

# CRANIAL MORPHOLOGY OF THE HADROSAURIAN DINOSAURS OF NORTH AMERICA

JOHN H. OSTROM

BULLETIN  
OF THE  
AMERICAN MUSEUM OF NATURAL HISTORY  
VOLUME 122 : ARTICLE 2    NEW YORK : 1961

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OF NORTH AMERICA

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SUBMITTED IN PARTIAL FULFILLMENT OF THE  
REQUIREMENTS FOR THE DEGREE OF  
DOCTOR OF PHILOSOPHY IN THE  
FACULTY OF PURE SCIENCE  
COLUMBIA UNIVERSITY

BULLETIN  
OF THE  
AMERICAN MUSEUM OF NATURAL HISTORY  
VOLUME 122 : ARTICLE 2  
NEW YORK : 1961

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 122, article 2, pages 33-186, text figures 1-78, plates 1-6

*Issued June 19, 1961*

*Price: \$2.50 a copy*

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## INTRODUCTION

THE PRESENT PAPER IS the product of an extensive investigation of the existing crania of North American hadrosaurian dinosaurs. Originally undertaken with the hope of discovering something about hadrosaurian mandibular musculature and the mechanical operation of the dental batteries, this study quickly expanded into a more comprehensive consideration of the total morphology and functional anatomy of the hadrosaurian head. The family Hadrosauridae forms an ideal group for a study of this kind, because of the wealth of finely preserved material and the diverse cranial features exhibited, including the sometimes grotesque supracranial crests which still stimulate and perplex the imagination. The unique and highly specialized dental apparatus of the hadrosaurs was a structure of considerable adaptive significance which undoubtedly had a profound influence upon gross cranial morphology as well as upon the living habits of these animals.

The earliest recorded reference to North American hadrosaurian remains is that of Joseph Leidy (1856) which describes some fragmentary material collected by F. V. Hayden in 1854-1856 from the Judith River valley of northern Montana and the "Great Lignite" (Hell Creek) formation of South Dakota. From this material, Leidy named the two earliest members of this now well-documented dinosaurian family: *Trachodon mirabilis*, based on several isolated teeth, and *Thespesius occidentalis*, based on two incomplete caudal vertebrae. In the century that has passed since these first discoveries, several hundred hadrosaurian finds have been recorded, including many notable discoveries of complete and unusually well-preserved specimens, such as the famous "mummy" specimens of *Anatosaurus annectens* (A.M.N.H. No. 5060 and S.M. No. R4036) collected by C. H. Sternberg and C. M. Sternberg in 1908 and 1910. Numerous persons have contributed to the large hadrosaurian collections that now are to be found in the museums of North America, to the extent that the hadrosaurs are probably better represented in these collections than

are any of the other dinosaurian families. The long list of references covering the North American hadrosaurian material is further testimony of the great interest which has been generated over the last century by these large and often bizarre creatures of the Cretaceous period. Outstanding among these many works is the monograph by Lull and Wright published in 1942.

The present investigation has been facilitated and encouraged by many individuals. My particular thanks go to Dr. Edwin H. Colbert, of the American Museum of Natural History and Columbia University, for his unlimited patience, unflinching encouragement, and invaluable advice. His sponsorship of this project and his efforts, both in reviewing and criticizing the manuscript and in making available the extensive hadrosaurian collections of the American Museum, are deeply appreciated. I am also indebted to Dr. Bobb Schaeffer, of the American Museum of Natural History and Columbia University, for his advice and continued encouragement and his critical review of the manuscript, and to Mrs. Rachel Nichols, of the American Museum of Natural History, who provided so much assistance in the location of both fossil specimens and innumerable literary references in the American Museum collections. I am equally grateful to Dr. John Imbrie, of Columbia University, and Dr. Joseph Gregory, formerly of Yale University, now of the University of California, who reviewed the complete manuscript and offered many helpful suggestions. To Dr. Georg Haas, of Hebrew University, Israel, I owe a debt of gratitude for his many suggestions and stimulating hours of discussion.

My thanks also go to Mr. Charles M. Bogert and Dr. Richard G. Zweifel, of the Department of Herpetology of the American Museum of Natural History, who graciously provided me with cranial material of numerous recent reptiles and specimens of *Ctenosaura*, *Varanus*, *Amblyrhynchus*, *Alligator*, and *Sphenodon* for cranial dissections. Dr. Loris S. Russell and Dr. Wann Langston, Jr., of the National Museum of Canada, made available the very fine hadrosaurian collec-

tions of that institution. Mr. C. M. Sternberg unselfishly contributed much of his time to the location of specimens and to relating his personal knowledge about this collection. The remarkable collections of the Royal Ontario Museum were placed at my disposal by Mr. Levi Sternberg and Dr. Gordon Edmund. Dr. Joseph Gregory arranged for the author's examination of the hadrosaurian material in the Yale Peabody Museum of Natural History. Dr. C. Lewis Gazin and Dr. David H. Dunkle, of the United States National Museum, most kindly made it possible for the author to examine the hadrosaurian material in the national collections, and Dr. Rainer Zangerl, of the Chicago Natural History Museum, arranged for the loan of the cranial material of the Fruitland specimen of *Parasaurolophus cyrtocristatus* from New Mexico and further facilitated my investigations of other hadrosaurian specimens in the collections under his care.

Grants from the James F. Kemp Fund of Columbia University and the E. I. DuPont Fund of Beloit College supported various phases of this investigation.

Figures 7 to 10 and 17 were drawn by E. S. Christman in 1917 and kindly provided by Dr. Colbert for inclusion in this paper. Figures 23 and 24 were drawn by Mr. Michael Insinna of the American Museum staff for a previous paper by Dr. Colbert and the present author. Figure 73 is reproduced with the permission of the United States National Museum. All other figures were prepared by the author.

The catalogued collections of several institutions are referred to throughout this report. In such references, the institutional names are abbreviated as follows:

- A.M.N.H., the American Museum of Natural History
- A.N.S.P., Academy of Natural Sciences of Philadelphia
- C.N.H.M., Chicago Natural History Museum
- N.M.C., National Museum of Canada, Ottawa
- R.O.M., Royal Ontario Museum, Toronto
- S.M., Senckenberg Museum, Frankfurt, Germany
- U.S.N.M., United States National Museum
- Y.P.M., Peabody Museum of Natural History, Yale University

## GEOLOGIC AND GEOGRAPHIC DISTRIBUTION

THE PRINCIPAL HADROSAUR-BEARING strata of North America belong to the Montana and Lance groups of late Cretaceous age. Among the more important of these are the Belly River, Two Medicine, Judith River, Edmonton, Hell Creek, and Lance formations of Wyoming, Montana, and Alberta, with the Belly River being several times as productive as any other single unit. Many other local formations in various parts of the continent have produced other hadrosaurian specimens, but each of these units may be partially or completely correlated with the classical hadrosaur-bearing formations, the Belly River, the Edmonton, and the Lance formations. (See fig. 3.)

The distribution of hadrosaurian species within the Belly River-Edmonton-Lance sequence is illustrated in figure 1. From this it would appear that the Belly River interval, which included at least 18 hadrosaurian species as compared with eight from the Edmonton and only five from the Lance, marked the peak of hadrosaurian diversification. Furthermore, it appears that this peak is actually the reflection of the obvi-

RELATIVE DIVERSITY

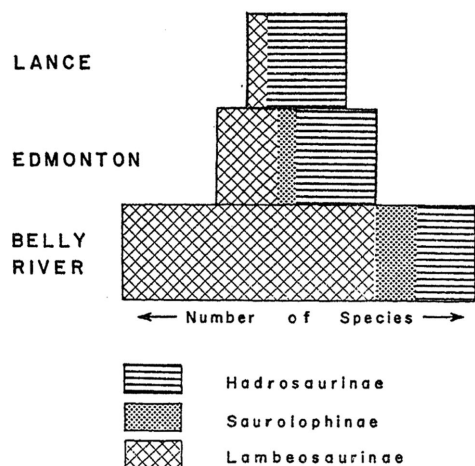


FIG. 1. Hadrosaurian diversity. The total width of each horizontal bar is proportional to the number of valid species known for that interval (Belly River, 18 species; Edmonton, eight species; Lance, five species). The relative importance of members of the three subfamilies is indicated by the width of the appropriate pattern.

RELATIVE ABUNDANCE

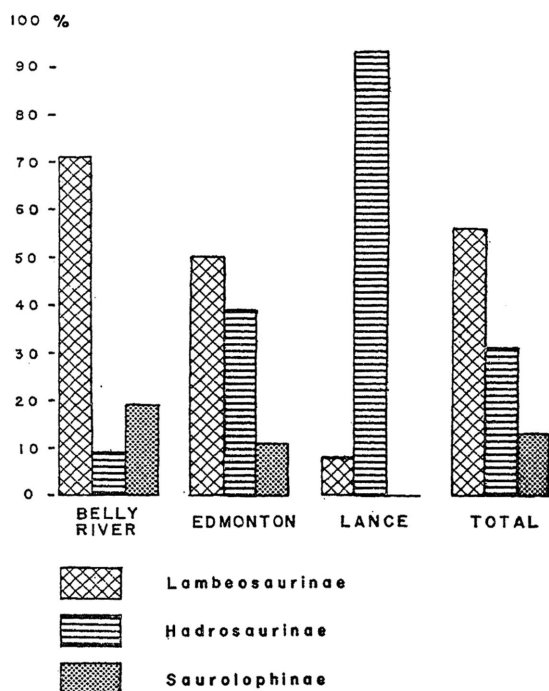


FIG. 2. Relative abundance of the Hadrosauridae. The histograms indicate the percentage of contemporaneous individual specimens, which have been assigned to the species of each of the three hadrosaurian subfamilies, for each of the three intervals of hadrosaurian history. The fourth histogram, showing the same data for the entire Belly River-Lance interval, is based on the total sample (77 specimens).

ously successful adaptive radiation of the hadrosaurian subfamily Lambeosaurinae. In terms of numbers of species, the lambeosaurs completely account for the hadrosaurian decline from Belly River to Lance times, for the number of non-lambeosaurian species remained almost constant throughout this period. Fifty-eight per cent of the hadrosaurian species are of Belly River age, 26 per cent of Edmonton age, and only 16 per cent of Lance age.

The relative abundance of the three principal hadrosaurian subfamilies, as illustrated by the graphs in figure 2, show similar trends

		ALBERTA		MONTANA		DAKOTAS		WYOMING		COLORADO	
UPPER	CRETACEOUS		Hell Creek	Lance	Hell Creek	Lance	Lance		Denver		
								Arapahoe			
								Laramie			
		Edmonton	Lennep		Fox Hills		Lewis	Fox Hills			
		Bearpaw	Bearpaw		Pierre	Mesaverde		Pierre			
		Belly River	Two Medicine	Judith River		Steele					
				Claggett							
				Eagle							
		Upper Benton	Niobrara		Niobrara		Niobrara	Niobrara			
		Cardium	Carlile		Carlile		Carlile	Carlile			
Lower Benton	Frontier		Greenhorn		Frontier	Greenhorn					
Graneros			Graneros								
Upper Kootenai	Mowry		Dakota		Mowry	Dakota					

FIG. 3. (This page and opposite page.) Upper Cretaceous correlation chart of selected regions. Only those regions that have produced a significant number of hadrosaurian specimens are included. The italicized names indicate rock units that are hadrosaur bearing.

for the chronologic distribution of the hadrosaurs. The frequencies given here are derived from the 77 specimens listed in a following section of this paper, and, while admittedly incomplete, they must constitute a fairly representative sample of the known hadrosaurian remains of North America, as they include most of the specifically identified hadrosaurs. Once again it is clear that the majority of the identified hadrosaurian remains belong to the Lambeosaurinae (55 per cent). Thirty per cent of the hadrosaurs have been identified as members of the Hadrosaurinae and the remaining 15 per cent as belonging to the Saurolophinae. Also, it appears, from this relatively small sample, that lambeosaurian species were more than seven times as abundant as those of the Hadrosaurinae and almost three times as abundant as saurolophine species during the Belly River interval. During Edmonton time, the Lambeosaurinae were only slightly more common than the Hadrosaurinae, but they were more than four times

as abundant as the Saurolophinae. And during the Lance interval, the hadrosaurian fauna apparently consisted entirely of species belonging to the Hadrosaurinae, with the single possible exception of one crested species, *Parasaurolophus tubicen* from the Ojo Alamo formation of New Mexico.

In reviewing these figures of hadrosaurian diversification and relative abundance, one must keep in mind that these are based on fragmentary evidence at best. The sample in question (the 77 specimens listed on p. 51) is statistically inadequate, so that the composition of the original biota cannot be determined.

If the faunal record is incomplete, the zoogeographic record must be even less complete. To date, hadrosaurian remains are known only from the North American and Eurasian continents. In North America, where hadrosaurian remains appear to be most common, these reptiles seem to have been restricted to two general areas (see figs. 4, 5, and 6), the re-



NEW MEXICO	TEXAS	KANSAS	ALABAMA MISSISSIPPI	NORTH CAROLINA	NEW JERSEY
<i>Ojo Alamo</i>					
McDermott					
<i>Kirtland</i>	Tornillo				
<i>Fruitland</i>				Pedee	<i>Monmouth</i>
Pictured Cliffs					
Lewis					
Mesaverde	<i>Aguja</i>	Pierre	<i>Selma chalk</i>	<i>Black Creek</i>	<i>Mafawan</i>
	Terlingua				
	Boquillas	<i>Niobrara</i>	Eutaw		Magothy
Mancos	Eagle Ford	Benton		Middendorf	
			Tuscaloosa		
Dakota		Dakota			Raritan

FIG. 3. (See legend on opposite page.)

gion currently described as the Atlantic and Gulf coastal plains of the east and the great plains belt along the eastern flank of the Rocky Mountains (some remains are also recorded from California) in the west. The western region, from New Mexico northward to Alberta and Saskatchewan, has produced most of the North American hadrosaurian material. Comparatively little material has been recovered from the eastern areas.

Paleogeographic evidence, as well as faunal differences between these two regions, suggests that these areas were separated by a broad inland sea (Niobrara and Pierre seas) which extended from Mexico through eastern New Mexico and western Texas northward across most of Saskatchewan, throughout most of the late Cretaceous interval. By Lance time, this sea had diminished considerably, but it apparently still extended as a narrow arm of the ocean, reaching as far north as the present latitude of the international border between North Dakota and Saskatchewan. Very possibly this late Cre-

taceous sea constituted an effective barrier to hadrosaurian migrations, at least until Lance time. Although the hadrosaurs were semi-aquatic in their adaptations, the absence of hadrosaurian remains in late Cretaceous marine sediments (with the notable exception of *Clasaurus agilis* from the Niobrara chalk of Kansas) seems to support such an interpretation. The existence of an inland sea, which reached its maximum extent during Coloradoan (Niobrara) and Montanan (Pierre) times, therefore suggests that hadrosaurian dispersals must have taken place earlier, by mid-Cretaceous (early Gulfian) time at least.

In spite of a number of discoveries, particularly in New Jersey, North Carolina, Alabama, and Mississippi, very little hadrosaurian cranial material has been recovered from the late Cretaceous of the eastern region. Most of the eastern hadrosaurian remains consist of isolated vertebrae and other fragmentary, post-cranial skeletal material, nearly all of which have been assigned to the

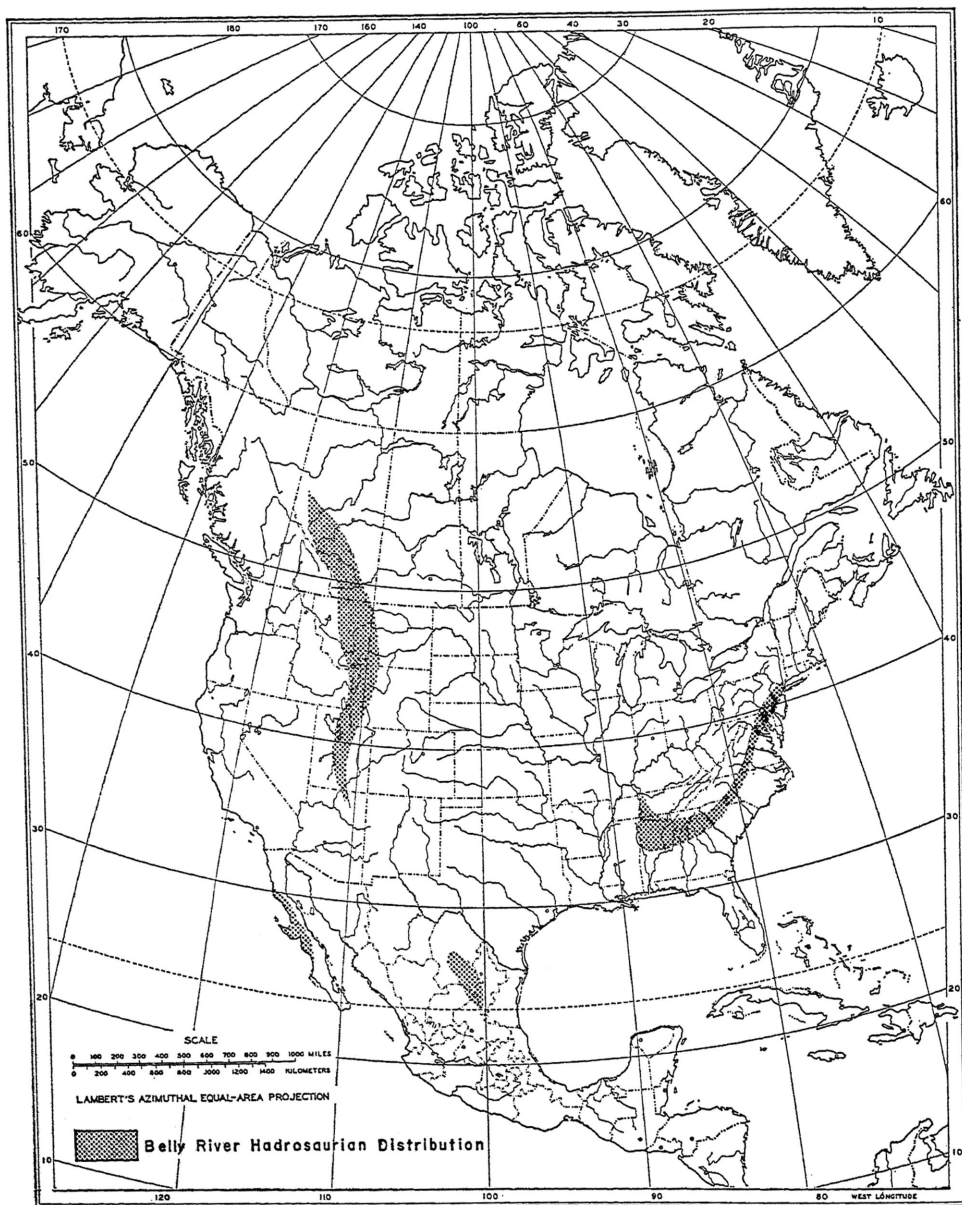


FIG. 4. Hadrosaurian distribution in North America during Belly River time. The pattern indicates the approximate areas where hadrosaurian remains have been found in the Belly River group and equivalent rock units. (Goode Base Map Series, published by the University of Chicago Press; copyright by the University of Chicago.)

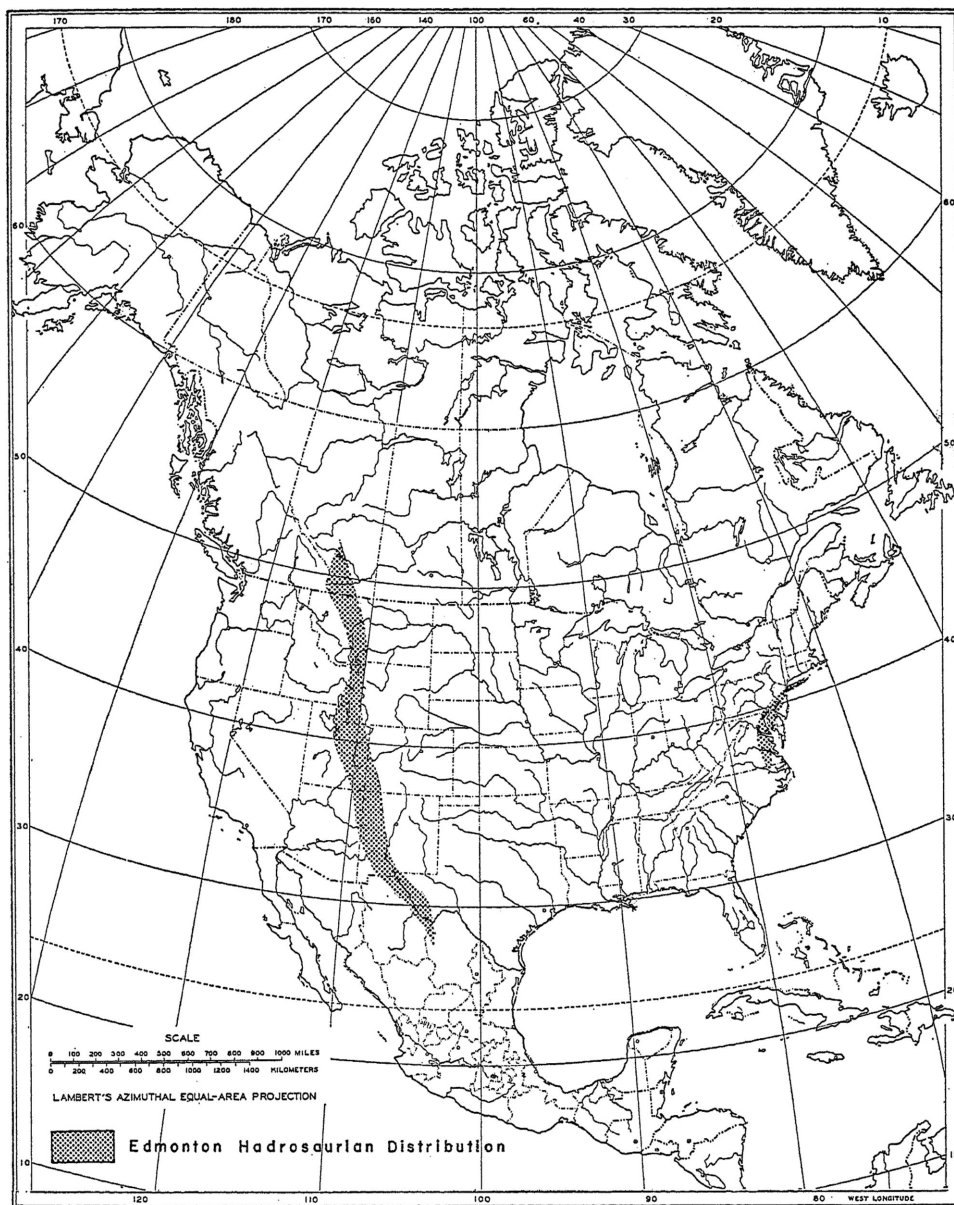


FIG. 5. Hadrosaurian distribution in North America during Edmonton time. The pattern indicates the approximate areas where hadrosaurian remains have been found in the Edmonton formation and equivalent rock units. (Goode Base Map Series, published by the University of Chicago Press; copyright by the University of Chicago.)

