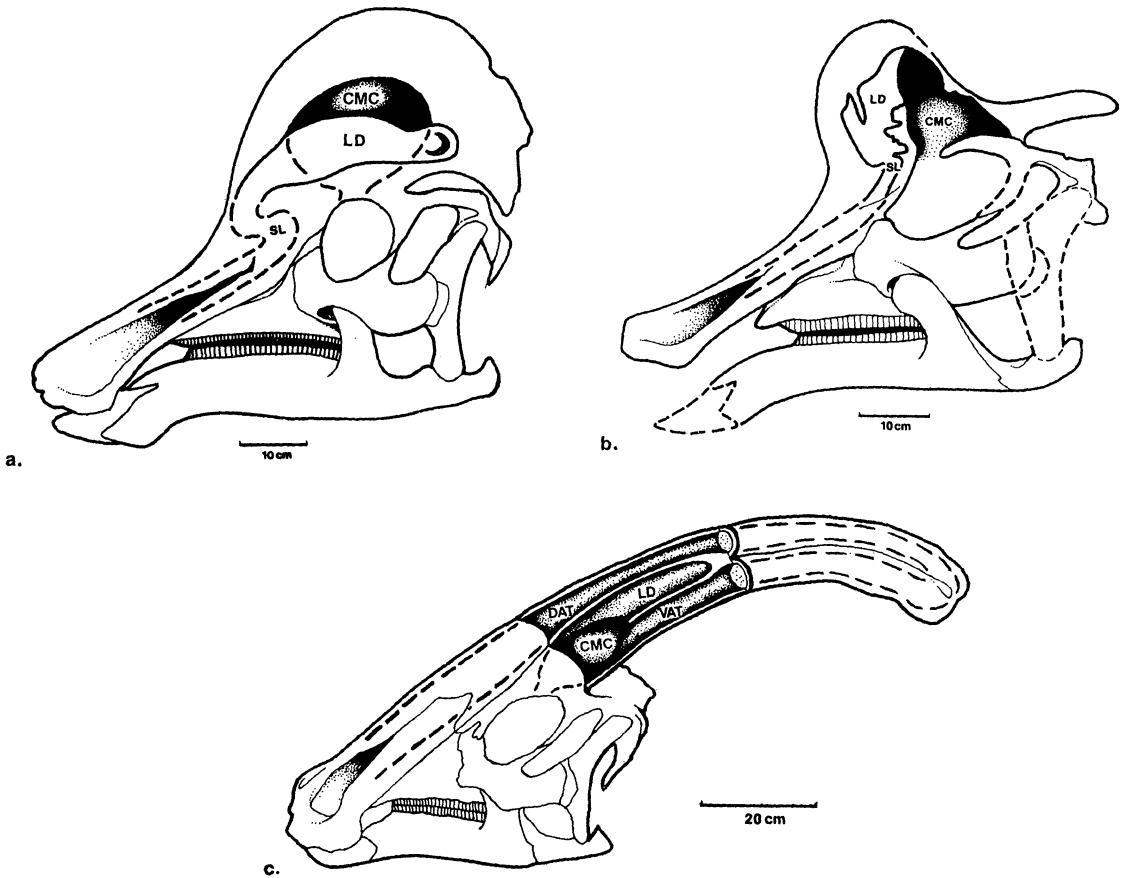


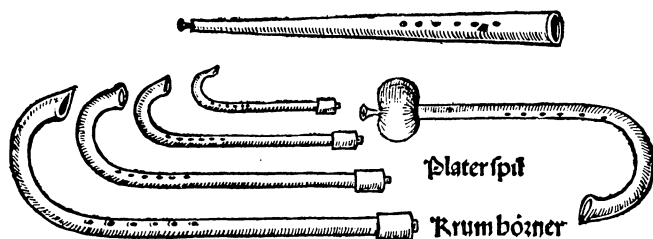
FIGURE 2. Internal anatomy of lambeosaurine crests. a. *Corythosaurus casuarius*; b. *Lambeosaurus lambei*; c. *Parasaurolophus walkeri*. Abbreviations: CMC, common median chamber; DAT, dorsal ascending tract; DT, descending tract; LD, lateral diverticulum; SL, S-loop; VAT, ventral ascending tract.

