THE VERTEBRATE FAUNA OF THE SELMA FORMATION OF ALABAMA

PART V
AN ADVANCED CHELONIID SEA TURTLE

RAINER ZANGERL

PART VI
THE DINOSAURS

WANN LANGSTON, JR.

FIELDIANA: GEOLOGY MEMOIRS
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THE VERTEBRATE FAUNA OF THE SELMA FORMATION OF ALABAMA

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THE DINOSAURS

WANN LANGSTON, JR.
CURATOR OF VERTEBRATE PALAEONTOLOGY
NATIONAL MUSEUM OF CANADA

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The Dinosaurs

INTRODUCTION

Chicago Natural History Museum's collection of Upper Cretaceous vertebrates from the Selma formation of Alabama contains remains of three dinosaurs from the lower Mooreville Chalk member in Dallas County. The specimens comprise an incomplete skeleton of a new and interesting hadrosaur, the ilium of a nodosaur, and a phalanx of a theropod. The fossil assemblage includes marine turtles, mosasaurs, plesiosaurs, and fishes. Zangerl believes (personal communication) that the sediments were laid down a mile or so offshore, in relatively quiet waters.

Dinosaur bones, mostly hadrosaurian, had been found previously in this and adjacent regions in beds of similar age, but the specimens were so incomplete that they were of little importance except as simple records of occurrence. The fact that one of them represented perhaps the largest known hadrosaur is interesting but not particularly significant. The hadrosaur skeleton in the Chicago collection has, on the contrary, proved especially interesting from an anatomical standpoint, although it too is of little systematic or stratigraphic importance. The nodosaur and theropod discoveries are in the same category as the earlier finds in so far as their scientific significance is concerned.

The discovery of terrestrial dinosaur remains in marine deposits, once the occasion for much excitement, has in recent years become almost commonplace. Ordinarily these finds are only isolated bones or single individuals in widely scattered beach deposits at different stratigraphic levels. Discovery of three unrelated dinosaurs close together within near-contemporaneous rocks is noteworthy when it is recalled that the sediments are non-clastic, offshore deposits.

Chances for this kind of burial may be limited, but the mode of deposition at least seems fairly clear in some cases. A few paleontologists have thought—I believe with little reason—that some fairly complete skeletons, for example, nodosaurs in the Niobrara formation, indicated marine adaptations; others have invoked bottom currents, marine scavengers, etc., to explain such seemingly anomalous occurrences.

Carcasses of many kinds of vertebrates may be seen on present-day beaches. The upper sides are often dried and hardened while below the cadaver is disintegrating under moist conditions. When disturbed by waves or scavengers heavy bones tend to fall away from the under side while smaller elements remain in place, held by dry and hardened connective tissues. Such remains are light in weight and float easily if swept into the water, where many more bones may drop away before sufficient water has been absorbed to cause the remainder of the carcass to sink. If soaking has not been thorough and deposition occurs in relatively quiet water something of the original death pose may be retained.

The condition of the hadrosaur skeleton from the Selma formation suggests this course of events. It was partly articulated; the head was present but most of the neck had been lost; all terminal phalanges of the hands were found but the arm bones and scapulae were missing; and the hind limbs retained their normal flexion while the right and *lower* femur was nowhere to be found. The interesting thing about these and similar occurrences is the fact that, like the Alabama nodosaur and theropod, isolated and seemingly non-buoyant bones occur in situations that imply considerable transportation before burial. The obvious explanation of simple flotation has for some reason appeared unattractive to some paleontologists.

AGE OF THE SELMA DINOSAURS

Beyond the fact that they are Upper Cretaceous forms the Selma dinosaurs provide no hint of their geological age. All of them came from about the upper third of the Mooreville profile near Marion Junction (Zangerl, personal communication). According to Zangerl's correlation chart (1948, fig. 2) this should be a little below the horizon of the Arcola limestone member of the Selma formation. Interpolations between Zangerl's chart and correlations by Stephenson, *et al.* (1942), from which the chart was adapted, suggest that the Mooreville dinosaurs came from beds of early Campanian and thus early Senonian age.

If the long-range geographic correlations of composite marine and terrestrial sections are accurate, the dinosaur-bearing Mooreville Chalk is older than much, if not all, of the Two Medicine and Judith River formations of Montana, the Oldman formation of Alberta, the Fruitland formation of New Mexico, and the Aguja beds of Trans-Pecos Texas. Among western dinosaur-bearing beds only the Eagle sandstone and perhaps the lowest part of the Two Medicine formation of Montana, the Colorado shale of Wyoming, and the Milk River formation in Alberta are older (Russell, 1930). Farther east a hadrosaur and a nodosaur from the Kansas Niobrara formation are certainly older than the Mooreville animals, as perhaps are also some of the Cretaceous dinosaurs from New Jersey.

The two previously reported hadrosaur localities in Alabama (Lull and Wright, 1942), in Autauga and Dallas Counties, appear to be a little lower stratigraphically than the Marion Junction sites, but are presumably also in the lower marl member of the Selma formation (see map, Monroe, 1941). The Black Creek formation of North Carolina which has yielded dinosaurs is in part equivalent to the Mooreville Chalk member, but the horizons where dinosaurs were encountered are not recorded.

Thus, the animals from near Marion Junction, Alabama, are among the oldest, but are by no means the oldest Upper Cretaceous dinosaurs from North America.

SYSTEMATIC DESCRIPTIONS

Order **Ornithischia**

Suborder **Ornithopoda**

Family **Hadrosauridae**

Subfamily **Hadrosaurinae**[1]

Lophorhothon,[2] new genus

Diagnosis.—Crested hadrosaurines with elevated cranium and short snout, broad orbits and wide temporal fenestrae; pyramidal crest on nasals resembling crest of *Prosaurolophus* but situated well forward of the orbits. Immature individuals with large fronto-nasal fontanel. Teeth with heavily crenulated enamel surfaces and denticulate coronal margins.

Type of genus.—*Lophorhothon atopus,* new species.

Lophorhothon atopus,[3] new species

Type.—An incomplete skeleton, Chicago Natural History Museum no. P27383. Collected in 1946 by Rainer Zangerl, William Turnbull, and C. M. Barber.

Locality.—Site 9 (Zangerl, 1948, p. 10 and pl. 3), southeast of Marion Junction, and 10 miles west of Selma, Dallas County, Alabama, on the Moore Brothers' farm.

Horizon.—Mooreville Chalk member of the Selma formation, in white to yellow marl, 5 feet below the wooded surface visible south of site 9 and near the upper third of the Mooreville profile. Age: early Campanian.

Diagnosis.—Same as for genus.

Description of materials.—The type and only known skeleton of *Lophorhothon atopus* is very incomplete. The following parts have been identified: Much of the disarticulated skull and part of the predentary; 44 vertebrae, representing every segment of the column; numerous incomplete ribs and chevrons; parts of the hands, including the terminal phalanges; most of one and part of the other ischium; a femur; both lower legs and feet, which are practically complete. In addition, there are several large fragments which I am unable to identify.

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[1] I follow Sternberg's (1954) classification of the Hadrosauridae, in which two subfamilies, Hadrosaurinae and Lambeosaurinae, are recognized.

[2] λόφ[os], a ridge or crest on the head, +o+ῥώθων, nose.

[3] *ατοπος*, out of place, an allusion to the form and position of the nasal crest.

Some of these bones are distorted almost beyond recognition owing to the extreme "plastic" deformation to which they have been subjected.[1] The problematica probably result from this distortion. The specimen occupied an area of slightly more than a yard square near the top of a low, rounded hill. The skull was partly weathered out, but most of the skeleton remained *in situ* and partly articulated.

This is a small skeleton; the animal in life was perhaps no more than 15 feet long and thus comparable in size to an adult *Cheneosaurus*. The generally incomplete state of ossification of the skeleton (hadrosaur chondroskeletons are relatively less ossified than those of related dinosaurs) suggests that the individual was immature. The possibility that here is a dinosaurian personification of "Case's Law" does not seem very likely because certain dermal bones of the skull show incomplete ossification and imperfect suturing. Both of these are presumably juvenile features. A young hadrosaur skeleton in the National Museum of Canada which may belong to *Prosaurolophus* is as large as the specimen from Alabama but shows less marked juvenile characteristics. Hence the adult *Lophorhothon* may have bulked with the largest hadrosaurs, and it may be recalled that a caudal vertebra from roughly correlative beds in Sampson County, North Carolina, represents the largest known hadrosaur (Lull and Wright, 1942).

Of the skull (fig. 146) we have both nasals, the united frontals with the anterior parts of the parietals and postorbitals attached, the prefrontals, the lacrimals, parts of both squamosals and quadrates, a fragment of a quadratojugal, a badly damaged maxilla, an incomplete pterygoid, parts of the laterosphenoids and orbitosphenoids attached to the frontals and postorbitals, the basioccipital and exoccipitals, the basisphenoid, the opisthotics and the proötics. None of these bones is complete, although by contrast with the rest of the skeleton most of them are little distorted.

An unusual feature of this skull is the presence of a nasal crest which at first caused the nasal bones to go unrecognized. However, a short section of the left crested bone fits laterally into a longitudinal sulcus on the anterior dorso-medial edge of the left prefrontal. When so placed the bone falls into the expected position of a nasal, and its broken posterior process, if extended, should reach the transverse groove provided for the postero-lateral part of the nasal bone on the anterior edge of the frontal. When correctly oriented, the nasals, though incom-

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[1] Zangerl (1948) has discussed this phenomenon in turtle fossils from the Mooreville Chalk. Such deformation seems peculiar to fine-grained sediments which retained a high percentage of water for some time after deposition. Commonly it is the more massive bones that have suffered most, whereas delicate and plate-like structures with a high proportion of compacta, and relatively open skulls often escaped damage. This is because the fine sediments fill in around the plate-like parts of a skull almost immediately upon burial and thereafter offer resistance of the same order to pressures exerted by the fluid sediments outside. More massive bones with thick walls but relatively hollow interiors, and especially those composed mostly of spongiosa, offer less resistance until they have been filled with matrix or crystalline material. Cracks through which matrix may enter the bones rarely appear until a great deal of distortion has occurred.

plete, show striking similarities to those of *Prosaurolophus*, a crested hadrosaurine, and superficially, behind, to those of *Cheneosaurus*, a low-hooded lambeosaurine. In the reconstructed skull the nasal crest lies farther forward relative to the orbits than in *Prosaurolophus*—more in the position of the *Kritosaurus* crest. Laterally it bears two shallow, roughly concentric depressions that open forward toward the nares. These are perhaps homologous to the excavations variously developed in several hadrosaurines, for example, *Edmontosaurus* and *Prosaurolophus*, and faintly even in some kritosaurs. The thickened posterior pyramid of the crest descends steeply behind into the posterior process of the nasal bone that meets the frontal. This process is longer but otherwise similar to *Prosaurolophus*, except that it bounds a median fontanel instead of meeting the opposite nasal bone in the mid-line. Anteriorly the nasals meet to form a sharp-edged ridge above the nares, of whose boundaries, however, nothing remains.

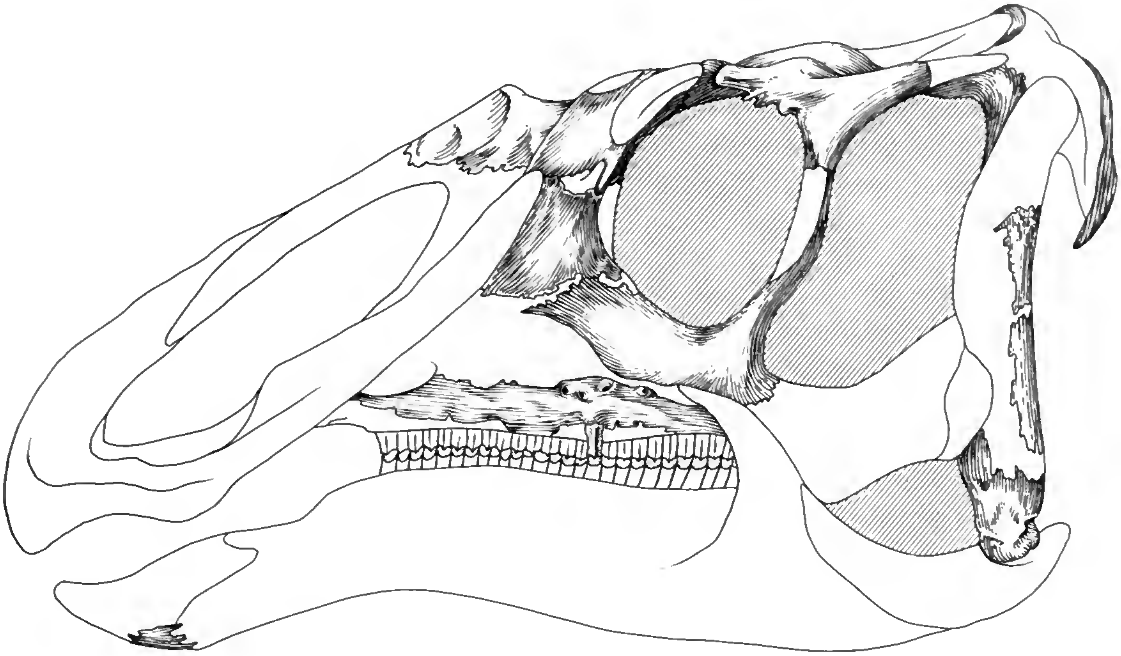


FIG. 146. *Lophorhothon atopus*. Reconstruction of skull of type specimen (CNHM–P27383); × ⅓. Shaded areas represent parts preserved; lacrimal, maxilla, and part of quadrate drawn from right side. In making this reconstruction, contacts between nasals, prefrontals, postorbitals, and parietals were available, and areas of overlap were clearly indicated on the right lacrimal; elsewhere cutouts from drawings and photographs were arranged to give the most satisfactory compromise between damaged bones. Results probably show the general shape of the skull except anteriorly, where the rostrum is completely conjectural. The mandible, represented only by a fragment of the predentary bone, is shown in conformity with the usual method of illustrating hadrosaur skulls.

The fontanel (fig. 147) is large, almost diamond-shaped, and, so far as I am aware, is unique in hadrosaurs. It is bounded anteriorly by the nasal bones, whose edges are smooth, posteriorly by the frontals, which send into the opening several flattened finger-like processes whose long axes radiate roughly from the center of frontal ossification toward the center of the fontanel. Two small fragments near the apex of the fontanel suggest separate ossifications, perhaps parts of the nasal bones, but these pieces are continuous below with the frontals. The frontals are strongly domed. This is unusual in hadrosaurines, for the cranial roof between the orbits is generally flat or even concave. The frontal-prefrontal suture is irregularly W-shaped. The frontal thickens toward the suture, which is of the usual tongue and groove construction. The frontal-postorbital suture is simple. All of these sutures have raised edges on the frontal bone. The suture between frontal and parietal is heavily denticulate. Seen from above it describes a broad wedge with apex anterior and the parietals extending on either side as far forward as the anterior edge of the supratemporal fenestrae. The frontal may just have been excluded from the fenestra by union of parietal and postorbital. The frontals are thick. They are broadly arched above the orbits to whose rims they contribute a wide process between prefrontals and postorbitals. Ventrally the vaulted roofs above the orbit and above the cerebral chamber are separated by a heavy ridge that runs diagonally forward and outward to join the internal orbital flange of the prefrontal bone. A secondary vault occurs around the edges of the fontanel and is separated from the vaulted area on either side by a low ridge that grades backward into the ventral surface of the frontal. These ridges are reflected antero-dorsally by the triangular branches of the W-shaped frontal-prefrontal suture. A broad ridge crosses the two frontals transversely below in front of and above the sphenoidal bones. The olfactory grooves are hardly distinguishable across this ridge as they pass from the cerebral chamber.