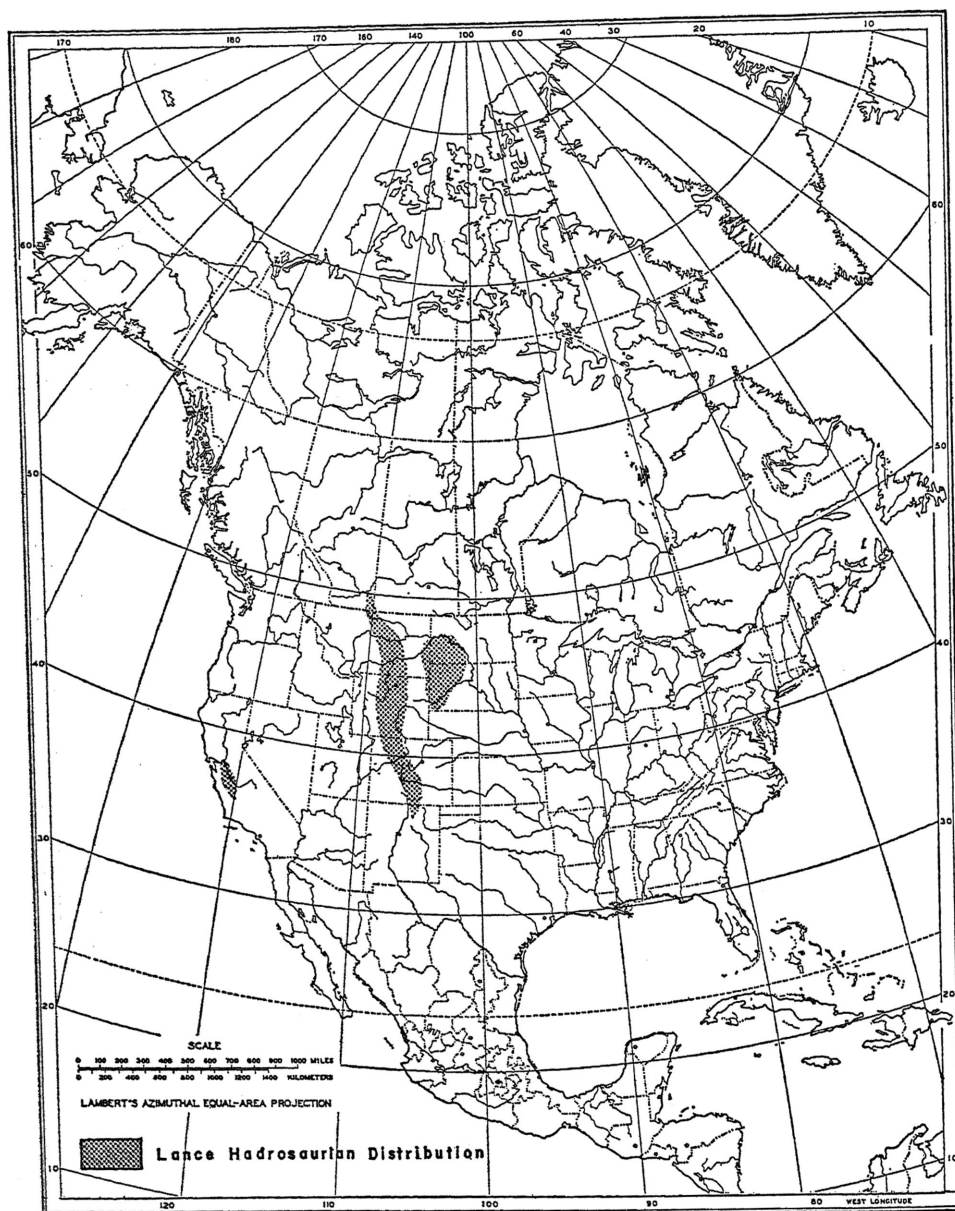


FIG. 6. Hadrosaurian distribution in North America during Lance time. The pattern indicates the approximate areas where hadrosaurian remains have been found in the Lance formation and equivalent rock units. (Goode Base Map Series, published by the University of Chicago Press; copyright by the University of Chicago.)

genus *Hadrosaurus* which at present cannot be identified as either flat-headed or crested. No proved lambeosaurian or saurolophine species have as yet been discovered in the Atlantic and Gulf coastal regions, and so far none of the eastern hadrosaurian species has been recognized with certainty in the western region. While such a statement may be questioned by some individuals, it appears that the hadrosaurian faunas of eastern and western North America developed independently and remained quite distinct following a mid-Cretaceous dispersal. Verification of this hy-

pothesis, however, must await the discovery of additional hadrosaurian material from the eastern Cretaceous deposits.

Lull and Wright (1942, p. 49) suggested that the western flat-headed species represented a wave of migration from the east at a time when the late Cretaceous sea was restricted (Lance time). This of course is a distinct possibility, but it does not seem to be supported by any evidence. Flat-headed species have been recovered from numerous western localities from strata ranging from Belly River to Lance in age.

## TAXONOMY

IN 1869, COPE proposed the name Hadrosauridae for the reception of various bipedal, herbivorous ornithopods of the North American Cretaceous, basing this group on Leidy's (1858) *Hadrosaurus foulkii* from the Woodbury clay of New Jersey. Lydekker (1888) and Marsh (1890) used the term Trachodontidae, based on Leidy's (1856) earlier species *Trachodon mirabilis* and for a number of years both terms were used to designate these late Cretaceous ornithopods. *Trachodon mirabilis*, however, was based on a few teeth and tooth fragments from the Judith River formation of Montana, and as yet no other hadrosaurian material has been found which is assignable to this species. Therefore, in 1918 Lambe, emphasizing the inadequacy of the type material of *T. mirabilis*, urged that this genus was not definable and that the prior term Hadrosauridae be adopted as the family name.

A cursory review of the many genera and species assigned to this family at the present time quickly demonstrates the wide range of cranial adaptations and the relative conservatism of post-cranial anatomy. Indeed, with the exception of some minor postcranial features, the principal diagnostic characters are concentrated in the hadrosaurian skull. As a result, the several classifications that have been proposed have been based almost entirely on cranial characters. Brown (1914b) established two hadrosaurian subfamilies, the Trachodontinae, to include the flat-headed forms, and the Saurolophinae, for the reception of the crested genera. Lambe (1918), objecting to the use of the term Trachodontinae (also Trachodontidae), because of the inadequacy of the type material, proposed that the term Hadrosaurinae be substituted for Brown's subfamily name. Later Lambe (1920) proposed a threefold division of the family, again based on cranial characteristics. Lambe's subfamilies were the Hadrosaurinae (flat-headed species), the Saurolophinae (species bearing incipient crests), and the Stephanosaurinae (crested species). With the subsequent invalidation of *Stephanosaurus marginatus*, the genotype of Lambe's new subfamily, Parks (1923) sug-

gested the name *Lambeosaurus lambei* for Lambe's new crested hadrosaur and proposed the appropriate change of the subfamily name to Lambeosaurinae. In 1942, Lull and Wright removed *Procheneosaurus* and *Cheneosaurus* from the Lambeosaurinae and erected a new subfamily, Cheneosaurinae, for the reception of these genera. Charles M. Sternberg (1953, 1954) has been a consistent opponent of the continued splitting of the Hadrosauridae, persistently arguing that there is little difference between *Procheneosaurus* and *Cheneosaurus* and the other members of the Lambeosaurinae. Similarly, Sternberg is of the opinion that *Prosaurolophus* and *Saurolophus* are closely related to the members of the Hadrosaurinae and should not be placed in a separate subfamily. On this basis, he has argued that a fourfold division of the family is unwarranted and that the Saurolophinae and Cheneosaurinae should be reincorporated into the Hadrosaurinae and Lambeosaurinae, respectively.

Sternberg's proposed twofold division appears to be a sound classification based on the principal distinctions among the genera concerned: the presence or absence of a cranial crest. However, the consideration of the type genus of the family immediately presents a major problem, which Lambe was aware of but failed to reconcile. The cotypes of *Hadrosaurus foulkii* (A.N.S.P. Nos. 9201, 9202, 9203, and 10005), which constitute the genotype of the family (and obviously also of the subfamily Hadrosaurinae), consist of 28 vertebrae, the larger forelimb and hind limb bones, parts of the pelvis, parts of the pes, nine isolated teeth, a portion of one mandible, and two small fragments of the maxilla. This material is quite sufficient to identify the remains as belonging to this family, but it is certainly an inadequate basis for the family definition. Furthermore, as the hadrosaurian subfamilies are now defined, it is quite impossible to place *Hadrosaurus* in any of these categories, for, with the exception of the maxillary fragments, no cranial material is known that is assignable to this genus.

Lambe (1918) and others have noted the questionable position and validity of this

genus, but most students have assumed that *Hadrosaurus* was non-crested. Such an assumption has been based largely on the tapering form of the incomplete distal end of the ischium. Numerous workers have attested to the reliability of the "footed" or distally expanded ischium as a diagnostic feature of the crested hadrosaurs, while non-crested forms are characterized by a "non-footed," tapering ischium. The fact that the distal extremity of the type ischium is missing, and that the cranium is unknown, makes the position of *Hadrosaurus* an unknown quantity. Any assumption as to the condition of these diagnostic characters in *Hadrosaurus* is of extremely significant taxonomic import, because both the family and the subfamily rest on this genus. The Hadrosaurinae, as currently defined, include the non-crested hadrosaurian species, which are characterized by normal nasals and premaxillaries, straight narial passages, and a "non-footed" ischium, conditions that cannot be demonstrated in the type genus. Therefore, this genus cannot with certainty be included among other hadrosaurian genera that are so characterized.

The obvious solution to this taxonomic problem is to suppress the term Hadrosauridae and to select a new, definable genus as the type genus of the family. The indeterminate position of *Hadrosaurus* would then have no influence on the group taxonomy. This incautious suggestion, however, seems most undesirable at this late time, for the removal of a family name so firmly embedded in the literature and in current usage would only promote confusion and additional undesirable synonymy. An alternative solution, which would remove all known flat-headed genera from the Hadrosaurinae, with the reconstitution of this subfamily as a monogeneric category (to include only the type genus until such time as the diagnostic characteristics of this genus can be ascertained), seems equally undesirable, because there is no evidence at present to indicate that *Hadrosaurus* is distinct from any of the better-known genera. In effect, such a decision would create a taxonomic category for the reception of doubtful or indeterminate genera.

As undesirable as the present situation

may be, the conservative answer requires that *Hadrosaurus* be accepted as a flat-headed form. Until it can be demonstrated that it should be otherwise, *Hadrosaurus* must be included with the non-crested genera in a single subfamily in order to preserve the value of this category and to minimize hadrosaurian synonymy.

As pointed out by Charles M. Sternberg (1953, 1954), the subfamily Chenoosaurinae of Lull and Wright (1942) appears to be a superfluous category. In support of Sternberg's position, it is proposed here that the members of this subfamily be reincorporated into the Lambeosaurinae. The differences between these two subfamilies are not great. In fact, the caudal expansion of the premaxillaries and nasals forming a supracranial crest, which is penetrated by the looped narial passages, although differing in degree is characteristic of both subfamilies. In addition, the expanded extremity of the ischium is typical of all species presently assigned to both subfamilies.

Close examination of hadrosaurian crania has led the present author to conclude that a third natural group is recognizable within the Hadrosauridae. The presence in *Prosaurolophus*, *Saurolophus*, and *Brachylophosaurus* of a "pseudo-narial" crest, which is not involved with the narial passages, is a condition quite distinct from that displayed in the members of either the Hadrosaurinae or the Lambeosaurinae. These three genera appear to be intermediate between the hadrosaurs with flat heads and those bearing a "true narial" crest. For this reason, it is proposed that the subfamily Saurolophinae be retained. As reconstituted, the Hadrosauridae includes three subfamilies: the Hadrosaurinae, Saurolophinae, and Lambeosaurinae.

The position of *Claosaurus*, as noted by Lull and Wright (1942) and Charles M. Sternberg (1953, 1954), is uncertain. The absence of a skull is very unfortunate, for certain features of the nearly complete postcranial skeleton and the fragmentary dentition, together with the stratigraphic position of this genus in the Niobrara chalk (the oldest known occurrence of a hadrosaur), suggest that *Claosaurus* may represent the most primitive member of the family. Additional discoveries may very well demonstrate the

need for erecting a more primitive hadrosaurian subfamily to include this genus. Evidence now available, however, does not warrant such action at the present time. The complete hadrosaurian classification proposed here follows.

#### ORDER ORNITHISCHIA SEELEY

#### SUBORDER ORNITHOPODA MARSH

#### FAMILY HADROSAURIDAE COPE

#### SUBFAMILY HADROSAURINAE

GENERA: *Anatosaurus*, *Edmontosaurus*, *Hadrosaurus*, and *Kritosaurus* (*Gryposaurus*).

DIAGNOSIS: Skull long and generally low, non-crested. Preorbital length very long. Muzzle broad and usually depressed. Edentulous section of maxilla and dentary quite long. Extremity of dentary not greatly depressed. Nasals normal, not expanded. Premaxillaries long, but not extended behind or far above the lacrimals. Nasal passages direct, not looped. External nares large and elliptical, usually surrounded by a strongly concave depression. Frontals included in the supra-orbital rim. Orbit oval and very large, always larger than the infratemporal fenestra. Post-orbital large and enclosing a moderate to large pouch or cavity. Humerus usually longer than radius. Ischium long and straight, with distal end tapered, not expanded.

#### SUBFAMILY SAUROLOPHINAE

GENERA: *Brachylophosaurus*, *Prosaurolophus*, and *Saurolophus*.

DIAGNOSIS: Skull long, generally somewhat higher than in the Hadrosaurinae. Small to moderate-sized crest formed exclusively of the nasals. Premaxillaries normal and not involved in crest formation. Nasals moderately to greatly expanded dorsocaudally. Crest not penetrated by narial passages ("pseudo-narial" crest). Narial passages direct, not looped. Preorbital region long. Muzzle slightly depressed and very broad, bearing a narrow reflected margin. Toothless portion of maxilla and dentary very long. Orbit oval and smaller than the infratemporal fenestra. Postorbital smaller than in

the Hadrosaurinae, lacking any pouch or cavity. Frontals contributing to the supra-orbital rim, except in *Prosaurolophus*. Humerus-radius ratio variable, with humerus longer than radius in *Prosaurolophus*, but shorter in *Saurolophus* and *Brachylophosaurus*. Ischium also variable, being "non-footed" in *Prosaurolophus*, but distally expanded in *Saurolophus*. Ischium unknown in *Brachylophosaurus*.

#### SUBFAMILY LAMBEOSAURINAE

GENERA: *Cheneosaurus*, *Corythosaurus*, *Hypacrosaurus*, *Lambeosaurus* (*Stephanosaurus*), *Parasaurolophus*, and *Procheneosaurus* (*Didanodon*, *Tetragonosaurus*).

DIAGNOSIS: Skull shorter and narrower but of greater height than that of other hadrosaurs. Crest moderately to extremely developed. Crest of the "true narial" variety, penetrated by the looped narial passages. Nasals and premaxillaries moderately to greatly expanded dorsocaudally, generally overriding the roof of the skull. Nasals receded or displaced posteriorly. Premaxillaries split into upper and lower rami, the lower branch enclosing the anterior portion of the narial passage. External nares small and elongate, located anteriorly on snout. Muzzle relatively narrow, not broadly expanded as in the Hadrosaurinae. Dentary strongly deflected anteriorly. Preorbital region somewhat shorter than in other hadrosaurs. Edentulous portion of maxilla and dentary relatively short. Frontals excluded from the orbital rim. Orbit oval to circular and nearly equal in size to the infratemporal fenestra. Humerus usually shorter than radius, except in *Parasaurolophus walkeri*. Ischium expanded at its distal extremity. Prepubis large, postpubis short and slender.

#### HADROSAURIDAE INCERTAE SEDIS

GENERA: *Claosaurus*, *Ornithotarsus*, *Thespesius*, and *Trachodon*.

#### GENERA OF DOUBTFUL VALIDITY OR IDENTITY

*Cionodon*, *Claorhynchus*, *Diclonius*, *Dysganus*, *Hypsibema*, *Pneumatoarthrus*, and *Pteropelyx*.



## MORPHOLOGY

### CRANIAL MATERIAL EXAMINED

THE FOLLOWING is a list of the hadrosaurian specimens that were examined during the course of this study. Several complete or fragmentary skulls are not included here for one reason or another, but it should be apparent that a majority of the available hadrosaurian cranial material of North America has been examined. At least one skull of every firmly established hadrosaurian genus has been studied, and in many cases several skulls were available for examination. The only North American species that was not examined is *Parasaurolophus tubicen*, for the only known material of this species is in the collections of the University of Upsala, Sweden. All other North American species for which cranial material is available are represented in this list.

#### HADROSAURIDAE

##### HADROSAURINAE

- Anatosaurus annectens*, U.S.N.M. No. 2414
- Anatosaurus annectens*, Y.P.M. No. 2182
- Anatosaurus annectens*, A.M.N.H. No. 5046
- Anatosaurus annectens*, A.M.N.H. No. 5060
- Anatosaurus annectens*, U.S.N.M. No. 3814
- Anatosaurus annectens*, U.S.N.M. No. 4737
- Anatosaurus copei*, A.M.N.H. No. 5730
- Anatosaurus copei*, A.M.N.H. No. 5886
- Anatosaurus saskatchewanensis*, N.M.C. No. 8509
- Anatosaurus edmontoni*, N.M.C. No. 8399
- Anatosaurus edmontoni*, R.O.M. No. 5851
- Anatosaurus longiceps*, Y.P.M. No. 616
- Anatosaurus* sp., Y.P.M. No. 618
- Anatosaurus* (?), A.M.N.H. No. 5236
- Edmontosaurus regalis*, N.M.C. No. 2288
- Edmontosaurus regalis*, N.M.C. No. 2289
- Edmontosaurus regalis*, U.S.N.M. No. 12711
- Edmontosaurus regalis*, R.O.M. No. 5167
- Edmontosaurus regalis*, C.N.H.M. No. P15003
- Kritosaurus notabilis*, N.M.C. No. 2278
- Kritosaurus notabilis*, R.O.M. No. 5859
- Kritosaurus notabilis*, A.M.N.H. No. 5350
- Kritosaurus incurvimanus*, R.O.M. No. 4514
- Kritosaurus navajovius*, A.M.N.H. No. 5799

##### LAMBEOSAURINAE

- Lambeosaurus lambei*, N.M.C. No. 2869
- Lambeosaurus lambei*, A.M.N.H. No. 5353
- Lambeosaurus lambei*, A.M.N.H. No. 5373
- Lambeosaurus lambei*, R.O.M. No. 5131

- Lambeosaurus lambei*, R.O.M. No. 1218
- Lambeosaurus lambei*, C.N.H.M. No. 1479
- Lambeosaurus clavinitialis*, N.M.C. No. 8703
- Lambeosaurus clavinitialis*, N.M.C. No. 351
- Lambeosaurus clavinitialis*, Y.P.M. No. 3222
- Lambeosaurus magnicristatus*, N.M.C. No. 8705

- Lambeosaurus* sp., N.M.C. No. 8502
- Corythosaurus casuarius*, A.M.N.H. No. 5240
- Corythosaurus casuarius*, A.M.N.H. No. 5338
- Corythosaurus casuarius*, A.M.N.H. No. 5348
- Corythosaurus casuarius*, N.M.C. No. 8532
- Corythosaurus casuarius*, R.O.M. No. 5857
- Corythosaurus excavatus*, N.M.C. No. 8676
- Corythosaurus excavatus*, R.O.M. No. 5505
- Corythosaurus intermedius*, R.O.M. No. 4670
- Corythosaurus intermedius*, R.O.M. No. 4671
- Corythosaurus bicristatus*, R.O.M. No. 5852
- Corythosaurus frontalis*, R.O.M. No. 5853
- Corythosaurus brevicristatus*, R.O.M. No. 5856
- Corythosaurus* sp., R.O.M. No. 1933
- Corythosaurus* sp., A.M.N.H. No. 5359
- Corythosaurus* (?), R.O.M. No. 1940
- Procheneosaurus praeceps*, R.O.M. No. 3577
- Procheneosaurus praeceps*, A.M.N.H. No. 5340
- Procheneosaurus erectofrons*, R.O.M. No. 3578
- Procheneosaurus erectofrons*, A.M.N.H. No. 5461
- Procheneosaurus cranibrevis*, N.M.C. No. 8633
- Procheneosaurus* sp., U.S.N.M. No. 16600
- Cheneosaurus tolmanensis*, N.M.C. No. 2246
- Cheneosaurus tolmanensis*, N.M.C. No. 2247
- Hypacrosaurus altispinus*, A.M.N.H. No. 5278
- Hypacrosaurus altispinus*, A.M.N.H. No. 5357
- Hypacrosaurus altispinus*, R.O.M. No. 4974
- Hypacrosaurus altispinus*, R.O.M. No. 702
- Hypacrosaurus altispinus*, N.M.C. No. 8501
- Hypacrosaurus* sp., U.S.N.M. No. 7948
- Parasaurolophus walkeri*, R.O.M. No. 768
- Parasaurolophus cyrtocristatus*, C.N.H.M. No. P27393

##### SAUROLOPHINAE

- Saurolophus osborni*, A.M.N.H. No. 5220
- Saurolophus osborni*, A.M.N.H. No. 5221
- Prosaurolophus maximus*, A.M.N.H. No. 5386
- Prosaurolophus maximus*, N.M.C. No. 2870
- Prosaurolophus maximus*, N.M.C. No. 2277
- Prosaurolophus maximus*, U.S.N.M. No. 12712

*Prosaurolophus maximus*, R.O.M. No. 1928

*Prosaurolophus maximus*, R.O.M. No. 1929

*Prosaurolophus maximus*, R.O.M. No. 4971

*Prosaurolophus* (?), R.O.M. No. 667

*Brachylophosaurus canadensis*, N.M.C. No. 8893

HADROSAURIDAE *incertae sedis*

*Claosaurus agilis*, Y.P.M. No. 1190

## OSTEOLOGY

This section is devoted largely to the cranial osteology of the holotype and plesiotype of *Corythosaurus casuarius* (A.M.N.H. Nos. 5240 and 5338), but occasional comparisons with other hadrosaurian species are included in order to present the cranial characteristics of the family as a whole. While all species included in this family conform in certain characters, there is a wide degree of variation, particularly in the development of the skull,

which requires extensive analysis of certain cranial structures in several hadrosaurian species.

The holotype of *Corythosaurus casuarius* (A.M.N.H. No. 5240) was collected in 1912 from the upper part of the Belly River beds along the Red Deer River near Steeveville, Alberta. A second and more complete specimen (A.M.N.H. No. 5338), designated the plesiotype, was collected from approxi-



FIG. 7. Skull of *Corythosaurus casuarius*, plesiotype, A.M.N.H. No. 5338. Abbreviations: Ar., articular; De., dentary; Ju., jugal; La., lacrimal; Ma., maxilla; Na., nasal; Pa.P., paroccipital process; Pd., prementary; Pf., prefrontal; Pm., premaxilla; Pm<sub>1</sub>, upper branch of premaxilla; Pm<sub>2</sub>, lower branch of premaxilla; Po., postorbital; Qj., quadratojugal; Qu., quadrate; Sa., surangular; Sp., splenial; Sq., squamosal. Approximately  $\times \frac{1}{2}$ .