in the sternum of the trumpeter and whistling swans (*Olor cygnus* and *O. columbianus*; Fig. 3b), believing this structure to be functionally analogous to the looped nasal cavity in *Parasaurolophus* (and other lambeosaurines). He suggested that sound created by the lambeosaurine vocal organ resonated within the elongated nasal cavity.

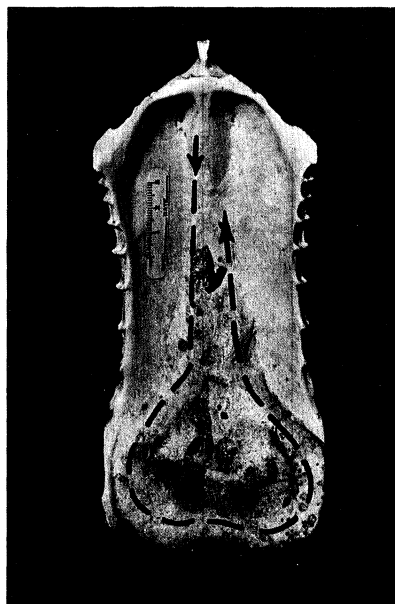
A vocal organ located between the lungs and pharynx of lambeosaurines would be well placed for the nasal cavity to be used as a resonator. In *O. columbianus* and *O. cygnus* the vocal organ occurs in a functionally comparable position, between the right and left bronchi at the base of the more distally located trachea. This position of the vocal organ relative to the looped trachea is believed to modify the vocal frequencies of these swans (A. S. Gaunt, pers. comm. 1976). The entire nasal cavity in species

of *Parasaurolophus*, excluding the lateral diverticula (discussed separately below), does not deviate significantly from a simple tubular configuration (Ostrom 1963; Weishampel 1981) and it is therefore relatively simple to make predictions of its resonant frequencies.

Sound produced by the vocal organ is transmitted via the pharynx and nasal cavity to the external nares, and the behavior of this sound within the passages is closely related to the shape and size of the passages which they traverse. The vocal organ introduces trains of air pulses (i.e. oscillating air pressure) into the vocal tract; the sound generated is a complex tone composed of the fundamental frequency of the vocal organ itself and a large number of harmonic partials. Standing waves are generated in the open-ended tubes when the length of the tube (nasal cavity length in *Parasaurolophus*) is



a.



b.

FIGURE 3. Functional analogs to the nasal cavity of lambeosaurine hadrosaurids. a. The krumlor or krumhorne. (A medieval illustration from Harrison and Rimmer 1964). b. Internal view of the sternum of *Olor columbianus*, the whistling swan. Dashed line indicates tracheal looping. (ROM Ornithology Collection 19891).

equal to an integral multiple of one half the wavelength of the sinusoidal wave pattern generated by the vocal organ:

$$L = n(\lambda/2) \quad n = 1, 2, 3, \dots \quad (1)$$

(L = tube length, n = resonance mode, λ = wavelength). Such standing waves are less attenuated and therefore radiate with higher relative amplitude than other sound waves. The static pattern of pressure oscillations (resonance) has maximum amplitude at either end of the tube (antinodes) and zero amplitude at points between (nodes). The effect of curvature of the tube on wavelength (and thus on frequency) is insignificant (Rayleigh 1896, p. 62) so that the extreme curvature at the end of the crest in *Parasaurolophus*, and the S-loops in the nasal passages in other lambeosaurines, may be ignored in acoustic modeling. Several examples of open-ended resonance are given in Fig. 4.