The fragmentary parietals preserve the undistorted contours of part of the cranial vault. They bend downward from their contact with the frontals and contract rapidly behind the dome-like vault. There is no trace of a sagittal ridge, which would have been destroyed, if ever present.

Although abraded, the left prefrontal is better preserved than the right. Part of the longitudinal groove which lodged the lateral edge of the nasal bone is preserved dorsally. Postero-dorsally thickened processes fitted into corresponding notches in the anterior edge of the frontal, where the contact surfaces of the prefrontal are very spongy, implying a zone of continuing ossification. Interlocking sutures are just beginning to form between these bones. Antero-laterally there is an area that was probably covered by the tip of the postero-dorsal maxillary branch of the premaxilla. Opposite this, the bone overlapped a dorsal flange of the lacrimal. Antero-ventrally, at the external edge of the orbit, is a deep vertical notch which received in complex interlocking relationship a process from the lacrimal. This produced a strong coupling which is variously developed in all hadrosaurs and evidently prevented distortion of the orbit in their loosely articulated skulls. Postero-medially the prefrontal is deflected into the orbit where a thickened flange was continuous above with the antero-posterior ridge on the under side of the frontal, and below with the orbital flange of the lacrimal. The orbital rim may have been thickened outwardly as well, but abrasion has destroyed part of the bone. It is clear, however, that any thickening here was

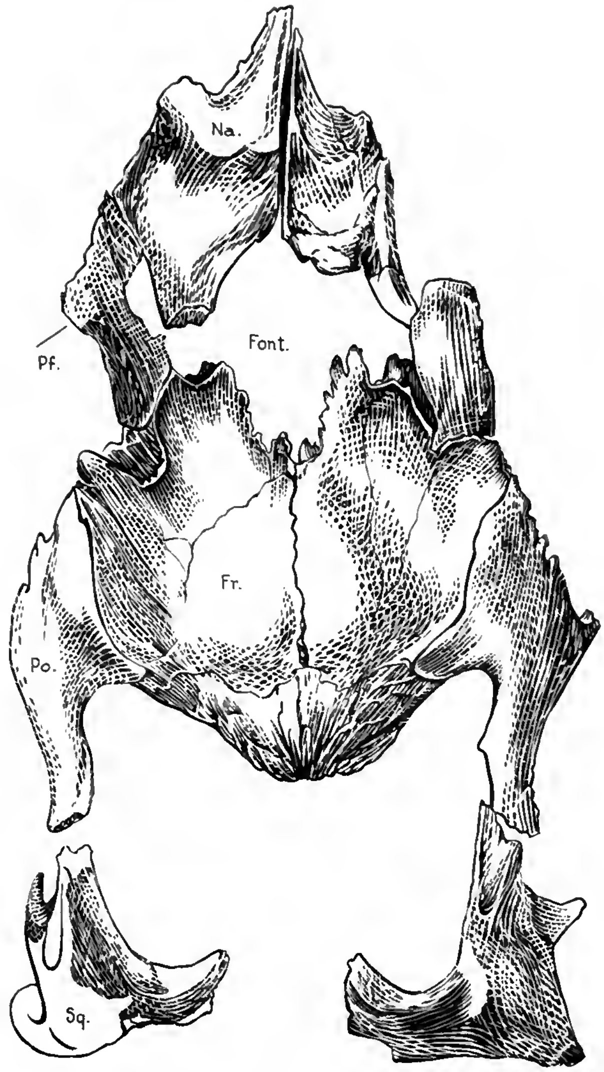


FIG. 147. *Lophorhothon atopus,* holotype (CNHM–P27383), cranial roof, superior aspect; × ½. Bones are shown as preserved except for some restoration of the left squamosal.

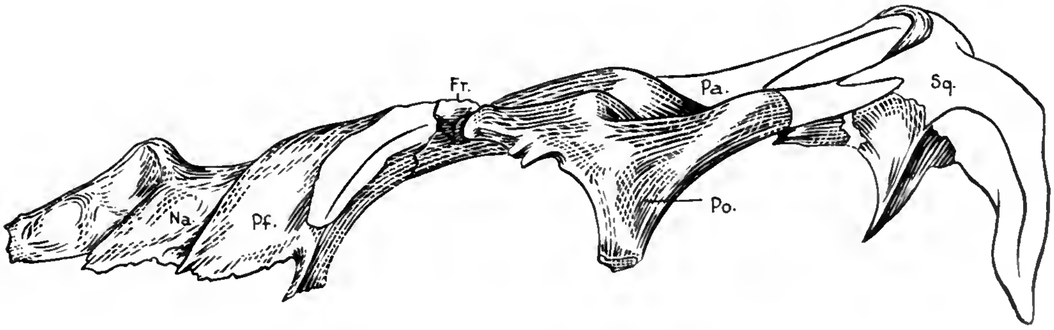


FIG. 148. *Lophorhothon atopus,* holotype (CNHM–P27383), upper part of skull, left lateral aspect; × ½. Prefrontal, parietal, postorbital, and squamosal partly restored.

not of the order seen in non-crested hadrosaurines like *Edmontosaurus* and *Anatosaurus,* where an angular vault occurs at the antero-superior corner of the orbit.

The right lacrimal (fig. 149) is fairly well preserved, but most of its thin dorsal and anterior edges have been damaged. Little if any surface detail remains externally. Relationships to adjacent bones were characteristically hadrosaurian. When articulated the bone was broadly overlapped laterally by the prefrontal above, the premaxilla anteriorly, and the jugal below, so that only about half of its surface was visible from the side. The lacrimal appears relatively large for a skull of this size. It is characteristically wedge-shaped with its apex anterior, but the antero-dorsal margin is broadly concave. The bone is very thin except along the ventral edge and along the margin of the orbit, where there is a slight thickening externally; internally there was the usual shelf that continues downward to meet an inner buttress on the jugal, and upward to join the orbital flange of the prefrontal. The large but narrow naso-lacrimal canal passed through the flange at about mid-height of the lacrimal into a broad shallow channel on the inner face of the bone. This channel must have housed an enlargement of the naso-lacrimal duct. It is sharply bounded above and below by bony ridges but opens out anteriorly where these ridges diverge and disappear. A deep triangular notch in the ventral margin of the lacrimal just anterior to the jugal buttress received from the jugal a dorsal process which helped lock the two bones together around the orbit. The device is analogous to the coupling between the lacrimal and prefrontal.

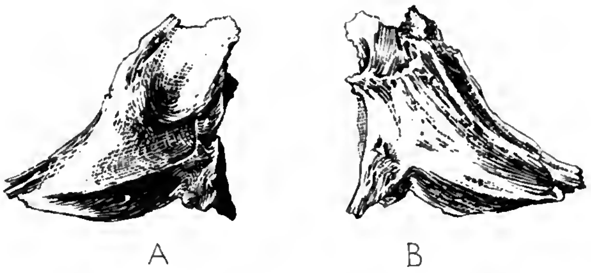


FIG. 149. *Lophorhothon atopus,* holotype (CNHM–P27383), right lacrimal: A, from within; B, lateral aspect. × ½. Margins of this bone are incomplete.

The jugal (fig. 150) has lost the thin edges of its maxillary plate, the articular surface for the lacrimal, the dorsal end of the postorbital process, and most of the subtemporal bar. The bone is basically hadrosaurian in form but its proportions differ somewhat from those of other North American hadrosaurs; for example, the part that articulates with the maxilla ends farther posteriorly than usual, beneath the middle of the orbit, and the infraorbital part of the bone, customarily deep, is no deeper than the antero-posterior diameter of the base of the postorbital process. The subtemporal plate seems also to have been unusually slender, at least anteriorly. On the other hand the postorbital process is relatively massive, particularly toward its base. It is more than six times longer than its antero-posterior diameter at mid-height. The process is excavated antero-laterally to receive the descending process of the postorbital bone which overlay half the length of the process. The antero-ventral edge of the jugal is paper-thin and was evidently not expanded downward as was usual in hadrosaurs. The anterior process of the maxillary plate which projects between maxilla and lacrimal is relatively very long and slender. It tapers to a point anteriorly. Although the part of the jugal which overlaps the lacrimal near the anterior rim of the orbit has been lost, the notch which received it on the lacrimal indicates that it was not expanded into a strong backwardly turned process, which is a common but not universal feature of hadrosaur jugals.

FIG. 150. *Lophorhothon atopus*, holotype (CNHM-P27383), left jugal; × ½. The arrow indicates the point of most posterior contact with maxilla.

Only the tips of the temporal bars are missing from the postorbital bones. The postorbital is characteristically triradiate. Its orbital margin is much roughened as are also the edges of the frontals between the prefrontals and postorbitals. Its broad supraorbital plate is in simple sutural contact with the frontal. From this contact the dorsal surface sags downward toward the center of ossification where the temporal and postorbital processes arise. The bone encloses postero-dorsally a concave area at the postero-dorsal corner of the orbit. This concavity becomes a large pocket of undetermined function in *Edmontosaurus* and *Anatosaurus*, but here it is not very pronounced and only continues the upper wall of the orbit around the upper corner. The posterior wall of the cavity forms a thin partition between the orbit and the temporal spaces; it is continuous proximally with the ventral keel on the parietal buttress of the laterosphenoid. A deep pit just behind the ridge receives the blunt end of the buttress. There is no indication of fusion between postorbital and laterosphenoid, and the osseous part of the buttress, no doubt capped by cartilage in life, does not fill the pit completely. The medial surface of the supratemporal bar is deeply channelled to receive the corresponding branch of the squamosal; there is no sign of fusion, but there was also no movement between the bones.

The squamosals are incomplete and somewhat distorted. Contacts with adjacent bones have been lost except where the right cotylus receives the proximal end of the quadrate. Nevertheless the position of the squamosal in the skull can be ascertained without difficulty by projecting the temporal process of the postorbital backward a short distance where it would have fitted into the correspondingly complex trough on the temporal ramus of the squamosal. The squamosals thus oriented formed all the posterior borders and something less than half of the lateral margins of the superior temporal fenestrae. The bones were not in osseous contact at the mid-line behind; the intervening space was occupied by unossified tissue, but whether this was of squamosal or parietal origin is unknown. Almost certainly the parietal was involved, however, and the space between the medial ends of the squamosals is much wider than in any other hadrosaur. The temporal bar was composed of squamosal and postorbital in about the ratio of 2:1. It was long, unusually slender, and more like *Kritosaurus* than other hadrosaurs. The long, slender and gently tapering diagonal process that forms the postero-dorsal edge of the lateral fenestra and limited forward movement of the quadrate is completely unlike the massive blunt process of *Edmontosaurus* and *Anatosaurus*. The lateral temporal opening was not greatly constricted toward the top. Behind the quadrate cotylus, hadrosaur squamosals generally have a plate-like process that is closely applied to the antero-lateral face of the paroccipital process. The process has been destroyed in this specimen, but its broken base on the right squamosal suggests that it was not much expanded.

Part of the distal half of the left quadrate and the proximal end of the right are preserved. This bone was long, straight, and slender. The proximal end is rounded; it is irregularly ovate in horizontal section, with the lateral outline sloping gently forward. An elongate roughened surface on the postero-lateral edge of the bone indicates the point of attachment of a strong ligament possibly associated with the tympanic membrane, if one was present in the space between the quadrate and the posterior squamosal flange. The distal end of the quadrate is poorly formed. The articular condyles have featureless convex surfaces that terminate anteriorly and medially near the end of the bone, but the lateral condyle rises some distance onto the edge of the bone behind. The weak medial condyle seems to have been displaced posteriorly in preservation. The pit on the internal surface of the quadrate for the quadrate buttress from the pterygoid is not well defined. The notch for the quadratojugal on the anterior edge of the bone was of moderate depth, to judge from the part preserved. A small thin irregular fragment probably represents the quadratojugal. Its edges are lost and the specimen is otherwise not definable. There is nothing noteworthy about the left pterygoid, which is preserved only where the various lamellar rami meet.

The maxilla is poorly preserved, with little of its external surface remaining; there is no trace of the maxillary-jugal surface, and several channels for twigs of the maxillary branch of the facial nerve are exposed. Anteriorly most of the notch which characterizes hadrosaur maxillae is preserved and there also remains some of the anteriorly directed process above it which was attached to the under side of the maxillary process of the premaxilla. The bone is incomplete behind. Twenty-five alveoli can be seen, 18 of them containing teeth. Probably no more than two additional alveoli were present and it is possible that 25 is the total number. Some of the groove which lodged the maxillary process of the premaxilla is preserved antero-dorsally. The backward and upward inclination of this groove provides evidence in hadrosaurs of the relative proportions of the maxilla. In the present case the angle is low, indicating a long and fairly slender bone with a low lacrimal flange. But distortion has obviously altered the natural contours of the bone, which probably resembled that of *Kritosaurus* in having a relatively elevated (for a hadrosaurine) lacrimal flange.

Except for the loss of the supraoccipital the neurocranium is fairly complete, but anteriorly the orbitosphenoids are represented only by fragments. The right one is best preserved. It was a moderately thick plate-like bone that met the laterosphenoid behind and joined the opposite orbitosphenoid anteriorly in a median suture below the olfactory tracts. Union with the frontal is sutural where small fingers of orbitosphenoid bone fit into pits on the under side of the frontal plate. A small foramen passes through the neurocranial wall between the orbito- and laterosphenoid at or just below their point of contact with the frontal. Anteriorly the orbitosphenoid is unfinished and presumably extended on as the cartilaginous planum supraseptale.

The preserved part of the right laterosphenoid is triangular; its inner surface is concave, continuing downward the spherical walls of the cerebral chamber. The bone contacts the frontal antero-dorsally in a strong interdigitating suture and sends dorso-laterally the massive laterosphenoid buttress which is lodged distally in a pit on the under side of the postorbital. The process is triangular in cross section. Its sharp ventral keel together with a medially turned ridge on the postorbital bone forms a partial partition between the orbit and the space occupied in life by the temporal musculature.

