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THE CRANIAL CRESTS OF HADROSAURIAN DINOSAURS

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INTRODUCTION

Ever since 1914 when Lawrence Lambe described and figured the first of the hooded dinosaurs, there has been considerable speculation and debate about the function of the hadrosaurian cranial crest. Although the debate has subsided somewhat in recent years, it has not been because general agreement has been reached. Dozens of crested hadrosaurs have been collected and described since that first discovery and one cannot help but be impressed by the variety of crestal shapes and sizes represented. There are the relatively small, almost incipient crests of *Procheneosaurus* and *Cheneosaurus*, the large "Corinthian helmets" of *Corythosaurus* and *Hypacrosaurus*, the "top hats" of *Lambeosaurus*, and the curved, tubular crests of *Parasaurolophus*. But in spite of the number and diversity of available specimens, the crestal function has remained quite elusive.

In 1920, Lambe discovered that the hadrosaurian crest was not a solid bony structure, but was instead constructed as a thin and delicate bony sheath which enclosed folded and sometimes complicated passages and chambers. Prior to this dis-

covery, most paleontologists had viewed these cranial prominences simply as interesting decorative features. Lambe's revelation, however, made such an interpretation quite untenable and a rash of hypotheses attempting to explain these structures ensued. The aquatic adaptations of the hadrosaurs had already been noted by this time and consequently many of these theories related the complex crestal cavities to the probable semi-aquatic habits of these ornithischian dinosaurs.

In spite of some popular appeal, and what may appear to be a certain degree of adaptive significance, most of the crestal hypotheses that are correlated with an aquatic mode of life involve serious weaknesses that have generally been overlooked. This situation, together with certain recently acquired information, warrants a careful reconsideration of the hadrosaurian crest problem.

ACKNOWLEDGMENTS

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ABBREVIATIONS

Reference is made to specimens in the collections of several institutions, and in such references the institutional names are abbreviated as follows:

A.M.N.H. — American Museum of Natural History
C.N.H.M. — Chicago Natural History Museum
N.M.C. — National Museum of Canada, Ottawa
R.O.M. — Royal Ontario Museum, Toronto
Y.P.M. — Peabody Museum of Natural History, Yale University.

Abbreviations used in the text figures are as follows:

AC. — Anterior chamber of nasal capsule
AS. — Anterior space of olfactory chamber
AT. — Anterior nasal tube of nasal capsule
CO. — Concha
CT. — Choanal tube
EN. — External naris
IN. — Internal naris
LC. — Lateral crest cavity
MC. — Medial crest cavity
OB. — Olfactory bulbs
OC. — Olfactory chamber of nasal capsule
OS. — Antorbital space of olfactory chamber

PREVIOUS THEORIES

William Parks was the first to succumb to the temptation of theorizing about the functional significance of hadrosaurian crests. In his description of *Parasaurolophus walkeri* (1922) he argued rather persuasively that the crest of this species had been joined to the neural spines of the anterior dorsal vertebrae by means of a strong muscular or ligamentous connection. By inference, at least, this would have facilitated movement of the rather large and unwieldy head. Parks' hypothesis, however, was based almost entirely upon what appears to the present writer to be a pathologic aberration of the sixth and seventh dorsal spines.

In opposition to Parks' interpretation, it must be noted that no identifiable muscle or ligament scars can be seen on the crest of *P. walkeri*, or on that of any other crested hadrosaur. It might also be pointed out that other hadrosaurs, such as *Edmontosaurus* and *Kritosaurus*, possessed far larger heads, but failed to develop such supporting or leverage structures. Furthermore, the crest of *P. walkeri* itself is largely responsible for the unwieldy nature of the head and therefore it cannot be seriously considered as an adaptation to counteract its own disadvantageous effects. And finally, Parks' hypothesis, published two years after Lambe's discovery, in no way accounts for the passages within the crest.

In 1924 Othenio Abel published the more fanciful suggestion that hadrosaurian crests were defensive structures, perhaps used in mating combat. In the same paper Abel very briefly considered the possibility that the crest cavities were also related to olfaction and he compared the crested hadrosaurs with crocodiles and their somewhat intensified olfactory powers. This paper was followed in 1929 by Nopcsa's sex character hypothesis wherein he presumed the crests to be secondary sex characters, the crested forms being the "males" and the non-crested varieties the "females." Again, with the exception of olfaction, neither Abel's nor Nopcsa's suggestion accounts for the presence of crestal passages, and Nopcsa's hypothesis proves somewhat inadequate on other grounds as well. (With the exception of *Parasaurolophus tubicen*, only non-crested "females" have been recovered from the Lance and equivalent stratigraphic units.)

Carl Wiman's resonating chamber theory (1931) was the first to give serious consideration to the most striking feature of hadrosaurian crests—the crestal cavities. That these cavities may have served as resonating chambers similar to those found in certain modern birds, appears entirely plausible, especially in view of the notoriously noisy habits of modern crocodiles. In fact, this suggestion is perhaps the best of any theory proposed so far, but it does seem somewhat improbable that this activity alone could have been responsible for such extensive cranial modifications.

A. S. Romer (1933) initiated the aquatic adaptation school with his comment that there may have been external narial openings near the top of the crest through which the animal could have breathed while almost completely submerged. An elevated or dorsal position for the external nares is a well known adaptation in certain living and extinct, air breathing, aquatic animals, but to date no such condition has been verified in the hadrosaurian crests, in spite of some comments to the contrary.

A series of papers by Martin Wilfarth (1938, 1939, 1940, and 1947) expanded the suggestion of Romer's relating the crests to an aquatic mode of life. In the first of these papers, Wilfarth suggested that the flat-headed hadrosaurs were

proboscis-bearing reptiles in which there existed a large muscular, "telescoping air tube" that rose from the preorbital fossae of the snout. This device enabled the animal to "reach" up to the surface for air without interrupting its underwater feeding. The deep excavation of the snout is interpreted by Wilfarth as the origin scar of the large proboscis muscles. In the crested hadrosaurs, a similar muscular "snorkel" was pictured as attached to the crest, but strangely enough, in the same paper, Wilfarth accepts Parks' ligamentous connection between the dorsal vertebrae and the crest in *Parasaurolophus*. In later papers, the "snorkel" interpretation is greatly elaborated by Wilfarth. The crested hadrosaurs are represented with unique "upper" external nares located high on the crests. The usual narial openings situated rostrally on the snout are considered as nonfunctional relicts closed in life by skin and other tissues. The large surface area of the crest presumably provided large areas for the origins of proboscis muscles and inspired air was conducted down the flexible "breathing tube," through dorsal "nares" into the crest cavities and then to the mouth cavity and trachea. It is further suggested that this remarkable breathing tube may also have been prehensile and therefore useful in feeding.