Wavelength is also a function of both wave velocity and frequency:

$$\lambda = v/f \quad (2)$$

(v = velocity of sound, f = sound frequency). The relation between actual frequency, mode,

and tube length is given by combining equations (1) and (2):

$$f = n(v/2L) \quad (3)$$

Resonant frequencies can be predicted from equation (3) and are given in Table 1 for species of *Parasaurolophus*. In *P. walkeri*, these frequencies range from 48 to 240 Hz (corresponding approximately to the range of musical notes from G two octaves below Middle C to B below Middle C, with higher harmonics possible). Using similar data from *P. cyrtocristatus*, we obtain ranges from 75 to 375 Hz (D one octave below Middle C to F# above Middle C). Such low frequencies have important implications for intraspecific communication, to be discussed below.

Resonance and the Nasal Cavity in Non-parasauroloph Lambeosaurines

The nasal cavity in species of *Corythosaurus*, *Lambeosaurus*, and *Hypacrosaurus* is more complex and variable in shape than that of *Parasaurolophus*, and the problem of the amount of soft tissue within the nasal cavity and the degree to which it modified the shape of the

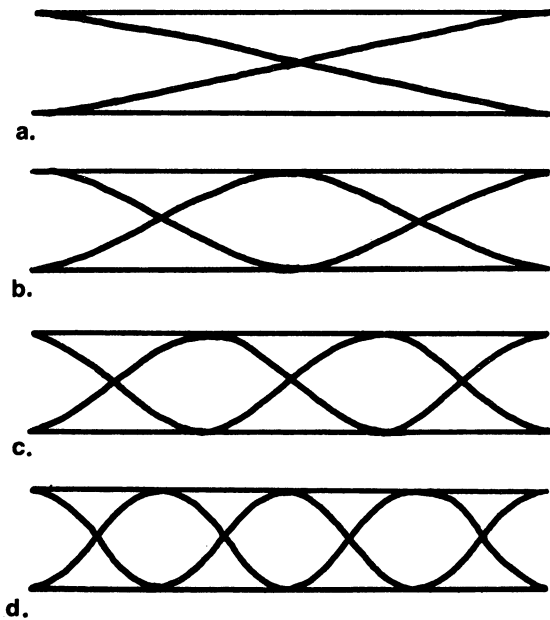


FIGURE 4. a. Fundamental condition for an open-ended tube. b. First harmonic. c. Second harmonic. d. Third harmonic.

bony-walled cavity is more significant in these lambeosaurines. For instance, the portals between the nasal vestibule, lateral diverticula, and common median chamber, and between the common median chamber and nasopharyngeal duct (as well as soft tissue elaboration within each region) may have had a great effect on topographic details within the nasal cavity. The uncertainties of soft tissue development as well as problems of mathematically modeling the form of the nasal cavity in these animals (viz., Rayleigh 1896, p. 66) preclude resonance analyses such as those performed on *Parasaurolophus*. However, it is important to examine some of the ways in which sound waves might interact with the nasal cavity in these lambeosaurines.

The nasopharyngeal duct in *L. lambei*, *C. casuarius*, and *H. altispinus* is roughly tubular, and in this region sound waves would have resonated with maximum amplitude at both ends (open-ended resonance). The standing waves that passed through the aperture between the nasopharyngeal duct and the common median chamber continued within the chamber until they reached the enclosing walls. The shape of

TABLE 1. Resonant frequencies of the nasal cavity in species of *Parasaurolophus*. *P. walkeri* frequencies based on a tube (nasal cavity) length of 346 cm; *P. cyrtocristatus* based on 221 cm length.