The otico-occipital segment is shown semidiagrammatically (figs. 151–153). The exoccipital is of characteristic hadrosaur form; it contributes a little to the occipital condyle, bounds the foramen magnum laterally and above, is separated from the opposite exoccipital narrowly in the floor of the foramen magnum by the basioccipital, and forms the body of the paroccipital process. The exoccipital is broad and low in posterior aspect, reflecting the low wide outline of the cranium. The paroccipital process is not as sharply downturned or as long and slender as in many hadrosaurs. The exoccipital pedicle encloses four foramina and impinges on a fifth. Largest and most posterior of these is the ovate exit for a posterior branch of cranial nerve XII. It passes diagonally downward and backward from the medullary cavity to emerge from the exoccipital at a point some distance behind its entrance. Anterior to this and a little lower down is a smaller, nearly round passage presumably for an anterior branch of the same nerve. It enters the exoccipital almost in the exoccipital-basioccipital suture (a cartilaginous area in this specimen) and passes upward and a little posteriorly to exit well above the suture. The most anterior foramen, completely surrounded by the exoccipital, is almost as large as the posterior hypoglossal foramen. It leaves the cranium postero-laterally, having run diagonally through the bone. This has often been called the jugular foramen in hadrosaurs, and is generally assumed to have carried some combination of nerves IX–XI. As I have explained subsequently, I believe it served only nerves X and XI and the perilymphatic duct.

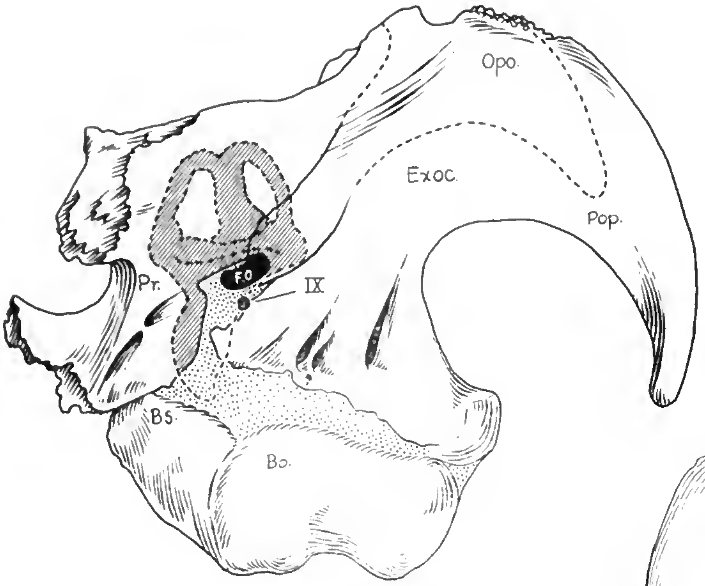
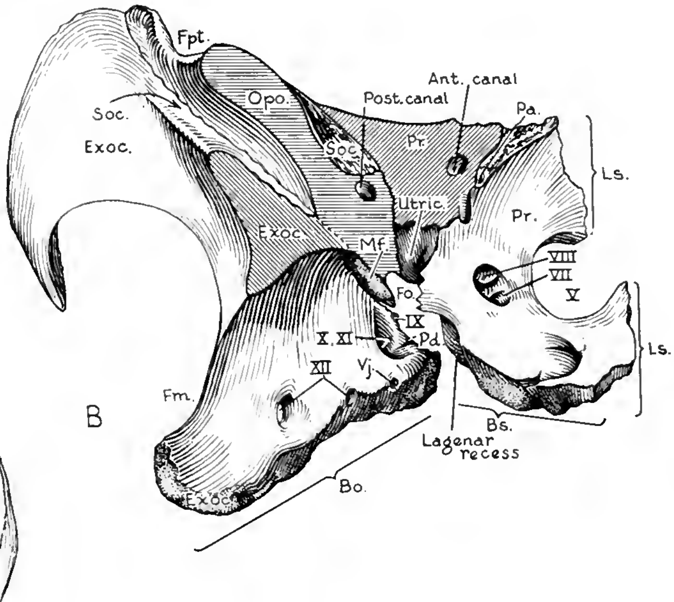


FIG. 151. *Lophorhothon atopus*, holotype (CNHM-P27383), otico-occipital segment of skull, left lateral aspect, semidiagrammatic; × 1. Extent of the bony labyrinth within the otic bones is shown by diagonal lines; dots indicate areas occupied in life by cartilage. Positions of fenestra ovalis and presumed glossopharyngeal foramen are indicated but outlines are conjectural. Presumed extent of paroccipital flange of opisthotic drawn from right side and indicated by broken line. See also figure 152.



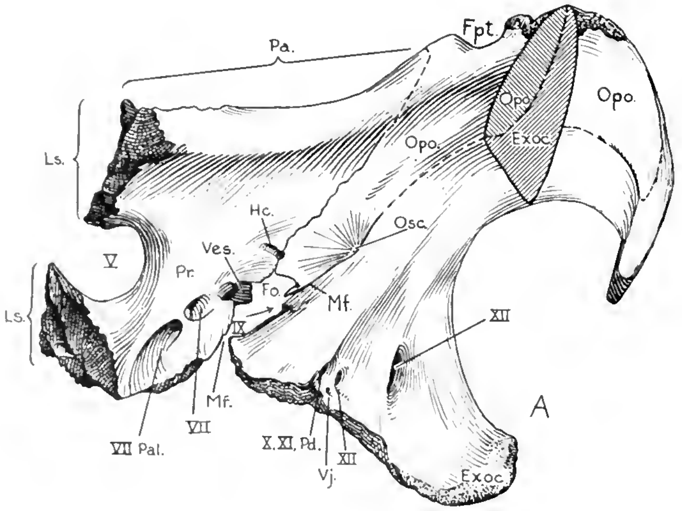


FIG. 152. *Lophorhothon atopus*, holotype (CNHM-P27383), otico-occipital segment of skull: A, left lateral aspect; B, parasagittal section of braincase, semidiagrammatic. Approximately × 1. Paroccipital process sectioned to show relative contributions of exoccipital and opisthotic. In B, the section through the proötic and opisthotic bones lies in a diagonal plane lateral to the vertical plane in which the exoccipital is sectioned. The exoccipital is sectioned somewhat lateral to the mid-line, where a similar section would show the space occupied by the supraoccipital entering the roof of the endocranial chamber and separating the exoccipital from the opisthotic. Surfaces marked *Bo.*, *Bs.*, *Ls.*, and *Pa.* are apposed to the basioccipital, basisphenoid, laterosphenoid, and parietal, respectively. The space occupied by the supraoccipital is indicated by *Soc.*; *Osc.* indicates the lateral ossification center of the opisthotic bone. *Hc.* shows where the horizontal semicircular canal has been exposed by breakage of the thin lateral wall. Drawings by John Crosby.

A tiny round canal which probably transmitted the internal jugular vein enters the exoccipital almost confluently with the so-called jugular foramen. It leads downward and forward to enter the endocranial cavity through a gap between the basioccipital and exoccipital.

Anteriorly the exoccipital forms the postero-ventral margin of a large irregular opening which is bounded anteriorly by the proötic and postero-dorsally by the opisthotic. The upper part of this opening is the fenestra ovalis, which leads directly into the vestibule. The opening has no lower bony boundary in this immature animal; there is a wedge-shaped space between exoccipital and proötic. A transverse channel whose course is indicated on the antero-dorsally facing edge of this gap passed below the fenestra ovalis and probably carried the ninth nerve.

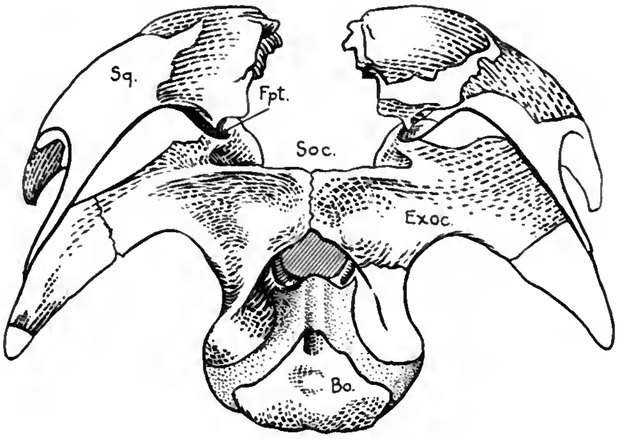


FIG. 153. *Lophorhothon atopus*, holotype (CNHM–P27383), occiput; approximately × ½. The area formerly occupied by the supraoccipital has been left blank. Dots indicate the areas occupied in life by cartilage. Space between the squamosals was probably filled by the parietals and incompletely ossified parts of the squamosals.

The opisthotic bone forms the posterior margin of the fenestra ovalis, encloses much of the bony labyrinth, and sends backward a flattened process that closely adheres to the antero-lateral surface of the exoccipital in the paroccipital process. The outline of the bone along the process is not well defined, but it certainly extends beyond the middle. The opisthotic had a complex association with the supraoccipital, but this will be discussed later (see p. 347). The bone formed all of the lower border of the post-temporal foramen and was narrowly visible below this opening on the posterior face of the paroccipital process.

The proötics retain much of their sutural surfaces. Each bone is a massive but cavernous wedge-shaped element which abuts on the laterosphenoid anteriorly and the basicranium (mostly basisphenoid) below, laps over the opisthotic behind, and meets the parietal above. It did not have osseous contact with the exoccipital, and contributed little if anything to the paroccipital process. Both proötics are damaged supero-medially and their supraoccipital surfaces are mostly destroyed. The proötic surrounds about three-fourths of the huge circular foramen ovale above, below and behind. It bounded the fenestra ovalis antero-dorsally. A large oval opening lies about midway between the foramen ovale and the inner ear chamber. It opens directly into an irregular pocket within the proötic. This pocket communicates with the bony labyrinth behind, and continues via a tubular passage downward and forward to open externally in the narrowly ovate facialis foramen midway between the foramen ovale and the fenestra ovalis. The foramen has across its exit a flattened bar of bone that divided two branches of the facial nerve immediately upon its emergence from the cranium. A groove on the side of the proötic presumably carried the palatine branch downward anteriorly; a similar groove for the main facialis trunk leads postero-dorsally and loops backward in the direction of the fenestra ovalis. There is no indication that the proötic extended much below the brain and it certainly did not take part in the formation of the dorsum sellae. The bony labyrinth will be described fully in the discussion of the hadrosaurian inner ear.

The supraoccipital bone was not preserved. It may have been incompletely ossified in this young individual, but the space which it occupied is clearly shown and will be discussed subsequently in connection with the hadrosaurian supraoccipital problem.

Most of the basicranium is very badly crushed and distorted, but the basioccipital is in good condition and does not seem to differ much from the usual hadrosaurian pattern. It was, of course, less completely ossified than in older individuals. Apparently, bony contacts with adjacent elements had not yet formed. The basipterygoid process of the basisphenoid was well formed. The presphenoid terminates in a cartilaginous ending anteriorly; the parasphenoid rostrum appears to have been broken off. The sella turcica is deep and its side walls were incompletely ossified. The dorsum sellae was evidently composed exclusively of basisphenoid. There is a deep notochordal pit on the occipital condyle. The condyle is about twice as wide as high. The basisphenoidal tubera are well formed but have not fused with the covering plates of the basisphenoid bone.

Measurements of individual skull bones from this specimen are not particularly useful; the illustrations furnish a clearer idea of relative proportions.

The lower jaw is represented only by the very incomplete predentary bone. This shows the usual posterior processes and part of the large foramen that normally passes through the bone dorso-ventrally in hadrosaurs. The bone was apparently flattened dorso-ventrally and therefore must have been broadly expanded, as is characteristic of advanced hadrosaurines.

None of the teeth in the maxilla is well exposed, but an unworn maxillary tooth was recovered during excavation. Two other dissociated teeth are from the dentaries. The maxillary tooth, (fig. 154, A, B) has a crown 21.6 mm. high, a maximum width of 10.0 mm., and a greatest transverse diameter of 9.6 mm. Its enamelled labial surface is narrowly and asymmetrically diamond-shaped, and the tip is bluntly pointed. It has a very distinct mid-ridge which reaches its maximum sharpness slightly above the center of the crown. There are no secondary ridges in the deep troughs on either side of the mid-ridge, but the edges of the enamel surface in the lower half of the crown are thickened and regularly serrated.

The dentary teeth have more broadly diamond-shaped enamel surfaces which are also more asymmetrically formed than those of the maxillary tooth. The more complete tooth (fig. 154, C, D) has a worn tip. Its crown is 17.2 mm. high and has a maximum width of 10.6 mm.; its greatest transverse diameter is 9.0 mm. The dentary teeth have low but sharp mid-ridges and a low supplementary ridge on either side. The posterior ridge gives off posteriorly two or three still smaller ridges which diverge downward, and near its base there appears another slight ridge that runs upward diagonally, in the direction of the mid-ridge. All the supplementary ridges roughly parallel the edges of the crown instead of the mid-ridge. Their development is variable, however, and in the second dentary tooth they are almost if not quite invisible. The edges of these dentary teeth are thickened and bear small, fairly regular marginal serrations which are much less pronounced than those of the maxillary tooth. The angle between the enamel crown and the root of the more complete dentary tooth, in so far as it can be accurately measured, is 140 degrees. The ratio of the transverse diameter of the base of the crown of this tooth to the greatest width of the crown is only 0.85.

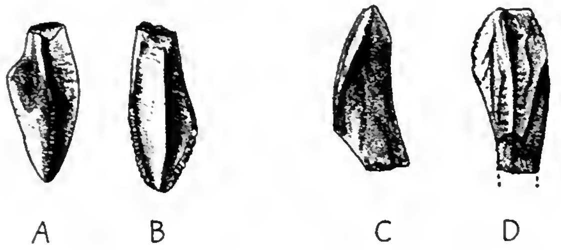


FIG. 154. *Lophorhothon atopus*, holotype (CNHM-P27383), teeth; × 1. A, maxillary tooth, anterior aspect; B, the same, lateral aspect; C, dentary tooth, anterior aspect; D, the same, lingual aspect.

There were about 25 vertical rows of teeth in the maxilla.

Not one of the 44 vertebrae preserved is complete and the distortion of some of the centra is fantastic. Neural spines and pedicles have also been much flattened.

Nowhere is the youthful nature of this animal more apparent than in the vertebral column. The bases of all the pedicles were cartilaginous and the characteristically toothed neurocentral surfaces were just beginning to form. The neural spines were capped by cartilage, and the anterior convexities that characterize the opisthocoelous centra of adult hadrosaurs are ossified only in the most anterior part of the dorsal series and in the cervicals. The odontoid process, if ossified, was not coalesced with the centrum of the axis. Except in one instance there is no trace of fusion between any of the sacral vertebrae, and even chevron facets are not distinctly formed on the caudals.

The massive centrum of the axis is uncrushed. It encloses about half of the neural canal in contrast to the dorsal and particularly the caudal centra where the canal is almost surrounded by the neural arch. Posteriorly this centrum is flat instead of deeply concave in usual hadrosaurian fashion. The sides are moderately excavated and the lateral surfaces meet below in a low, rounded median keel. No transverse trough is developed on the anterior face of the centrum for reception of the atlantal intercentrum. The centrum is 55 mm. long, 51 mm. wide anteriorly at the level of the parapophyses, 40 mm. wide posteriorly and 50 mm. high anteriorly (including the walls of the neural canal). The part of the canal registered on the centrum is 11 mm. deep and 19 mm. wide posteriorly. A badly distorted mid-cervical centrum is 47 mm. long and 47 mm. high posteriorly. This centrum is strongly opisthocoelous and has fairly deep pleurocoels and no ventral keel.