Wilfarth's imaginative solution to the hadrosaurian crest problem, appealing and exotic as it may be, is not supported by any evidence. In the first place, not all of the hollow hadrosaurian crests are characterized by the required external openings which Wilfarth has interpreted as external nares. The crest of *Cheneosaurus tolmanensis*, for example, is not penetrated by any lateral or dorsal openings. The same is also true of *Corythosaurus frontalis*, *Corythosaurus brevicristatus*, and *Hypacrosaurus altispinus*. And in spite of Wilfarth's implications to the contrary (1947), there are no terminal openings in the crest of either *Parasaurolophus walkeri* or *P. tubicen* and they appear to have been absent in *P. cyrtocristatus* as well. Furthermore, the highly varied and irregularly shaped crestal openings that do occur in some specimens, (*Corythosaurus casuarius*, *Lambeosaurus lambei*, and *Procheneosaurus praeceps*) appear to be due to incomplete ossification at bone margins, and the areas involved were probably closed by

cartilage or membrane. Still more doubt is cast on Wilfarth's hypothesis by the lack of any discernible muscle scars on any of the hadrosaurian crests. Although the preorbital fossae of the non-crested hadrosaurs might be considered as excellent scars left by proboscis muscles, it seems much more likely that these excavations contained narial sphincter muscles together with relatively large nasal organs.

Although perhaps not comparable, proboscis-bearing mammals are generally characterized by a marked reduction in the size of the nasal bones rather than an enlargement as is the case in many of the crested hadrosaurs. Furthermore, the nearest thing to a homologous structure, the elephant trunk, is not used as a "snorkel," but is a prehensile feeding mechanism and it apparently has always been such a device. If the hadrosaurian snorkel-like proboscis were also prehensile, as suggested, it would hardly seem to be functionally advantageous together with an expanded beak, as C. M. Sternberg (1939) has already pointed out.

Two additional explanations that have received a much greater degree of acceptance are similarly correlated with the semi-aquatic habits of the hadrosaurs. C. M. Sternberg (1935, 1939, 1942, and 1953) and L. S. Russell (1946) considered the crest as a trapping device which prevented the entrance of water into the narial passages and lungs while the animal was submerged. According to this thesis, the S-shaped narial loop is considered analogous to an inverted U-tube, and the greatly elongated crest of *Parasaurolophus* is represented as the functional peak of this adaptation. In contrast to the trap theory is the air storage hyothesis put forward by E. H. Colbert (1945 and 1955) and Romer (1933 and 1945). Here, the crestal cavities are interpreted as chambers for retaining a reserve supply of air which would have enabled the animal to remain submerged for longer periods. Both of these capabilities would seem to be highly advantageous adaptations for air breathing, aquatic animals. However, neither of these functions seems possible for the structure involved.

The U-tube trap explanation is unsatisfactory for several reasons. First, the mere presence of an inverted loop in the narial passage could not in itself have prevented the entrance of water into the narial passages, or even into the lungs. Water

does not rise in the inverted U-tube for the simple reason that pressures at both ends of the tube are equal. In the case of the hadrosaurian loop, equal pressures on opposite sides of the loop could only occur in the emerged state. Even at shallow depths, hydrostatic pressure would have exceeded the air pressure within the crestal cavities and lungs. Such excessive hydrostatic pressure would have resulted in compression of crestal air and the entrance of water into the narial passages — even in an upward path against the force of gravity. Only excessive lung pressure (over hydrostatic pressure) could have prevented water from rising within the narial loop with the consequent admission of water into the nasal chambers and possibly into the lungs as well. No modern air breathing vertebrates, aquatic or semi-aquatic, rely solely on lung pressure to prevent drowning. Moreover, when one considers that the far simpler and more effective sphincter valves or vascularized narial tissues have been developed repeatedly for this very same function in such diverse aquatic animals as cetaceans, sirenians, pinnepeds, rodents, crocodiles, lizards, snakes and amphibians, the proposed water trapping function of the hadrosaurian crests loses much of its appeal.

Storage of a reserve air supply, for the purpose of prolonging the period of submergence, at first glance seems to be a very plausible and practical adaptation for semi-aquatic, air breathing animals. However, two quite unrelated factors make such a thesis highly improbable—if not impossible. First, the available volume of the crestal chambers appears totally inadequate in comparison with the probable lung capacity. A very conservative estimate of the lung capacity of *Corythosaurus casuarius*, (A.M.N.H. No. 5338) for example, is approximately 65,000 cc., or less than one fifth of the total volume of the rib cage. If it be assumed that the entire crest volume of this species could have been utilized as storage space, the total available volume of the uncrushed crest probably did not exceed 2500 cc. Thus in this particular species, the crest volume at best represented only about four per cent of the total lung capacity, and it is more than likely that it actually represented a much smaller fraction. Species with much smaller crests, such as *Procheneosaurus* and *Cheneosaurus*, would have had an even

less significant volume of reserve air. It therefore seems unlikely that such extreme structural modifications were related to air storage. Furthermore, it seems somewhat anomalous that a semi-aquatic vertebrate should have undergone such extreme modifications for this purpose when purely aquatic air breathers have been so conservative with regard to such adaptations.

Finally, if we consider the manner in which the proposed storage cavities would have been utilized, it is immediately apparent that highly undesirable or totally impossible conditions would have resulted. For example, in order to withdraw this "reserve air supply" from the crest cavities and into the lungs, something (either air or water) must have displaced it. Water seems a most unlikely agent in view of its adverse effects and the numerous effective precautions against just such circumstances that have been repeatedly developed in other aquatic tetrapods. Air as a displacing substance, obviously was available only in an emerged state—in which case the "reserve air supply" was unnecessary. If narial sphincter muscles or vascularized narial valves prevented the entrance of water into these narial passages, as seems probable, these very same valves must have prevented air withdrawal from the crest during submergence. Thus, in spite of the attractiveness of the air storage theory, it seems quite improbable on the basis of current evidence.

NASAL APPARATUS IN MODERN REPTILES

Partial or complete dissection of several hadrosaurian crests has shown that the crestal cavities are continuous with the rostrally situated external nares and demonstrates most clearly that this structure was largely, if not entirely, related to the nasal apparatus and to some phase of respiratory activity. It is necessary therefore to examine the nasal anatomy of modern reptiles and to consider the various functions of the tetrapod nasal system.

The primary function of the nasal apparatus quite obviously is the conduction of air from the exterior to the lungs. In addition, this principal activity requires other preparatory functions such as cleansing, warming (or cooling), and humidifying of the inspired air. (The trapping hypothesis relates to the first

of these.) It should not be necessory to consider each of these functions in detail in order to arrive at the respective merits of each as an explanation of the structures under consideration. It is true that temperature regulation or humidification of inspired air may be the proper explanation, but all of these seem improbable in view of the humid, temperate to subtropical conditions indicated for the hadrosaurian environment.