Mode of resonance	Frequency (in Hz)	
	<i>P. walkeri</i> (ROM 768)	<i>P. cyrtocristatus</i> (FMNH P27393)
1	48	75
2	96	150
3	144	225
4	192	300
5	240	375

these walls determined the behavior of these sound waves as they distributed themselves throughout the inside of the crest. Figure 5 suggests that the common median chamber acted as a collector of sound from the nasopharyngeal duct and as a distributor to the lateral diverticula, at least in *Corythosaurus* and *Hypacrosaurus* and perhaps in *Lambeosaurus*. From the common median chamber, pressure waves then passed through the lateral diverticula to the nasal vestibule. The unusual acoustic properties of the lateral diverticula are described below. The paired, tubular passages of the nasal vestibule are open at both ends and resonance becomes a function of the length of the passages and of the sound spectrum generated within the common median chamber and lateral diverticula. The frequencies at the diverticulum/vestibule portal resonate over a relatively long distance before exiting at the external nares. Vocal frequencies therefore depend on the compatibility of acoustic behavior of the various segments of the nasal cavity.

The Effect of Resonance Within the Lateral Diverticula

The lateral diverticula of *Parasaurolophus* are moderately long, tubular blind pockets that extend caudodorsally within the nasal vestibule. Because the lateral diverticula are closed at their caudal ends, they act as closed-ended resonators branched from the main portion of the nasal cavity and have resonant frequencies that relate to their length (Table 2).

The conditions created by lateral diverticula in *Parasaurolophus* are similar to resonant conditions in which resonators suppress sound tra-

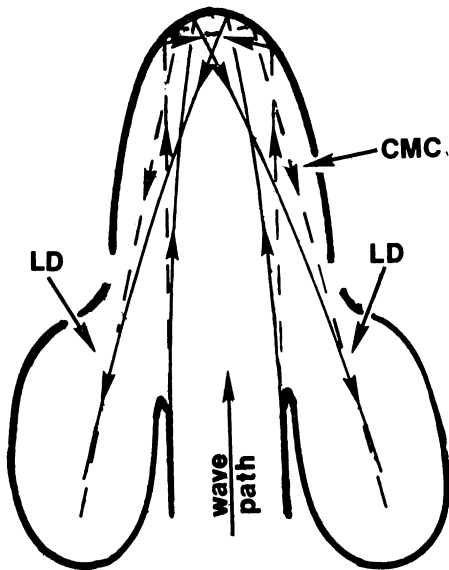


FIGURE 5. Wave trajectories within the common median chamber and lateral diverticula in *Corythosaurus casuarius*, rostral view.

versing a tube (Rayleigh 1896, p. 209). These conditions hold that, when a standing wave within a tube encounters a resonator of identical pitch extending from the side of the tube, the wave is suppressed at the mouth of the resonator and no sound is emitted at the far end of the tube. In *P. walkeri*, the lateral diverticula will resonate at frequencies corresponding to the 4th, 12th, and 19th harmonics of the entire nasal cavity (with higher harmonics possible), and, therefore, these frequencies will be suppressed if encountered during vocalization.

The lateral diverticula in *L. lambei*, *H. altispinus*, and *C. casuarius* are significantly more complex than those of *Parasaurolophus* (Weishampel 1981). They may have behaved as closed-ended resonators like those in *Parasaurolophus* to the extent that portions of each cavity lay beyond the direct air flow. However, these diverticula also form an integral portion of the continuous flow from the common median chamber to the nasal vestibule, unlike those in *Parasaurolophus*, and so it is not clear in which manner they may have functioned acoustically in life.

The lateral diverticula in species of *Parasaurolophus* (and perhaps in other lambeosaurines) likely acted as resonators (viz., Hopson 1975),

TABLE 2. Resonant frequencies of the lateral diverticula in *Parasaurolophus walkeri* (length = 45 cm) and *P. cyrtocristatus* (length = 28 cm). * For closed-ended resonance: $L = (2n - 1)(\lambda/4)$ $n = 1, 2, 3, \dots$ and $f = (2n - 1)(v/4L)$ $n = 1, 2, 3, \dots$