Perhaps five centra and ten neural arches and spines belonged to the dorsal series. One neural arch which lacks the spine and most of the transverse processes can be reassociated with its uncrushed centrum. This vertebra (fig. 155) is presumably from near the middle of the thorax. Its centrum is biconcave and the sides are moderately constricted; the edges are greatly thickened and strongly beveled below. In transverse section this centrum is more triangular than the others preserved, but there is no ventral keel. It is about two-thirds as long as high, and about as high as wide. The neural canal was largely enclosed by the neural arch and thus differed from an *Anatosaurus* dorsal described by Lull and Wright (1942), in which the canal is said to excavate the centrum so that at least half of its cross section lies below the plane of the neurocentral suture. The pedicle is almost as long as the centrum. It is relatively high. As in the other dorsals preserved, the lateral trace of the neurocentral suture is broadly W-shaped in contrast to the V- and U-shaped sutures of the caudals. There is no parapophysis and the capitular facet is borne laterally on the paradiapophyseal buttress where it runs into the lateral edge of the prezygapophysis. The spine was inclined to the rear. Another neural arch is longer and lower and the spine is more strongly slanted posteriorly. Of the remaining centra only one shows even the slightest anterior convexity, and all are concave behind. One, possibly the last dorsal, is moderately excavated above by the wide neural canal. This centrum has a more rounded cross section than the one just described.

The dorsal centra vary in length from 43 to 44 mm., in height from 63 to 65 mm., and in anterior width from 55 to 63 mm.

Six sacral centra are preserved. Four have flattened ends and were not fused with other centra. The other two, whose identity as vertebrae is hardly recognizable owing to distortion, seem to be solidly united. There is a suggestion of a ventral keel on one vertebra, but there is no trace of the ventral median groove that often appears in hadrosaurian sacra. The sides show varying degrees of constriction and the transverse diameters of the centra vary considerably, as usual. The bones bear shallow intervertebral facets laterally for the insertion of the cartilaginous sacral rib heads. These ribs, of which eight are preserved (including two pairs), are simple structures that show no sign of fusion to the vertebrae or to each other distally, whereas in adult hadrosaurs the expanded ends of the ribs join to form a massive iliac buttress. The position of the ribs within the sacrum is not clear, but the centrum with the greatest transverse diameter, possibly the third sacral, when combined with the longest sacral ribs—which obviously did not belong to this vertebra—shows that the sacrum could not have exceeded 120 mm. in width.

The caudal vertebrae are characteristically hadrosaurian. They require no detailed description, but several features are worthy of mention. There is a deep pit laterally below the neurocentral suture on all the larger centra. In the largest vertebra (fig. 156) the pit extends across the suture onto the side of the pedicle. These pits received the cartilaginous heads of caudal ribs in the normal reptilian fashion; the "transverse processes" of authors are clearly caudal ribs in hadrosaurs. The high "shoulders" which are sometimes seen on anterior caudal diapophyses (for example, *Hypacrosaurus*) are not present on this vertebra.

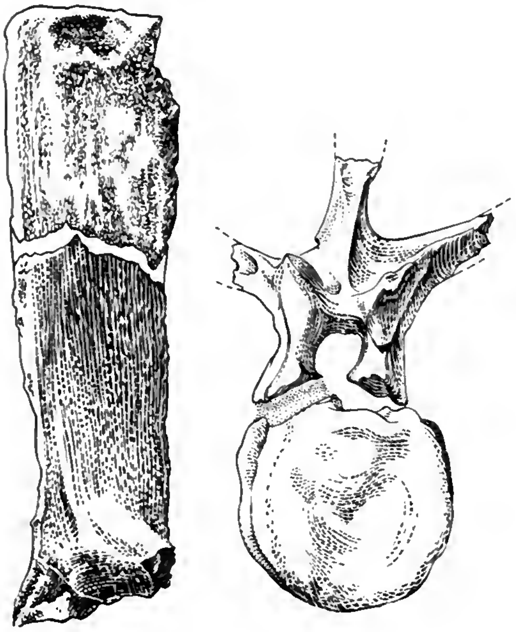


FIG. 155. *Lophorhothon atopus*, holotype (CNHM–P27383), mid-dorsal vertebra, anterior aspect, and dorsal neural spine, lateral aspect; × ½. Dots indicate areas occupied in life by cartilage.

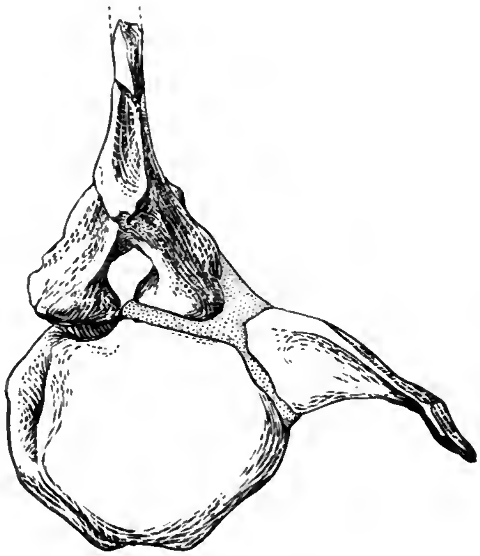


FIG. 156. *Lophorhothon atopus*, holotype (CNHM–P27383), anterior, possibly first, caudal vertebra, posterior aspect; × ½. The right caudal rib is shown in place; facet for the left rib is clearly shown. Dots indicate space occupied in life by cartilage.

Ventrally the caudal centra are strongly beveled at either end, where chevron facets are not distinctly formed. There are no longitudinal haemal grooves. The neural arches are massive, particularly toward the bases of the pedicles. These bases are expanded medially and in the anterior vertebrae the pedicles from either side almost meet below the neural canal. In some distal centra the deep excavations in the centra which lodged the pedicle bases do meet in the mid-line. What is probably the first caudal centrum is 34 mm. long, 68 mm. high, and has a greatest transverse diameter posteriorly of 78 mm.

Numerous neural spines are preserved. Three, which are probably from posterior dorsal or sacral vertebrae, are 148, 156, and 158 mm. high, or roughly 2.5 times the height of the largest dorsal centrum preserved. These proportions are reminiscent of hadrosaurines like *Kritosaurus*, in which the ratio is about 1:3, rather than the long-spined lambeosaurines such as *Hypacrosaurus*, with dorsal spines five times as high as the centra. The same spines are 32, 29 (distorted), and 35 mm. wide at the base, and 45, 37+ and 48+ mm. at the top. As preserved they are plate-like, the thickest not exceeding 14 mm. in transverse diameter, but there is an incomplete and otherwise smaller dorsal spine which has a transverse diameter of 14 mm. near the top. A caudal spine which is only half as wide as the dorsals above described is 16 mm. thick. This suggests that *Lophorhothon* had club-shaped spines like *Kritosaurus* and that the large flattened dorsal spines have suffered subtile distortion.

Ossified tendons, which occur so commonly in hadrosaur skeletons, were not present in this specimen.

I am unable to recognize cervical ribs in this specimen, and dorsal ribs are represented by fragments only. The sacral ribs have already been described. Part or all of at least nine caudal ribs are preserved. Their heads were not fully ossified and all are dissociated from their vertebrae. One which may have belonged to the first caudal is 70 mm. long.

Several chevrons, mostly anterior ones, are preserved, but none is quite complete. One is 143 mm. long and more than 30 mm. wide across the proximal rami; another is somewhat heavier, with a transverse diameter proximally of at least 52 mm. The bones are long, slender, straight, and seemingly flattened anteroposteriorly. There is no sign of distal expansion in any anterior chevron, but a bone from the mid-caudal region widens from 6 mm. above to 16 mm. below. It is 50 mm. long.

Of the hands only the unguals and one other phalanx were recovered. The unguals are the usual spade-shaped bones with cylindrical proximal shanks. The longest ungual, probably from digit II, has a length of 65 mm. and a maximum width of 42 mm.

The pelvis is represented only by parts of the ischia. The right bone lacks part of the proximal end and the distal tip; the left shows part of the region around the acetabulum. The ischium of *Lophorhothon* was long, straight, and slender, and obviously lacked the distal expansion which characterizes lambeosaurines. Had this been present some indication would be seen in the preserved part of the right ischium, which has lost at most only a few millimeters of the distal end. There is a blunt obturator process; only a wide obturator notch was present. The bone around the acetabulum is unusually thin and plate-like and even the iliac peduncle is not much expanded transversely. This may have resulted from crushing. From the two bones we know about 590 mm. of the ischium. The general proportions of the bones suggest that the complete ischium was no longer than the femur (which itself is not completely preserved).

The left femur is preserved but is so damaged that it is of little value. Like the other bones of the hind limb it gives an impression of unusual length and slenderness. In the case of the femur this is somewhat illusory owing to loss of the expanded ends and reduction in the diameter of the shaft in the vicinity of

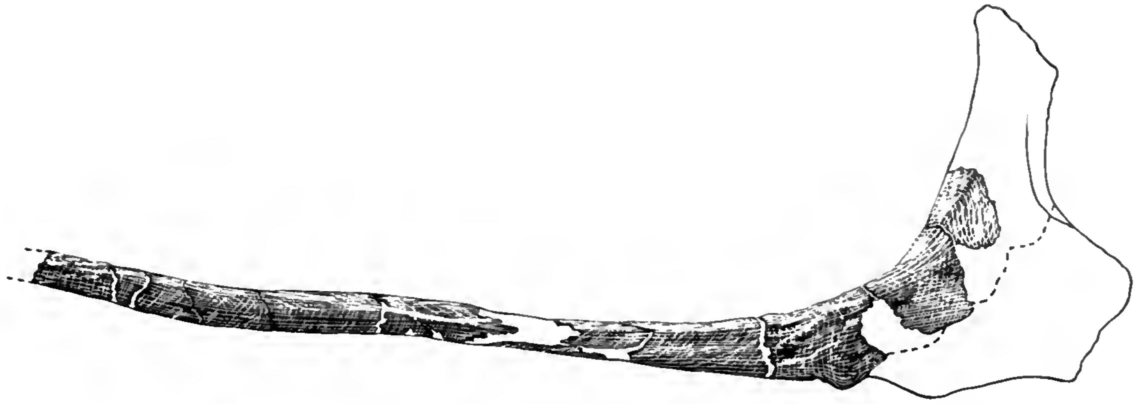


FIG. 157. *Lophorhothon atopus*, holotype (CNHM-P27383), ischium; × ¼. Shaded parts drawn from right ischium; area enclosed by broken line from left bone.

FIG. 158. *Lophorhothon atopus*, holotype (CNHM-P27383), right tibia, anterior aspect; × $^2/_7$.

the fourth trochanter resulting from post-mortem distortion. The proximal trochanters have been destroyed and what remains of the fourth trochanter extends for about a fourth of the length of the bone, its heaviest part roughly at mid-length of the shaft. The preserved part of the femur is 613 mm. long; the entire bone probably was about 635 mm. in length. Least transverse and fore-and-aft diameters of the shaft are 55 and 42 mm. respectively.

Both tibiae are comparatively well preserved, although one is damaged proximally, the other distally. The cnemial crest as seen on the right bone was smaller than is usual in hadrosaurs and had a smoothly rounded dorsal outline. The shaft of the tibia seems unusually long and slender, but this may result in part from the fact that the ends, particularly the distal ones, are less expanded than usual and the sharp fibular flange that extends laterally up the shaft from the distal end is not as widely expanded as in larger animals. The astragalar surface was characteristically hadrosaurian, and as elsewhere in the skeleton there is every suggestion that ossification was incomplete. The left tibia is about 580 mm. long and 141 mm. wide at the distal end, and has a transverse diameter at mid-length of 58 mm. If the femur was at least 635 mm. long the ratio of femur length to length of tibia was about 1 : 0.910. The femur : tibia relationship varies between 1 : 0.790 and 1 : 0.903 in hadrosaurines, and between 1 : 0.926 and 1 : 0.980 in lambeosaurines (Lull and Wright, 1942, tables 4–8).

There are two well-preserved fibulae of characteristic hadrosaurian form. As elsewhere in this skeleton the muscle scars on the bones are less well defined than in adult animals. The left fibula shows some evidence of injury just above mid-length of the shaft, where there is some roughening of the medial surface of the bone. The opposing surface of the left tibia also shows this roughening. The right fibula is 537 mm. long and has a widest diameter proximally of 74 mm. The left fibula is a few millimeters longer.

The hind feet are represented by numerous bones, mostly distorted. Present are both calcanea, an astragalus, all the metatarsals and half the phalanges, but the relative positions of the various bones in the feet are difficult to ascertain. The left astragalus is almost complete but much flattened dorso-ventrally by crushing. The characteristic hadrosaurian ascending process was apparently not very massive. The development of this process, however, is somewhat variable in different hadrosaur genera, a few of the largest animals having relatively smaller processes than smaller forms. The calcaneum was well formed, but like the astragalus its surfaces appear unfinished, particularly where it opposed the distal end of the fibula. There was, of course, no fusion between astragalus, calcaneum and adjacent elements. Pads of cartilage probably separated these bones.

The metatarsals probably retain their approximate lengths and distal widths despite considerable crushing. Even in their accidentally flattened (and expanded) condition they appear to have been relatively slender. The proximal phalanges seem relatively a little longer than usual, but no conclusions are possible regarding their transverse diameters. A few more distal and seemingly undistorted phalanges are definitely a little longer than corresponding bones in some large hadrosaurs with which I have compared them. A flattened and incomplete ungual phalanx with a long proximal neck probably belonged to left digit II. It has the characteristic hadrosaur hoof-like end, and does not differ perceptibly from many similar ungual phalanges from large hadrosaurs in the National Museum of Canada.

MEASUREMENTS
(In millimeters)

	Right Pes			Left Pes		
Digit	II	III	IV	II	III	IV
Metatarsal						
Length	184	234	175	183	245	178
Width*	55	72	..	53	68	..
Proximal phalanx						
Length	..	..	..	80	97	95
Width	..	..	..	52	63	60
Second phalanx						
Length	?35	37	..	..	43	..
Width	?61	71	..	..	72	53
Third phalanx						
Length	..	..	24	62†	30	23
Width	..	..	54	52+	62	51
Fourth phalanx						
Length	..	..	26	..	..	..
Width	..	..	41	..	..	..

* All widths measured at distal end; each is maximum width.

† Ungual phalanx.

Relationships

The hadrosaurian affinities of *Lophorhothon* are obvious from the foregoing descriptions. The hoodless cranial roof, the absence of a distal expansion on the ischium, and the angle between the crown and the root of dentary teeth imply close affinities with the hadrosaurine subfamily. But the imperfection of the type specimen and this animal's immaturity make a more refined appraisal of its relationships somewhat uncertain.