A second major function involving the nasal apparatus is that of olfaction. It is surprising that this activity, which is associated with respiratory activities in all tetrapods, has not been considered more seriously before this. Perhaps the reason for this may lie in the general impression that modern reptiles do not possess a highly developed sense of smell. This is certainly true, if one compares them with mammals—particularly with macrosmatic mammals, but the fact that reptiles do have olfactory powers cannot be disputed.

Mammals which are characterized by a highly developed sense of smell show a corresponding expansion of the olfactory sensory epithelium. This is reflected in the expanded and complex turbinal and ethmoid systems. There is of course no comparable "ethmoid-turbinal complex" in the hadrosaurs, but the crestal cavities could well have contained analogous structures. The question to be answered here is—what was the purpose of the greatly elongated and complex path of the narial passages? Might not this expanded passage have been a means of increasing the surface area of sensory epithelium? The form, pattern and size of the cavities are quite variable, but in every crested hadrosaur there has been some increase in the length of the narial passages through which the inspired air traveled. This is the only common denominator for all lambeosaurine crests.

Examination of the nasal capsule in modern reptiles reveals some interesting morphologic evidence pertinent to this subject. The reptilian nasal capsule (see fig. 1), which is largely cartilaginous, encloses the membranous nasal sac. The sac itself consists of four major parts: the anterior nasal tube, the anterior chamber, the olfactory chamber, and the choanal tube (Beecker, 1903; Pratt, 1948; Bellairs and Boyd, 1950; and Oelrich, 1956). Each of these regions may vary from one form to another, but they are at least partly distinct from each

other functionally as well as morphologically. The anterior chamber is principally a preparatory mechanism (filtering, humidifying, and temperature regulating), while the olfactory

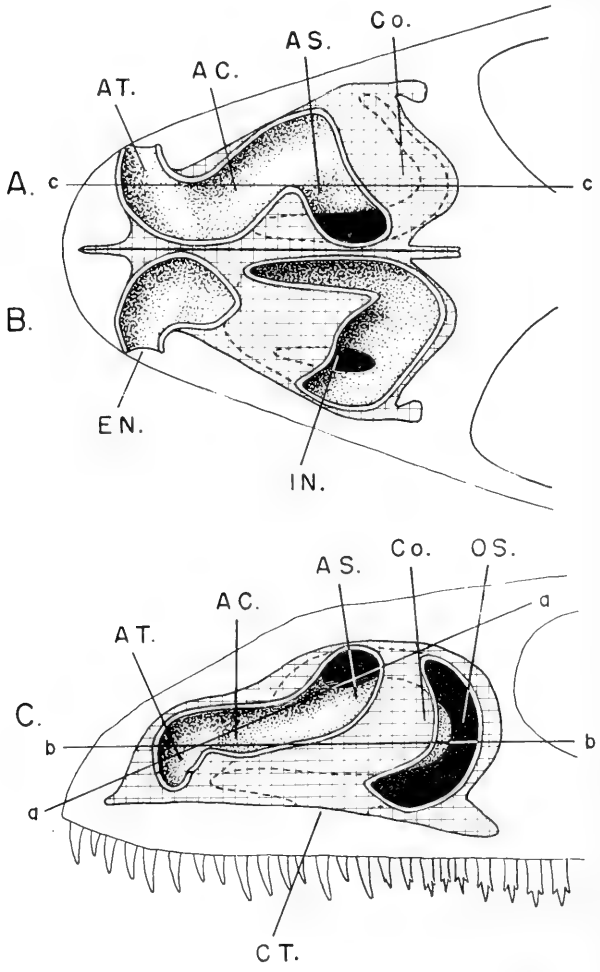

Fig. 1. Cartilaginous nasal capsule of *Ctenosaura pectinata*. A. Dorsal view of capsule as seen in rostrally inclined section (see line a - a in diagram C.) showing the anterior part of the nasal canal. B. Dorsal view as seen in horizontal section through the center of the capsule (see line b - b in diagram C.) showing the posterior and ventral parts of the nasal canal. C. Lateral view of the capsule as seen in parasagittal section (see line c - c in diagram A.) For abbreviations see text.

chamber is in large part sensory in function. The olfactory chamber is further divisible into three regions relating to an epithelial swelling or protuberance of its lateral wall—the concha. These are: the anterior space (anterior to the conchal swelling), the conchal zone, and the antorbital space (posterior to the concha) (Oelrich, 1956). Ventrally the olfactory chamber (usually in the conchal zone) opens into the choanal tube and thereby communicates with the oral cavity.

In *Sphenodon* (see fig. 2) a short anterior nasal tube passes posteromedially from the laterally situated external naris to a

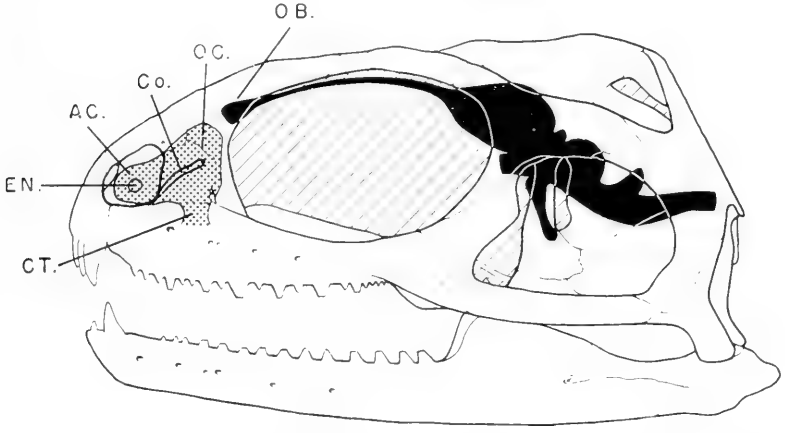

Fig. 2. Lateral view of the skull of *Sphenodon punctatum* illustrating the locations and relative sizes of the cartilaginous nasal capsule (stippled pattern) and the olfactory structures of the brain. Notice the long olfactory stalks and the olfactory bulbs situated just behind the relatively small nasal capsule.

short but slightly expanded anterior chamber adjacent to the nasal septum. The anterior chamber is continuous with a larger olfactory chamber behind. (Although the olfactory chamber of *Sphenodon* is larger than the anterior chamber, it is relatively smaller than the olfactory chamber in most lizards [Pratt, 1948].) Within the olfactory chamber, the anterior space is restricted and the concha occurs as a very weakly developed swelling of the lateral wall. The antorbital space is also restricted. Sensory epithelium is limited to relatively small

areas on the medial and dorsal surfaces of the restricted concha, a relatively much smaller proportion of the available area as contrasted with certain lizards (Pratt, 1948). Olfactory nerve fibers arise from these small areas of olfactory epithelium and pass posteriorly along the lateral wall of the antorbital space and through the posterior wall of the nasal capsule (planum antorbitale) where they join the olfactory bulb just behind. It is important to note here that in spite of the relatively weak development of the olfactory chamber, the small olfactory bulbs are situated immediately behind the short nasal capsule anterior to the orbits.