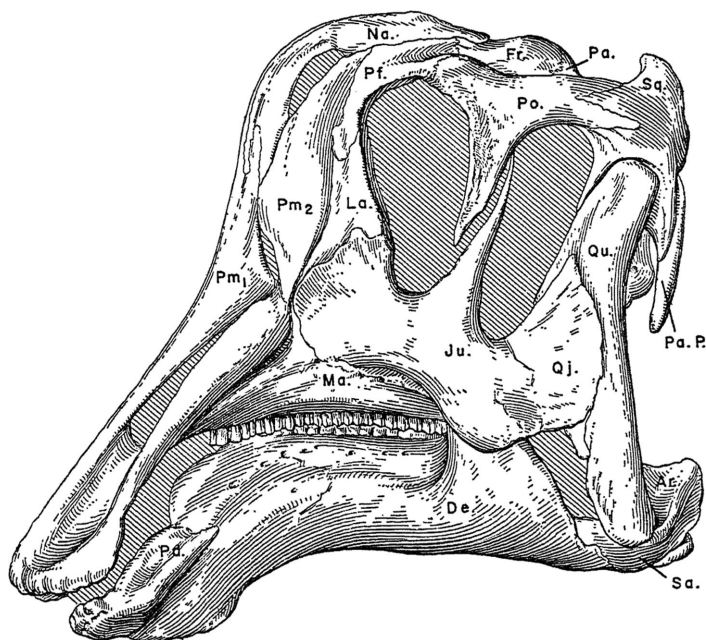


FIG. 8. Skull of *Procheneosaurus erectofrons*, A.M.N.H. No. 5461. Abbreviations: Ar., articular; De., dentary; Fr., frontal; Ju., jugal; La., lacrimal; Ma., maxilla; Na., nasal; Pa., parietal; Pa.P., paroccipital process; Pd., premaxilla; Pf., prefrontal; Pm<sub>1</sub>, upper branch of premaxilla; Pm<sub>2</sub>, lower branch of premaxilla; Po., postorbital; Qj., quadratojugal; Qu., quadrate; Sa., surangular; Sq., squamosal. Approximately  $\times \frac{1}{2}$ .

mately the same vicinity and horizon two years later. Brown (1914b) erected the genus and species on the first of these specimens in a very brief description of the skull. Later (1916b) he gave an equally brief description of the postcranial skeleton, musculature, and epidermis of the holotype. Since Brown's descriptions, there have been only occasional brief references (Parks, 1923, 1935b; Charles M. Sternberg, 1935; Wilfarth, 1938, 1939; Gilmore, 1924b; and Lull and Wright, 1942) to this species, and as yet no detailed description of *Corythosaurus casuarius* is available.

The following discussion is presented in part to correct this deficiency, but also to describe the cranial skeleton of one of the American hadrosaurs and thereby provide points of reference for the subsequent discussions of hadrosaurian musculature and neurology as well as the detailed treatment of the functional morphology of the hadrosaurian skull.

#### SKULL FORM IN *CORYTHOSAURUS CASUARIUS*

This species is characterized by a high, rounded, laterally compressed crest which is composed entirely of the premaxillaries and nasals. The anterior margin and the anterior inferior portions of the crest are formed by the premaxillaries, while the nasals form the remaining 80 per cent of this cranial structure. The crest rises from the snout just in front of the orbits, extending to its highest point directly above the eye region. From its summit, the crest margin descends in a smooth curve to a posterior, hook-like termination which overlaps the squamosals and the supraoccipital region. As in most other corythosaurian species, the crest is laterally compressed to form a thin, blade-like helmet, which houses the rather complex and sinuous narial passages. This crest, which nearly doubles the height of the skull, creates the impression of an extremely large and massive skull. Actually, such is not the case,

however, for the skull length and height (excluding the crest) are proportionately less than in most other hadrosaurs. The skull of *Procheneosaurus*, with its much smaller crest, by way of contrast emphasizes the dominant role of the corythosaurian crest.

The muzzle of *Corythosaurus* is relatively shorter and less expanded anteriorly than that of other members of the family, and the edentulous portion accounts for approximately one-third of the mandibular length. The large oval orbit is situated high on the lateral surface of the skull on a level with the upper end of the quadrate. The frontal is excluded from the supraorbital rim, as it is in all the Lambeosaurinae.

The mandible length represents only about 80 per cent of the skull length, chiefly because of the caudal extension of the crest behind the occipital surface. The massive and robust form of the mandible, so characteristic of all members of the family, provided a sturdy foundation for the large dental battery which occupies more than half of the total mandibular length.

#### NEUROCRANIAL SEGMENT

To aid the reader and to simplify the presentation of subsequent material, it seems preferable to present the cranial osteology in two sections, dealing with the neurocranial segment or cranium (occipital segment of Versluys and others) and the maxillary segment separately. Such a division is purely one of convenience and, as will be seen, cannot be mechanically justified, as these two segments are firmly united in the akinetic hadrosaurian skull. However, these portions of the skull are treated as separate and independent units in the later discussion of certain phases of cranial dynamics.

The neurocranial segment of *Corythosaurus casuarius*, as does that of all other hadrosaurian species, forms a relatively massive, firmly united brain case. Both dermal and endochondral elements contribute to its formation, although the sphenoidal and occipital elements are the most important. The hadrosaurian brain case has, ever since the earliest studies, presented problems, which are still far from solved, concerning the identification of the various components. Sutures are usu-

ally partially or completely obliterated between certain cranial bones. Even in juvenile specimens, such as *Anatosaurus annectens* (A.M.N.H. No. 5046), extensive fusion of adjacent elements has largely obscured the cranial sutures.

The hadrosaurian cranium is formed by the large exoccipitals and the supraoccipital posteriorly, the opisthotics and prootics laterally, the parietals and frontals dorsally, the basioccipital and basisphenoid ventrally, and the laterosphenoid, orbitosphenoid, parasphenoid, and presphenoid complex in front. Each of these elements is discussed separately.

#### SUPRAOCCIPITAL

This element has been variously located by different authors, and the holotype and plesiotype of *Corythosaurus casuarius* do not completely solve the problem. In both specimens the sutures between the supraoccipital and the exoccipitals cannot be located with any degree of certainty, although the condition of the plesiotype (A.M.N.H. No. 5338) is very suggestive. The plesiotype of *C. excavatus* (N.M.C. No. 8676), however, illustrates quite well the shape and the location of the supraoccipital, as does the fine specimen of *Procheneosaurus erectofrons* (A.M.N.H. No. 5461). In the latter (fig. 10), the supraoccipital occurs as a small, subtriangular bone situated with its greatest width ventrally and tapering abruptly upward to the apex. The very distinct sutures that define this bone clearly indicate its exclusion from the foramen magnum below. Located dorsal to the foramen magnum in the midline of the posterior cranial wall, the supraoccipital is bounded by an almost straight, horizontal suture ventrally and by slightly irregular, digitate, and inclined lateral sutures. Conspicuous medial expansions of the exoccipitals meet in the midline ventral to the supraoccipital, thereby separating the supraoccipital from the foramen magnum. Laterally, the extremities of the supraoccipital meet the laterodorsal expansion of the exoccipitals, while dorsally the apex of the supraoccipital comes in contact with the ventral surface of the squamosals and the parietals. Although not so well preserved, the same condition may be seen in the plesiotype of *C. excavatus*.

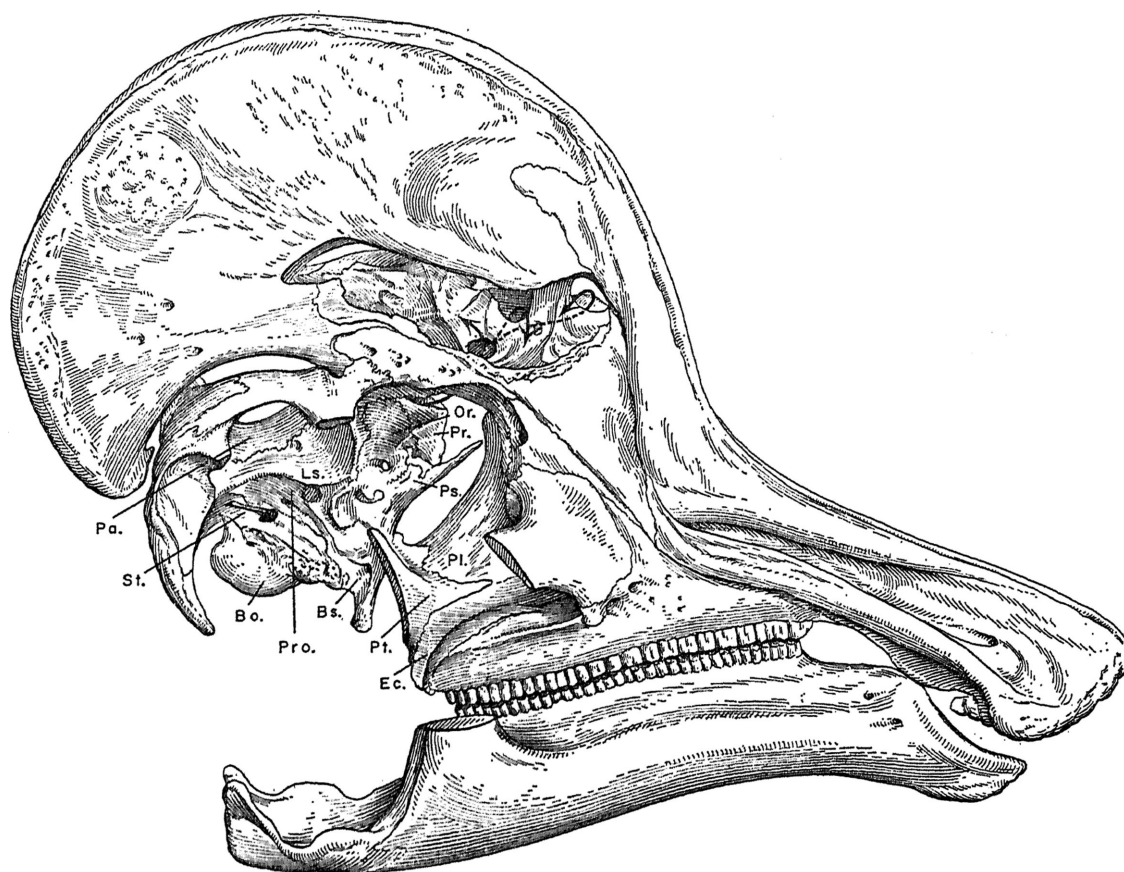


FIG. 9. Skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338. Some of the superficial lateral elements are removed to show the relationship of the neurocranial segment to the maxillary segment. The arrows trace the hypothetical path of the olfactory nerve fibers from the endocranial cavity into the crestal cavities. Abbreviations: Bo., basioccipital; Bs., basisphenoid; Ec., ectopterygoid; Ls., laterosphenoid; Or., orbitosphenoid; Pa., parietal; Pl., palatine; Pr., presphenoid; Pro., pro-otic; Ps., parasphenoid; Pt., pterygoid; St., stapes. Approximately  $\times \frac{1}{4}$ .

(N.M.C. No. 8676) as well as in *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), *Hypacrosaurus altispinus* (N.M.C. No. 8501), and *Brachylophosaurus canadensis* (N.M.C. No. 8893).

Lull and Wright (1942) note that the limits of the supraoccipital cannot be defined in *Anatosaurus* or *Edmontosaurus*, but they presume that it occupies a typical position at the upper margin of the foramen magnum. Lambe (1920) and Parks (1923) also reconstructed the supraoccipital as forming the upper limit of the foramen magnum, but subsequent works by Gilmore (1924c, 1937) and Charles M. Sternberg (1926, 1935, and 1953)

have established quite certainly that, where the sutures are preserved, the hadrosaurian supraoccipital occupies a position dorsal to and excluded from the upper margin of the foramen magnum.

The type specimens of *C. casuarius*, as stated above, fail to show these relationships, but the plesiotype does exhibit a subtriangular depression, like that of *Procheneosaurus*, which is bordered by the squamosals above and a continuous bony mass (probably the exoccipitals) laterally and ventrally. Here, as in *Procheneosaurus* and *C. excavatus*, the depressed supraoccipital forms the floor of the nuchal notch.

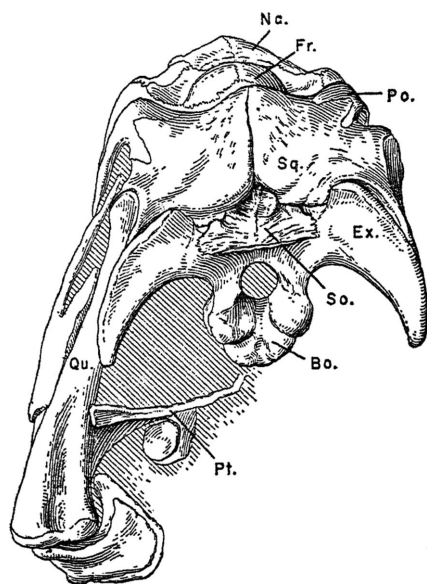


FIG. 10. Skull of *Procheneosaurus erectofrons*, A.M.N.H. No. 5461, in posterior view, showing the form and location of the supraoccipital. Abbreviations: Bo., basioccipital; Ex., exoccipital; Fr., frontal; Na., nasal; Po., postorbital; Pt., pterygoid; Qu., quadrate; So., supraoccipital; Sq., squamosal. Approximately  $\times \frac{1}{2}$ .

#### EXOCCIPITAL

The exoccipitals form an unknown portion of the occipital cranial surface, because as yet their sutural borders have not been completely determined in this family. The only exoccipital sutures known are those bordering the basioccipital and the supraoccipital. The opisthotic suture has not been observed in any member of the family.

Although none of the exoccipital sutures is preserved in the type specimens of *C. casuarius*, it is reasonable to assume that they were similar to those preserved in other hadrosaurian specimens. The well-preserved exoccipital-basioccipital suture seen in *Procheneosaurus cranibrevis* (N.M.C. No. 8633) and *Procheneosaurus erectofrons* (A.M.N.H. No. 5461) clearly demonstrates the role of the exoccipital in the formation of the occipital condyle. In both specimens, this suture traverses the condyle from the lower lateral margin of the foramen magnum to the lateral inferior surface of the condyle. Thus the exoccipitals form each lateral third of the occipital condyle, while the ventral or medial third is

formed by the basioccipital. Fragmentary evidence indicates that a very similar condition exists in *C. excavatus* (N.M.C. No. 8676), *Hypacrosaurus altispinus* (N.M.C. No. 8501), and *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), and may have been true of *C. casuarius* also. The exoccipital-basioccipital suture continues forward across the lateral inferior cranial wall in both specimens of *Procheneosaurus*. Because the union of the exoccipital with the opisthotic has not been located, the extent to which the exoccipital (or opisthotic) contributes to the lateral cranial wall is unknown.

As seen in *P. erectofrons* (A.M.N.H. No. 5461), the exoccipitals complete the upper as well as the lateral margins of the foramen magnum. Complete fusion has united the exoccipitals in the midline, thereby obliterating any medial suture. The posterior surface of the skull, lateral to the supraoccipital, flares upward and outward into the broad paroccipital process which is deflected downward distally into a tapering, hook-like process posterior to the quadrate. This process is quite solid and continuously ossified, without any visible sutural breaks. The exoccipital probably contributes to the medial portions of this structure, but it is believed that the opisthotic is responsible for the largest part of the paroccipital process, as in most reptilian groups. None of the presently known hadrosaurian specimens exhibits, however, any evidence concerning the composition of this structure.

#### BASIOCCIPITAL

Again, because of the high degree of fusion in the type specimens of *C. casuarius*, it is necessary to refer to other members of the family for adequate definition of the basioccipital. Typically this element forms the ventral third of the occipital condyle and the posterior part of the floor of the brain case. *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), *Procheneosaurus cranibrevis* (N.M.C. No. 8633), and *Kritosaurus notabilis* (A.M.N.H. No. 5350) all demonstrate this condition, in addition to showing several of the sutures with adjacent bones. These three specimens show the dorsolateral margin of this element particularly well in the form of a nearly horizontal, medially inclined, su-

tural contact with the overlying exoccipital. The anterior extension of this suture between the basioccipital below and the exoccipital and opisthotic above is also finely preserved in the holotype of *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), but it could not be recognized in either type specimen of *C. casuarius*.

In the above-mentioned specimens, the basioccipital displays a subrectangular form which is expanded at each end and constricted strongly in the center. The posterior expansion, which is the largest, forms the ventral part of the occipital condyle. The anterior enlargement forms the caudal portion of the large, bulbous, spheno-occipital tubercles. Anteriorly, the basioccipital is terminated by a digitate, transverse suture which crosses the floor of the brain case, nearly bisecting the spheno-occipital tubercles. Other specimens that display this suture are *C. excavatus* (N.M.C. No. 8676), *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), and *Procheneosaurus cranibrevis* (N.M.C. No. 8633). Parks (1923) states that this basioccipital-basisphenoid suture is also preserved in the ventral midline depression between the spheno-occipital tubercles of *Corythosaurus intermedius* (N.M.C. No. 4670), and Lambe (1920) noted a similar suture partially preserved in the paratype of *Edmontosaurus regalis* (N.M.C. No. 2289).

In *C. casuarius*, the basioccipital is slightly enlarged laterally and ventrally to form part of the occipital condyle. Anteriorly, it appears to contribute to the caudal portions of the spheno-occipital tubercles, but the extent of the contribution is not known.

#### OPISTHOTIC

The plesiotype of *C. casuarius* shows poorly defined breaks which may represent the sutures between the opisthotic and the pro-otic in front and the parietal above. No sutures could be detected between this element and the exoccipital, as is noted above. The holotype of *Anatosaurus saskatchewanensis* (N.M.C. No. 8509) also shows the sutures between the opisthotic and the pro-otic and parietal, as well as a possible suture between the opisthotic and the basioccipital, but again no suture is visible between the opisthotic and the exoccipital.

It appears, after examination of most of the known American hadrosaurian skulls, that the opisthotic fused very early with the exoccipital behind and the basioccipital and basisphenoid below. The junctions with the pro-otic and parietal are also typically obliterated by fusion, but occasional specimens do show these latter sutures partially preserved. In view of this situation, the hadrosaurian opisthotic cannot be accurately defined.

As suggested by Gilmore (1937), the opisthotic undoubtedly forms the posterior part of the inferior lateral wall of the brain case, bordered posteriorly by the exoccipital, ventrally by the basioccipital and perhaps by the basisphenoid, anteriorly by the pro-otic, and dorsally by the parietal. This region of the cranium is relatively thick and firmly united with adjacent elements in all hadrosaurian skulls. Its lateral surface is marked by a prominent horizontal ridge, which is the forward extension of the ventromedial angle of the paroccipital process. Located below this ridge, within the probable area of the opisthotic, are the more caudal foramina of the cranial nerves. The fenestra ovalis, which is easily recognized behind the trigeminal and facialis foramina, is probably located at the anterior margin of the opisthotic. This interpretation is based largely on the suture preserved in *Anatosaurus saskatchewanensis*, which passes almost vertically in each direction from the fenestra ovalis. If this interpretation is correct, three distinct foramina penetrate the opisthotic of *C. casuarius*. These have elsewhere been interpreted as the exits of the ninth through twelfth cranial nerves. Lambe (1920) extends the opisthotic forward in a similar manner, in his description of *Edmontosaurus regalis*, to include the area penetrated by these most posterior cranial foramina, and, although the opisthotic-pro-otic suture is not preserved in the type specimens, Lambe also suggests that this junction was situated in the region of the fenestra ovalis.

Lambe (1920), in his description of *Edmontosaurus*, and Lull and Wright (1942) suggest that the opisthotic forms the entire paroccipital process, a condition commonly found in modern reptiles. Whether or not this condition is true of the Hadrosauridae has never been established. To what extent

the opisthotic, or exoccipital, contributes to the formation of this large, hook-like process is impossible to estimate at present.

#### PRO-OTIC

The hadrosaurian pro-otic occupies a position in the inferior lateral wall of the brain case surrounded by the opisthotic behind, the basisphenoid below, the laterosphenoid in front, and the parietal above. The only visible suture found in *C. casuarius* is located in the vicinity of the fenestra ovalis and apparently defines the posterior margin of this bone. Although this suture is poorly preserved and quite doubtful, it agrees with the well-preserved opisthotic-pro-otic suture in *Anatosaurus saskatchewanensis*, which is described above. A similar feature can be seen in *Corythosaurus excavatus* (N.M.C. No. 8676).

The sutures between this element and the basisphenoid and laterosphenoid could not be located in *Corythosaurus casuarius*, or in any other hadrosaurian species for that matter. The upper margin of the pro-otic could not be recognized in this species either, but what appears to be the parietal-pro-otic suture can be seen in *Anatosaurus saskatchewanensis* (N.M.C. No. 8509) horizontally traversing the upper lateral surface of the cranium immediately above the trigeminal foramen. This suture continues forward, apparently marking the junction of the parietal with the laterosphenoid.

Owing to the lack of sutures between the pro-otic and the laterosphenoid in front and the basisphenoid below, no precise description of the hadrosaurian pro-otic can be given at present. Its posterior and dorsal margins have been reconstructed from the several specimens cited above. The trigeminal foramen is presumed to occupy the typical reptilian position between the pro-otic and the laterosphenoid, although no sutural evidence supports such an assumption. Ventrally, the pro-otic has fused firmly with the basisphenoid in the inferior lateral wall of the cranium between the basipterygoid process and the spheno-occipital tubercles.

The external surface of the pro-otic is marked by a nearly horizontal ridge, which is continuous with the ridge described above in the discussion of the opisthotic. Above this

ridge the pro-otic is moderately convex, while below it is distinctly concave and marked by cranial foramina. Midway between the fenestra ovalis and the trigeminal foramen a small opening marks the point of emergence of the seventh cranial nerve.

Lull and Wright (1942), although noting the high degree of fusion between this element and adjacent bones, describe an essentially similar condition of the pro-otic in *Edmontosaurus* and *Anatosaurus*. Lambe (1920) also was unable to discern the anterior and posterior pro-otic sutures, but he suggested that these limits were located at the level of the trigeminal foramen and fenestra ovalis, respectively.

#### BASISPHEOID

This element cannot be precisely defined in any of the existing hadrosaurian specimens. The typical reptilian basisphenoid forms a portion of the cranial floor just anterior to the basioccipital. Surrounding it are the basioccipital behind, the laterosphenoids and pro-otics above, and the parasphenoid in front. Both the anterior and posterior sutures are partially preserved in *C. casuarius*. The basioccipital suture is very poorly preserved in the type specimens of *C. casuarius*, but it is partially or completely retained in *C. excavatus* (N.M.C. No. 8676), *Procheneosaurus cranibrevis* (N.M.C. No. 8633), *Edmontosaurus regalis* (N.M.C. No. 2289), and *Corythosaurus intermedius* (N.M.C. No. 4670).