It is necessary to compare *Lophorhothon* with hadrosaurs that occur geographically and stratigraphically close to it. These are few and fragmentary. From North Carolina we have *Hadrosaurus tripos* Cope and *Hypsibema crassicauda* Cope; from New Jersey, *Ornithotarsus immanis* Cope, *Hadrosaurus minor* Marsh, and *H. faulkii* Leidy. According to Lull and Wright (1942) all except *Ornithotarsus* and *H. faulkii* are *nomina nuda*. The type caudal vertebra of *H. tripos* has a deep ovoid depression ventrally between the anterior and posterior chevron facets. I find no sign of this in caudals of *Lophorhothon*. *Hypsibema* is said to resemble *Hadrosaurus tripos* in the structure of the caudals; no other comparisons with *Lophorhothon* are possible. *Ornithotarsus* seems to be characterized by a tibia whose distal end is wide, relative to its dorso-ventral diameter. *Lophorhothon* shows an opposite condition. *Hadrosaurus minor,* which is only a little larger than the type of *L. atopus,* shows a slight hollow on the ventral surface of the posterior dorsal vertebrae. *Lophorhothon* dorsals have a convex, almost keeled ventral surface.

Hadrosaurus faulkii is the best known of the eastern hadrosaurs, but it has not been really adequately defined. Lull and Wright (1942, p. 141) state that about "the only characteristic features of the vertebral series as preserved are the pronounced rake of the spinous processes and the relative shortness of the anterior caudals." The presumed first caudal of *Lophorhothon* is relatively wider than the average of three anterior caudals of *H. faulkii.* It is impossible to be certain of the inclination of the vertebral spines, but they seem to have been rather upright, in keeping with their relatively great height. The ischium of *Lophorhothon* is perhaps more slender, a difference of little consequence in animals of such disparate bulk. Similarly, there seems no point in comparing the limb bones.

Thus, although I am unable to show important differences between *Lophorhothon* and the other hadrosaurs from the eastern part of the United States, I have not found resemblances of significance between them. Comparisons with better known species from western North America are a little more illuminating. First, however, the unique fontanel between the frontals and the nasal bones of *Lophorhothon* requires an explanation because of its possible bearing on the relationships of the genus.

Perhaps a frontal-nasal fontanel was a normal feature of very young hadrosaurs: a subadult *Anatosaurus saskatchewanensis* skull in the National Museum of Canada (no. 8509) is almost three feet long, but has frontals only a millimeter or so thick near the frontal-nasal junction. The Senckenberg Museum's famous *Anatosaurus* mummy has a small opening in the skull roof at this point (Versluys, 1923). Even in adult hadrosaurines, except *Kritosaurus,* the frontal bones are generally thin where they roof the olfactory tracts, but in two young skulls that I have examined the fontanel has closed—if it was ever present. The frontal roof is much thickened in adult lambeosaurines, where the hood rests upon this part of the skull.

The configuration of the unfinished edges of the fontanel suggests that continued ossification of the frontal bones would have closed the opening in this animal. The corresponding edges of the nasals are smooth and this probably anticipates the simple internasal suture and the overlapping or inserting, but not interdigitating, frontal-nasal suture customarily found in hadrosaurines. In *Kritosaurus* the nasals abut bluntly into the frontal plate, where a deep transverse groove is developed for their reception. The posterior tips of the nasals of *Lophorhothon* evidently were lodged in somewhat comparable grooves that have already appeared antero-laterally on the frontals. *Prosaurolophus* nasals diverge posteriorly much as in *Lophorhothon,* but the roof above the olfactory tracts is completed between the nasal processes by a triangular tongue of the frontals. Absence of this tongue would give a distinctly *Lophorhothon*-like appearance to this part of the *Prosaurolophus* skull; either a *Prosaurolophus*- or *Kritosaurus*-like frontal-nasal contact may have been present in the adult *Lophorhothon*.

In some lambeosaurines the bones comprising the hood apparently shifted ontogenetically, and the frontals sometimes have a gap between them anteriorly where they underlie the hood. The edges of this gap are always rugose and much thickened. It is not improbable that the frontals of the crested hadrosaurine *Saurolophus* had similarly formed frontal bones, and young individuals may have possessed a crest more like *Prosaurolophus*, that is, a low hump on the nasal bones more anteriorly situated than in the adult *Saurolophus*. Perhaps (though I think it improbable) the young *Saurolophus* crest resembled that of *Lophorhothon*. In *Lophorhothon* I find nothing in the structure and relationships of the nasal bones that seems to foreshadow backward extension of the nasal crest. Hence it is logical to assume that the present development of the *Lophorhothon* crest reflects essentially adult conditions. The presence of the frontal fontanel must then be attributed to immaturity of the individual and probably has no systematic significance in presently used generic criteria in the Hadrosauridae.

The skull as a whole was evidently much like those of *Kritosaurus* and *Prosaurolophus*. Its general shape was probably more similar to that of *Kritosaurus*, where the orbits were relatively large. *Lophorhothon* is perhaps intermediate between the two genera in the size of the lateral temporal openings, but certainly more like *Kritosaurus* in the shape of these openings and the large semi-quadrangular superior temporal fenestrae (fig. 147). The nasal crest, though similarly situated, is already more complex structurally than in *Kritosaurus*. Its resemblance to *Prosaurolophus* has already been noted: On the assumption that the nasal crest migrated ontogenetically, the conclusion that *Lophorhothon* was in fact an immature *Prosaurolophus* would be tempting indeed, had we nothing to go on but the fragmentary nasal and frontal bones.

The jugal is a remarkably slender bone for a hadrosaur, and the plate through which it joined the maxilla is relatively less developed than in any other North American hadrosaur, but most nearly resembles the jugal of *Kritosaurus* in that group. Only a small portion of the rim of the orbit is formed by the jugal. The broad orbital rim of the lacrimal precludes the possibility of later development on the jugal of an antorbital margin like that of lambeosaurines or *Edmontosaurus*. The subtemporal ramus of the jugal was evidently no broader than the base of the postorbital bar. This plate is also relatively slender in some specimens of *Kritosaurus*, but the only really comparable jugal seems to be that of the European Upper Cretaceous hadrosaur, "*Limnosaurus*" *transylvanicus* Nopcsa (1918).[1] The Asiatic *Tanius* and *Bactrosaurus* also have slender jugals with but slightly expanded maxillary plates—characters that may be primitive as well as juvenile in hadrosaurs.

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[1] *Limnosaurus* Nopcsa (1899) is preoccupied by *Limnosaurus* Marsh (1872), a supposed sebecosuchian crocodile (Langston, 1956). "*Limnosaurus*" *transylvanicus* was once referred to *Orthomerus* Seeley by Nopcsa, but he later reverted to the use of *Limnosaurus*.

Exposure of the frontal bone in the orbital rim is said to be characteristic of later North American hadrosaurines (Lull and Wright, 1942). This also happens in *Bactrosaurus* and *Tanius*, where the degree of frontal contribution seems fairly comparable to that in *Lophorhothon*. The feature appears variable in *Kritosaurus*. It is possible that the frontal would be excluded from the orbit by continued growth of prefrontals and postorbitals in *Lophorhothon*, but the great rugosity of the dorsal rim of the orbit here and in *Kritosaurus* is a feature not present in other hadrosaurs, where the frontal reaches the edge of the orbit. The bone's lateral exposure seemingly would have resembled that of a skull referred to *Kritosaurus notabilis* by Lull and Wright (1942, p. 168) but is relatively shorter and higher as a whole.

The medial ends of the squamosals show that these bones did not meet in the mid-line as is usual in most hadrosaurs, but were very widely separated probably by a tongue of the parietals as in *Edmontosaurus* and *Kritosaurus*.

The occiput of *Lophorhothon* is very broad. Among North American genera it is most closely approached in this regard by *Kritosaurus*, but the paroccipital processes are much shorter than they are in that genus. The occiput is also lower than in any hadrosaur known to me with the exception of *Bactrosaurus*, and this may reflect a combination of juvenile and primitive features.

The teeth, though clearly hadrosaurian in construction, show less similarity in details to those of other members of the family than does the rest of the skeleton. There is in the Royal Ontario Museum, Toronto, a specimen (both dentaries and left nasal bone) of a young *Kritosaurus* which was almost exactly the same size as the specimen of *Lophorhothon*. Teeth can be found in the dentaries that resemble closely the isolated dentary teeth of *Lophorhothon*. However, most of the crowns of the *Kritosaurus* teeth seem to lack any kind of marginal denticulations and those crowns which have secondary ridges on either side of the sharp mid-ridge appear to be relatively more slender and lanceolate than the two *Lophorhothon* dentary teeth. On both these specimens the relative breadth and irregularly crenulated enamel surfaces of the dentary teeth are vaguely reminiscent of iguanodont conditions, and probably reflect the primitive construction expressed in these hadrosaurs as a feature of immaturity. Crenulations do occur in other hadrosaurs, perhaps most often among lambeosaurines, where, however, they more nearly parallel the mid-ridge of the elongate lanceolate enamel crowns. Marginal denticulations vary greatly in development in many (mostly lambeosaurine) hadrosaurs.

Sternberg (1936) has emphasized the systematic importance of the external angle between crown and root (=fang) in hadrosaur dentary teeth, although the universality of his generalizations has not been certainly demonstrated. Sternberg's drawings (see fig. 159, this volume) show this angle to range from 130 to 140 degrees in hadrosaurines (*Hadrosaurus faulkii*, *Kritosaurus* sp., and *Anatosaurus* sp., respectively), and from 148 to 150 degrees on lambeosaurines (*Lambeosaurus clavinitialis* and *Cheneosaurus tolmanensis*). The angle of 140 degrees in *Lophorhothon* agrees best with that in Sternberg's *Anatosaurus* sp. The ratio of the transverse diameter at the base of the crown to the widest diameter of the enamel surface is also supposed to be important, being never less than 1.00 in hadrosaurines. The ratio 0.85 in *Lophorhothon* is therefore more like lambeosaurines, but this comparison may be suspect owing to the great disparity in the relative width and length of *Lophorhothon* and lambeosaurine teeth, which are usually very slender. The number of vertical rows of teeth in the dental magazines once so confidently employed as a generic or specific "character" among the Hadrosauridae is probably misleading, for the number of rows evidently increases throughout the life of the individual. The relatively few rows (25) in the maxilla of *Lophorhothon* vary from a few less to slightly more than half the number encountered in adult hadrosaurines. It is closest to *Mandschurosaurus* (Gilmore, 1933) and agrees almost exactly with some adult *Bactrosaurus*. It much exceeds half the number present in most adult lambeosaurines. The number of rows also seems to vary with absolute size; species that most nearly approach *Lophorhothon* in tooth count are comparable to it in size irrespective of the individual's age.

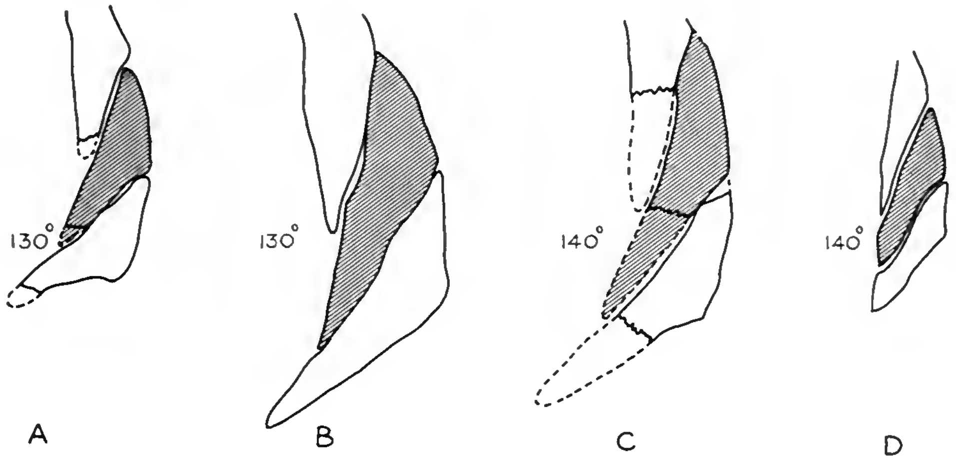

FIG. 159. Mandibular teeth of hadrosaurine dinosaurs compared in transverse section. Drawings to scale, angulation between enamel face and root indicated in degrees. A, *Hadrosaurus;* B, *Kritosaurus;* C, *Lophorhothon atopus,* holotype (CNHM-P27383); D, *Anatosaurus.* (A, B, and D modified from Sternberg.)

The remainder of the skeleton is of little value systematically. The neural spines, though incompletely formed dorsally, are already relatively longer than in *Prosaurolophus* and resemble those in *Kritosaurus* in proportions and probably in the expansion or "clubbing" of the upper ends. This apparent slenderness of the limb bones is probably attributable to the relatively small size of the animal, and in any case the bones are so badly preserved that comparisons of measurements are not systematically useful.

In its totality of traits *Lophorhothon* resembles *Kritosaurus* more closely than it does other hadrosaurs. The similarity of the nasal crest to that of *Prosaurolophus* suggests a relationship to the saurolophs as well. It may retain primitive features of the *Kritosaurus* and *Prosaurolophus* ancestors. That it is an ancestor of either, possible on chronological grounds, seems improbable on morphological grounds because the crest is already more complex than in *Kritosaurus,* whereas elsewhere the skeleton seems much closer to this genus than to *Prosaurolophus.*

It would be pointless in the present state of our knowledge to try to analyze *Lophorhothon* in more detail respecting its primitive and juvenile characters. The specimen proves, however, that a review of the Hadrosauridae (including Old World forms) emphasizing ontogenetic variation is much needed. Immature specimens like the animal from Alabama should contribute much to such a study.

Order **ANKYLOSAURIA**

Family **NODOSAURIDAE**

Genus and species indet.

An incomplete left ilium (P27469) of a small nodosaurid records this family in the Selma formation. The specimen was found isolated about 20 feet west of the small wooded area directly west of "site 4" (Zangerl, 1948, pl. 3), and stratigraphically below the skeleton of *Lophorhothon.* There has been a great deal of dorso-ventral flattening, and some of the pre- and post-acetabular parts are missing. Details are obscure, but the general shape of the bone in dorsal outline is shown in figure 160, A.

Viewed from above, this ilium had the form of a very depressed elongate triangle whose apex, now lost, lay anteriorly. The postacetabular length, measured from the center of the acetabulum, was much shorter than the preacetabular part. The pubic peduncle was evidently massive, though now it is much reduced in volume by crushing. The ischiadic peduncle was broad, low, and flattened in characteristic nodosaurid fashion. The edge of the ilium is somewhat thickened laterally. The area of primary sacral attachment is also thickened, but anterior to the level of the middle of the acetabulum the bone diverges sharply to the side and the median edge here becomes almost paper-thin. This is in the region where posterior dorsal ribs underlay the iliac blade, but I find no trace of facets or grooves on the under side of this blade. The dorsal surface of the ilium is fairly smooth. The bone as preserved is 520 mm. long and has a greatest transverse diameter of 200 mm.; the acetabulum is about 100 mm. long.