The relatively short preorbital length, together with the large eyes of *Sphenodon*, limits the available space for the nasal capsule and undoubtedly is related to the restricted development of the olfactory chamber and concha. The latter apparently is not related, however, to the limited olfactory sensitivity of *Sphenodon*, because even the available surface area of the olfactory chamber is not fully utilized for sensory functions. The limited olfactory powers (Pratt, 1948) would appear to be in contradiction to the nocturnal, predatory nature of the animal where an acute sense of smell would seem to be advantageous, but on the other hand it is consistent with the burrow-living (but possibly not fossorial) habits of *Sphenodon*.

Stebbins (1943 and 1948) and Pratt (1948) have demonstrated that there is considerable variation in the respective parts of the lizard nasal sac depending upon the mode of life. For example, in deserticolous lizards the trapping and humidifying functions are more critical and there is a corresponding enlargement of the anterior chamber. In arboreal lizards, vision is of greater importance than olfaction and the visual apparatus seemingly has expanded and limited the development of the olfactory chamber. In cursorial forms, particularly in the non-burrowing varieties, vision and olfaction are both important. Thus there commonly exists a relatively large eye which limits the expansion of the olfactory chamber in front. However, in such cases, the concha is usually greatly expanded and it appears that conchal expansion is an alternative method of maintaining or increasing the available area for olfactory epithelium when other factors (orbital expansion or short snout

length) restrict expansion of the olfactory chamber itself (Pratt, 1948).

In *Ctenosaura* (see figs. 1 and 3), the anterior nasal tube extends for a short distance anteromedially from the anterolaterally placed external naris. Adjacent to the nasal septum it turns abruptly backward and upward, extending to a long and expanded anterior chamber. This is continuous dorsomedially with a narrow anterior space and inflated conchal zone. Posteriorly, a large antorbital space extends ventrally and then forward to the choanal tube. Within the olfactory chamber, olfactory epithelium lines the medial and dorsal walls, the medial and posterior surfaces of the concha, and the posterior wall of the antorbital space (Oelrich, 1956). Olfactory nerve

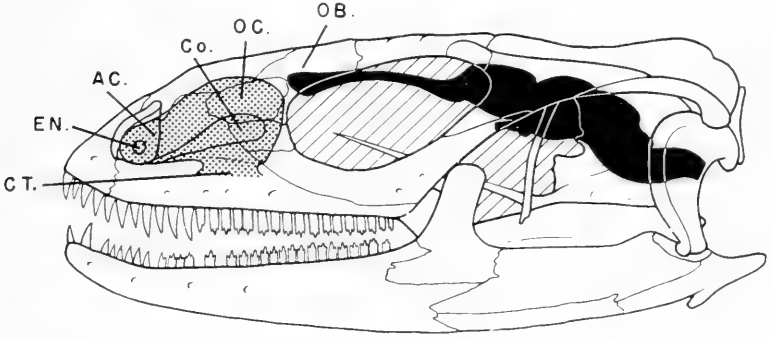

Fig. 3. Lateral view of the skull of *Ctenosaura pectinata* showing the locations and relative sizes of the nasal capsule (stippled pattern) and the olfactory centers of the brain.

fibers pass posteriorly from these areas, penetrate the planum antorbitale and unite with the olfactory bulb situated anterior and dorsomedial to the orbits.

Relative to *Sphenodon*, *Ctenosaura* possesses enlarged olfactory chambers and considerably more extensive olfactory epithelium. As in *Sphenodon*, the olfactory bulbs are situated far forward, immediately behind the planum antorbitale of the nasal capsule and in front of the orbits.

In *Alligator* (see fig. 4), an extremely short anterior nasal tube descends from the dorsally situated external naris. At its

ventral limit it turns abruptly backward and opens into a very long and slightly inflated anterior chamber that reaches caudally to the anterior extremity of the palatine. Although compressed dorsoventrally, the anterior chamber expands laterally reaching its maximum width at about mid-length Posteriorly, the anterior chamber is continuous with a rather large olfactory chamber. A very prominent concha occupies most of the olfactory chamber with the result that both the anterior space and the antorbital space are restricted in volume, although both are of moderate size. The total length of the nasal

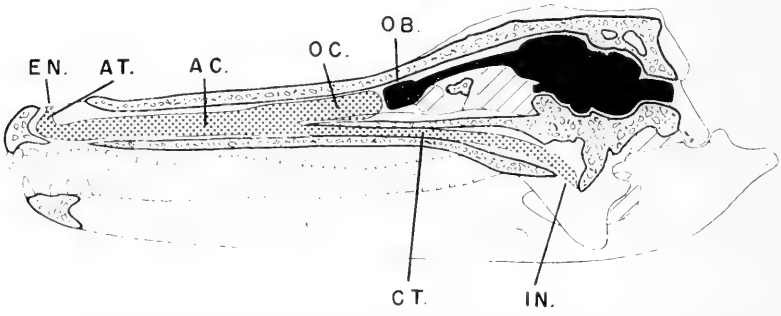

Fig. 4. Skull of *Alligator mississipiensis* as seen in near-sagittal section, showing the relationships between the olfactory centers of the brain and the enlarged nasal capsule (stippled pattern). Notice the enlarged anterior chamber and olfactory chamber as well as the elongated choanal tube.

capsule is approximately equal to the total preorbital skull length, the planum antorbitale being situated just beneath the anterior rim of the orbit.

Olfactory epithelium lines portions of the medial, dorsal, and ventral walls of the olfactory chamber, the dorsal, medial, and ventral surfaces of the concha, and the posterior wall of the antorbital space. From these rather extensive sensory areas, olfactory nerve fibers extend dorsoposteriorly to the moderately sized olfactory bulbs that are placed dorsomedially at the level of the anterior margins of the orbits. As in *Sphenodon* and in lizards, the olfactory bulbs lie immediately behind the rear wall of the nasal capsule.

Generally speaking, there is a marked reduction in the olfactory sensitivities of aquatic animals, but this does not seem

to be true of the Crocodilia. The long snout has provided space for a relatively long nasal capsule that extends over the entire preorbital length. Extensive development of sensory epithelium, an expanded concha, and moderately sized olfactory bulbs all indicate a significant (if not acute) level of olfactory sensitivity.