In all the above specimens, the basisphenoid-basioccipital suture traverses the ventral wall of the brain case at the level of the rather bulbous spheno-occipital tubercles. In view of its constancy in these forms, it appears quite logical to assume a similar position for this suture in other members of the family.

The basisphenoid of *C. casuarius* is situated directly beneath the trigeminal foramen, ventral to the pro-otic and laterosphenoid. Its upper limits are unknown, as it is completely fused with these superior bones. Posteriorly, the strong ventrolateral expansions form the anterior part of the spheno-occipital tubercles. In front of these tubercles it is strongly constricted both laterally and ventrally beneath the trigeminal foramen. The anterior portion, however, is greatly expanded ventrolaterally into the laterocau-



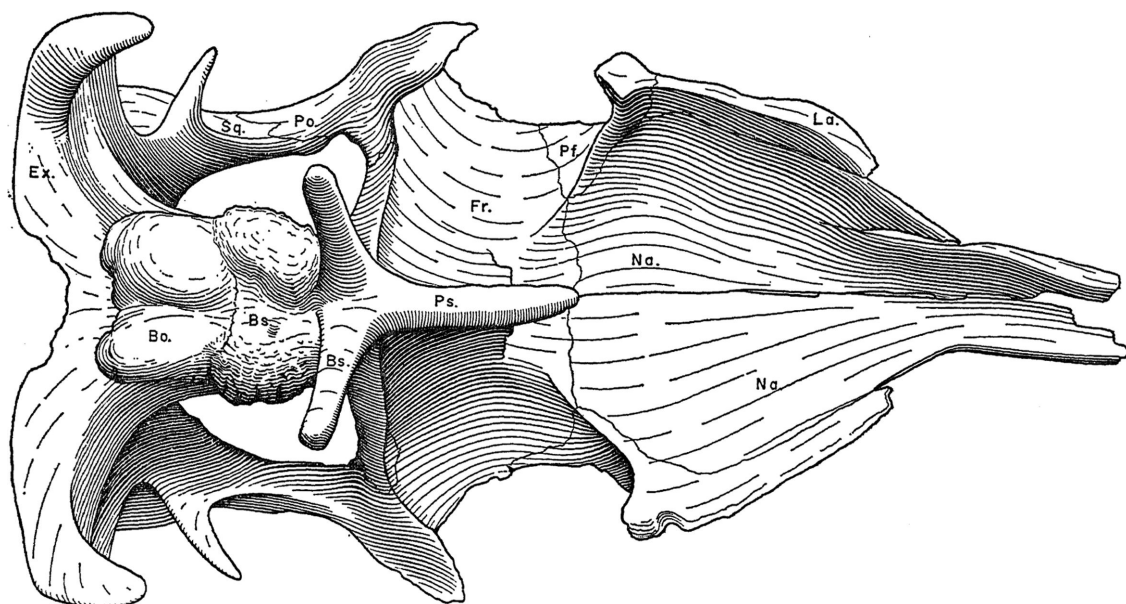


FIG. 11. Brain case and skull roof of *Kritosaurus notabilis*, A.M.N.H. No. 5350, in ventral view. Abbreviations: Bo., basioccipital; Bs., basisphenoid; Ex., exoccipital; Fr., frontal; La., lacrimal; Na., nasal; Pf., prefrontal; Po., postorbital; Ps., parasphenoid; Sq., squamosal.  $\times \frac{1}{2}$ .

dally directed pterygoid processes. These processes taper distally but are expanded at their extremities to form large, blunt, articular surfaces, which articulate with the quadrate processes of the pterygoids. These latero-caudal projections are the most prominent features of the basisphenoid and one of the strongest arguments for articular mobility within the hadrosaurian skull, a matter that is discussed at length elsewhere in this report. Anterior to the pterygoid process, the basisphenoid tapers rapidly and passes continuously into the long, narrow parasphenoid. A nearly vertical suture passing through the oculomotor-abducens foramen marks this junction of the basisphenoid and parasphenoid.

The hadrosaurian basisphenoid is pierced by two small foramina, one on each side immediately behind and above the base of the pterygoid process on the ventrolateral margin of the cranium. It is partially concealed by a thin, triangular flange which projects caudolaterally from the brain case just above the base of the pterygoid process. This opening, which is elsewhere interpreted as the passage for the internal carotid artery, is not always exposed by preparation, but it can

readily be seen in *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), *Corythosaurus excavatus* (N.M.C. No. 8676), *Corythosaurus intermedius* (R.O.M. No. 4670), *Lambeosaurus lambei* (R.O.M. No. 5131), and *Kritosaurus notabilis* (A.M.N.H. No. 5350). Lambe (1920) describes another foramen situated just anterior to the lateral flange of the basisphenoid, which he interprets as the passage of an upper branch of the internal carotid artery (probably the palatine artery). This canal is preserved on both sides of the cranium in *Edmontosaurus*, but it could not be detected in either of the type specimens of *Corythosaurus casuarius*.

Although not visible in most of the hadrosaurian specimens, the thick ventral portion of the basisphenoid encloses the hypophyseal cavity, which is continuous with the brain cavity via the canal of the infundibulum. The upper surface of this bone, as shown by the endocranial casts of *Edmontosaurus regalis* (N.M.C. No. 2289) and *Kritosaurus notabilis* (A.M.N.H. No. 5350), is pierced by the rostrally descending passages of the abducens nerves. The similarity of these two endocranial casts, with regard to these canals and the

location of the pituitary body, seems to be sufficient evidence on which to reconstruct the general hadrosaurian condition. It therefore seems probable that the basisphenoid of *C. casuarius* also enclosed the infundibulum and pituitary body as well as the trunks of the sixth cranial nerves.

#### PARASPHENOID

This bone, typically forming the most anterior of the ventral axial elements of the cranium, is completely fused with the basisphenoid in most hadrosaurian specimens. The plesiotype of *C. casuarius*, however, displays a nearly vertical fracture which passes from the ventral surface of the cranium up across the foramen of the third and sixth cranial nerves. This appears to represent the sutural union of the basisphenoid with the parasphenoid and presphenoid in front. The parasphenoid of *Corythosaurus* extends forward and slightly upward as a thin, tapering continuation of the basisphenoid. The posterior third of the parasphenoid is in contact with the overlying presphenoid, the remainder projecting freely forward between the orbital cavities. Throughout its entire length, its height exceeds the width.

The posterior portion of the parasphenoid apparently forms the floor of a narrow canal which is roofed over by the presphenoid, a condition similar to that which was reported by Lambe (1920) in his description of *Edmontosaurus regalis*. The extent of this feature, which is very poorly preserved in *C. casuarius*, is not known nor is its precise function understood with any degree of certainty. A similar canal appears in *Kritosaurus notabilis* (A.M.N.H. No. 5350). Discussion of this median canal is deferred to a following section, where it is correlated with a median branch of the internal carotid artery.

No distinct sutures between the parasphenoid and the overlying presphenoid were detected in either of the type specimens of *C. casuarius*, but the location is presumed to approximate that described by Lambe (1920) in *Edmontosaurus*, which would place the union of the parasphenoid and presphenoid ventral to the emergence of the optic nerve, probably extending forward from the foramen of the oculomotor and abducens nerves.

#### LATEROSPHEOID

The laterosphenoid (alisphenoid of some authors) is almost completely coalesced with the adjacent elements in both type specimens of *C. casuarius*. The only possible exception noted is a rather obscure break above the oculomotor-abducens foramen, which appears to be a continuation of the basisphenoid-parasphenoid suture, and may represent the junction of the laterosphenoid with the presphenoid-orbitosphenoid complex in front. Such a possibility cannot be verified, however, as no similar suture has been observed in other hadrosaurian specimens. It should also be noted here that this portion of the cranium is badly crushed in the plesiotype of *C. casuarius*. With the exception of this one doubtful suture, no other margins of the laterosphenoid could be recognized in *Corythosaurus*. It is very probable, however, that the laterosphenoid occupied a typical reptilian position anterior to the pro-otic and forming the lateral wall of the brain case dorsal to the basisphenoid. Presumably the laterosphenoid is bounded by the orbitosphenoid and presphenoid in front, and the parietal, frontal, and postorbital dorsally, but such is pure speculation.

Gilmore (1924b, fig. 8) illustrates the dorsal suture with the parietal, frontal, and postorbital in a partial brain case of *Lambeosaurus* (N.M.C. No. 8502), which appears similar to a partial suture separating the laterosphenoid and parietal in *Anatosaurus saskatchewanensis* (N.M.C. No. 8509). Lambe (1920) describes a distinct suture between the laterosphenoid and pro-otic in *Edmontosaurus*, as well as a dorsal suture with the parietal. The former descends from the ventral margin of the parietal across the dorsolateral wall of the brain case to the dorsal rim of the trigeminal foramen. The latter runs forward from the upper end of the pro-otic suture to the posterior margin of the postorbital. Lull and Wright (1942) note that the orbitosphenoid-laterosphenoid (alisphenoid) suture is preserved in *Anatosaurus annectens* (Y.P.M. No. 618).

If it be assumed that the laterosphenoid of *C. casuarius* occupied a similar position with essentially corresponding margins, the posterior border may be placed at the level of the

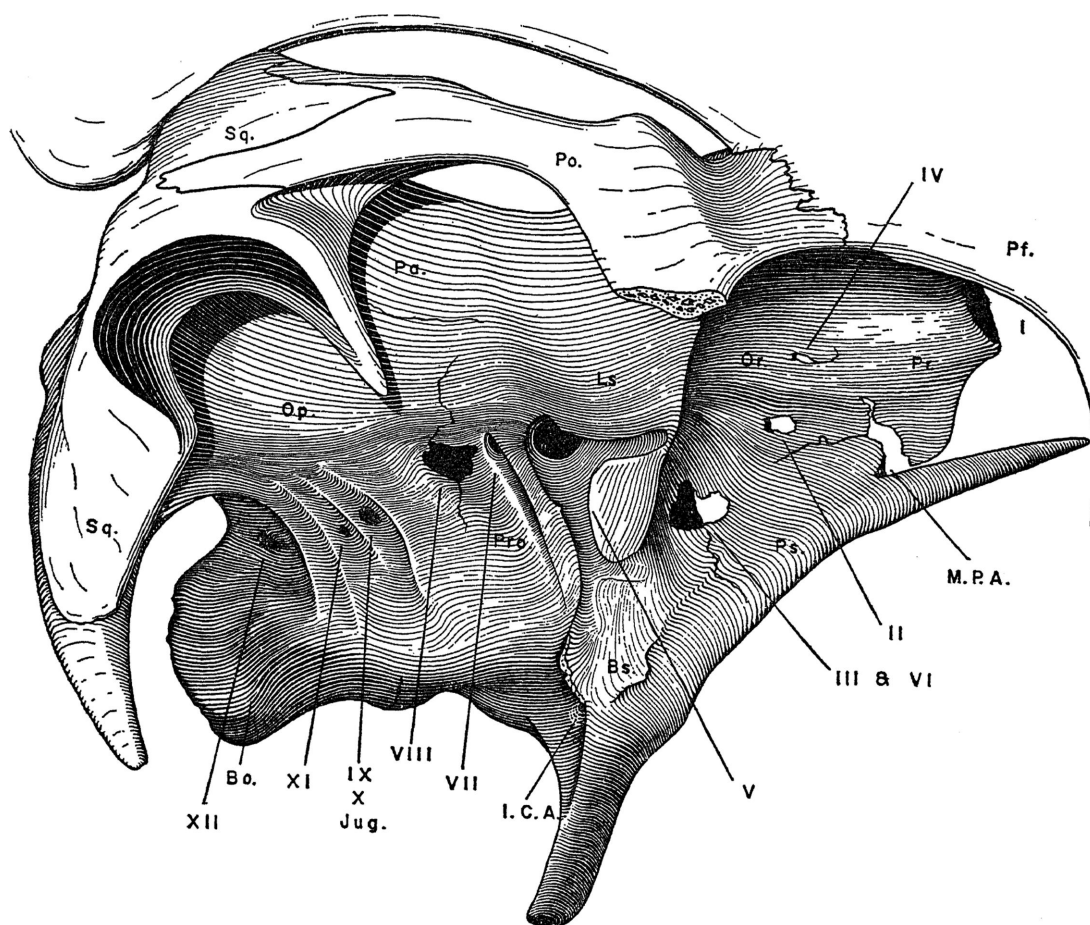


FIG. 12. Brain case of *Corythosaurus casuarius*, A.M.N.H. No. 5338, in lateral view. **Abbreviations:** Bo., basioccipital; Bs., basisphenoid; I.C.A., foramen for internal carotid artery; Jug., foramen for jugular vein; Ls., laterosphenoid; M.P.A., canal for median palatine artery; Op., opisthotic; Or., orbitosphenoid; Pa., parietal; Pf., prefrontal; Po., postorbital; Pr., presphenoid; Pro., pro-otic; Ps., parasphenoid; Sq., squamosal; I–XII, foramina for the respective cranial nerves. Approximately  $\times \frac{1}{2}$ .

trigeminal foramen, as in *Edmontosaurus regalis*. The anterior margin probably coincided with the prominent, near vertical ridge which ascends from in front of the trigeminal foramen to buttress the postorbital. This ridge, in effect, separates the infratemporal fossa from the orbital cavity and, topographically at least, is the most likely position for the union of the laterosphenoid with the orbitosphenoid and presphenoid.

The corythosaurian laterosphenoid is penetrated by a single foramen, the trigeminal foramen, at its posterior margin. Ventral and anterior to this opening, the external surface

of the laterosphenoid is marked by two very deep grooves which mark the passage of the two deep branches of the trigeminal nerve. Both grooves are open, but several hadrosaurian crania (*Lambeosaurus lambei*, R.O.M. No. 5131, to cite one) exhibit a partially or completely roofed-over canal for the profundus or ophthalmic branch.

#### PRESPHENOID AND ORBITOSPHEOID

The bony surfaces situated anterior to the trigeminal foramen, forming the incomplete interorbital septum, are only partially preserved in the type specimens of *C. casuarius*.

Although no sutures are recognizable, it is probable that this region is formed by the orbitosphenoid and presphenoid, the latter contributing to the lower part of this septum just dorsal to the parasphenoid, and the former to the floor of the olfactory canal. These elements are bounded by the parasphenoid below, the laterosphenoid behind, and the frontal above, the last-named forming the roof of the olfactory canal. Lull and Wright (1942) note that an orbitosphenoid-presphenoid suture is preserved in *Anatosaurus annectens* (Y.P.M. No. 618), traversing this septum from the laterosphenoid ridge forward and slightly upward. These elements are too poorly preserved in the species under consideration to allow adequate description.

Lambe (1920) refers to a specimen of *Stephanosaurus* (*Lambeosaurus*) in which the posterior margin of these elements is marked by a suture extending between the oculomotor-abducens foramen and the laterosphenoid ridge, upward to the frontal. Lambe failed to note the particular specimen, however, and the present author was unable to find such a suture in any of the specimens of *Lambeosaurus* examined.

The dorsal margin of the presphenoid-orbitosphenoid complex is clearly visible in the form of a sinuous suture at the ventral border of the frontal in *Edmontosaurus regalis* (N.M.C. No. 2289). This same specimen exhibits a well-preserved suture at the ventral junction of this complex with the parasphenoid.

The fused orbitosphenoid and presphenoid of *C. casuarius* are presumed to be like those of *Edmontosaurus* and, as in this genus, penetrated by several foramina for the emergence of the anterior cranial nerves. Four distinct openings can be seen in this region in the type specimens of *C. casuarius*. The largest of these is located in the midline between the orbitosphenoids and undoubtedly marks the emergence of the olfactory tracts. Ventral and posterior to the olfactory canal, just in front of the laterosphenoid ridge, is a prominent opening in the lateral surface of this complex which is believed to have provided for the passage of the optic nerve. Immediately ventral and posterior to this, located at the probable posterior margin of the orbito-

sphenoid-presphenoid complex, is a larger opening which is elsewhere interpreted as the common exit for the third and sixth cranial nerves. Above the optic foramen is a small canal believed to represent the route of the trochlear nerve. A fifth opening associated with these elements, mentioned in the discussion of the parasphenoid, occurs as a long narrow canal between the presphenoid region and the underlying parasphenoid. This midline passage, which apparently extends from the hypophyseal cavity in the basisphenoid forward to its exit in the interorbital region, is discussed at length elsewhere.

#### PARIETAL

The parietals of *C. casuarius*, as in most members of the family, have coalesced to form a single, median bone situated between the frontals and the squamosals. As the posterior roof of the brain cavity, the parietals extend the entire length of the supratemporal fenestrae and in effect separate these two openings. The length of the parietals is approximately twice the width, although this varies in other species. Dorsally the junction of the parietals along the midline is raised in a strong, laterally compressed, sagittal crest, which rises almost to the upper level of the supratemporal arch. A distinct gap exists between the upper surface of the parietals and the ventral margin of the overlying nasal crest, presumably to allow for the expansion of the mandibular muscles which arose within the supratemporal fossa. The lateral surfaces of the parietals, which form the medial walls of the upper temporal openings, are moderately concave both horizontally and vertically.

The fused parietals meet the frontals at the anterior limit of the supratemporal fossa in a distinct, digitate, transverse suture. There is no interposition of the parietals between the paired frontals as described by Gilmore (1924b) in *Lambeosaurus*. Laterally, a less prominent, longitudinal suture can be seen between the parietal and the pro-otic region of the cranium. Very possibly this anterior segment of the parietal suture was extended both forward and caudally, separating the laterosphenoid, opisthotic, and exoccipital from the parietal, but these parts have been obliterated by fusion or crushing

in the plesiotype of *C. casuarius*. As mentioned above, the lateral margin of the parietal is partially or completely preserved in several other hadrosaurian species and is best displayed in *Anatosaurus saskatchewanensis* (N.M.C. No. 8509). Here it extends forward from the region of the opisthotic to the rear margin of the postorbital.

The posterior margin of the parietal differs in *Corythosaurus casuarius* from that of some hadrosaurian species in that these coalesced elements extend beyond the posterior limit of the upper temporal opening to form the medial and dorsal part of the stout occipital crest. Lambe (1920) describes and figures a similar narrow extension of the parietals as passing between the squamosals, back to the occipital surface of the cranium. This is apparently in contact with the dorsal and anterior surface of the supraoccipital and completely divides the squamosals in the midline. In the plesiotype of *C. casuarius* a similar condition exists. Here, the parietals extend back as a broad bone, forming nearly the entire posterior wall of each upper temporal opening and restricting the squamosals to the lateral walls of these fossae and the dorsal and posterior surfaces of the occipital crest. The largest part of the occipital crest is formed by this broad, median extension of the parietals between the squamosals. However, the squamosals are not completely separated by this extension, as they meet in the midline dorsal to the supraoccipital and dorsal and posterior to the parietals on the caudal surface of the occipital crest. The sutures defining the squamosal and parietal limits in this area are quite well preserved on the plesiotype but are not visible on the holotype. Within the supratemporal fossa, however, the squamosal-parietal suture is obscure, owing largely to the crushed state of the plesiotype and incomplete preparation of the holotype. Sectioned hadrosaurian skulls, such as those of *Anatosaurus* (Y.P.M. No. 618, A.M.N.H. No. 5236), show that in certain species the parietal extends caudally beneath the squamosals to coalesce with the anterior limit of the supraoccipital in a broad bony union. In these specimens, the squamosals form a thin, superficial overlap dorsal to the caudal extremity of the united parietals, creating a large part of the occipital crest.

The superficially incomplete passage of the parietals between the squamosals in *C. casuarius* appears to be intermediate between the condition seen in *Edmontosaurus regalis*, in which the squamosals fail to meet in the midline at all, and that of *Anatosaurus*, described by Lull and Wright (1942), in which the parietal is excluded from the occipital surface of the skull. Gilmore (1924c) states that the separation of the squamosals by the interposition of the parietals is true of many of the hadrosaurs, but rarely is this separation complete. *Edmontosaurus regalis* and *Kritosaurus notabilis* are the only species, to the best of my knowledge, in which the squamosals fail to meet in the midline at all. It is true that many of the hadrosaurian species show varying degrees of parietal interposition, but generally it is a relatively short caudal extension in the midline, and usually it is restricted to the anterior surface of the occipital crest. The majority of the hadrosaurian species exhibit an occipital crest formed largely by the paired squamosals. It is interesting to note that this parietal interposition is much less extensively developed in other corythosaurian species than it is in *C. casuarius*; in fact it is hardly developed at all in some corythosaurian specimens.

#### FRONTAL

The small frontals of *C. casuarius* are only partially exposed just behind the base of the nasal crest at the anterior margin of the supratemporal fossae. Anteriorly they are overlain by, and in sutural contact with, the nasals and premaxillaries. The ventral margin of the nasal crest rises in a gentle arch over the supratemporal fenestrae, exposing the posterior portions of the paired frontals, which form the moderately convex roof of the cerebral chamber.

The frontals articulate with the parietals posteriorly, the nasals and premaxillaries anteriorly, the prefrontals and postorbitals laterally, and the orbitosphenoids ventrally. Many of these sutural unions are preserved in the type specimens of *C. casuarius*, although the union between the frontal and the orbitosphenoid is not. The digitate, transverse suture between the frontals and the parietals is the most conspicuous, extending across the convex cranial roof at the anterior

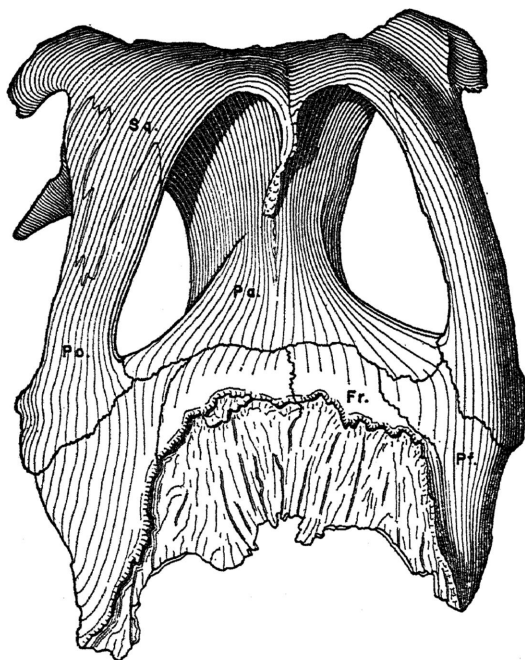


FIG. 13. Cranial roof of *Corythosaurus* sp., R.O.M. No. 1940, in dorsal view. Notice the broad, rugose, anterior surface of the frontals which formed a solid base for the crest. Abbreviations: Fr., frontal; Pa., parietal; Pf., prefrontal; Po., postorbital; Sq., squamosal.  $\times \frac{1}{2}$ .

limit of the upper temporal openings. The restricted contacts of the prefrontal and postorbital with the frontal are largely concealed by the lateral position of these elements with respect to the frontal. However, partial sutures can be seen in the dorsal wall of the orbit in the plesiotype of *C. casuarius*. The frontal, together with the prefrontal and postorbital, forms a considerable portion of the dorsomedial orbital wall.