It is difficult to compare nodosaurid ilia, because they are often incomplete, distorted, hidden by osteoderms or matrix, and not often clearly illustrated in the literature. However, general comparisons may be made between the bone from Alabama and several nodosaurid ilia, even though the value of the comparisons varies with the quality of available illustrations (see fig. 160). The bone seems closely similar to that of certain broad-backed nodosaurs like *Polacanthus, Nodosaurus, Ankylosaurus,* and *Stegopelta.* The general shape as preserved, without the complete iliac blade, is much like an ilium of *Stegopelta* figured in Moodie (1911, pl. 55). The flange from which probably originated the ilio-femoralis ex-

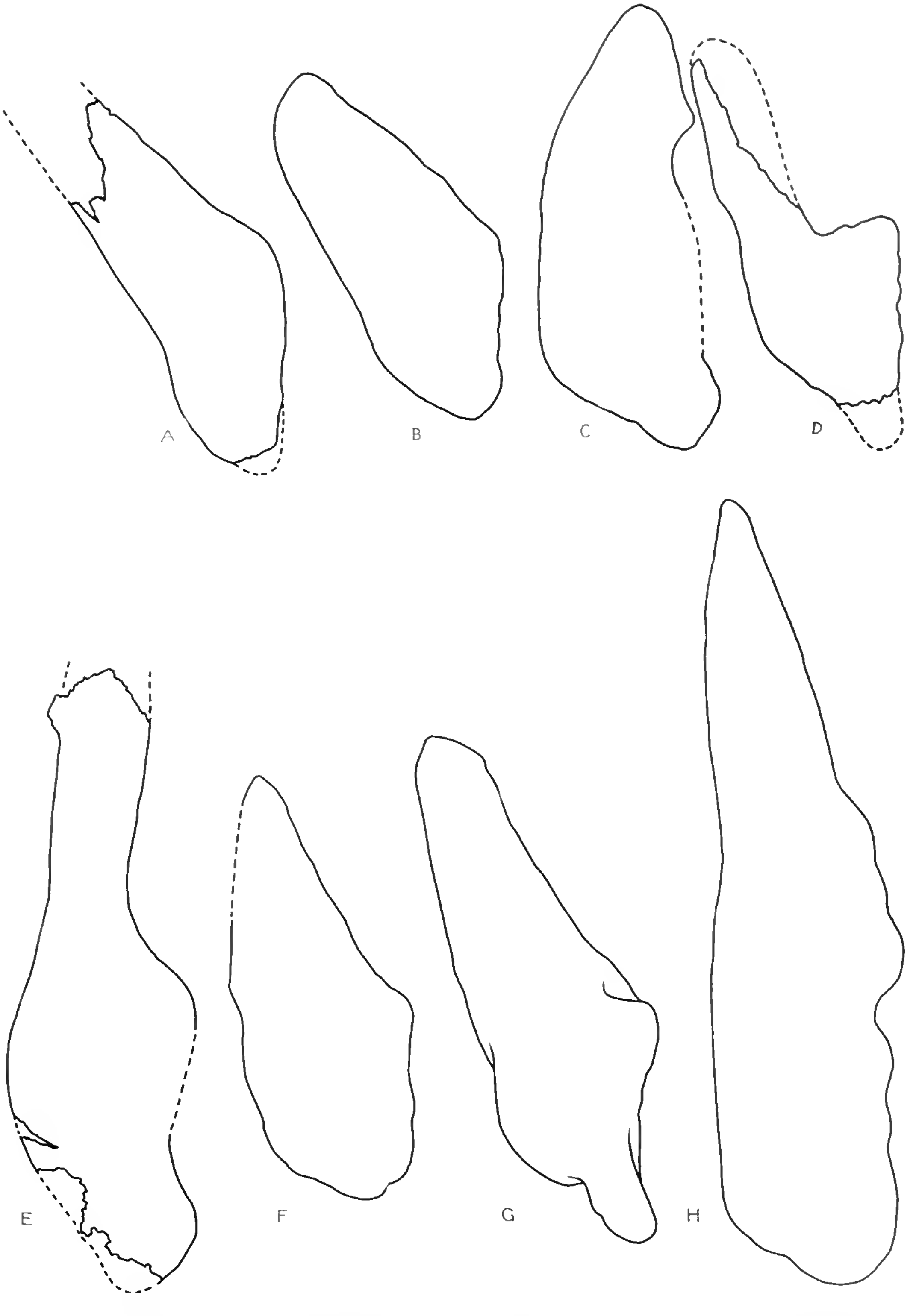

FIG. 160. Schematic drawings of left ilia of various nodosaurs, dorsal aspect. All figures reduced to same width across widest transverse diameter. A, nodosaurid, gen. and sp. indet. (CNHM–P27469); B, *Stegopelta landerensis* Williston; C, *Nodosaurus textilis* Marsh; D, *Dyoplosaurus acutosquameus* Parks; E, *Edmontonia longiceps* Sternberg (NMC 8531, holotype, drawing reversed from right ilium); F, *Polacanthus;* G, *Ankylosaurus;* H, *Scelidosaurus.* (B from a photograph by Moodie; C from a photograph by Lull; D from a photograph by Parks; F, G, and H adapted from Romer.)

ternus muscle (Romer, 1927) appears to be intermediate in development between those of *Ankylosaurus* and *Nodosaurus*. The postacetabular part of the ilium is relatively shorter than in the former and longer than in the latter. Ilia of *Scolosaurus, Scelidosaurus, Dyoplosaurus,* and *Edmontonia,* so far as can be seen, had relatively more elongate and more slender anterior blades.

Order **SAURISCHIA**

Suborder **THEROPODA**

Genus and species indet.

A phalanx of a theropod, presumably a carnosaurian dinosaur (fig. 161) was picked up at "site 2" about 640 yards west of the *Lophorhothon* locality (Zangerl, 1948, pl. 3). It bears the number P27398.

FIG. 161. Carnosaur phalanx (CNHM-P27398); × ½.

This bone, which I take for the proximal phalanx of the third left pedal digit, has suffered much from weathering and has lost all surface detail and most of the compacta. The animal to which it belonged was less than half as large as the type of *Gorgosaurus libratus* Lambe and hence ranks with the smaller carnosaurs. The bone appears fairly slender in its present condition and resembles more the phalanges of *Gorgosaurus* than those of the more primitive megalosaurs. The proximal end is not deeply cupped; the distal condyles are widely separated. The bone is 77 mm. long, 39 mm. high, and 43 mm. wide proximally. Its narrowest diameter (roughly dorso-ventral at mid-length) is 21 mm.

NOTES ON HADROSAURIAN CRANIAL ANATOMY

The general state of preservation of the type skeleton of *Lophorhothon atopus* is bad; had it been found in the hadrosaur-rich terrestrial Cretaceous deposits of the west, it might have been thought unworthy of the collector's attentions. But owing to a combination of fortuitous circumstances, for example, the incomplete fusion of certain cranial elements in the immature skull, the differential permineralization of the bone, which tends to accentuate the ossification lattices of certain bones, and the soft calcareous matrix that can be completely removed, this specimen reveals anatomical details hitherto unobserved in all of the excellently preserved hadrosaur material that has come to light in the last hundred years. On the other hand, the loss of the supraoccipital from this specimen contributed directly to the determination of whether or not a supraoccipital ossification occurs in hadrosaurs, and the nature of its relationships to other bones of the cranium.

The anatomical discussions to follow concern mostly conservative structures, and I believe that the generalizations here stated will prove valid for hadrosaurs as a group. The net result of this study is to show that structurally hadrosaurs conformed more closely to a generalized archosaurian pattern than has sometimes been supposed.

The Supraoccipital Problem

The hadrosaur supraoccipital has received scant attention owing to its cryptic position within the cranium. One suspects from their descriptions that some authors even doubted its existence. Lull and Wright (1942) describe it erroneously in *Edmontosaurus* and *Anatosaurus* and mislabel it in their illustrations (op. cit., figs. 4, 6, 7).

Gilmore, however (1937), described and figured a well-preserved supraoccipital in a young lambeosaurine cranium, Brown (1914) shows the bone in a sagittal section of a large hadrosaurine braincase, and Sternberg (1926) has correctly interpreted it in *Anatosaurus saskatchewanensis.* Most other authors have mistaken parts of adjacent bones for the supraoccipital and have usually assumed that it entered the foramen magnum, although Gilmore and Brown both showed that it did not do so in their specimens.

The supraoccipital bone was not recovered with the skeleton of *Lophorhothon* described above, wherein it was probably incompletely ossified and not firmly united to contiguous elements. A strong transverse bar composed of exoccipitals (figs. 152, 153) is suturally divided in the mid-line above the foramen magnum just as Gilmore (1933, fig. 22) found it in *Bactrosaurus.* In sagittal section this bar is triangular with apex anterior and hypotenuse antero-dorsal as in Brown's specimen (1914, pl. 36). The upper surface of the bar is clearly marked for attachment of the supraoccipital, which would have entered the endocranial vault some distance in front of the foramen magnum. In the National Museum of Canada there is a complex bilaterally symmetrical bone (pl. 34) whose identity has been a mystery since its discovery in 1910. It fits almost exactly the space formerly occupied by the supraoccipital in the *Lophorhothon* cranium, and comparison with many hadrosaur crania in the collection confirms that it is the supraoccipital of a hadrosaur. It differs somewhat from the lambeosaurine element described by Gilmore and also from the supraoccipital of several non-crested hadrosaurines; so further description is in order.

Viewed from behind and in proper orientation with respect to the occiput, the bone is about two and one-half times as wide as high. Gilmore described his specimen as triangular, but he apparently viewed it with the longitudinal axis vertically instead of diagonally oriented. The ventral surface which opposed the upper face of the transverse exoccipital bridge is nearly flat, with only a slight downward bowing toward the mid-line. At either side of the supraoccipital an obtusely rounded peg-like boss was inserted into an opposing pit in the under side of the squamosal. In some hadrosaurs, if not in all, this boss is completed laterally by the opisthotic (Gilmore believed by the exoccipital). Its surface is unfinished, so a cartilage pad was evidently intercalated between it and the squamosal. The boss is apparently not homologous to the lateral pedestal of the crocodilian supraoccipital. The supero-median part of the supraoccipital, the ossified portion of the processus ascendens of the synotic tectum, is a broad, low, longitudinally grooved block-like mass that extends antero-dorsally to a blunt, unfinished end. Gilmore describes the process as "bilobed" in the lambeosaurine and believed that complete ossification and fusion with the parietals might occur in old individuals. This seems highly improbable after inspection of several hadrosaurian parietals; the oft-noted dorso-median cerebral protuberance of hadrosaur endocranial casts reflects the parietal fossa, thus recording the gap between the end of the bony supraoccipital and the parietal roof.

On either side of the median supraoccipital (=nuchal) crest there is a shallow, elongate and narrow depression which probably gave tendinous insertion to the rectus capitis posterior muscle. This whole area is raised and bounded laterally by a low, sharp ridge. A broad and moderately deep longitudinal channel crosses the supraoccipital on either side of the median elevation. It leads forward, outward and upward for some distance and thence downward and outward into the temporal space. This is the bottom of the small post-temporal foramen which was completed above by the squamosal. Its size varies greatly in different hadrosaurs, and in many it is almost undetectable owing to downward crushing of its squamosal roof.

The parietals meet the supraoccipital suturally on either side of the processus ascendens, where broad, forked, longitudinally furrowed grooves on the side of the bone receive blunt finger-like processes of the parietal. Below and in front of this articular area is a small antero-dorsally directed apex with an unfinished end. It was doubtless continued forward by cartilage of the taenia marginalis. Below the apex the anterior edge of the supraoccipital bears the posterior margin of a foramen that was evidently completed anteriorly in cartilage and pierced the cranial wall near or at the junction of parietal, laterosphenoid and proötic. Perhaps it carried the vena capitis dorsalis.

Seen from the side, the ventral margin of the supraoccipital has a broadly V-shaped outline. The margins were sutured and firmly fused in adult hadrosaurs to the proötic in front and the opisthotic behind. Postero-ventrally the bone lay upon the exoccipital bar above the foramen magnum.

The supraoccipital part of the endocranial vault is ∩-shaped. Except for some encroachment medially by the otic capsule, the endocranial surface is smooth and featureless. The supraoccipital encloses most of the dorsal loops of the vertical semicircular canals which lead below into the recess for the common crus. Apparently only the medial wall of this tunnel was contained in the supraoccipital; the remainder lay in the otic elements.

It is evident from the foregoing that the hadrosaur supraoccipital bone is well formed and has basically sauropsid relationships with adjacent elements. It is longer, more upright in position, more broadly exposed in occipital aspect, and more triangular in posterior outline in lambeosaurines than in hadrosaurines (fig. 162). The bone labeled "supraoccipital" in *Edmontosaurus* by Lambe (1918, figs. 5, 6) is actually the transverse bar of cojoined exoccipitals. The "supraoccipital" of *Anatosaurus* shown by Lull and Wright (1942, fig. 6) is also clearly part of this bar, and the true supraoccipital is distinctly shown in the "nuchal pit" above it. In both genera the bone was much flattened dorso-ventrally and bore little resemblance to the supraoccipital of lambeosaurines when viewed from behind.

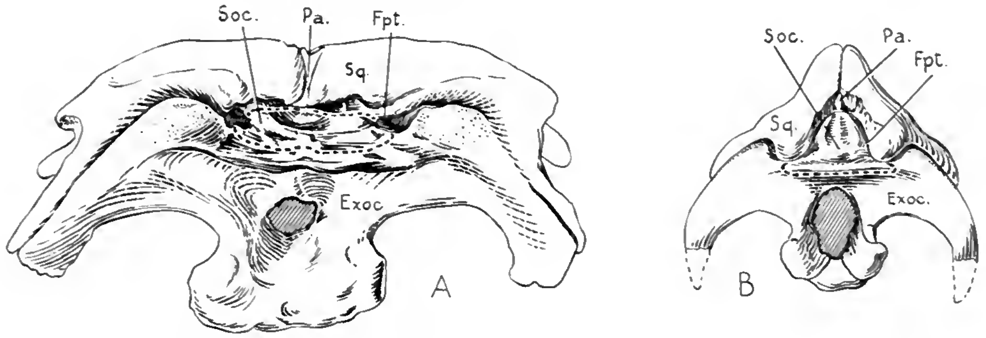

FIG. 162. Occipital aspect of crania of (A) a hadrosaurine dinosaur, *Edmontosaurus regalis* (NMC 2289), and (B) a lambeosaurine, *Cheneosaurus tolmanensis* (NMC 2246), showing differing shapes of the supraoccipital bone in the two hadrosaurian subfamilies. Drawn to scale, much reduced.

Exclusion of the supraoccipital from the margins of the foramen magnum is not uncommon in dinosaurs. This is usual in saurischians and in many ornithischians, except, for example, in armored forms, the Protoceratopsidae, primitive camptosaurs, and *Hypsilophodon*. The hadrosaur condition is easily derivable from a camptosaur stage where the supraoccipital somewhat resembled the bone of *Bactrosaurus*, is relatively large and more superficial in position than in hadrosaurs, and enters the foramen magnum. The camptosaur occipital plane is vertical or slants slightly forward, and the paroccipital processes are relatively short and project more or less transversely. The postero-superior margin of the skull is almost straight transversely. The head was presumably carried in an extended position. In hadrosaurs the angle between the longitudinal axes of the head and neck became progressively more acute until head and neck were carried nearly at a right angle to each other, and in response the postero-dorsal edge of the skull shifted backward relative to the plane of the condyle. This has produced in

Edmontosaurus and related anatosaurs a roof-like structure which overhangs the occipital and anterior cervical region. The paroccipital processes lengthen greatly and the posterior sagittal crest becomes concave transversely (this feature is apparently often accentuated in hadrosaur skulls owing to crushing from side to side). A transverse bar of the exoccipitals develops between the extending paroccipital processes and finally forms in hadrosaurs a bridge across the occiput behind the supraoccipital and hence above the foramen magnum. In the most advanced hadrosaurines (*Edmontosaurus* and *Anatosaurus*) the supraoccipital is exposed on the occipital surface only within a deep "nuchal" pit bounded below by the massive transverse exoccipital bar, above by an incipiently frill-like sagittal crest, and on either side by the paroccipital processes. Furthermore, in adult individuals it becomes firmly fused with adjacent bones on the occipital surface. It is small wonder that the supraoccipital has been so often misinterpreted or overlooked.