NASAL APPARATUS OF THE HADROSAURIDAE

Turning our attention back to the group in question, the Hadrosauridae are subdivided into three subfamilies (four by Lull and Wright [1942] and certain other workers) chiefly on the basis of cranial anatomy. The three subfamilies recognized here are the Hadrosaurinae, characterized by flat, non-crested skulls; the Lambeosaurinae, possessing hollow bony crests composed of the premaxillaries and nasals extending over the top of the cranium; and the Saurolophinae, which bear less prominent, solid, bony crests composed exclusively of the nasals. The lambeosaurine crests have been referred to as "true narial" crests because they are all hollow and enclose parts of the elongated and sometimes complicated narial passages. The various species of *Prochenecosaurus*, *Chenecosaurus*, *Corythosaurus*, *Lambeosaurus*, *Hypacrosaurus*, and *Parasaurolophus* all display variations of the true narial crest. Crests of the Saurolophinae (*Saurolophus*, *Prosaurolophus*, and *Brachylophosaurus*) have been labeled "pseudo-narial" crests, because of their solid construction and the fact that they do not enclose any part of the nasal apparatus (Ostrom, 1961b).

Correlated with these cranial conditions is the construction of the hadrosaurian snout. Those hadrosaurs which bear true narial crests have greatly reduced snouts, while all other hadrosaurs are characterized by a long and inflated snout. As a result, all members of the Hadrosaurinae and the Saurolophinae have conspicuous preorbital fossae, while the Lambeosaurinae have virtually no preorbital space available in the snout. It is quite reasonable to assume that the prominent preorbital excavation of the hadrosaurine and saurolophine premaxillaries and nasals housed (at least in part) rather large nasal organs as suggested by Versluys in 1936. In the Lambeosaurinae, on the other hand, the snout is greatly compressed dorsoventrally

and there is no large excavation of these bones. Instead, the premaxillaries and nasals have been prolonged dorsocaudally and inflated at a more dorsal and posterior level forming the true narial crest.

In *Procheneosaurus* the inflated region occurs dorsal to the maxillaries immediately in front of the orbits. In *Cheneosaurus* it occupies a similar position, but has expanded dorsocaudally and lies over the orbits as well. The inflated zone of *Corythosaurus*, *Hypacrosaurus*, and *Lambeosaurus* has expanded still

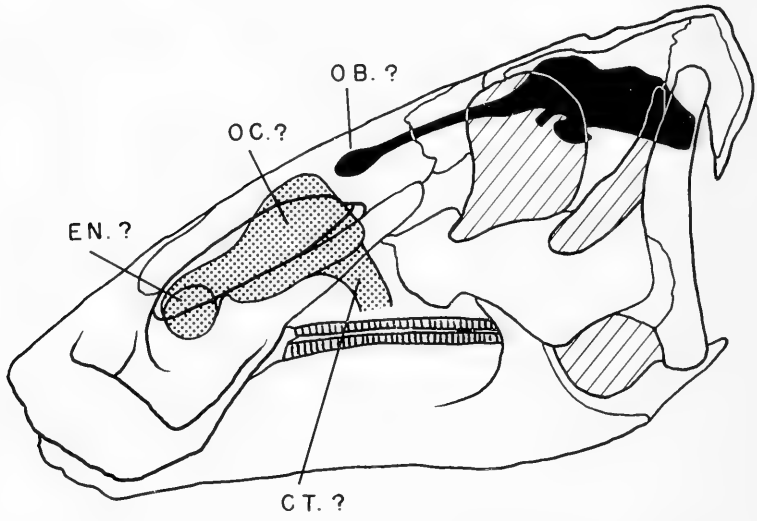

Fig. 5. Outline sketch of the skull of *Edmontosaurus regalis* (N.M.C. No. 2288) illustrating the probable position of the cartilaginous nasal capsule (stippled pattern) in the preorbital fossa. The preorbital position of the olfactory bulbs suggested here is based upon the close proximity of nasal capsule and olfactory bulbs found in all modern reptiles. Notice that the expanded snout of the Hadrosaurinae provides ample space for a nasal capsule and narial sphincter muscles.

further dorsocaudally so that in nearly every instance it lies well above and behind the orbital level in a supracranial position. And in *Parasaurolophus*, an extreme expansion has carried the inflated region well behind the cranium, as well as above it, to a postcranial position. These hadrosaurs would seem to form a sequence of structural stages through which the

nasal apparatus has expanded and shifted from a rostral position on the snout to a preorbital, to a supraorbital, to a supracranial, and finally to a partially postcranial position. (See figs. 6-9.)

Considering the true narial crests in more detail, they all involve a dorsal and caudal expansion of both the premaxil-

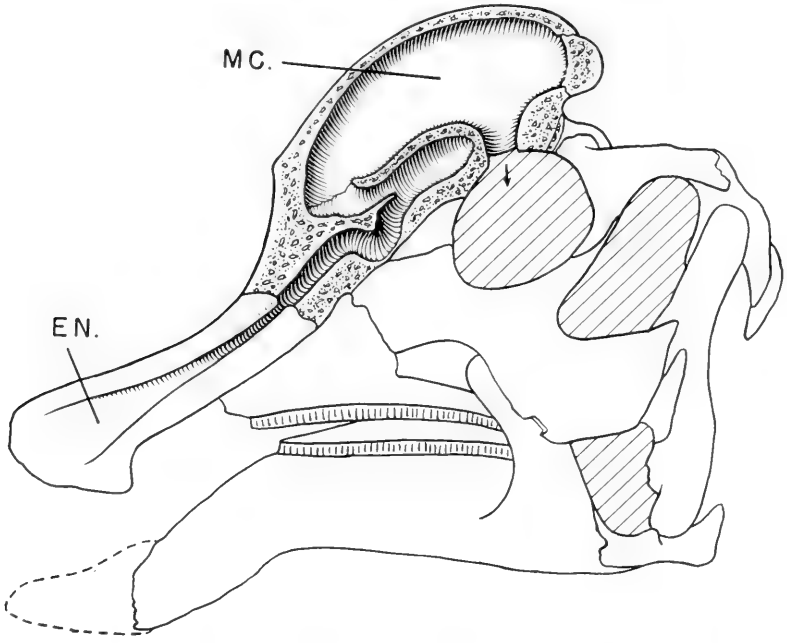

Fig. 6. Outline sketch of the skull of *Prosaurolophus cranibrevis* (N.M.C. No. 8633) showing a reconstruction of the narial passages of the crest. The left premaxillary and nasal have been partially removed to show the paired lower canals and the "undivided" medial cavity and "choanal" tube. The arrow indicates the passage of the "choanal" canal from the crest. (From Ostrom, 1961b.)

laries and the nasals, the degree of expansion and the relative participation of each varying considerably between different species. Most conservative are those of the three species of *Prosaurolophus* (*P. praeceps*, *P. erectofrons*, and *P. cranibrevis*) and the only known species of *Saurolophus* (*S. tolmanensis*). In these species the premaxillaries are split into

superior and inferior rami or lobes lying above and below the nares. Both lobes ascend caudally, almost completely enclosing the anterior portion of the narial passage. The nasal bone occupies a dorsal position between the upper extremities of the premaxillary lobes and encloses the upper part of the narial canal.