The most interesting of the frontal sutures is that formed by the dorso-anterior frontal surface which articulates with the base of the nasal crest. Although not visible in either of the type specimens of *C. casuarius*, this surface is finely preserved in a number of specimens. One of the best of these is a cranium, probably of *Corythosaurus* (R.O.M. No. 1940), which displays a very broad, strongly grooved, anterior frontal surface (see fig. 13). This surface, which is slightly broader than the posterior frontal width, slopes rather steeply forward, with its pronounced longi-

tudinal grooves offering a maximum area for the solid attachment of the nasals and premaxillaries. The inclined surface constitutes more than half of the total length of the frontal. Gilmore (1924b) describes a very similar feature in a partial cranium of *Lambeosaurus* (N.M.C. No. 8502). In this specimen the frontals are greatly reduced in size and, as in the above specimen, are wider than long. Anteriorly these bones terminate in a nearly vertical, strongly grooved, sutural surface. Still a third specimen (U.S.N.M. No. 11893), an unidentifiable partial cranium of a crested hadrosaur described by Gilmore (1937), exhibits this same grooved surface. It is quite apparent from these specimens that the anterior surface of the frontals provided a large part of the foundation for the hadrosaurian nasal crest. The exact nature and extent of the contact between the frontals and the nasals and premaxillaries are not known in *C. casuarius*, but they are believed to be patterned after the condition displayed in these fragmentary specimens.

#### MAXILLARY SEGMENT

The skull elements discussed in this section are directly or indirectly attached quite firmly to the brain case or neurocranial segment of the skull, but they are included in this separate section for purposes of simplification and organization. As here conceived, the maxillary segment includes all those skull bones that are not directly involved in the formation of the brain case.

The maxillary segment of *Corythosaurus casuarius* is in effect a superficial envelope of dermal bones, which very nearly surrounds the neurocranial segment. This external encasement of bone is obviously penetrated by a number of external openings or fenestrations of varying size, but with the exception of these and the exposed posterior occipital surface, the brain case is well shielded by these superficial elements. It is these maxillary elements that give *Corythosaurus* its characteristic crested head form.

The skull of *C. casuarius* is quite long (837 mm. in the holotype) and nearly as high (708 mm.). In profile, the narrow snout, which slopes steeply forward, swings upward in front of and at the level of the orbits to form the nearly vertical anterior margin of the

nasal crest. The muzzle is relatively short and narrow but is expanded into a broad, bill-like beak anteriorly. Rising from the rear of the snout and extending back over the remaining skull length is the high and laterally compressed nasal crest. In both type specimens this crest is nearly semicircular in profile. The highest point of the crest is situated above the orbit, and the caudal extremity overhangs and projects behind the occipital surface. The crest is formed entirely by the dorsal and posterior expansions of the premaxillaries and nasals, although Brown (1914b) and others originally believed that the frontals and prefrontals contributed to a large extent in the formation of this structure.

With the exception of the narial crest and the muzzle, the corythosaurian skull is strongly camptosaurid, although it is somewhat higher and more fenestrated. Lying behind and beneath the long premaxilla, the massive maxilla forms the anteroventral skull margin. Springing out from the lateral maxillary surface the broad but rather thin jugal extends back to the quadratojugal and quadrate, defining the posteroventral margin of the skull as well as the ventral borders of the orbit and infratemporal fenestra. The relatively small lacrimal, prefrontal, and postorbital define the upper margin of the orbit, the last two, together with the squamosal, forming the upper temporal arch. The long stout quadrate completes the nearly vertical posterolateral limit of the skull.

The various bones of the maxillary segment are, in general, firmly united by digitate or squamose sutures and are solidly joined to the brain case. There appears to be little, if any, articular freedom within the corythosaurian skull, a condition considered to be characteristic of the entire family.

#### PREMAXILLA

The premaxilla accounts for much of the distinctive corythosaurian profile. The entire muzzle is formed by the anterior portions of the premaxillaries, while the posterior expansions of these bones contribute greatly to the anterior and ventral portions of the crest. At their anterior limits the premaxillaries flare out laterally to form the broad beak. The upper surface of this beak is strongly con-

cave, a feature that is characteristic of all hadrosaurian species. Caudally the premaxilla narrows moderately, as does the dorsal concavity which posteriorly forms a tapering groove leading into the external nares. Ventrally the premaxilla forms the concave lower margin of the muzzle, which is completely devoid of dentition. The rounded anterior margin in both type specimens is marked by slight irregularities, creating a subdued digitate margin. This pattern, which is preserved in several hadrosaurian species, has been interpreted as the attachment scar of a horny bill or beak such as is found in modern turtles. Such a bill has apparently never been preserved, but impressions of this have been described in specimens of *Anatosaurus annectens* (A.M.N.H. No. 5060, S.M. No. R4036) and *Corythosaurus excavatus* (N.M.C. No. 8676) (Cope, 1883; Versluys, 1923; Charles M. Sternberg, 1935).

Dorsal to the narial opening, the premaxilla rises steeply as the anterior margin of the dorsal hood or crest. This dorsal expansion of the premaxilla is separable into two portions commonly designated the upper and lower branches or lobes of the premaxilla and separated by an external supranarial groove ventrally and the interposition of the nasal dorsally. It is the narrow upper branch of the premaxilla which forms the anterior crestal margin. The lower branch, which is somewhat broader and more irregular in shape, forms almost half of the ventral crest margin, reaching slightly posterior to the orbital region. Except for the narial opening, the premaxilla is not penetrated by any foramina or fenestrae. There is no infraorbital fenestra or expanded naris in *C. casuarius*, as in most flat-headed forms.

The sutures bounding the premaxilla are well preserved in both the holotype and plesio-type. Opposing elements meet in a straight, midline suture which is visible from the anterior periphery of the muzzle to the top of the crest, along the anterior crestal margin. Ventrally the premaxilla meets the dorso-anterior margin of the maxilla in a rather feeble junction. A firmer sutural contact is quite distinct between the lower branch of the premaxilla and the lacrimal and prefrontal, forming the ventral margin of this lower branch. The remaining margins of the pre-



maxilla are bounded by the greatly expanded nasal. The posterior border of the lower premaxillary branch is marked by a strong digitate suture between this and the nasal, a condition that is also characteristic of the entire junction of the upper branch with the nasal. However, much of the dorsal margin of the lower branch fails to articulate with the interposing nasal, thus leaving a somewhat sinuous and elongate opening which leads into the crestal cavities. Examination of the crestal cavities and their relationship with the nasal passages suggests that this lateral crestal opening was closed in life, probably by a membrane. Brown (1914b), in his original description of *Corythosaurus*, correctly interpreted the anterior part of the muzzle as the premaxilla, but he believed the upper branch to be the nasal and the lower branch the prefrontal. Lambe (1920) first noted and published the presently accepted interpretation.

In all essential characters, this element is very similar to that found in other species of *Corythosaurus*. The most prominent variation of this element within the genus is the degree of contribution to crestal formation. The greatest deviation from the condition seen in *C. casuarius* was noted in *C. frontalis*, in which the crest is much lower and is formed largely by the expanded branches of the premaxilla, the nasal being relatively small. Even greater variation is found among the other lambeosaurian genera, as figures 14 and 15 clearly illustrate.

#### MAXILLA

The maxilla is typically hadrosaurian in form, differing only in minor features from that of other members of the family. Bearing the large dental battery, this large, wedge-shaped bone is situated along the lateroventral margin of the skull. It is bordered by the premaxilla anteriorly and superiorly, the lacrimal dorsally, the jugal posterolaterally, and the ectopterygoid posteriorly. Medially the vomer meets the maxilla inferiorly, while the palatine and pterygoid (slightly) join it above. These last three elements are inadequately exposed in the type specimens of *C. casuarius*, and as a result their contacts with the maxilla cannot be accurately described.

The contact of the maxilla and the lower branch of the premaxilla is not firmly united. As a result, this junction is most obvious in

both the holotype and the plesiotype. The lacrimal is firmly united, however (by an irregular, grooved suture), to the upper extremity of the maxilla, but this junction is usually almost completely concealed by the overlapping jugal. The jugal itself articulates by a broad, squamose suture with the dorsolateral surface of the maxilla. The lateral surface of the maxilla, behind its articulation with the jugal, is marked by a prominent, horizontal ridge, which separates this external surface into an inferior concave surface directed ventrolaterally and a superior concave shelf directed dorsolaterally. This latter surface, which in its posterior part is overlapped by the thin and narrow ectopterygoid, is elsewhere interpreted as the site of origin of part of the M. pterygoideus.

The corythosaurian maxilla is penetrated by a number of foramina. Externally, two openings of moderate size are located immediately ventral to the jugal articulation, and two smaller foramina are situated anterior to the jugal. Although these could not be completely explored, it seems probable that they provided passage for both vascular and neural elements supplying the lateral buccal tissues and possibly the salivary glands. The more anterior of the two large foramina is probably the external maxillary foramen, which connects with the lacrimal canal.

The lingual surface of the maxilla is marked by a prominent pattern of foramina arranged in a gently curving horizontal row, with the extreme pores located closest to the alveolar margin and the centrally situated foramina more dorsally placed. The size of individual foramina varies with the position in this row. The largest openings are situated centrally, while the foramina closer to each end of the series decrease in size progressively, a situation that is closely paralleled by tooth size in the maxillary dental battery. The number of foramina varies in individual specimens, but it appears to agree with the number of tooth rows in the battery in all hadrosaurian specimens, thus indicating a definite relationship with the dentition. The most frequent interpretation of this feature is one of vascular and nerve passage, but Edmund (1957) has demonstrated that this is quite improbable. Edmund suggests that these foramina provided for the passage of germ teeth from the dental lamina into the alveolar cavities.



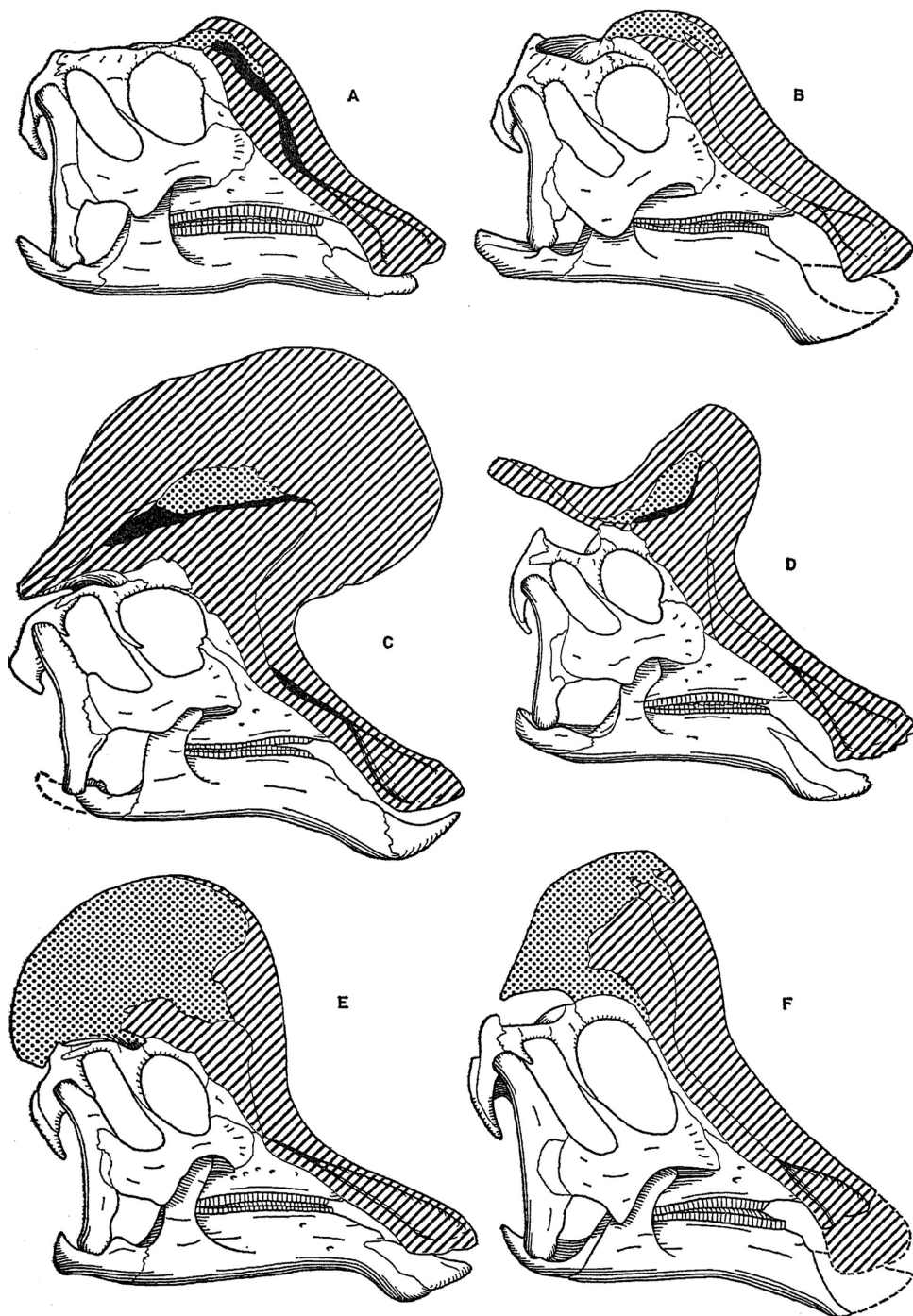


FIG. 14. Comparison of narial crests in six lambeosaurian species, illustrating the relative importance of the premaxilla (oblique pattern) and nasal (stippled pattern). Quadrate-premaxilla length drawn to unit scale. A. *Procheneosaurus praeceps*, R.O.M. No. 3577. B. *Cheneosaurus tolmanensis*, N.M.C. No. 2246. C. *Lambeosaurus magnicristatus*, N.M.C. No. 8705. D. *Lambeosaurus lambei*, N.M.C. No. 2869. E. *Corythosaurus casuarius*, A.M.N.H. No. 5240. F. *Hypacrosaurus altispinus*, N.M.C. No. 8501.

## NASAL

This distinctive element, along with the expanded premaxilla, is responsible for the formation of the large, helmet-like crest of *Corythosaurus*. In *C. casuarius*, the nasal accounts for at least 75 per cent of the crestal surface. The large size of the crest in this species is directly related to the very large size of the nasal, and the smaller crests seen in other species of *Corythosaurus* result in large measure from the smaller size of this element. However, the large size of the crest in other members of the Lambeosaurinae (with the exception of *Hypacrosaurus* which is generally considered a descendant of *Corytho-*

*saurus*) has resulted from a very pronounced expansion of the premaxillaries. In both *Lambeosaurus* and *Parasaurolophus*, the nasal is relatively small (exceedingly small in the latter, according to Russell's interpretation of 1946), while the two branches of the premaxilla are greatly expanded to form nearly the entire crest. (See figs. 14 and 15.)

The limits of the nasal are quite distinct in the plesiotype of *C. casuarius* and somewhat less obvious in the holotype. Forming the entire upper and posterior portions of the crest, the nasal creates the superior and posterior crest profile. Anteriorly it is closely united with the posterior margin of the upper branch of the premaxilla. Inferiorly, for about

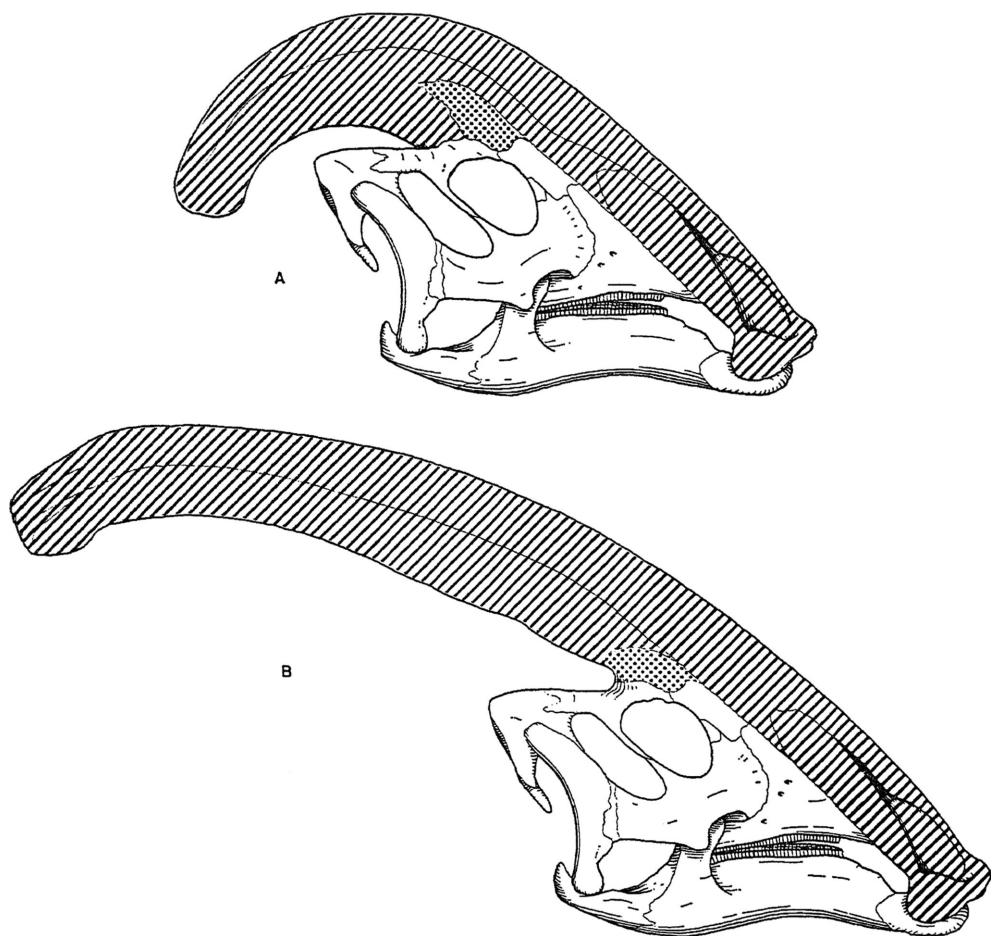


FIG. 15. Comparison of nasal crests in two lambeosaurian species, illustrating the relative importance of the premaxilla (oblique pattern) and nasal (stippled pattern). Quadrate-premaxilla length drawn to unit scale. A. *Parasaurolophus cyrtocristatus*, C.N.H.M. No. P27393 (skull reconstructed from *P. walkeri*). B. *Parasaurolophus walkeri*, R.O.M. No. 768.

half of its total length, it meets or terminates close to the upper border of the lower branch of the premaxilla. This junction is incompletely developed and generally is marked by an elongate opening between these two bones. Posteroventrally the nasals appear to unite firmly by a strongly grooved sutural surface with the underlying frontals, as in *Lambeosaurus* (N.M.C. No. 8502) and several partial crania of crested hadrosaurs (R.O.M. No. 1940, U.S.N.M. No. 11893).

The two nasals meet in the midline of the crest along a distinct peripheral suture. In all specimens of *C. casuarius* the nasals, and the crest in general, are surprisingly thin. Other species (*C. intermedius* and *Hypacrosaurus altispinus*) show a greater inflation of the nasals. Obviously both type specimens of *C. casuarius* have been distorted by lateral crushing, and it is reasonable to assume that the crest now exhibits less than its original thickness.

Internally the nasal is characterized by a relatively large and complex system of narial cavities and passages. The separated narial passages of the premaxillaries meet in a common cavity just prior to their entrance into the nasal portion of the crest. Within the nasals this cavity appears to become at least partially redivided into two lateral cavities, one in each nasal, enclosed by lateral and medial bony walls. These nasal cavities appear to extend almost to the posterior limit of the nasal and to occupy approximately half of its total height. The median septum, formed by the medial nasal wall and separating these lateral narial pockets, is incompletely preserved in the partial crest of *C. casuarius* (A.M.N.H. No. 5348). Whether or not the separation of these lateral cavities, either by bone or membrane, was complete during life has not been determined. It does appear that the narial passages enter a common chamber ventrally in the various crested hadrosaurs, for a single opening can be seen at the ventral margin of the nasal in *C. excavatus* (N.M.C. No. 8676) just rostral to the frontals. These narial passages are discussed in detail in a following section of this report.

#### JUGAL

This element is particularly distinct in the plesiotype of *C. casuarius*. Situated beneath

the orbit and the infratemporal fossa, it forms the ventral margin of the skull. It is a thin, elongate bone with rather sinuous upper and lower margins and appears to have been convex laterally in its uncrushed form. This lateral bowing undoubtedly provided for the movement of the coronoid process beneath it, as well as for the lateral bulging of the mandibular muscles during adduction of the mandibles.

Anteriorly the jugal is quite broad in its dorsoventral dimension, thereby forming a broad base for articulation with the maxilla and lacrimal. This broad articular surface provides a roughly grooved sutural contact with these adjacent elements. Immediately behind the union with the maxilla, there is a marked vertical constriction; the upper margin of the jugal at this constriction forms the lower border of the orbit. A slender, tapering process ascends from the midpoint of the jugal just behind the orbit to meet the descending process of the postorbital and thereby separates the orbit from the infratemporal fenestra behind. The ventral margin of the jugal is marked by a pronounced ventral lobe which descends to the level of the maxillary dental battery in the vicinity of the coronoid process. In general, the ventral margin is quite thin and obviously did not accommodate any muscular attachment, although the ventral lobe of the jugal, which is a universal hadrosaurian character, was considered as a possible attachment area of the *M. levator anguli oris*.

The posterior extremity, as is its opposite, is expanded in a vertical plane to provide a large squamose articulation with the quadratojugal. The lower limit of the infratemporal fenestra is defined by the posterior half of the jugal. The overlapping junction of the jugal with the quadratojugal, while not a firm union, certainly would appear to have allowed little if any movement between these elements. Examination of these surfaces in numerous hadrosaurian skulls failed to turn up any evidence of sliding motion in this area. Displacement of the quadratojugal is not uncommon in hadrosaurian specimens, but the sutural surfaces of the bones in question always lack true articular facets, which might be expected in areas of significant mobility. It therefore seems quite certain that the

quadratojugal and jugal were joined in a moderately firm union.

#### QUADRATOJUGAL

Situated between the quadrate and the jugal and largely overlain superficially by the latter is the small, thin, oval-shaped quadratojugal. Anterolaterally this bone articulates by an extensive, squamose-like suture with the jugal. The posterior margin is somewhat thickened and flattened where it butts against the anterolateral quadrate margin. This contact apparently was not firmly ossified, for this element is frequently displaced or missing, but there is no evidence of any mobility between these bones. The lack of articular facets, along with the buttress type of contact between the quadratojugal and quadrate, appears to eliminate this region as one of significant motion.

#### QUADRATE

This stout bone creates the nearly straight, vertical, posterior profile of the corythosaurian skull and in lateral or posterior aspect is one of the dominant cranial elements. The main body of the quadrate forms a slightly curved shaft, which descends from the squamosal to its junction at midlength with the jugal and quadratojugal, and from which point it continues ventrally to the mandibular cotylus.