Mode of resonance	Frequency (in Hz)*	
	<i>P. walkeri</i> (ROM 768)	<i>P. cyrtocristatus</i> (FMNH P27393)
1	184	296
2	552	895
3	919	1505

to modify the harmonic spectrum of sounds traveling through the nasal cavity. Similar complex resonators are known or suspected to operate in this fashion in a diverse assortment of vertebrates, ranging from microchiropteran bats (Roberts 1973) and howler monkeys (Schön 1971), to delphinid cetaceans (Evans and Maderson 1973) and, finally, to some crocodylians (Martin and Bellairs 1977). The functional significance of resonance is different for each group, but all groups utilize the resonators to modify the vocal harmonic spectrum in a regular fashion. It can be expected then that the lateral diverticula in *Parasaurolophus*, and to a certain extent in *Lambeosaurus*, *Corythosaurus*, and *Hypacrosaurus*, promoted or suppressed portions of the harmonic spectrum characteristics of the nasal cavity. It is significant that the size, shape, and position of the lateral diverticula in the sympatric *C. casuarius* and *L. lambei* differ and thus maintained distinct vocal frequencies and discontinuities.

Auditory Sensitivity in Hadrosaurids

Inasmuch as predicted vocal frequencies are available for species of *Parasaurolophus*, it is relevant to compare these frequencies with predictions of auditory sensitivity. Both middle and inner ear structures are represented in hadrosaurids. In the middle ear (e.g. *C. casuarius*, AMNH 5338; Colbert and Ostrom 1958), the ratio between potential tympanic membrane area (approximately 22 cm²) and oval window area (approximately 3 cm²) is large and indicates a potentially high degree of sensitivity to a wide range of airborne frequencies (Manley 1973).

In the inner ear of tetrapods, the length of the basilar membrane, and thus the length of the lagena or cochlear duct that accommodates

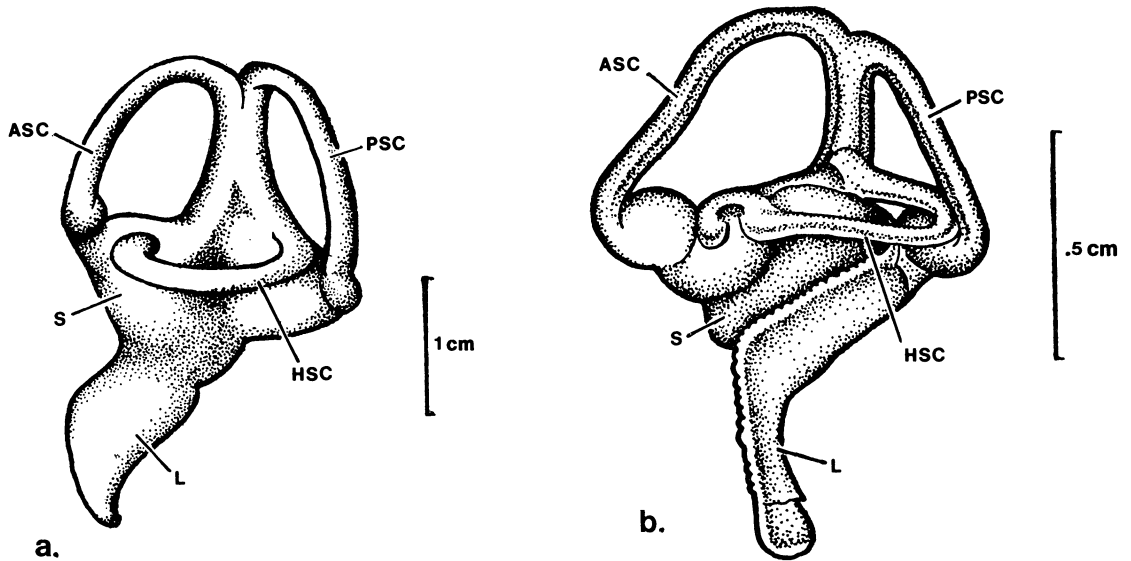


FIGURE 6. a. Lateral view of restored left inner ear of *Lophorhynchon atopus* (FMNH P 27383) showing elongate lagena (modified from Langston 1960). b. Lateral view of left inner ear of *Alligator mississippiensis* (modified from Retzius 1884). ASC: anterior semicircular canal; HSC: horizontal semicircular canal; L: lagena; PSC: posterior semicircular canal; S: sacculus.