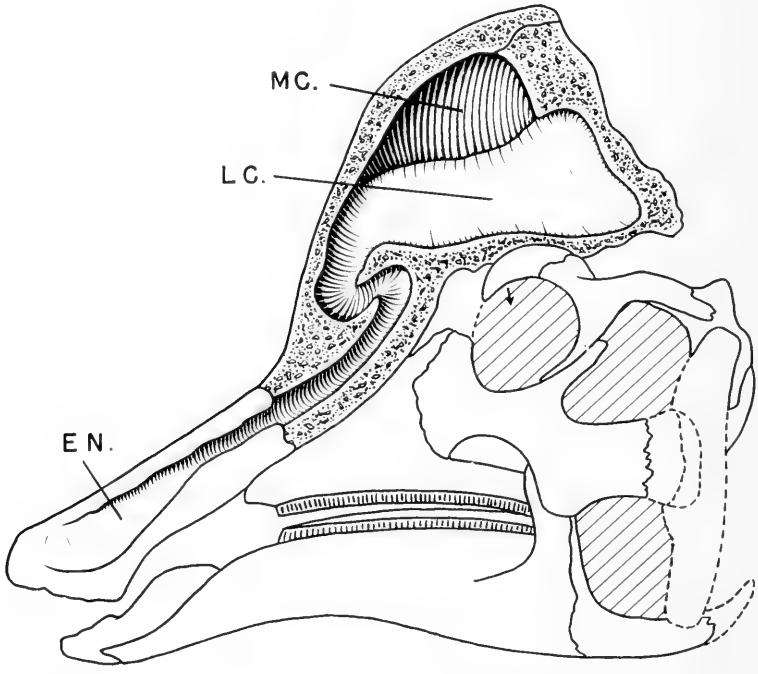

Fig. 7. Outline sketch of the skull of *Corythosaurus excavatus* (N.M.C. No. 8676) showing a reconstruction of the narial passages of the crest. The left premaxillary and nasal have been partially removed to show the paired lower canals and lateral cavities and the "undivided" medial cavity. The arrow indicates the approximate passage of the "choanal" canal from the crest. (From Ostrom, 1961b.)

Within the crest of *Prochencosaurus* (as may be seen in *P. cranibrevis*, N.M.C. No. 8633) the narial passages ascend as separate canals from the rostrally situated external nares. (See fig. 6.) This portion of the canal, although quite long, may be analogous to the anterior nasal tube of modern reptiles. Dor-

sally, at the anterior limit of the nasal bone, the narial canals loop forward and then upward in an S-shaped curve and finally enter a common medial crest cavity anterior to and at the level of the orbits. (This medial cavity quite probably was divided by cartilage or membranous tissues in life, consistent with the paired conditions of modern reptilian nasal structures.) Ventroposteriorly, a single (also probably paired in life) "choanal" canal descends from this medial crest cavity into the interorbital region. The latter feature is certainly comparable to the choanal tube of the modern reptilian nasal capsule and the undivided cavity above it would appear to represent the location of paired olfactory chambers. The S-shaped curve of the nasal passage then seems to represent the anterior chamber.

The crest of *Corythosaurus excavatus* (N.M.C. No. 8676), although differing in details, displays a very similar pattern (see fig. 7). In this and most other species of *Corythosaurus*, the nasal is a very prominent bone forming a major part of the crest. Again, separate narial passages (anterior nasal tubes?) ascend posteriorly from the external nares, enclosed for most of their length by the two lobes of the premaxillaries. In front of and slightly above the level of the orbits, the two passages turn forward and then upward and back again, forming separate S-shaped curves (anterior chambers?) similar to those of *Procheneosaurus cranibrevis*. Unlike the condition in that species, however, the paired narial canals lead into paired lateral cavities above and posterior to the S-shaped loops. These lateral cavities (olfactory chambers?) occupy the lower half of the crest, but dorsally they open into a common medial cavity that extends well up into the crest. Although this latter cavity could not be fully explored, it apparently extends ventrally as a single "choanal" tube between the lateral cavities to the interorbital region just anterior to the olfactory canal of the brain case. These relationships indicate a great expansion of the lateral (olfactory) chambers back around the more medially placed "choanal" tube.

Two specimens of *Lambeosaurus* (*L. lambei*, N.M.C. No. 2869, and *L. clavinitialis*, Y.P.M. No. 3222) display similar narial patterns characterized by the independently ascending passages (anterior nasal tubes?) and the S-shaped loops

(anterior chambers?) (see fig. 8). In both of these specimens, however, the canals remain separated for some distance behind these loops before entering the large undivided medial cavity in the posterior half of the crest. As in other forms, this medial

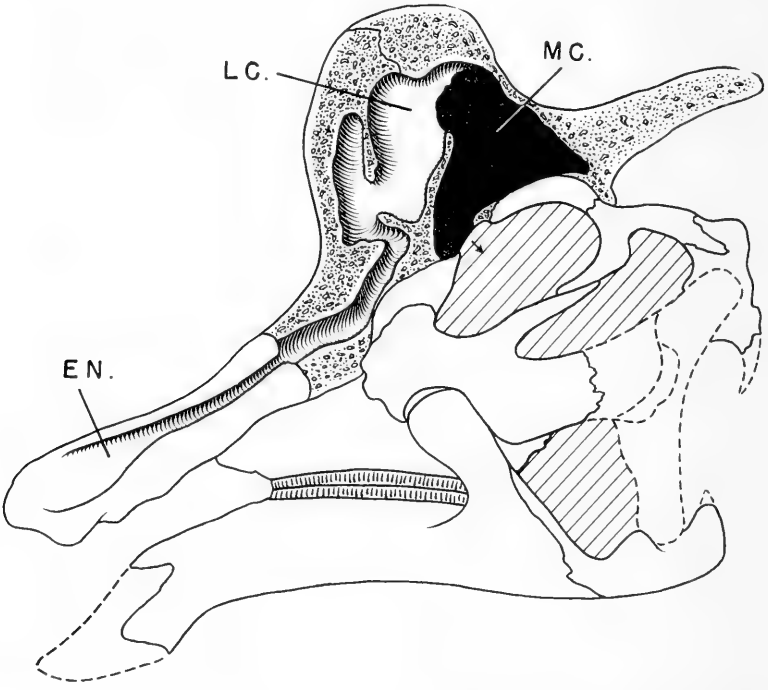

Fig. 8. Outline sketch of the skull of *Lambeosaurus clavinitialis* (Y.P.M. No. 3222) showing a reconstruction of the narial passages of the crest. The lateral elements of the crest have been partially removed to show the paired condition of the lower canals and the "undivided" dorsal (posterior) cavity and "choanal" tube. Organic material, perhaps representing cartilaginous tissues, found in the posterior cavity indicates this cavity may have been divided by a median septum in life. The arrow indicates the passage of the "choanal" canal from the crest. (From Ostrom, 1961b.)

crest cavity (site of the olfactory chambers?) is continuous ventrally with an unpaired "choanal" tube leading to the interorbital region just anterior to the brain case.