In lateral aspect the quadrate presents a slightly convex lateral surface and an elongate and slightly curved outline. Its anterior surface is deeply excavated into a pronounced, elongate concavity extending nearly the full length of the quadrate between the laterally situated quadrate shaft and the more medial pterygoid flange of the quadrate. Thus a horizontal transverse section of the quadrate at midlength resembles a strongly asymmetrical V, with the stoutest portion located posteriorly and laterally at the apex of the section.

The dorsal end of the quadrate is well rounded and is united with the strongly concave, socket-like surface of the squamosal. The squamosal "cotylus" would seem to have allowed some movement of the rounded quadrate head, but the precotylar process of the squamosal situated immediately anterior to the "cotylus" seems to eliminate this pos-

sibility. The ventral end of the quadrate is also rounded for articulation of the suspensorium with the mandible.

The pterygoid process of the quadrate is triangular in outline, with the apex directed anteromedially. This thin but broad process articulates by a broad, overlapping, squamose suture with the quadrate process of the pterygoid medially. The posteromedial surface of the quadrate shaft displays a slight medial projection or ridge, against which a stout posterior shaft of the pterygoid abuts anteriorly, apparently reënföring quadrate immobility. (See fig. 74B.)

#### SQUAMOSAL

An important union between the cranium and the maxillary segment is effected by the squamosal. Situated at the dorsal, posterolateral corner of the skull, it forms the lateral portions of the occipital crest as well as the posterior region of the upper temporal arch.

The anterior process of the squamosal meets the postorbital in an irregular oblique suture. Medially a strong digitate suture unites the parietal with the squamosal, while on the occipital surface of the skull a pronounced sutural contact is visible between the squamosal and supraoccipital medially and the exoccipital-opisthotic complex laterally. As noted above in the discussion of the parietal, the squamosals meet in the midline in a very narrow junction on the occipital cranial surface. The posterior extension of the parietals between the squamosals has almost completely separated these elements in the type specimens of *C. casuarius*. Sectioned crania, however, show that the ventral surface of the squamosals has fused with the dorsal surface of the supraoccipital, thereby firmly uniting the cranium and the maxillary segment in this region.

The ventrolateral region of the squamosal is marked by two prominent ventral processes: the precotylar and postcotylar processes which border the upper part of the quadrate shaft. Between these processes is the deep, laterally exposed, and rounded quadrate "cotylus" which provides a relatively limited articular socket for the head of the quadrate. In general, the squamosal is irregularly quadriradiate, relatively massive and strongly convex externally, with an equally

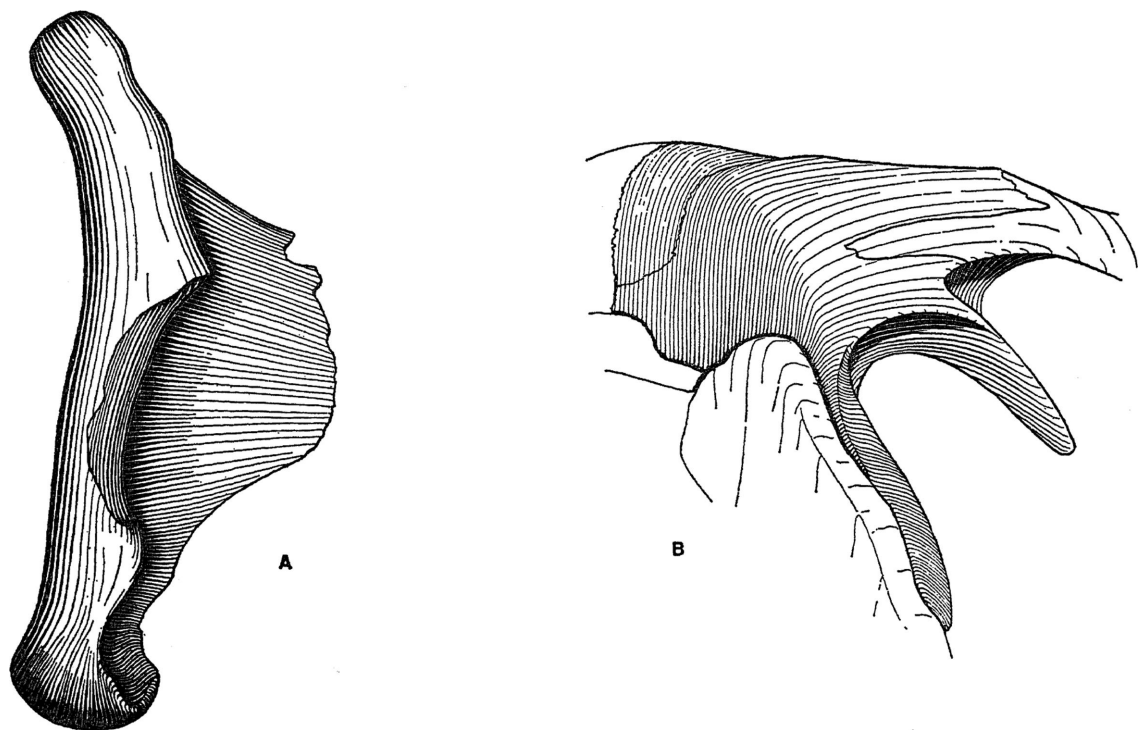


FIG. 16. A. Right quadrate of *Corythosaurus casuarius*, A.M.N.H. No. 5338, in anterolateral view.  $\times \frac{1}{2}$ . B. Right squamosal of *Corythosaurus casuarius*, A.M.N.H. No. 5338, in posterolateral view, showing the socket-like "cotylus."  $\times \frac{1}{2}$ .

concave medial surface forming the latero-posterior wall of the supratemporal fossa. The precotylar process closely adjoins the quadrate shaft, although it is not fused with this bone, while the postcotylar process, resembling the paroccipital process, is joined with that hook-shaped process laterally. (See figs. 16B and 74A.)

#### LACRIMAL

Superficially the lacrimal appears to be a thin, triangular bone situated between the jugal and the prefrontal, forming the anterior orbital rim. Actually this bone is more nearly subrectangular in lateral view, but the overlapping jugal obscures its lower portion. It is bordered ventrally by the maxilla, ventrolaterally by the jugal, anteriorly by the premaxilla, and dorsally by the narrow anterior process of the prefrontal. All these contacts are broadly overlapping sutures which create the impression of a somewhat smaller bone than is actually the case.

The broad concave posterior surface of the

lacrimal, which forms the anterior wall of the orbital cavity, is penetrated by a moderately large foramen which has been interpreted as the lacrimal canal by several authors (Lambe, 1920; Lull and Wright, 1942). The route of this canal could not be determined in any corythosaurian material, but Lambe (1920) describes its course in *Edmontosaurus* in some detail.

#### PREFRONTAL

The prefrontal forms a large part of the upper orbital rim between the lacrimal and the postorbital. Although figured as a narrow, elongate bone by Lull and Wright (1942) in their figure of the holotype of *C. casuarius*, this bone is probably incomplete. The plesio-type displays a much larger triangular bone which rises higher on the crest and overlaps the lower part of the nasal. The lateral surface is gently convex and terminates in a strong ventral ridge, the superior orbital rim. Its ventral surface, which forms the dorsal wall of the orbital cavity, is strongly concave.

In both the holotype and plesiotype, the prefrontal is firmly united by digitate sutures with the lacrimal in front and the postorbital behind. Dorsally it abuts, but is not united with, the lower branch of the premaxilla, and dorsoposteriorly it articulates by a squamose suture with the lower part of the nasal. Its medioposterior extremity is in contact with the anterior lateral border of the frontal.

#### POSTORBITAL

Lying posterior to the prefrontal on the dorsolateral margin of the skull is the four-pronged postorbital, interpreted by Gilmore (1924b) as the fused postorbital and postfrontal, and termed the postfrontal by some authors. In *Corythosaurus casuarius* this bone forms the posterior part of the dorsal as well as most of the posterior rim of the orbit. A stout anterior process of the postorbital extends forward over the orbit where it meets the prefrontal in a digitate suture. A very slender descending process meets the ascending process of the jugal in an oblique overlapping contact to form the delicate postorbital bar and separate the large oval orbit from the high, narrow, infratemporal fenestra. Extending caudally, a rather stout and long process forms much of the upper temporal arch. This articulates posteriorly with the anterolateral margin of the squamosal by an irregular, digitate suture. Medially, a broad and massive prominence of the postorbital meets the frontal in a strong digitate suture which indicates a solid union at this point between the neurocranial and maxillary segments. Although cranial sutures in the interorbital region are obscure, it appears that the postorbital, in its most posterior contact with the cranium, overlaps and is united with the anterior portion of the laterosphenoid. This, however, has not been definitely established in any of the corythosaurian specimens, as the precise condition of the orbital wall is not completely known.

#### PTERYGOID

Although incompletely exposed in most articulated skulls, the pterygoid is one of the more unusual and complex bones of the hadrosaurian skull. Situated ventral and slightly lateral to the brain case and medial to the jugal, it is distinctly triradiate in form.

Long, thin, and frequently broad alar processes provide the contacts with adjacent elements—the quadrate, maxilla, and palatine.

From the topographic center of the pterygoid, a point almost directly medial to the ventro-anterior corner of the lateral temporal fenestra, the most obvious extension is the broad "wing" of the quadrate process which extends posterolaterally almost to the quadrate shaft where it is overlapped laterally by its counterpart of the quadrate. The dorsal margin of this quadrate process ascends steeply posteriorly, giving the appearance of a greatly expanded projection. The main portion of this "wing" is very thin, except for a stout medial ridge or bar, which forms its ventral margin. This ridge extends laterocaudally to an articulation against the medial surface of the quadrate shaft, forming a strong buttress. (See fig. 74B.)

A second, shorter, and more massive extension of the pterygoid, the ectopterygoid process, extends ventrally to articulate with the posteromedial surface of the ectopterygoid and the caudal extremity of the maxilla. The large, but thin, anterior process of the pterygoid is the most inadequately known portion of this bone because of its position concealed beneath the superficial maxilla and premaxilla. Ascending as a broad "wing" towards the preorbital region, it appears to articulate with the upper medial surface of the palatine. Its ventral portion may also articulate with the dorsal margin of the maxilla and vomer, but such articulation has not yet been established in this species.

Situated as the pterygoid is between the maxillary and neurocranial segments, with its articulations located in three widely separated areas of the superficial skull segment, the next pterygoid articulation is most critical. On its ventromedial surface, at the base or anterior extremity of the quadrate process, it comes in contact with the pterygoid process of the basisphenoid. Although each of the previously mentioned contacts is an overlapping articulation which appears not to have permitted any sliding between elements, this articulation with the basisphenoid very definitely appears to be a mobile junction. The basisphenoid process, extending ventrolaterally, fits into the medial groove of the quadrate "wing" of the pterygoid. There is no

fusion of these bones in any of the hadrosaurian skulls examined, and the smooth, rounded surfaces at the point of contact certainly suggest some degree of mobility at this point. These surfaces might very well be the result of articular abrasion. This question of intracranial mobility requires more detailed consideration, which is deferred to the following section on functional anatomy.

#### ECTOPTYERGOID

Situated on the lateral and posterior surface of the maxilla, this small bone forms the posterior part of the maxillary shelf. It is a long, narrow bone, which is quite thin except posteriorly where it attains its greatest thickness. Ventrally and medially it is united by an extensive squamose suture with the maxilla. Posteromedially it articulates with the caudal process of the pterygoid. Frequently this bone is poorly preserved or inadequately exposed by preparation, but it is well displayed and easily defined in the plesiotype of *C. casuarius*.

#### PALATINE

Only the posterior portion of the palatine is observable in either of the type specimens of *C. casuarius*, but this appears basically similar to that which is well exposed in *C. excavatus* (N.M.C. No. 8676). Here the palatine is roughly triangular in shape and quite thin, except at its ventral margin. Ventrally and anteriorly it overlaps the dorsal margin and part of the lateral surface of the maxilla in the area medial to the jugal. The upper portion of its anterior margin meets the posterior extremity of the vomer. Dorsally the large anterior (or palatine) process of the pterygoid laterally overlaps the upper edge of the palatine. This squamose articulation, which is similar to that between the pterygoid and quadrate, may have permitted some degree of sliding between these elements, but again there is no evidence in these surfaces of any motion in this region.

#### VOMER

This bone is not visible in either of the type specimens of *C. casuarius*, and therefore it again becomes necessary to rely on the plesiotype of *C. excavatus*. In view of the general similarities between these two species,

it is considered worthwhile to include a brief description of this bone in the latter species.

Situated along the midline between the ascending processes of the maxillaries and the dorso-anterior portions of the palatines are the small vomers. In *C. excavatus* the vomer is long, thin, and tapered, the greatest width occurring close to the posterior termination. Anteriorly it tapers uniformly to a sharp anterior extremity. The vomer articulates with its counterpart medially and with the dorso-medial surfaces of the palatine and maxilla laterally.

#### MANDIBULAR SEGMENT

The hadrosaurian mandible is unique among reptiles in its unusually massive character. Undoubtedly this is the result of the extensive modification of the dentition and the development of the large dental batteries which required a strong foundation.

The mandible is formed of six distinct bones, of which the dentary is by far the most important, accounting for more than 80 per cent of the mandibular length. The total mandibular length in *Corythosaurus casuarius* is 645 mm. in the plesiotype and 670 mm. in the holotype, of which more than half is occupied by the mandibular dental battery. The robust coronoid process rises from the lateral dentary surface approximately 185 mm. from the caudal end in the plesiotype. Posteriorly the retroarticular process is upturned and is strikingly short in view of the immense size and weight of the mandible. Perhaps the shortness of this process is a reflection of this great size, as the weight of the lower jaws would be a significant factor in the depression of the mandible, thereby making a reduction in the necessary length of the retroarticular process possible. Anteriorly the mandibular rami meet in a short and weakly developed symphyseal union.

In lateral aspect the mandible is moderately curved, convex downward in its posterior portion, and concave downward in its anterior half. In dorsal view the mandible is slightly convex laterally, with both ends converging towards their counterparts.

#### PREDENTARY

The prementary is a median, unpaired, scoop-shaped element, which articulates

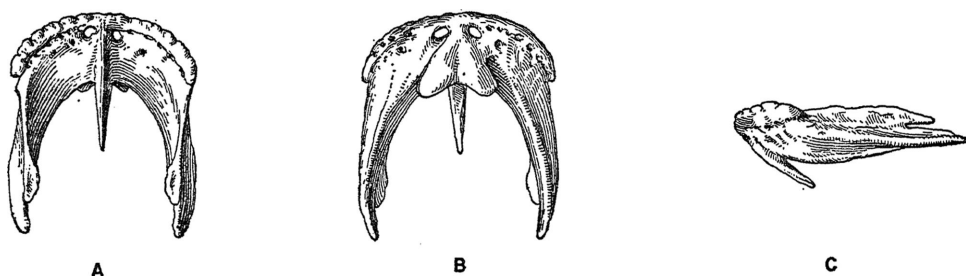


FIG. 17. Predentary of *Corythosaurus casuarius*, A.M.N.H. No. 5338. A. Dorsal view. B. Ventral view. C. Lateral view.  $\times \frac{1}{2}$ .

rather loosely with the distal extremities of the paired dentaries. While present in both of the type specimens, it is best preserved in the plesiotype. Here its anterior margin is rounded and quite broad, terminating in a slightly thickened, denticulate border which is irregularly penetrated by numerous foramina that probably represent circulatory passages. Posteriorly, two well-developed caudal processes overlap the dentaries laterally. A smaller medial process extends back over the symphysis dorsally, while an even shorter bilobed ventral expansion articulates with the ventral surface of the symphyseal region. The predentary is strongly concave along its posterior margin and thus U-shaped in dorsal aspect. The superior surface is likewise strongly concave, creating the scoop-like form of this bone.

The denticulated and perforated nature of the anterior margin, like that of the premaxilla, has been interpreted as the scar of attachment of a lower horny beak. No such structure, however, is known to have been preserved (except as impressions) in any hadrosaurian material.

#### DENTARY

This is the largest of the mandibular bones, measuring 510 mm. in the plesiotype, in which the total jaw length is 645 mm. Anteriorly the dentary ends in a rather blunt termination which is very weakly joined with its opposite. The overlapping predentary and its horny sheath may have greatly strengthened this articulation, but such a possibility cannot be verified. Passing caudally from the symphysis, the edentulous anterior portions of the dentaries are close together and essentially parallel. At about midlength, however,

they begin to diverge, sweeping laterally in a broad curve which places the coronoid processes a maximum distance apart. Behind the coronoid region the rami maintain this broad curve, thereby bringing the retroarticular processes closer together. Posteriorly the dentary terminates in two large, blade-like processes above and below the large Meckelian groove just posterior to the coronoid process. The posterior enlargement of the Meckelian groove determines the size and position of these caudal extremities of the dentary.

Anterior to the posterior terminations, the prominent coronoid process bows out from the lateral dentary surface and ascends medial to the jugal arch and well lateral to the plane of the dental batteries. It is interesting to note, in addition to the very robust nature of this process, its unique position and attitude. As a result, most likely, of the rearward expansion of the dentition, the coronoid process does not arise from the dorsal surface of the dentary. Instead it extends outward and upward from the strongly convex lateral surface well beneath the dorsal margin of the dentary and lateral to the plane of occlusion. The lateral surface of the coronoid, as is that of the dentary, is strongly convex. The medial surface is much less so and indeed is slightly concave in its upper part, perhaps reflecting an area of muscular attachment.

It should be further noted that, unlike the typical dorsoposterior inclination of the usual vertebrate coronoid process, the corythosaurian (hadrosaurian for that matter) process extends upward and forward. Thus the coronoid process extends towards the orbit rather than towards the supratemporal



fossa, a condition not found in any other vertebrate.

The medial dentary surface is moderately convex, with a thin bony plate concealing the medial surface of the mandibular battery. As in the maxilla, this medial plate overlapping the battery is penetrated by numerous small foramina arranged in a gentle curve which is concave upward. The size of these openings also varies with the position in the row, those nearer the extremities being smaller than the centrally situated foramina. The number again agrees with the total number of vertical tooth rows in the battery. The lateral dentary surface is pierced by half a dozen or more small foramina, including two rather pronounced openings in the anterior third, which Lull and Wright (1942) interpreted as mental foramina.

In the plesiotype, the mandibular battery occupies more than half of the dentary length. Here the battery length is approximately 297 mm., reaching from the dentary midpoint back to the caudal extremity. These proportions appear to be more or less characteristic of the entire family.

#### SPLENIAL

This is a small, wedge-shaped bone visible on the medial surface of the mandible ventral and posterior to the caudal portion of the battery. It, together with the uppermost of the two posterior dentary processes, forms the upper mandibular surface behind the battery, as well as roofing over the rear portion of the Meckelian fossa. Its lateral surface articulates with the medial surface of the dentary in the region of the coronoid process. It is not, however, firmly united with the dentary. The most posterior dental foramina of the dentary are concealed by this thin, overlapping bone.

#### ANGULAR

The angular of *C. casuarius* forms the ventral and ventromedial margin of the posterior half of the mandible. As a long, thinly tapering element, it is applied to the medial surface of the dentary ventral to the Meckelian groove. Its posterior half extends beyond the dentary, forming the ventral border of the post-battery portion of the mandible. Here it articulates with the medial

surface of the surangular. This very long, slender bone measures approximately 290 mm. in length in the plesiotype and is nearly equal to half of the mandibular length, but its slender form makes it far less important than the very massive dentary.

#### SURANGULAR

Forming the largest part of the mandible behind the dental battery is the surangular, which anteriorly articulates with both processes of the dentary, completing the posterior, lateral, and medial walls of the Meckelian fossa. Ventrally and ventromedially it articulates with the angular, and medially it comes in contact with the rear margin of the splenial. Together with the small articular, it forms the retroarticular process and the quadrate cotylus. Anteriorly the surangular sends a thin plate of bone upward along the posteromedial edge of the coronoid process for nearly two-thirds of the total height of this process.

#### ARTICULAR

Together with the angular and surangular, the articular forms the retroarticular process. It is situated above the angular and medial and posterior to the surangular, contributing to the posterior half of the articulation surface for the quadrate. In general it has a subrectangular form, with an irregularly rounded anterior extremity where it meets the surangular and splenial, the latter medially. Posteriorly it curves slightly upward in the caudally tapering retroarticular process. The upper surface is transversely and longitudinally concave, while the lower surface is wedge-shaped in its contact with the angular and surangular.

#### DENTITION

The dental apparatus of *Corythosaurus casuarius* is typically hadrosaurian and therefore need not be described in great detail here, as it has been so well discussed by Lambe (1920) and Lull and Wright (1942). As in other members of the family, the teeth in this species are arranged in closely spaced vertical series, with each series consisting of three to six teeth. These are successional series, which include replacement teeth as well as the active teeth, with the replacement

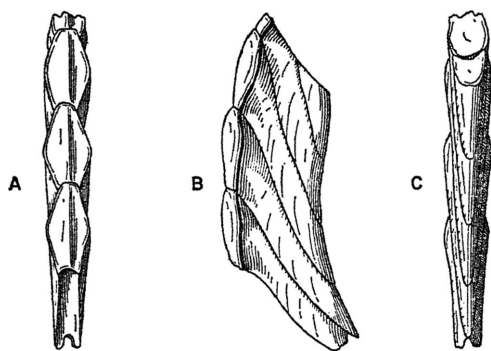


FIG. 18. Dentary teeth of *Anatosaurus annectens*, a single successional tooth series. A. Medial view. B. Anterior view. C. Lateral view. (After Lull and Wright, 1942, fig. 9.)  $\times \frac{1}{2}$ .

teeth pushing up and out of the alveolar groove and displacing the exposed and worn teeth. The plesiotype shows 39 vertical rows in the lower right battery and at least 40 rows in the right upper battery. In both the upper and lower batteries these closely spaced vertical rows form a large block or dental mosaic consisting of from 200 to 250 teeth.

Each individual tooth is diamond-shaped in cross section and fits tightly against two adjacent teeth in each of the two adjacent vertical rows. In longitudinal section each tooth is wedge-shaped, tapering towards the root and closely fitting against the preceding and succeeding teeth in its series. As illustrated in figure 18, each tooth is inclined with respect to the occlusal surface, so that two or three teeth may be functional in each row at the same time. Unlike the condition in most reptiles, the enamel is restricted to one side of the tooth or, more correctly, to the inclined crown face (the medial surface in the dentary battery and the lateral surface in the maxillary battery), so that the occlusal surface is obliquely situated with respect to the enameled crown. Thus the enamel is restricted to the medial margin of the lower occlusal surface, and the grinding surface of the dentary battery is formed chiefly by the worn dentine of the older teeth. In the upper battery, this enameled crown is concealed by the preceding tooth and therefore is not exposed just along one margin of the grinding surface but is distributed as narrow

bands between relatively thick bands of dentine (fig. 19).

The shape of the enameled crown is typically that of a diamond elongated in a vertical direction and blunted at the extremities. Each crown is marked by a pronounced vertical keel, which is continuous with keels of the crowns on preceding and succeeding teeth of the dentary battery. Because the enameled crown is overlain by the non-enameled fang of the preceding tooth in the rows of the maxillary battery, each crown is separated from crowns of preceding and succeeding teeth in the upper battery. Individual tooth size varies with the position in the battery, teeth located centrally being the largest and those nearer each end of the battery being progressively smaller.