The Paroccipital Process

Long, gracefully arched wing-like paroccipital[1] processes are characteristic of the hadrosaur skull. Even in the most primitive known species their length and curvature greatly surpass those of any other ornithopod dinosaur. The process has usually been recognized as a compound structure, but owing to early co-ossification of the cranial bones in the occipital and otic regions the elements comprising it have never been clearly defined; the process has been variously described as composed of exoccipital, proötic, and opisthotic singly and in various combinations.

Gilmore (1937) showed that the exoccipital formed most of the paroccipital process in a disarticulated lambeosaurine skull; Lull and Wright (1942) did not mention this bone in connection with the process but stated that the process of *Edmontosaurus* is formed of the "opisthotic portion" of the skull. Several *Edmontosaurus* skulls in the National Museum of Canada are more specifically interpretable here in light of the Alabama hadrosaur skull, where most of the process is clearly formed of exoccipital. This is doubtless the usual condition. However, the exoccipital part of the paroccipital process is overlapped and buttressed anteriorly by a thin postero-lateral continuation of the opisthotic, whose margins can be seen intermittently on the anterior surface of the paroccipital process in the *Lophorhothon* specimen (figs. 151, 152). Variations in the texture of the exoccipital indicate where the very thin opisthotic plate has been removed. Evidently its outline roughly paralleled the exoccipital, but it did not extend to the end of the paroccipital process.

The extent of proötic participation in the paroccipital process is not clear. If the bone reached it at all it must have overlapped the opisthotic in the same

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[1] The term "paroccipital" has often been used synonymously with "opisthotic," which in many reptiles, but not in hadrosaurs, forms most of the so-called paroccipital process. For the sake of uniformity it seems most useful to continue this practice, but abandonment of the term "paroccipital bone" in favor of "opisthotic" (which literally it is) may be advisable, inasmuch as the process is sometimes formed, as in hadrosaurs, of the exoccipital bone.

way that that bone overlapped the exoccipital. Gilmore indicates a strong sutural surface for the proötic in his lambeosaurine skull, but this does not quite reach the paroccipital process; the suture was probably for the opisthotic. Brown (1912, fig. 3) indicates a major proötic contribution to the process in *Saurolophus*, where he apparently thought the rest of the paroccipital was composed of opisthotic, a rather improbable situation. So far as interpretations are permitted by the thorough co-ossification in the paroccipital processes, I find no hadrosaur skulls in the National Museum of Canada that do not agree with conditions described above. The structure may easily have been derived from the paroccipital of a camptosaur by elongation and curvature of the exoccipital wing. The opisthotic which does not enter the process in camptosaurs simply maintained its contacts with the exoccipital as that bone attenuated.

The Hadrosaurian Inner Ear

Fossil material suitable for studies of the inner ears of dinosaurs is uncommon. The only previous detailed account of the structure in a hadrosaur is by Brown (1914), who studied endocranial and otic casts of a large species of undetermined genus, possibly *Saurolophus*. The otico-occipital segment of the *Lophorhothon* skull is well preserved and affords another opportunity to examine the bony labyrinth of a hadrosaur. The left labyrinth, though lacking the "epiotic" parts lost with the supraoccipital bone, and most of the endocranial wall of the cavum capsularis, is undistorted and has been completely freed of matrix. From it a satisfactory latex cast (fig. 163) was obtained in which the following parts of the bony labyrinth are reflected: a common utriculo-saccular recess with well-differentiated posterior and anterior utricular recesses, the proximal part of the recess for the superior utricular sinus, the lagenar recess, and three semicircular canals. A latex cast from the isolated supraoccipital bone already described shows the dorsal part of the common crus and the upper loops of the vertical semicircular canals. A cast of the endocranium and partial labyrinths was made from the skull of *Bactrosaurus johnsoni* Gilmore (AMNH 6366), which because it is better ossified shows some details more distinctly than the skull of *Lophorhothon*. The description that follows is based largely on these specimens, supplemented by Brown's descriptions and illustrations. It is probably applicable to hadrosaurs generally because the external architecture of the otico-occipital region does not seem to vary much in different genera, and the inner ear was presumably a conservative organ in these animals.

The osseous labyrinth comprises cavum capsularis with its voluminous vestibule and appendicular lagenar recess, semicircular canals, and recessus crus communis. It invades the proötic, opisthotic, and supraoccipital bones, and in adult animals is completely enclosed by these elements except for the usual openings. The cavum is not reflected externally on the otico-occipital wall of the braincase, but medially the bony capsule forms a flattened hemispherical bulge within the endocranium. This has sometimes been called an otic "bulla." The three bones of the capsule join in a **Y**-shaped suture in the wall of the "bulla."

The osseous semicircular canals do not seem to reflect details of the membranous canals, and ampullae are not clearly distinguishable in the casts. Their positions may, however, be determined from annular constrictions that occur at the ends of the various canals. The anterior canal is much the thickest of the three; it has an antero-posteriorly compressed cross section and is strangely shorter than the posterior canal, a feature noted also in Brown's specimen. The canal is less widely arched than the posterior one, but much more so than the horizontal canal, whose loop is relatively flattened. The horizontal canal is much shorter and more slender than the other two. It arises proximally from the broad tubular posterior utricular recess and loops just within the distal end of the posterior canal before turning anteriorly. Distally (anteriorly) the canal joins the large vertically ovate anterior utricular recess postero-lateral to and below the anterior ampullar region. The anterior third of the horizontal canal passes through the proötic bone; the posterior canal has a rounded cross section and is slender and more broadly looped than the others. The recessus crus communis, seemingly longer in Brown's specimen than in the ones at hand, was thick in *Lophorhothon*. The vertical canals describe a broad V as they diverge from the common crus. The vertical planes of the canals stand at an angle of just over 60 degrees to each other.

The roof of the vestibule is low and flat and slants outward and downward; there is no space here for a dorsal "ballooning" of the sacculus. ⅄-shaped grooves on the vestibular roof reflect something of the utricular sinuses. Utricular and saccular recesses are not distinctly separable in the casts.

A thin tongue of the opisthotic, the lagenar crest, projects into the posterior part of the cavum capsularis just below the level of the fenestra ovalis. The anterior (proötic) wall of the lagenar recess—all of the wall that was ossified in the *Lophorhothon* cranium—is somewhat constricted dorsally at about the level of the fenestra ovalis. The lagenar crest and this constriction partly separate the appendicular lagenar recess from the wide vestibule above. The recess has not been fully cleaned in other specimens at hand, but Brown's cast shows an equally elongate though perhaps more slender recess (labeled "fr" in his figures). The recess was slightly flattened from side to side in *Lophorhothon* and was clearly a little twisted outward below.

An opening that appears to have been a tubular passage leading from the lagenar recess directly into the endocranial cavity and thence turning sharply backward, downward, and outward through the large "jugular" foramen in the supraoccipital is faintly discernible in the *Lophorhothon* cast. A much sharper impression obtained from the *Bactrosaurus* cranium confirms the presence of this tube, which probably carried the perilymphatic duct. The paratype skull of *Edmontosaurus regalis* Lambe (NMC 2289) has a narrow bridge of bone deep within the large triangular depression that surrounds the "jugular" foramen. This bridge separates an ovate foramen that opens from the medullary space from a smaller round passage below that seems to turn sharply into the cavum

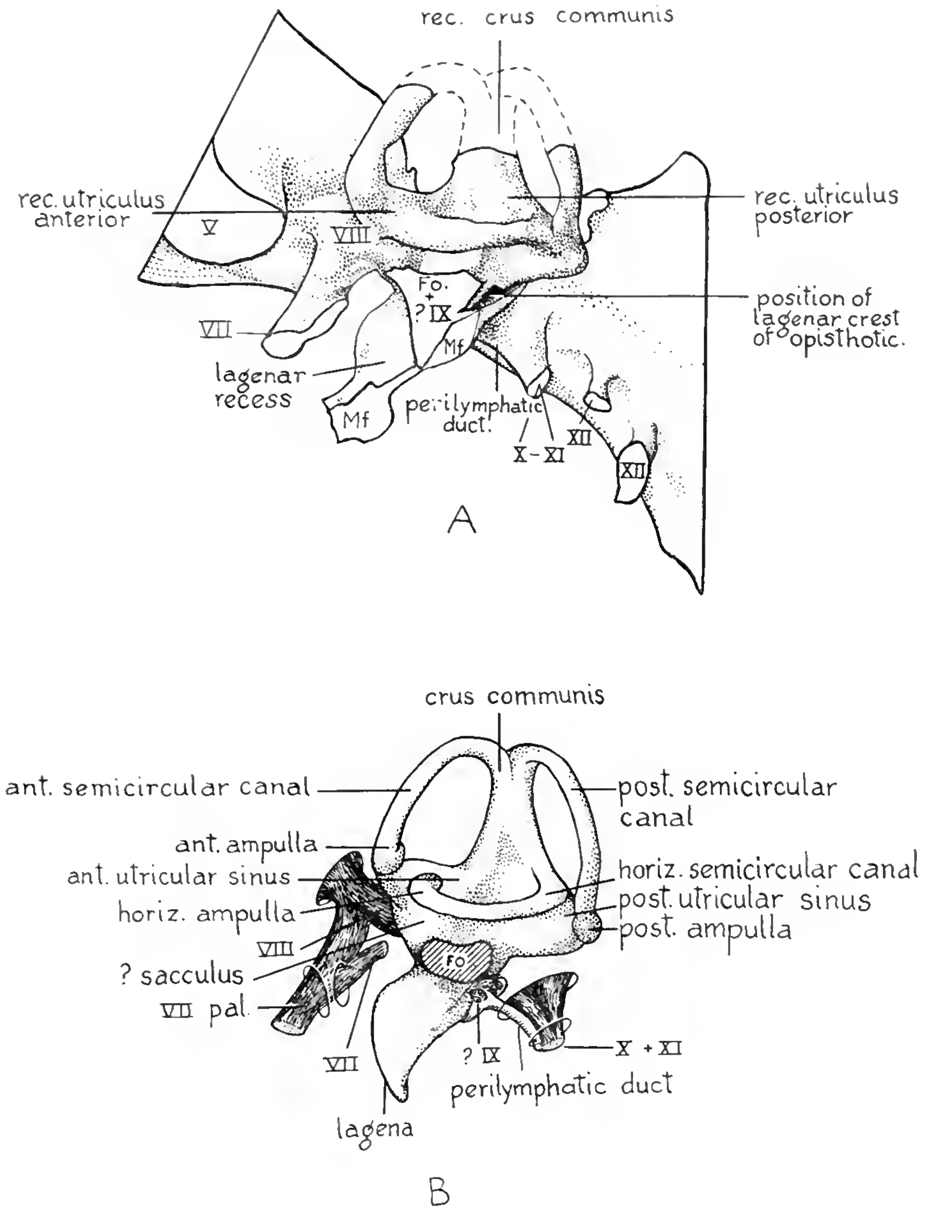

FIG. 163. The hadrosaurian inner ear. A, otic and partial endocranial cast from cranium of *Lophorhothon atopus*, holotype (CNHM–P27383). B, reconstruction of membranous labyrinth and adjacent structures, based on A, with supplementary data from a skull of *Bactrosaurus johnsoni* (AMNH 6366) and an isolated supraoccipital of an unidentified hadrosaur (NMC 0170).

capsularis without first entering the endocranial cavity. There was probably no fenestra rotunda, for a membranous covering in this region seems to be precluded by the proximity of the cranial nerves to the perilymphatic duct within the triangular depression, and the fact that in the other two specimens the perilymphatic duct emerged from the endocranium in concert with the nerves. No information regarding the endolymphatic duct is to be had from the damaged otic "bullae" of *Lophorhothon* or *Bactrosaurus*. A tiny opening, probably for the endolymphatic duct, leads dorso-medially from the otic capsule into the endocranial cavity in the paratype of *Edmontosaurus regalis* Lambe. Similarly placed but much larger openings are sometimes reflected in endocranial casts of hadrosaurs, and these have generally been interpreted as casts of the acoustic foramina. The large diameters are, however, almost certainly artificially produced by careless preparation. No sulci that might have lodged the endolymphatic duct endocranially are visible in any skull available to me.

The distribution of the acoustic nerve is difficult to ascertain from material at hand. If the paratype of *Edmontosaurus regalis* Lambe is representative of hadrosaurs generally, the small endolymphatic foramen and a larger opening below that leads into the lagenar recess provide the only direct routes between braincase and otic chamber. However, the corresponding lower passage apparently does not enter the otic chamber at all in *Bactrosaurus*, but passes directly through the neurocranium at right angles to the longitudinal axis of the head. This indicates that some other structure—probably another nerve—was involved here. The *Lophorhothon* cranium, and presumably other hadrosaur skulls as well, have a large elliptical chamber within the proötic bone just in front of the otic capsule. The large trunk of the facial nerve passed through this chamber, which communicates directly between the cerebral space and the outer wall of the neurocranium; but postero-dorsally a short tubular passage branches from this chamber and enters the anterior utricular recess. This passage must have transmitted at least the anterior branch of the acoustic nerve; I believe it carried the entire nerve, which probably ramified within the cavum capsularis.

Nothing resembling an otolith was encountered during preparation of the osseous labyrinth of *Lophorhothon*.

Certain deductions regarding the architecture of the hadrosaurian inner ear can be drawn from the foregoing. The labyrinth was dorso-ventrally attenuated. The semicircular canals described fairly regular loops, and although not unusually elongate the vertical canals were elevated. The posterior canal was longer than the anterior. Ampullae were small, the anterior and the horizontal widely separated. The tubular utriculus comprised a system of ⅄-shaped sinuses of which the anterior was most capacious, the posterior most elongate, and the superior most regularly formed. The crus communis was of moderate length and fairly thick. The vertical semicircular canals branched from it dorsally in broadly V-shaped fashion. There was no apex. The sacculus was small and lacked a dorsally expanded vesicle. The lagena was appendicular, elongate, and incipiently twisted distally. There were no otoliths. A large perilymphatic duct either entered the endocranial cavity and then, sharply reflected, passed outward through the exoccipital bone in concert with cranial nerves X and XI, or emerged independently via its own foramen without first entering the medullary space. In the apparent absence of a fenestra rotunda the duct probably terminated extracranially within soft tissues of the temporal region. A tiny endolymphatic duct passed directly from the otic capsule into the thick dura mater that seems to have been a general dinosaurian characteristic. The acoustic nerve left the endocranial chamber together with the large trunk of the facial nerve, turned back sharply within the proötic bone to enter the vestibule from in front, and ramified within the cavum capsularis.