The crest of *Parasaurolophus cyrtocristatus* (C.N.H.M. No. P27393) provides the most detailed information yet available

about hadrosaurian crestal cavities (Ostrom, Ms.) (see fig. 9). Dissection of one side of the crest illustrates that the narial canals extend as separate passages along the full length of the crest. From the rostrally situated external nares, the paired passages (anterior nasal tubes?) ascend in the upper half of the tubular crest. At the caudal extremity, they loop down to the lower half of the crest and pass forward to the roof of the skull. Only at the base of the crest, just above and behind the orbits do these paired passages join in a common cavity. (These inferior passages and the undivided basal cavity may represent the location of the olfactory chambers.) Thin medial lamellae

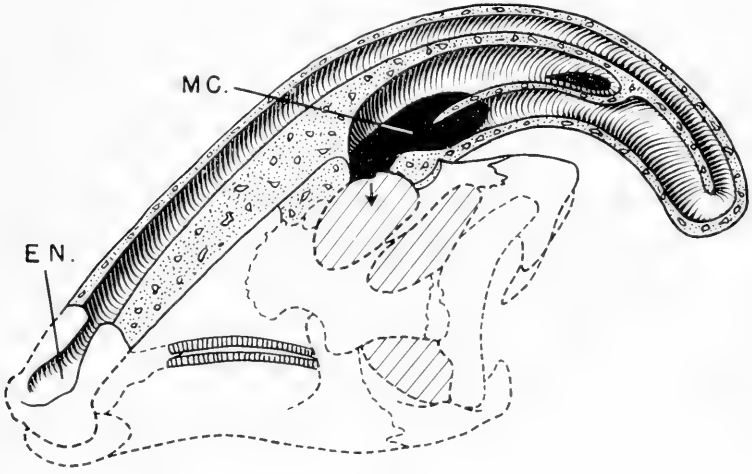

Fig. 9. Outline sketch of the crest of *Parasaurolophus cyrtocristatus* (C.N.H.M. No. P27393) with the lateral elements removed to show the pattern of the crestal cavities. The only "unpaired" portion of the passages occurs at the base of the crest just above the orbits. The "choanal" tube extends ventrally (arrow) from the medial cavity into the interorbital region. (From Ostrom, 1961b.)

of the premaxillaries form a continuous wall between the canals over their entire length, and similar transverse bony walls separate the upper and lower canals as well. The undivided medial cavity at the base of the crest communicates with the interorbital region by way of a "choanal" tube as in other crested hadrosaurs. The only subsidiary chambers discovered

in this relatively simple crest plan were a pair of elongated cavities situated between the upper and lower passages. These extend caudally from the common cavity for about half of the total crest length.

In each of these specimens, at least a part of the crest is occupied by a large undivided or unpaired chamber—that part of the narial cavities adjacent to the "choanal" canal. It is quite probable that this common cavity, as well as the "choanal" canal, was actually divided by cartilage or membranous tissue. In support of this are numerous patches of organic material dispersed throughout the matrix of these crestal cavities of both *Parasaurolophus cyrtocristatus* and *Lambeosaurus clavinitialis*. These appear to represent remnants of thin sheets of organic material—probably cartilage—which were originally situated within the crestal cavities. In view of the cartilaginous nature of the modern reptilian nasal capsule, it is quite possible that the hadrosaurian capsule was of similar construction and that these bits if organic material are remnants of this structure. No similar material could be discovered in the matrix outside of the crestal cavities, but most of the matrix had already been removed prior to the present study. None of the other crests which were examined showed any comparable material within the accessible parts of the crest.

OLFACTION IN THE HADROSAURS

That the hadrosaurian dinosaurs were like all other tetrapods in the possession of a nasal capsule, is not likely to be disputed. And that this capsule was concerned with the same fundamental activities as those of modern tetrapods is likewise beyond doubt. It even seems safe to assume that the hadrosaurian nasal capsule was probably of the same basic design as that of modern reptiles. But as to the precise capsule form and the relative importance of the several nasal functions there is considerable uncertainty.

The restricted construction of the lambeosaurine snout indicates that the nasal apparatus could not have been located rostrally. The crest, on the other hand, not only provides a likely site—it constitutes the only possible site for the lambeosaurine nasal capsule. Moreover, the construction of the crest

cavities seems to parallel in a very general way the basic pattern of the capsule in modern reptiles, consisting of a long narrow "anterior nasal tube," a more inflated and sinuous "anterior chamber," a large, inflated "olfactory chamber," and a "choanal tube."

The origin of this expanded nasal "capsule" cannot be explained by the primary nasal function—air conduction. Nor

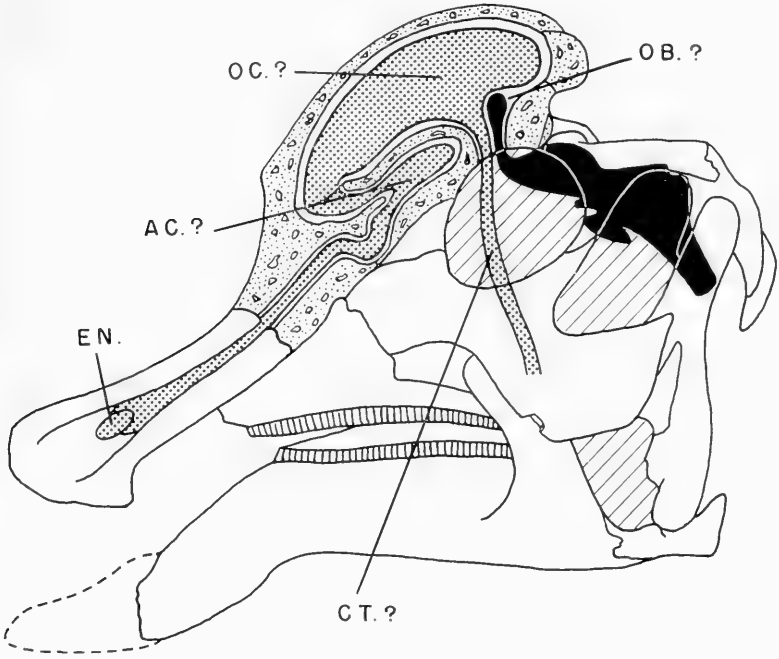

Fig. 10. Outline sketch of the skull of *Prochenecosaurus cranibrevis* (N.M.C. No. 8633) illustrating the dorso-ventrally compressed snout of the Lambeosaurinae and the inflated narial crest. The stippled pattern indicates the proposed disposition of the nasal capsule within the crestal cavities and its probable relationship to the olfactory bulbs.

does it seem probable that air preparation was a significant causal factor. Olfaction, on the other hand, appears very likely as a principal factor in the development of the lambeosaurine crest. As we have seen in the several modern reptiles

considered here, appreciable variation occurs in the total amount of olfactory epithelium, and the available surface area may be expanded in certain forms by an invagination (concha) of the olfactory chamber wall. In mammals, still more complex folding of the epithelium has resulted in an increase in sensory epithelial surface area and more acute olfactory powers. Within the lambeosaurine crest, the nasal passage has been elongated and in some sections greatly inflated. But not only has it been lengthened and inflated, the total surface area has also been increased, perhaps as a parallel means of increasing the total area available for olfactory epithelium. In support of this interpretation, it should be noted that the largest of the crestal cavities is always situated immediately adjacent to the "choanal" canal and it is this segment of the modern reptilian capsule that is usually involved with sensory activities.