The teeth of the lower battery are arranged in vertical rows which curve slightly outward. The enameled crowns form a mosaic pavement of keeled, diamond-shaped segments which face medially. The upper battery, however, consists of vertical series which curve inward to meet the lower battery (see fig. 71A). The occlusal surface, as a result, is inclined steeply outward, more nearly vertical than horizontal. The upper battery differs also

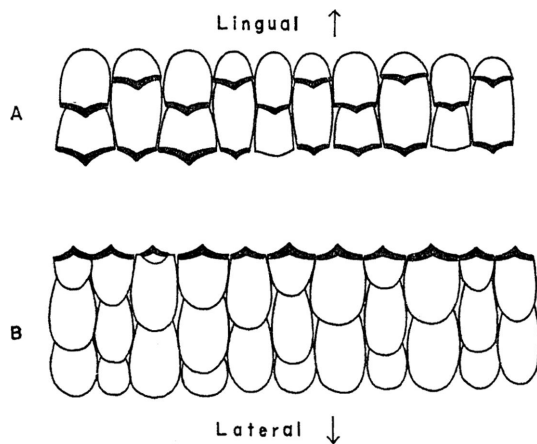


FIG. 19. Diagram of segments of the hadrosaurian occlusal surfaces. A. Right maxillary battery. B. Right dentary battery. The black bands indicate the positions of the enamel crowns of individual teeth. Notice that the enamel is restricted to the lingual margin in the lower battery but is distributed discontinuously over the grinding surface of the upper battery.

in that the enameled crowns of individual teeth are on the lateral rather than the lingual side of the teeth and, being concealed by the roots of preceding teeth, are not exposed in a broad, enameled pavement.

Lambe (1920) was the first to reveal the complexity and high degree of development of the hadrosaurian dental apparatus. Since 1920, relatively little additional light has been shed on these unique structures until Edmund's recent discussions (1957, 1960). Edmund's most recent study has shown that tooth replacement in the hadrosaurs was typically reptilian in pattern, with the replacement of the worn teeth of alternate vertical rows progressing in wave-like fashion from the rear to the front of the batteries. Replacement teeth became functional in alternate rows successively from the back forward. Figure 20A illustrates this normal

replacement pattern. An abnormal pattern, based on an unidentifiable specimen in the American Museum, is illustrated in figure 20B. This specimen was the only one examined in the course of this study that deviated significantly from the typical hadrosaurian pattern, and at present no attempt is made to explain this pattern.

Apparently the tremendous increase in the number of functional teeth and the increased efficiency of tooth replacement were necessary responses to the relative inefficiency of tooth structure and the grinding motion of the lower jaws. The restricted distribution of enamel on the occlusal surfaces must have contributed to rapid tooth wear and the necessity of developing a highly effective replacement mechanism. The tightly spaced tooth arrangement, creating a large, continuous occlusal surface, is correlated with a

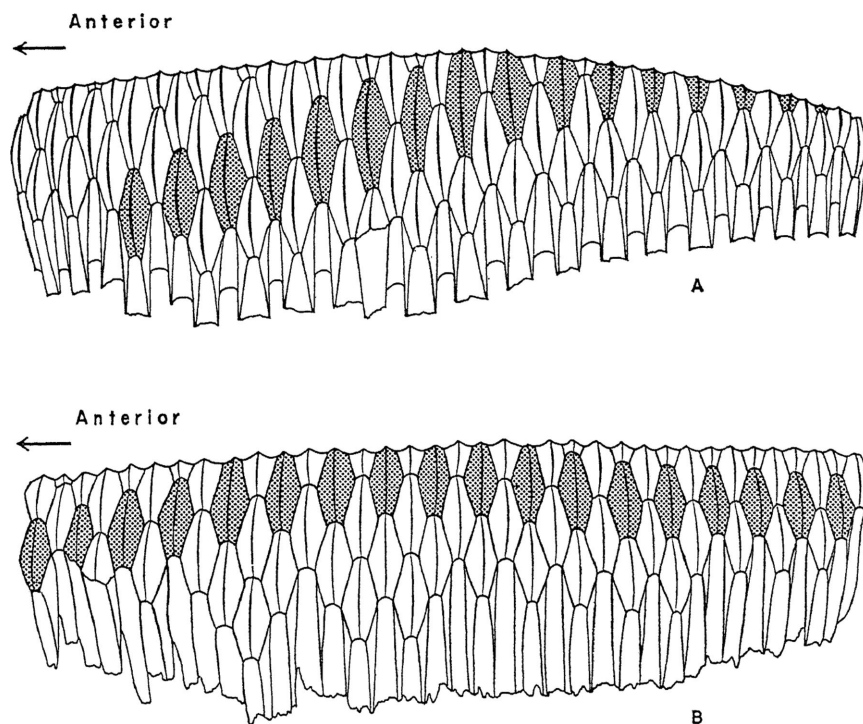


FIG. 20. Tooth replacement in hadrosaurian mandibular batteries. A. Medial view of mandibular battery, showing normal replacement pattern. Posterior teeth (to the right) are progressively more completely erupted, as shown by the tooth position of alternate vertical rows (stippled pattern). Sequence of tooth eruption is from back to front (right to left), with alternate rows subject to the same replacement cycle or wave. B. Medial view of mandibular battery of an unidentifiable hadrosaur, showing an abnormal replacement pattern. Note the high position of the central teeth in this replacement wave.

grinding type of mastication (discussed in detail in another section of this paper).

## ACCESSORY ELEMENTS

### HYOID APPARATUS

Elements of the hyoid apparatus are frequently associated with hadrosaurian remains. As noted elsewhere, hyoid bones have been found associated with the skeletal remains of *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), *Saurolophus osborni* (A.M.N.H. No. 5220), *Lambeosaurus lambei* (A.M.N.H. Nos. 5353 and 5373), and both type specimens of *Corythosaurus casuarius* (A.M.N.H. Nos. 5240 and 5338). In general, the remains of these elements are quite similar in all these specimens, so only those of *Corythosaurus* are described here.

In view of the similarity of the hyoid elements in each of these four genera and their high degree of ossification, they are considered to be the same bones in each case and are interpreted as the first ceratobranchials. In modern reptiles the first ceratobranchial occupies a dominant position in the hyoid system and is usually the most highly ossified of all modern reptilian hyoid elements, probably because of its intermediate position in the hyoid where it provides attachment areas for both the prehyoid and posthyoid musculature. The ceratohyal plays a comparatively minor role, the second ceratobranchial none at all, in the supporting framework of the hyoidal musculature. Therefore, it seems logical, in view of the frequency of preservation of this one element and the failure of any other hyoid bones to be preserved, to assume that this bone is the first ceratobranchial.

Both of the first ceratobranchials can readily be seen in the holotype of *C. casuarius* as it is presently displayed, located beneath

the posterior third of the mandibles and closely paralleling the rear margins of the lower jaws. The same bones, measuring 233 mm. in length, are also preserved in the plesiotype, although they are not so readily seen in this specimen. Each unit is strongly compressed anteriorly but becomes more cylindrical and tapering posteriorly, terminating in a rounded, blunt end which is bent upward in a slight curve similar to that of the retroarticular process. The elements preserved are obviously paired, being very nearly mirror images of each other. There is no evidence to suggest that they were articulated, nor is there any evidence indicating their relationship with other hyoidal elements.

### ORBITAL ELEMENTS

One of the exceptional features of the plesiotype of *C. casuarius* is the presence of the sclerotic plates, almost perfectly preserved in the orbital cavities. These elements are extremely thin and delicate, yet they have been preserved in their natural arrangement. Sclerotic ossifications are known in many vertebrates exclusive of modern amphibians and have been described in numerous dinosaurs, including *Plateosaurus*, *Diplodocus*, *Struthiomimus*, and *Centrosaurus*, to name only a few. Among the hadrosaurs they have been recorded in *Prosaurolophus maximus* (A.M.N.H. No. 5386), *Saurolophus osborni* (A.M.N.H. No. 5220), *Procheneosaurus praeceps* (A.M.N.H. No. 5340), *Procheneosaurus cranibrevis* (N.M.C. No. 8633), *Cheneosaurus tolmanensis* (N.M.C. No. 2246), *Anatosaurus annectens* (S.M. No. R4036), *Lambeosaurus lambei* (R.O.M. No. 1218), and now in *Corythosaurus casuarius* (A.M.N.H. No. 5338). Brown (1912b) was the first to describe these elements in a hadrosaur (*Saurolophus*). Edinger (1929b) described those of the Senck-

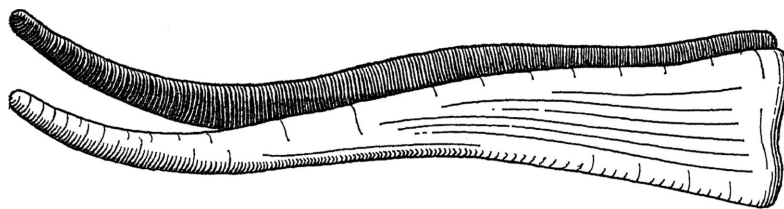


FIG. 21. The first ceratobranchials of *Corythosaurus casuarius*, A.M.N.H. No. 5338, lateral view from the right side.  $\times \frac{1}{2}$ .

enberg *Anatosaurus*, and Russell (1940) most recently described the sclerotic plates of *Lambeosaurus*.

Lemmrich (1931) notes that two basic arrangements have been observed in vertebrate sclerotic plates. The first of these, designated Type A by Lemmrich, consists of a ring of hexagonal plates which can be separated into four nearly equal quadrants. These quadrants are defined by four key plates which are visible in lateral view. Two plates, designated positive plates, laterally overlap both adjacent plates, while two others, designated negative plates, are overlapped by both adjacent plates. The two positive plates occupy dorsal and ventral positions within the sclerotic ring, while the negative plates are located anteriorly and posteriorly in this structure. These key plates divide the sclerotic ring into nearly equal quadrants, although the number of plates may not be the same in all quadrants. Lemmrich's second arrangement, Type B, is divided into distinctly unequal halves by a single, ventral, positive plate, which overlaps both adjacent plates, and a single, posterior, negative plate, which is overlapped by both adjacent plates.

Although Brown's reconstruction of the sclerotic ossifications in *Saurolophus* differs distinctly from both of these types (Brown restored the plates in a continuously overlapping series with each plate overlapped by the next plate clockwise), it appears certain that the hadrosaurian sclerotic ring is of the Type A pattern. Edinger (1929b) demonstrated the Type A arrangement in the Senckenberg *Anatosaurus*, as did Russell (1940) in his restoration of the sclerotic plates in *Lambeosaurus*. This condition is true also of the plesiotype of *C. casuarius*, and, if preservation permits, it most probably will be shown to exist in all other members of the family.

The sclerotic plates of *C. casuarius* are in the form of elongate hexagons, with all margins, except the inner edge, slightly denticulate. In most cases, they are all slightly concave laterally, although not uniformly so. A total of 14 plates (as compared with 13 in *Saurolophus*, 13 in *Anatosaurus*, and 14 in *Lambeosaurus*) are arranged in the Type-A pattern. Excluding the key plates, the antero-

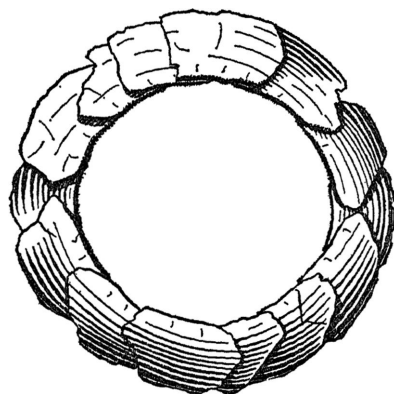


FIG. 22. Right sclerotic ring of *Corythosaurus casuarius*, A.M.N.H. No. 5338.  $\times \frac{1}{2}$ .

superior quadrant consists of two plates; the antero-inferior quadrant, of three plates; the postero-inferior quadrant, of two plates; and the posterosuperior quadrant, of three plates. While the pattern is consistent in *Corythosaurus*, *Lambeosaurus*, and *Anatosaurus*, the number of elements in specific quadrants varies. The dimensions also vary from approximately 60 mm. in outside diameter in *Lambeosaurus* to nearly 70 mm. in *Corythosaurus*.

Considerable discussion of the function of sclerotic plates has been recorded in the literature. Brown (1912b) suggested that they aided in the dilation of the pupil, a theory that is opposed by Edinger on the evidence gained from experiments on the lizard *Ophisaurus*. Others have suggested that they aided in supporting and maintaining the shape of the eyeball, which seems unlikely in view of the extreme diversity of the habitats occupied by the forms endowed with such structures and the presence in these same environments of related forms that are not similarly endowed. The function of these structures, therefore, has not yet been determined.

#### AUDITORY APPARATUS

It is fortunate that the preservation is so fine in the plesiotype of *C. casuarius*, for this specimen has contributed much of our knowledge about the auditory apparatus of the Ornithischia (Colbert and Ostrom, 1958). The left stapes is nearly completely preserved in its natural position in this remarkable specimen, marking the second known hadro-



FIG. 23. Left stapes of *Corythosaurus casuarius*, A.M.N.H. No. 5338. (From Colbert and Ostrom, 1958, fig. 9a.)  $\times 1$ .

saur in which this bone has been preserved. [Versluys in 1923 briefly mentioned the existence of a stapes in *Anatosaurus* (*Trachodon*) *annectens*, S.M. No. R4036.]

The stapes of *C. casuarius* has the form of a nearly cylindrical rod approximately 50 mm. in length, with a maximum diameter of about 2.5 mm. at its distal end. The proximal end is embedded in the fenestra ovalis at the anterior border of the opisthotic, just medial to the anterior margin of the dorsal end of the quadrate. No expanded foot plate was observed, and, in view of the position of the stapes, it seems likely that this structure is present within the fenestra.

The stapes passes posterolaterally to its slightly expanded distal termination just behind the quadrate and anterior to the paroccipital process, as illustrated in plates 5 and 6. The distal termination is medial to the external quadrate surface, indicating the probability of the existence of a more distally situated, extrastapedial element which completed the connection with a superficial tympanic membrane. The expanded distal end is interpreted as an enlargement for the articulation of this extracolumella.

The position of this stapes verifies the supposition that the ornithischian external ear was located between the quadrate and the paroccipital process, as suggested by Lull and Wright (1942). Indeed, their prediction of the position of the stapes and its dimensions is remarkably accurate. The presence of a tympanum is quite safely established with this discovery, because, lacking a tympanic membrane, there is no functional explanation for the existence of the columella auris. Similarly, a sense of hearing is indicated, for of all modern vertebrates only *Sphenodon* and specialized burrowing lizards and snakes have undergone reduction of the external auditory apparatus. Even in these forms, however,

hearing is retained, although it is effected largely through bone conduction.

### CRANIAL CRESTS

The hadrosaurs are primarily noted for the varied and strange crests or hoods which surmount the skulls of many species, although these structures are not characteristic of all members of the Hadrosauridae. Much has been written about the form, function, and taxonomic significance of these crests, but as yet there is little general agreement on these matters. The present discussion is simply a review of the morphology of the hadrosaurian crests. Their functional and taxonomic significance are reserved for discussion elsewhere.

Generally speaking, the hadrosaurian crests may be classified as two basic types: those that enclose a major portion of the narial passages and those that do not. The first type, which for purposes of clarity is referred to as the "true narial crest," is found in the various species of *Procheneosaurus*, *Cheneosaurus*, *Lambeosaurus*, *Corythosaurus*, *Hypacrosaurus*, and *Parasaurolophus* (and also, apparently, *Tsintaosaurus* from China). The second type, which is referred to as the "pseudo-narial crest," is characteristic of only three American species known to date: *Prosaurolophus maximus*, *Saurolophus osborni*, and *Brachylophosaurus canadensis*. All other hadrosaurs lack any crest whatsoever and commonly are referred to as the "flat-headed" hadrosaurs. These include the several species of *Anatosaurus*, *Edmontosaurus*, and *Kritosaurus* and presumably the less completely known species of *Hadrosaurus*, *Trachodon*, *Ornithotarsus*, *Thespesius*, and possibly also *Claosaurus*.

### NARIAL CRESTS

The true narial crests involve a dorsal and caudal expansion of both the premaxillaries and the nasals, the degree of expansion and the relative participation of these two elements varying considerably in different species, as illustrated in figures 14 and 15. Each of the narial crest varieties, however, is characterized by a dorsal and posterior elongation and complex folding of the narial passages. Most conservative of the narial crests are those typified by the three species of



FIG. 24. Skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, in posterolateral view, showing the position of the stapes. (From Colbert and Ostrom, 1958, fig. 4.)

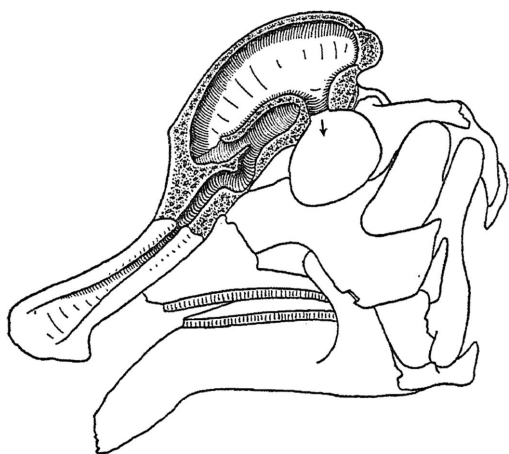


FIG. 25. Skull of *Procheneosaurus cranibrevis*, N.M.C. No. 8633, showing a reconstruction of the narial passages of the crest. Left premaxilla and nasal partially removed to illustrate the cavity pattern. The separate narial passages enter a common inflated chamber above the loop. A single opening at the base of the common cavity (arrow) communicated with the throat and trachea.

*Procheneosaurus* (*P. praeceps*, *P. erectofrons*, and *P. cranibrevis*) and the single species of *Cheneosaurus* (*C. tolmanensis*). In all these species the premaxillaries are split into superior and inferior branches lying above and below the nares. Both branches ascend caudally, almost completely enclosing the anterior limb of the narial passage on each side. The nasal occupies a position between the dorsal extremities of the two premaxillary branches, enclosing the upper portion of the narial loop.

As described by Charles M. Sternberg (1935), and illustrated here in figure 25, the narial passages ascended as separate canals from the external nares, chiefly within the lower branch of the premaxilla. Dorsally, at the anterior limit of the nasal, these canals looped forward and upward in an S-shaped curve before opening into a common median cavity at the peak of their ascent. This cavity extended slightly posteriorly, with a vertical canal descending from it to the "choana" at the level of the lacrimals and the anterior margin of the orbits. Thus the slightly inflated narial crests of *Procheneosaurus* and *Cheneosaurus* were penetrated by a looped narial passage consisting of two ascending

canals, a common dorsal chamber, and a single descending passage leading from the latter to the interorbital region.

More striking and complex are the narial crests of the numerous species of *Lambeosaurus*, *Corythosaurus*, and *Hypacrosaurus*. In *Lambeosaurus*, the very greatly expanded premaxillaries form the entire snout and nearly all of the crest (see fig. 14). The nasals are not expanded here as they are in other lambeosaurines, but they have been carried back by the posterior expansion of the premaxillaries where they form a small central area of the lateral crest wall. In contrast, with the exception of *Corythosaurus frontalis* in which the nasal is relatively small, the narial crests of all species of *Corythosaurus* and *Hypacrosaurus* are formed largely by the nasals. In these species, the premaxillaries contribute only to the anterior margin and the anteroventral part of the crest.

Most specimens of these three genera could not be disarticulated to reveal the internal pattern of the narial cavities, but a few specimens illustrate portions of these patterns. The details vary slightly with each specimen, but all indicate an expansion and complica-

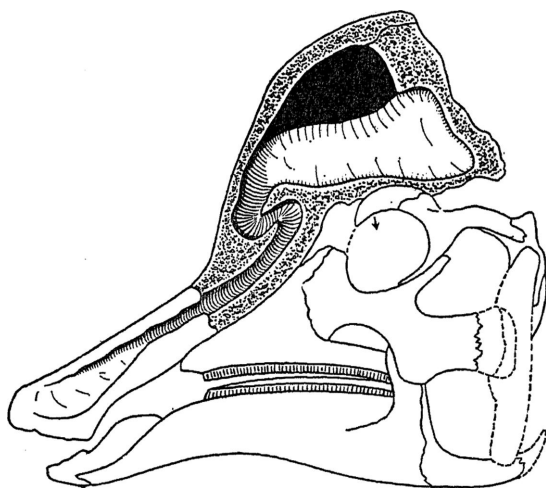


FIG. 26. Skull of *Corythosaurus excavatus*, N.M.C. No. 8676, showing a reconstruction of the narial passages of the crest. Notice that the narial passages ascend independently to a level above the preorbital loop, where they open into large lateral chambers. These open dorsally into a median chamber which leads to the interorbital region by a single canal (arrow).



tion of the same basic pattern found in *Procheneosaurus*. The plesiotype of *Corythosaurus excavatus* (N.M.C. No. 8676) best illustrates this advanced pattern (see fig. 26). Here, the separate narial passages ascend posteriorly, enclosed for most of their length by the lower rami of the premaxillaries. At the point of separation of the two premaxillary branches, both passages turn forward and then up and backward again, forming separate S-shaped curves which are divided by the median lamellae of the premaxillary upper branches. Above the S-shaped curves, the two passages expand into inferior lateral chambers which join in a common median cavity dorsally. This median cavity extends upward and caudally as a high vaulted chamber between the two premaxillaries and nasals in the upper half of the crest. At about the level of the anterior orbital margin a common canal descends from this chamber between the anterior lateral cavities to the internal nares. The lateral chambers are enclosed medially and laterally by the nasals and to a lesser extent by the inferior rami of the premaxillaries.

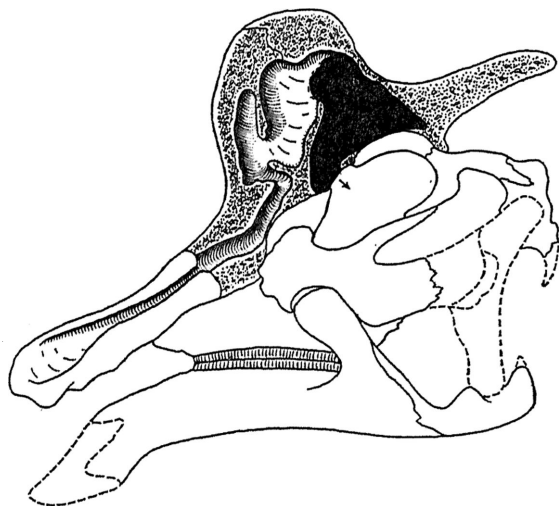


FIG. 27. Skull of *Lambeosaurus clavinitialis*, Y.P.M. No. 3222, showing a reconstruction of the narial passages of the crest. In this species the separate narial tracts become inflated above the preorbital loop in the anterior half of the crest. Posteriorly these communicate with the large median chamber which in turn is continuous with the internal nares via a common canal (arrow) in the interorbital region.