it, is related to frequency sensitivity (Manley 1971). The lagena in crocodylians is relatively longer than that of other modern reptiles (Retzius 1884; Baird 1970) and can be correlated with high auditory sensitivity in these animals over a range of 20 to 6000 Hz (Beach 1944; Wever 1971; Wever and Vernon 1957). Langston (1960) demonstrated the similarity of the lagena of the hadrosaurine *Lophorhynchon atopus* (FMNH P27383) to that of *Alligator* (Fig. 6), which supports the inference that some hadrosaurids were able to perceive a wide range of vocal frequencies. The sound range over which adult alligators vocalize (50 to 750 Hz), in combination with auditory sensitivity (20 to 6000 Hz), is fully consistent with the argument that hadrosaurids vocalized and were sensitive to low frequencies, based on lowest predicted frequencies in species of *Parasaurolophus* and potential auditory sensitivity from an *Alligator*-like lagena in hadrosaurids. Sensitivity to high frequency vocalization in adult crocodylians is related to vocal signalling between offspring and parent, where juveniles are known to vocalize at high frequencies (200 to 2000 Hz; Campbell 1973; Herzog and Burghardt 1977). Similarly, size of the nasal cavity in juvenile lambeosaurines suggests relatively higher vocal

frequencies than in adults and explains the potentially high frequency sensitivity from the elongate lagena. Adult sensitivity to juvenile vocalization is consistent with the parent-offspring sociality suggested by Horner and Makela (1979; see also Hopson 1977).

Discussion

The suggestions of Wiman (1931) and Hopson (1975) that lambeosaurine crests were resonating organs is consistent with available evidence from resonance analyses and auditory anatomy. Thus, distinctive vocalization is reasonably explained on the basis of selection for vocal communication. What then are the effects of growth and sexual dimorphism on lambeosaurine vocalization and what benefits might have been reaped from vocal distinctiveness beyond individual and/or species-specific recognition? In other words, why low frequency vocalization?

Changes in the form of the nasal cavity that accompany growth in *L. lambei* and *C. casuarinus* are discussed by Weishampel (1981), following Dodson's (1975) study of relative growth in these species. Juveniles do not possess lateral diverticula, but all other divisions of the nasal cavity are present. The smaller size of the nasal cavity in juveniles suggests that resonance oc-

curred at higher frequencies (discussed above) and the lack of lateral diverticula indicates that the sound spectra were relatively unmodified (i.e. no harmonics suppressed or enhanced) along their course from the common median chamber to the external nares. Presumably, these effects allowed age-specific vocalization: higher and perhaps over a somewhat more continuous range in juveniles, and lower and discontinuous (due to suppression and enhancement of harmonics) in adults.

Sexual dimorphism appears to occur in *C. casuarius* and *L. lambei* (Dodson 1975) and has been suggested for *Parasaurolophus*, with the type specimens of *P. walkeri* and *P. tubicen* being males and the type of *P. cyrtocristatus* being a female (Hopson 1975). I am unable to discern any dimorphic variation in the nasal cavity of specimens of *C. casuarius* or *L. lambei*, implying tonal similarity of male and female vocalization. However, the nasal cavities of *P. cyrtocristatus* (female?) and *P. walkeri* (male?) show dimorphic characters that are acoustically significant (Fig. 7). First, crest size is smaller in *P. cyrtocristatus* than in *P. walkeri* (although other skeletal elements indicate animals of similar body size; Ostrom 1963); thus, total length of the nasal cavity and length of the lateral diverticula are different in these two individuals. These differences indicate different resonant properties of the nasal cavity and different vocal ranges (Tables 1 and 2).