If the large chamber of the lambeosaurine crest did in fact house the olfactory chambers of the nasal capsule, how were the contained areas of olfactory epithelium innervated? Several specimens suggest an answer. *Corythosaurus casuarius* (R.O.M. No. 1933), *Corythosaurus excavatus* (N.M.C. No. 8676), *Lambeosaurus lambei* (N.M.C. No. 2869), and *Lambeosaurus clavinitialis* (Y.P.M. No. 3222) display a uniform relationship between the "choanal" passage from the crest and the olfactory foramen at the anterior limit of the brain case. In each of these specimens, the "choanal" passage opens into the interorbital region immediately in front of the olfactory nerve canal. The distance between the olfactory foramen of the brain case and the "choanal" opening of the crest never exceeds 40 mm. A fifth specimen, *Parasaurolophus cyrtocristatus* (C.N.H.M. No. P27393) displays the "choanal" opening located in a similar position that must have been immediately anterior to the brain case. Unfortunately, however, the brain case is not preserved so the relationship cannot be verified in this particular case.

The proximity of these two openings, together with their respective dimensions, indicate that the olfactory bulbs were probably located up in the crest cavities and the olfactory tracts passed downward out of the crestal cavities through the "choanal" canal and then turned backward into the endo-

cranial cavity (see figs. 10 and 11). In fact, no other suitable site for the olfactory bulbs seems to exist. Additional support for this interpretation was recently found in *Lambeosaurus clavinitialis* (Y.P.M. No. 3222) where remains of what appears to have been a cartilaginous extension of the walls of the olfac-

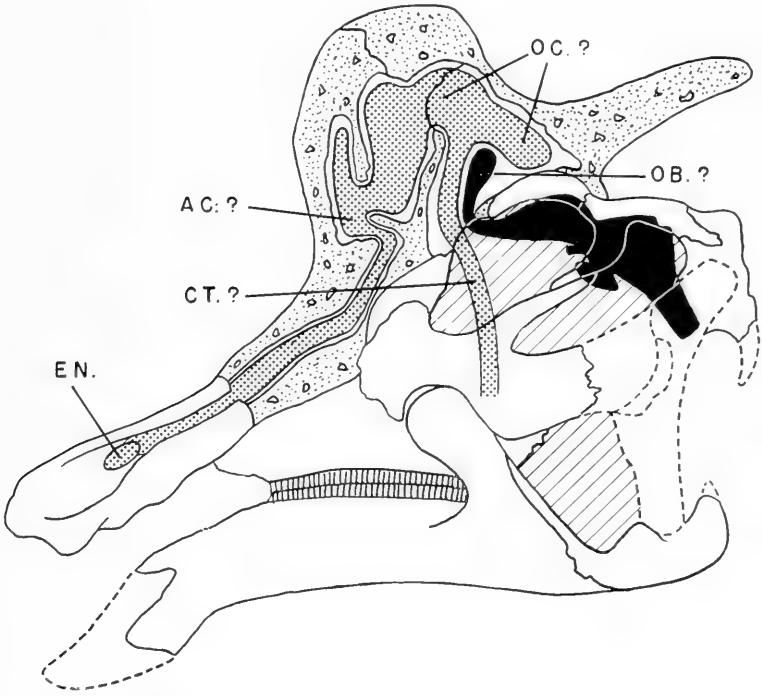

Fig. 11. Outline sketch of the skull of *Lambeosaurus clavinitialis* (Y.P.M. No. 3222) showing the dorso-ventrally compressed snout and the greatly inflated narial crest. The stippled pattern indicates the generalized arrangement of the nasal capsule proposed here together with the probable location of the olfactory bulbs.

tory nerve canal passes from the brain case up into the crestal cavities through the "choanal" canal. Strange as such a position may appear, it conforms only with a crestal position of the olfactory chambers and is entirely consistent with the modern reptilian condition where the olfactory bulbs are located immediately adjacent to the nasal or olfactory sac.

CONCLUSION

From all available evidence, it appears quite likely that the lambeosaurine crest was an adaptation for increasing olfactory sensitivity by providing an increase in the total surface area available for olfactory epithelium. (It also seems probable, in view of the very large and unique preorbital fossae, that the non-crested hadrosaurs had also developed enlarged or modified nasal apparatus situated in a more normal position in the inflated snout. See fig. 5.) But the inevitable question arises, why should the hadrosaurs, rather than any other dinosaur, have required superior olfactory powers? Of course this question cannot be answered to the complete satisfaction of everyone concerned, but some interesting possibilities are suggested by reconsidering hadrosaurian ecology.

It is quite probable that hadrosaurs lived a rather passive, perhaps even retiring existence as relatively slow moving, terrestrial or amphibious herbivores. That they were able to move about over the land is verified by their skeletal construction and that they may have been terrestrial browzers, at least in part, is suggested by Kräusel's(1922) analysis of the "stomach contents" of *Anatosaurus* (*Trachodon*) *annectens*. Other evidence (the large laterally compressed tail and the webbed manus) points to a certain dependency upon an aquatic environment—perhaps for food in the form of soft aquatic plants or perhaps as a place of refuge from terrestrial predators.

In comparing the hadrosaurs with other dinosaurian herbivores, it is striking that they alone lack any obvious defensive or protective adaptations. They possessed no horns, no claws, no sharp teeth, they carried no clubbed or spiked tail, and they had no bony armor. They certainly were not constructed for rapid flight and they cannot be considered giants for their time. In short, the hadrosaurs appear to have been quite defenseless—a most improbable plight. As an alternative it seems increasingly probable that they depended upon the relative security of lakes, swamps, or rivers and thereby escaped from their enemies.

However, such inland waters represented only *potential* safety as long as the individual was out on the land—potential safety contingent upon adequate advance detection of the im-

pending danger by one or more of the sensory systems. Here is where acute olfactory sensitivity may have had significant survival value for the hadrosaurs, just as it does for many modern mammalian herbivores.

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