The hadrosaurian inner ear thus appears to have been a typically sauropsid structure with some specialized features. Comparisons with Retzius' (1884) classic descriptions and figures reveal a general agreement with lacertilian conditions, but the lagena of the dinosaur was more highly developed than in any lizard, the semicircular canals less so than in most. Relative size of the canals is the reverse of conditions in the phytosaur *Machaeroprosopus* (Camp, 1930), where the external canal is largest and the anterior canal most slender of the three. The balloon-shaped expansion of the sacculus, so striking a feature of certain lizards and snakes, was totally lacking in the hadrosaur inner ear. Correlated with this is the absence of a saccular otolith. A posterior semicircular canal of greater length than the anterior one must be unique among reptiles. The lagena was more like that of a crocodile than that of other living or fossil sauropsids yet was neither as elongate nor as slender as in *Alligator*. It was even better differentiated (so far as can be deduced from the bony labyrinths) than in many therapsids (Olson, 1944). The perilymphatic duct, perhaps constructed as in *Lacerta*, was large and seems to have followed a somewhat tortuous path from the cavum capsularis. Distribution and ramification of the acoustic nerve may have paralleled conditions in several different groups of reptiles.

Useful interpretations of dinosaur otic casts are available for two ornithischians, *Protoceratops* (Brown and Schlaikjer, 1940) and *Anchiceratops* (Brown, 1914), and a saurischian, the great sauropod *Brachiosaurus* (Janensch, 1935). There is a strong basic resemblance between all of these which seem to differ less from each other than do some lizards, for example, *Iguana tuberculata* and *Phrynosoma cornutum*. Absence of a balloon-like sacculus and presence of an elongate lagena (not usually noted in descriptions) appear to be common dinosaurian features. As in living reptiles the greatest variation seems to involve the semicircular canals. These are much elevated and elongated in *Brachiosaurus*, which also has an extremely long and slender crus communis, and are shortest in *Pachycephalosaurus* (Brown and Schlaikjer, 1943), where this part of the labyrinth appears almost chelonoid and the anterior canal is "hardly recognizable." The canals of *Protoceratops* are intermediate in length between *Anchiceratops* and the hadrosaurs, but in all the ornithischians they are much shorter than in *Brachiosaurus*.

The hadrosaurs alone have the posterior canal longer than the anterior, and the horizontal canal seems disproportionately short in this family.

Some Cranial Foramina

While the foregoing notes on the hadrosaurian inner ear were being prepared, two openings were noted in the otico-occipital segment of the cranium. These, I believe, have been generally misinterpreted in hadrosaurs.

Fenestra ovalis.—The shape of this opening varies greatly in different hadrosaurs owing apparently to differential rates of ossification of the cartilage in the metotic fissure below it. Even in skulls where all otico-occipital sutures are closed the fenestra proper is not always completely bounded by bone. This had led most writers to conclude that the opening was much larger than it actually was. Exoccipitals and proötics have not established bony contact below the fenestra in the *Lophorhothon* skull, where much of the cavum capsularis and especially the lagenar recess is thus exposed to lateral view. The small tongue of opisthotic, the lagenar crest, partly bounds the persistent metotic fissure dorsally, thus separating it from the fenestra ovalis. The crest is visible in many hadrosaur skulls where it is ossified at an early age, but it lies deep within the depression on the otico-occipital wall that surrounds the fenestra and is not always exposed by shallow preparation. Continued ossification at the anterior end of the crest probably ultimately forms an entire bony lower edge of the fenestra. I have not seen a hadrosaur where ossification has progressed upward beyond the lagenar crest.

Glossopharyngeal foramen.—Below the fenestra ovalis and usually very close to it a small round foramen issues from the braincase. It may pass from the endocranial cavity through the lagenar recess (paratype of *Edmontosaurus regalis*) or through a distinct bony tunnel below the lagena (*Bactrosaurus*). It often appears confluent with the fenestra ovalis in lateral aspect and has usually been designated as part of the fenestra. The perilymphatic duct might have occupied a passage of this sort, but, as already noted, a more likely passage is available for this duct. The very direct route from the brain seen in *Bactrosaurus* suggests that the tunnel transmitted a cranial nerve. I believe this was probably the ninth, which in hadrosaurs is conventionally shown emerging in concert with cranial nerves X and XI.

When their boundaries became completely ossified, foramina carrying the ninth through the twelfth cranial nerves, the perilymphatic duct, and the jugular vein were all contained in the exoccipital bone. There was, as explained above, probably no fenestra rotunda, and the common exit for cranial nerves X and XI and the perilymphatic duct is not a "jugular" foramen in the usual sense. The opening that has usually been labeled "fenestra ovalis" is compound, and contains not only the fenestra but the glossopharyngeal foramen below and often part of the lagenar recess exposed through incomplete ossification of its lateral wall.

SUMMARY AND CONCLUSIONS

1. Poorly preserved remains of three dinosaurs have recently been recovered from marine Upper Cretaceous, presumably early Campanian, rocks southeast of Marion Junction, Dallas County, Alabama. The collection contains a partial skeleton of a new genus and species of hadrosaur, *Lophorhothon atopus,* an ilium of a nodosaurid, and a proximal pedal phalanx of a small carnosaur. The hadrosaur skeleton had evidently floated a mile or so seaward as a partly dried cadaver before it sank in relatively quiet water, where it was buried in partial articulation by sediments of the Mooreville Chalk member of the Selma formation. The nodosaurid and carnosaur bones presumably fell away from similarly floating carcasses.

2. These dinosaurs are among the oldest Upper Cretaceous dinosaurs from North America. They can be compared satisfactorily only with various forms from western North America.

3. The type specimen of *Lophorhothon atopus* was a very young individual whose cranial sutures were not completely closed, whose fronto-nasal fontanel was large, and whose replacement bones were not completely formed. The living animal was perhaps fifteen feet long, but adult individuals were probably among the largest of hadrosaurs. The hadrosaurine affinities of *Lophorhothon* are revealed by the hoodless cranium, the slender non-expanded ischium, and the angle between root and crown in dentary teeth. General skull shape and presence of a nasal crest suggest relationships to *Kritosaurus* and *Prosaurolophus* but similarities to *Kritosaurus* are more extensive and more basic in the skeleton as a whole. Geologically *Lophorhothon* was antecedent to both, but phylogenetically it was more closely (though not ancestrally) allied to *Kritosaurus,* which, however, possessed a more primitive nasal crest.

4. Ribs in the tail of the type of *Lophorhothon atopus* are not fused with their vertebrae, showing that the caudal transverse processes of authors are true caudal ribs in hadrosaurs.

5. The type specimen of *Lophorhothon atopus* was so preserved that some details of cranial anatomy hitherto unobserved in hadrosaurs are clearly shown. Examination of other material in light of these observations makes possible certain conclusions that are probably applicable to hadrosaurs generally:

(*a*) A large supraoccipital bone of normal sauropsid structure and relationships was present in hadrosaurs, but the bone was excluded crocodile-like from the dorsal margin of the foramen magnum by medially directed processes of the exoccipital bones.

(*b*) The paroccipital process in hadrosaurs is composed mainly of exoccipital with only a minor opisthotic contribution anteriorly.

(*c*) A tiny post-temporal foramen persists in most hadrosaurs, but owing to post-mortem effects it is rarely seen.

(*d*) Architecture of the occipital face of the hadrosaur cranium is easily derived from a primitive camptosaur pattern, most changes being related to strengthening of the phylogenetically attenuating paroccipital processes of hadrosaurs, and changes in the position of the head relative to the neck.

(*e*) The hadrosaurian inner ear had a vertically elongated labyrinth with large utriculus and small sacculus, moderately developed common crus, and appendicular incipiently twisted lagena of unusually large size. Semicircular canals were of unusual proportions: the posterior canal was somewhat longer than the anterior, the anterior of greatest, the horizontal of least diameter; ampullae were small, the anterior and the horizontal widely separated. A large perilymphatic duct emerged from the skull in concert with the vagus and accessory nerves, or via its own canal directly from the otic chamber. There was no fenestra rotundum. The endolymphatic duct was of small diameter. It passed directly into the thick dura mater within the cranium. The undivided acoustic nerve entered the otic chamber from in front and ramified within the labyrinth.

(*f*) The hadrosaurian inner ear resembled that of other dinosaurs, differing mainly in the construction of the semicircular canals, unusually long in the sauropod *Brachiosaurus*, unusually short in the ornithischian *Pachycephalosaurus*. The organ was fairly comparable to the inner ear of such a lizard as *Lacerta*, but it had a more highly developed lagena and like other dinosaurs lacked a dorsal enlargement of the sacculus.

(*g*) The fenestra ovalis has generally been misinterpreted in hadrosaurs, where it is usually depicted as a much larger opening than it actually was. Its lower margin is slow to ossify.

(*h*) The vagus and accessory nerves are contained in the exoccipital bone, but contrary to usual interpretations the glossopharyngeal nerve did not emerge with them through the "jugular" foramen, but passed independently below the fenestra ovalis through or just below the lagenar recess.

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Except as otherwise noted the drawings are the work of Mr. Pat Haldorsen.

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ABBREVIATIONS

ant. canal, anterior semicircular canal

Bo., basioccipital

Bs., basisphenoid

Exoc., exoccipital

Fm., foramen magnum

Fo., fenestra ovalis

Font., naso-frontal fontanel

Fpt., post-temporal foramen

Fr., frontal

Mf., metotic fissure

M. rec. cap. post., presumed surface for insertion of M. rectus capitis posterior

Na., nasal

Opo., opisthotic

Pa., parietal

Pd., presumed passage for perilymphatic duct

Pf., prefrontal

Po., postorbital

Pop., paroccipital process

post. canal, posterior semicircular canal

Pr., proötic

rec. crus communis, recess for common crus

Soc., supraoccipital

Sq., squamosal

utric., utricular recess

v. capitis dorsalis, presumed passage for dorsal head vein

Ves., vestibule

vj., presumed passage for internal jugular vein

V–XII, cranial nerve foramina, and reconstructed nerves

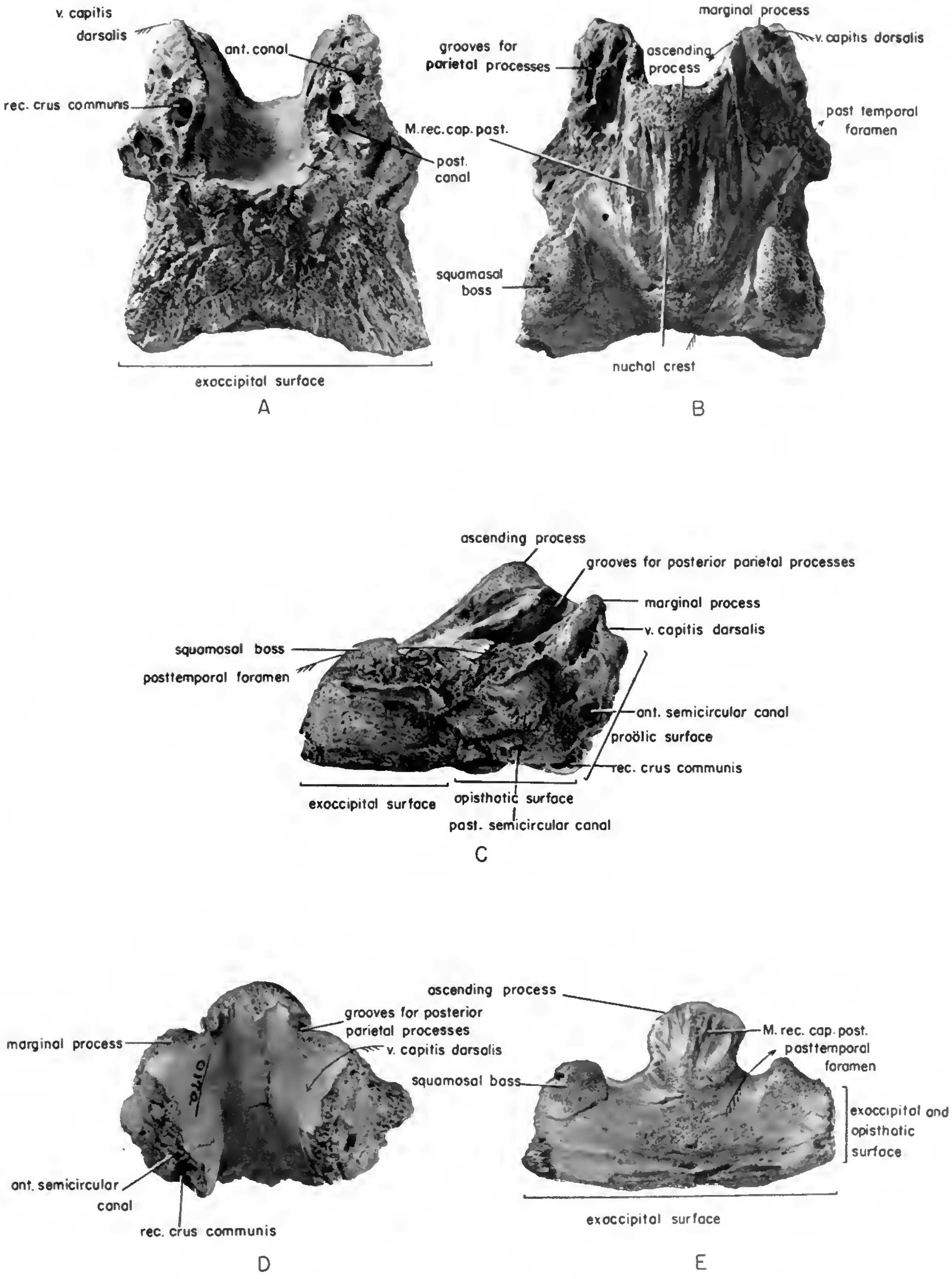
AMNH, American Museum of Natural History

NMC, National Museum of Canada. In older literature the same numbers were prefixed by GSC (Geological Survey of Canada)

CNHM, Chicago Natural History Museum

EXPLANATION OF PLATE 34

Supraoccipital bone of an unidentified, probably hadrosaurine hadrosaur (NMC 0170). About natural size. A, seen from below, with the broad roughened surface for the exoccipital vertical; B, from above, with the nuchal crest vertical; C, from the right side, with the exoccipital surface horizontal; D, from within, with the ascending process nearly vertical; E, from behind, with the exoccipital surface horizontal.


v. capitis dorsalis
ant. canal
rec. crus communis
M. rec. cap. post.
post. canal
exoccipital surface
A
grooves for parietal processes
marginal process
ascending process
v. capitis dorsalis
post temporal foramen
squamosal boss
nuchal crest
B
ascending process
grooves for posterior parietal processes
marginal process
v. capitis dorsalis
squamosal boss
posttemporal foramen
ant. semicircular canal
proötic surface
rec. crus communis
exoccipital surface
opisthotic surface
post. semicircular canal
C
marginal process
grooves for posterior parietal processes
v. capitis dorsalis
ant. semicircular canal
rec. crus communis
D
ascending process
M. rec. cap. post.
posttemporal foramen
squamosal boss
exoccipital and opisthotic surface
exoccipital surface
E