I have suggested that lambeosaurines vocalized over a wide, but predominantly low range of frequencies. It is possible to speculate on the factors that may have shaped this range. First, habitat structure places restrictions on efficient communication over long distances. For vocal frequencies below about 400 Hz the distance over which sound is carried is independent of habitat type, while above 400 Hz this distance is greatly decreased in grassland, but less so in forest areas (Morton 1975; Moynihan 1969; Garrick et al. 1978). Low frequency vocalization may have allowed lambeosaurines to exploit intraspecific communication in both open and closed habitats. Second, there are three cues potentially used to locate a sound source (Marler 1969): differences in 1) loudness, 2) direction, and 3) time of arrival of the sound at the two ears. Low frequency vocalization provides

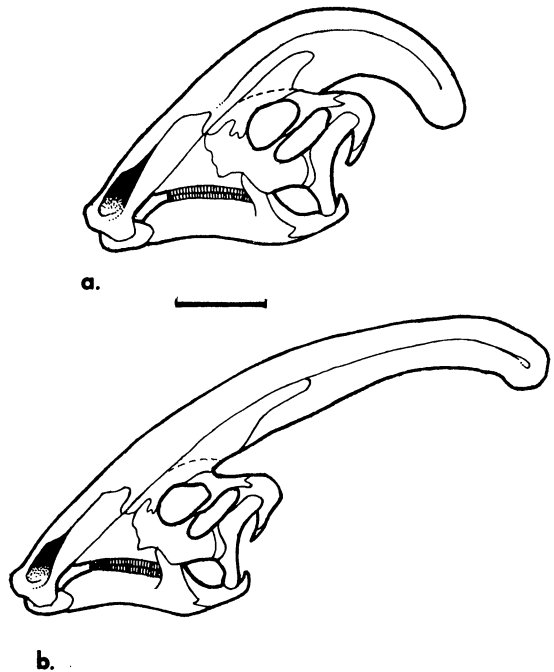


FIGURE 7. Skulls of (a) *Parasaurolophus cyrtocristatus*, interpreted as a possible female, and (b) *P. walkeri*, interpreted as a possible male, on the basis of the dimorphism in crest shape. Scale = 20 cm.

poorer cues about loudness and direction than do high frequency signals. However, low frequency signals, with wavelengths longer than the inter-ear distance of the receiver, make it possible for phase differences of the sound (and thus time of arrival at the two ears) to be determined in a way not possible at high frequencies (Garrick et al. 1978). Wavelengths for frequencies discussed in this paper for species of *Parasaurolophus* range from 720 to 55 cm, which are greater than the 30 to 40 cm inter-ear distances in these animals. Low frequencies additionally have the advantage of attenuating less rapidly over long distances than do high frequency signals. Lambeosaurine vocalization at low frequencies, then, may have been selected on the basis of 1) the distance or habitat across which vocal signals needed to be carried and 2) a localizing cue consistent with these habitat constraints on vocalization.

Summary

The structure of lambeosaurine crests is consistent with a hypothesis that these animals vo-

calized, particularly at low frequencies in adults (Wiman 1931; Hopson 1975). The lateral diverticula present in all but juvenile lambeosaurines acted to enhance or suppress portions of the sound spectra traveling through the nasal cavity and probably allowed for some differentiation of juvenile and adult vocalization. If the type specimens of *Parasaurolophus cyrtocristatus* and *P. walkeri* represent female and male of the same species, the resonance properties of their crests provide ample evidence that sexual dimorphism was present in their vocalizations. High frequency vocalization in juveniles and auditory sensitivity to these frequencies in adults suggest close parent-offspring ties, similar to those found in crocodylians. Low frequency vocalization in adult lambeosaurines probably relates to sound dispersal in varied habitats and/or localization with low attenuation of the vocal signal, both important to the high degree of sociality suggested for hadrosaurids (Hopson 1977; Horner and Makela 1979; Currie and Sarjeant 1979).

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