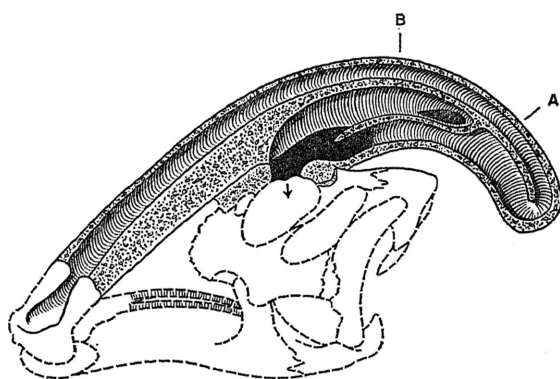


FIG. 28. Restored skull of *Parasaurolophus cyrtocristatus*, C.N.H.M. No. P27393, showing a reconstruction of the narial passages of the crest. The paired tracts are completely separate over their entire length, except at the base of the crest where they enter a common chamber. A pair of elongated chambers extend back from the common chamber between the upper and lower narial tracts. These communicate with each other posteriorly but are otherwise separated by a median septum. A "choanal" canal (arrow) is again situated above the interorbital region. The dashes above the crest indicate the positions of the cross sections of figure 29. (Skull restoration based on *P. walkeri*.)

A second specimen of *Corythosaurus* (R.O.M. No. 1933), probably of *C. casuarius*, illustrates almost exactly the same pattern, with the exception that the median chamber here appears to be somewhat less extensive dorsally and caudally. Two specimens of *Lambeosaurus* (*L. lambei*, N.M.C. No. 2869, and *L. clavinitialis*, Y.P.M. No. 3222) possess similar narial patterns characterized by the independent ascending canals with S-shaped turns. These specimens, however, differ from the above-mentioned patterns in that the median septa of the premaxillaries and nasals have not been preserved in the posterior part of the crest. The divided narial passages appear to enter the common median cavity at a more posterior position. The median cavity seems to have occupied the rear half of the crest and was divided by a median septum anteriorly. No evidence is preserved in either specimen to indicate the existence of any lateral cavities other than the inflated segments of the narial tracts in the anterior half of the crest. A common exit from the large median chamber

was again situated at the base of the crest close to the level of the orbits (see fig. 27).

Very little is known about the narial cavities of *Hypacrosaurus*. Only one incomplete crest (R.O.M. No. 702), identified as belonging to this genus, exhibits information about the crestal conditions. Here a large median chamber, apparently occupying the anterior dorsal part of the crest, is partially preserved. This probably communicated anteriorly with divided narial canals and ventrally with a common "choanal" canal. Lateral chambers or sinuses are also indicated in this specimen, occupying the ventro-posterior part of the crest as in *Corythosaurus excavatus*.

*Parasaurolophus* presents a much simpler situation than any of the hadrosaurs discussed above. Although originally reconstructed by Parks (1922) as composed of the nasals and frontals, Russell (1946) has shown

the *Parasaurolophus* crest to consist almost entirely of the premaxillaries, with the nasals contributing only to a small degree at the posterior basal region of the crest. The frontals, according to Russell, are completely excluded from this structure. As illustrated by Parks (1922), the very long crest of *P. walkeri* is traversed by four nearly circular tubes extending the full length of the crest. These are separated by horizontal and vertical bony septa. Russell (1946) first suggested that the upper pair of passages, which are continuous with the external nares, ascended to the end of the crest where they looped back beneath themselves as the lower pair of passages. These probably continued to the base of the crest, where they led down and back to the pharyngeal region. These long, paired, U-shaped passages, while apparently uncomplicated by other chambers or sinuses, form a greatly elongated but simplified version of

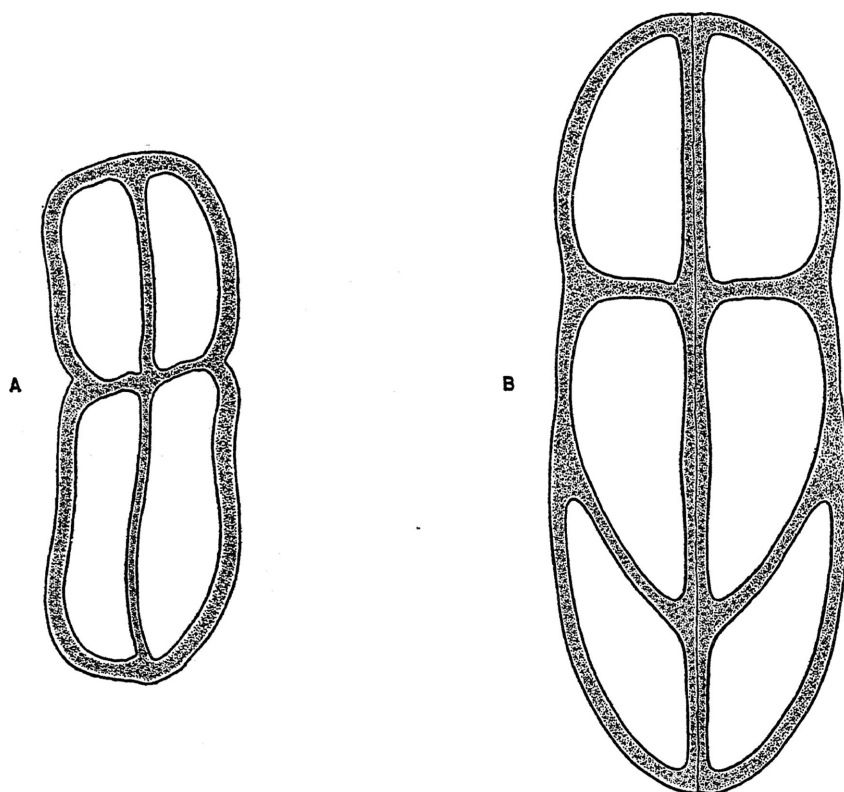


FIG. 29. Sections of the crest of *Parasaurolophus cyrtocristatus*, C.N.H.M. No. P27393. A. Distal cross section as seen in a natural break. B. Proximal section restored. (See fig. 28 for the location of these sections.)  $\times \frac{1}{2}$ .

the *Procheneosaurus* and *Corythosaurus* narial pattern.

*Parasaurolophus tubicen* differs from the type species in that the crest appears to have been traversed by a single passage. While a horizontal constriction, partially separating this passage into upper and lower tracts, may represent a formerly complete bony or membranous partition between ascending and descending passages, there is no indication in Wiman's (1931) restoration that these were ever divided by a median septum into paired passages.

A third specimen, *Parasaurolophus cyrtocristatus* (C.N.H.M. No. P27393), provides the most detailed information about hadrosaurian crestal cavities so far available. This specimen is represented by a nearly complete skeleton with a fragmentary skull bearing a complete, but much shorter and more strongly recurved crest. The total crest length in this specimen, from the crest base above the orbit to its posterior extremity, is approximately one-third of that of *P. walkeri*, and the latter species was probably slightly smaller than the former. The preservation of the skull of *P. cyrtocristatus*, unfortunately, does not permit a reliable determination of the crest components to be made, but it appears to be composed chiefly of one element: the paired premaxillaries.

Dissection of one side of the crest of *P. cyrtocristatus* established two important points, which are illustrated in figure 28. First, the narial passages extend as separate tracts over the full length of the crest. At the distal end of the crest, the paired passages loop forward and beneath themselves, passing to the base of the crest along its lower half. Only near the proximal end of these passages, in the base of the crest, do they join in a common cavity. Thin medial lamellae of the premaxillaries form a continuous wall between the canals over their entire length. A second feature, which was not suspected and which may or may not be present in *P. walkeri* and *P. tubicen*, is a pair of elongated, blind cavities situated between the upper and lower passages. These auxiliary cavities communicate with each other near their posterior limits and with the main narial passages anteroventrally. Figures 28 and 29 illustrate these cavities and their relationships.

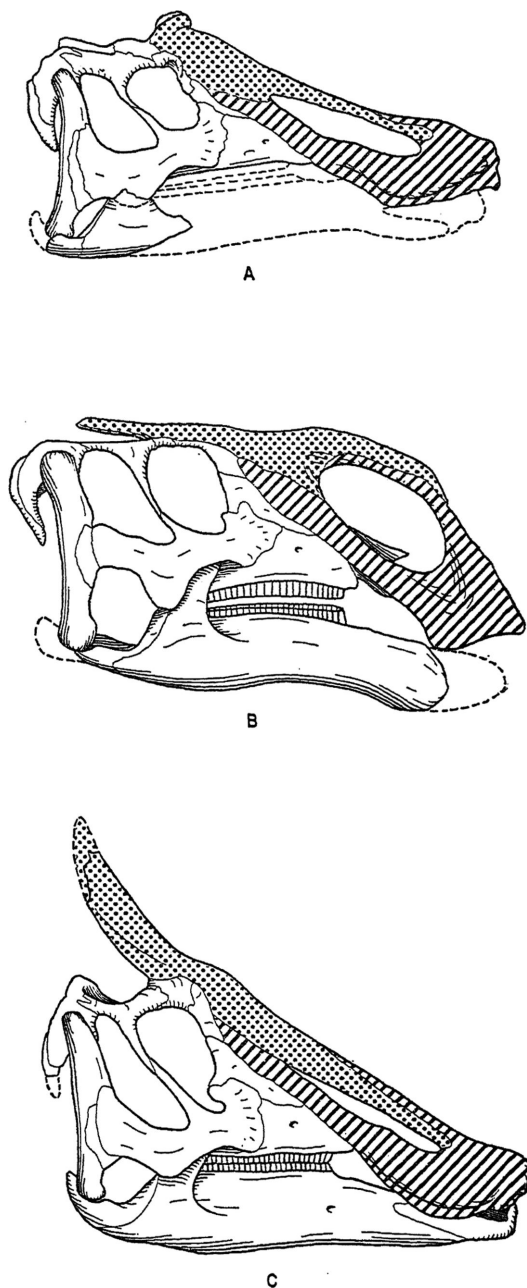


FIG. 30. A comparison of the skulls and pseudo-narial crests of the three saurolophine species. Quadrate-premaxilla length drawn to unit scale. A. *Prosaurolophus maximus*, A.M.N.H. No. 5386. B. *Brachylophosaurus canadensis*, N.M.C. No. 8893. C. *Saurolophus osborni*, A.M.N.H. No. 5220. Notice that the nasal (stippled pattern) forms the entire crest. The premaxilla (oblique pattern) fails to contribute to the formation of the crest.

## PSEUDO-NARIAL CRESTS

The pseudo-narial crests, exemplified by *Prosaurolophus*, *Saurolophus*, and *Brachylophosaurus* (see fig. 30), are quite distinct from the true narial crests in that they are not traversed by any part of the nasal system, in spite of their being constructed entirely of the nasal bones. The crest of *Prosaurolophus* is a small, anteriorly deflected protuberance which overlies the orbital region medially. At least two specimens (N.M.C. No. 2870 and U.S.N.M. No. 12712) clearly demonstrate this crest to be composed entirely of the dorsocaudal extremities of the elongated nasals, although it is strongly supported by the frontals behind and beneath. Most of the other specimens seem to substantiate this interpretation. Brown (1916a, p. 707), however, reported that this crest in the holotype (A.M.N.H. No. 5386) is "derived primarily and chiefly from the anterior lateral border of the frontals, supported at the base by the prefrontals and in front formed by the posterior prolongation of the nasals." This specimen certainly suggests such a condition, but the crushed state of the crest leaves some doubt concerning the location of the nasal-frontal suture.

The spike-like crest of *Saurolophus* is quite clearly composed of a dorsocaudal prolongation of the nasals, projecting freely above the

frontals. Neither the premaxillaries nor the frontals contribute in any way to this crest, as shown in figure 31. Although neither of the existing specimens has been sectioned, it appears that the "spike" of *Saurolophus* is not penetrated by the narial passages.

The recently discovered specimen of *Brachylophosaurus* (N.M.C. No. 8893), described by Charles M. Sternberg (1953), displays a crest which in some respects is quite dissimilar to that of *Saurolophus*. It is similar, however, in that it also is constructed entirely of the nasals and is definitely a pseudo-narial crest. The skull of *Brachylophosaurus*, which in over-all appearance closely resembles that of *Kritosaurus*, is characterized by a very broad, "paddle-like," posterior extension of the nasals (see fig. 32). The "paddle-like" crest extends back almost horizontally over the frontals and parietals, terminating above the occipital crest of the squamosals. This horizontally broad, but vertically thin structure completely conceals the superior aspect of the brain case and has the appearance of a long flat lid overlying the top of the skull and supratemporal openings. There is no doubt whatsoever that this crest is devoid of any narial passages. Most probably the narial tracts extended straight back from the external nares to an internal opening in the lower interorbital region.

From this brief review, it may be said that

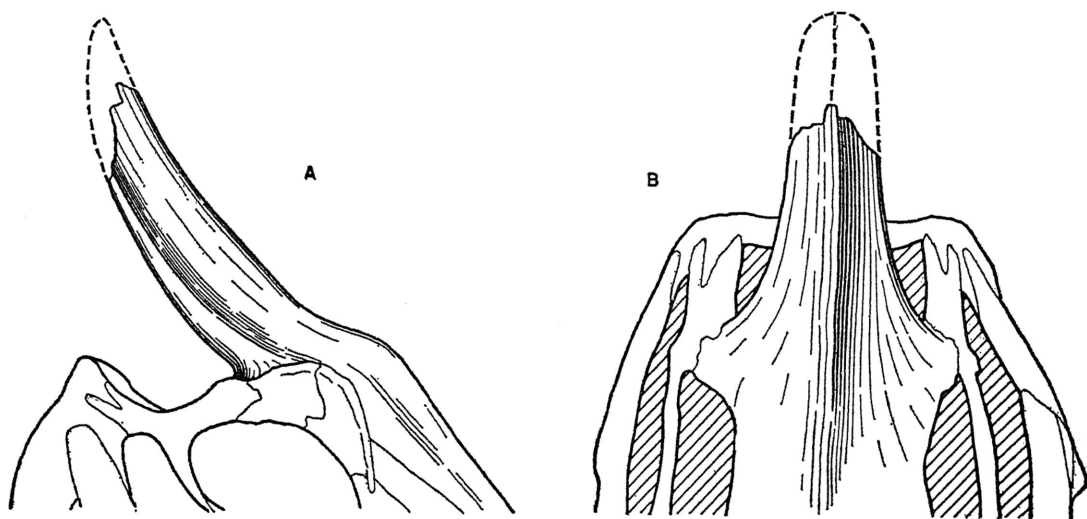


FIG. 31. Pseudo-narial crest of *Saurolophus osborni*, A.M.N.H. No. 5220. A. Lateral view. B. Anterodorsal view.

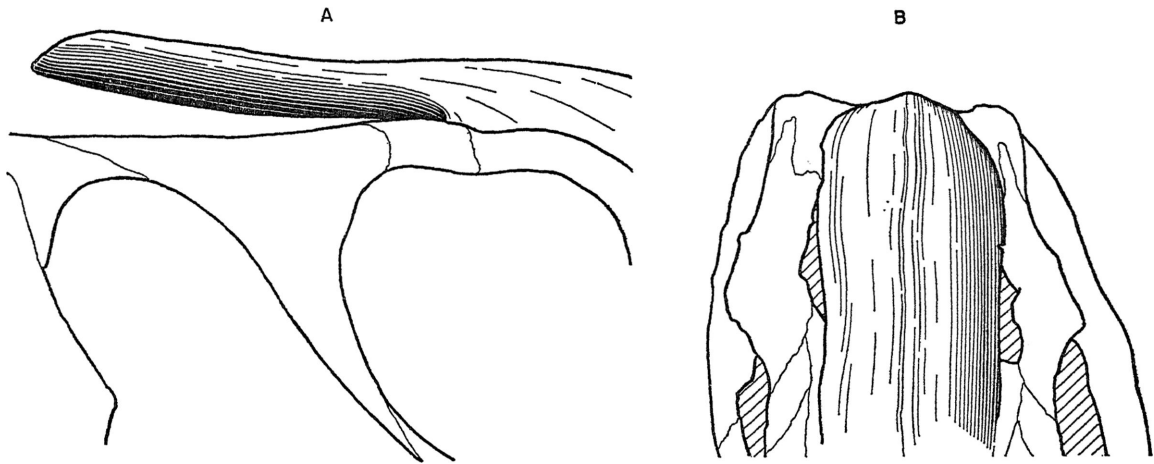


FIG. 32. Pseudo-narial crest of *Brachylophosaurus canadensis*, N.M.C. No. 8893.  
A. Lateral view. B. Dorsal view.

crested hadrosaurs were characterized by one of two distinct types of cranial crests: either the true narial crest, which enclosed the looped and in some cases chambered narial passages, or the pseudo-narial crest, which

did not enclose or include any part of the narial passages. The true narial crest is characteristic of the members of the Lambeosaurinae, while the pseudo-narial crest typifies species of the Saurolophinae.

### MYOLOGY

Reconstruction of the soft anatomy of fossil organisms can rarely be established with absolute certainty, yet frequently there is a wealth of information preserved in the skeletal remains which permits the partial reconstruction of various fleshy systems. A number of earlier works, such as those of Lull (1908), Gregory and Camp (1918), Adams (1919), Romer (1927), Russell (1935a), Anderson (1936), Olson (1936), Evans (1939), Säve-Söderbergh (1945), Colbert (1946), and Haas (1955), attempted to reconstruct the musculature of certain extinct vertebrates. Studies of this kind constitute an important part of our knowledge about ancient life, for only through such studies is it possible to approach a sound interpretation of the dynamic or functional anatomy of extinct vertebrates.

Two major difficulties are encountered in any attempt to reconstruct the musculature of fossil vertebrates, aside from the usual problem of incomplete or inadequate preservation of skeletal material. The first is the recognition of the areas of muscle attachment. These of course vary greatly with the

various muscles of a single individual, but the problem is further complicated by evolutionary differentiation, which has resulted in changes of muscle size and division and shifts in muscular attachments, as well as changes in function. Similar or identical locations and even similar functions cannot in themselves establish muscular homologies. Functional change is too well documented in the fossil record and modern comparative anatomy to allow acceptance of such homologies.

The impression of the musculature on the skeletal framework is highly variable, varying not only from muscle to muscle but from individual to individual and also with the ontogenetic stage of development. The prominence of muscular scars is partly a function of muscle size, although very small muscles may occasionally leave more distinct impressions than do much larger muscle masses. Most important of all is the manner of muscle attachment: whether by tendon or aponeurosis, or by a broad fascia of connective tissue forming a fleshy attachment. The fact that more than one muscle may attach by a common tendon presents still further complications.

It has been established by Bernhard (1924) and Augier (1931) that bony tissues react in specific ways to the stresses set up by muscular attachments and the contractions of these fibers. Bernhard states that the atrophy of bony elements results from muscular pressures, while tension, which usually develops at the point of attachment, causes the formation of bony crests and ridges. Augier, however, suggests that crests typically develop around the area of attachment rather than at the point of attachment. Thus areas of muscular attachment appear as depressions frequently defined by surrounding crests or prominences. Evans (1939) interprets such attachment as an indication that the greatest tensional stresses develop about the periphery of the attachment area, resulting in a moderate to strong crest surrounding a depressed or concave scar.

The second major problem encountered in "paleomyological" studies is the correct identification of the muscles involved. As suggested above, the problem of muscle homology is extremely complex as a result of the general inconstancy of vertebrate musculature. Muscles have repeatedly extended and shifted their attachment areas, as the skeletal framework has undergone transformation, and a division or fusion of muscle masses has occurred numerous times. With these changes there have been, of course, frequent changes in muscle function. No longer can we accept the function or position of a muscle as reliable evidence of muscular homology. Currently, however, muscle innervation appears to be quite conservative and relatively constant for most muscle masses regardless of changes in position or function. Embryological studies of muscular development generally support this concept, and at present muscular innervation is the primary basis for muscle identification.

The literature on recent reptilian musculature is quite extensive, but unfortunately much of this literature is confused by the application of mammalian terminology and implied or stated correlations with the anatomy of these more advanced tetrapods. Specifically, much of this confusion results from the extension of human anatomical nomenclature to the lower vertebrates, with the resulting erroneous implications. No attempt has been made here to unravel the existing muscle synonymy.

The major cranial muscle systems of the vertebrates can be separated into four groups: the mandibular, the branchial and hyoid, the axial, and the orbital. The orbital muscles are not discussed in this paper, simply because no impressions of the origins of these small muscles have been preserved in the hadrosaurs. The reconstruction of hadrosaurian myology that follows is based not only on the fossil evidence cited, but also on extensive dissections of numerous modern tetrapods. Occasional references to the conditions found in modern reptiles are made where these are considered significant, but detailed comparisons are not presented here, as the literature is already quite extensive.

#### MANDIBULAR MUSCULATURE

Luther (1914) contributed much to our early knowledge of vertebrate mandibular musculature in his classic study of amphibian trigeminal musculature. Subsequently, this knowledge has been supplemented by the works of Adams (1919), Lakjer (1926), Haas (1930, 1934), Edgeworth (1935), Brock (1938), Säve-Söderbergh (1945), Hofer (1950), Ingeborg Poglayen-Neuwall (1953, 1954), Ivo Poglayen-Neuwall (1953a, 1953b), Barnikol (1954), and others. Luther established the fundamental separation of the trigeminal musculature into the three functional units so characteristic of the fishes and the non-mammalian tetrapods. These three muscle groups (the adductor mandibulae, the constrictor dorsalis, and the constrictor ventralis or intermandibularis groups) are still considered to be the basic divisions of the trigeminal muscle system, having been carried on by Lakjer in his monumental work on the Sauropsida and more recently by Säve-Söderbergh (1945), Haas (1955), and others. It was Luther (1914) who also introduced the principles of adductor muscle classification according to the muscle position with respect to the branches of the trigeminal nerve.

The three groups of mandibular muscles are separated according to innervation and function rather than location. The adductor mandibulae group, which includes the superficial muscles in the temporal region, functions to close the jaws. Lying medial to this, in forms possessing kinetic skulls, is the constrictor dorsalis group, which elevates the maxillary segment. The intermandibular

muscles, extending between the mandibular rami, constitute the third functional group, which aids in swallowing and respiratory activities. In the discussion that follows, the terminology used is that of Luther and Lakjer.

#### ADDUCTOR MANDIBULAE GROUP

Luther's classification (1914) separates the adductors into external, internal, and posterior masses according to their relationships with the three branches of the trigeminal nerve. The *M. adductor mandibulae externus* is situated superficially in the temporal region, lateral to the second and third branches of the trigeminal nerve (external position). The *M. adductor mandibulae internus* lies medial to the externus and medial and anterior to the second branch of the trigeminal (intimus and internal positions). The *M. adductor mandibulae posterior* is situated medial and posterior to the third trigeminal branch (posterior position). These muscle locations appear quite constant throughout the lower vertebrates despite shifts in the positions of the origin and insertion areas or changes in muscle size. Figure 33 illustrates these trigeminal muscle positions.

The *M. adductor mandibulae externus*, and especially its most superficial portions, appear to be the most variable of the adductor muscles in modern fishes, amphibians, and reptiles. Typically the adductor externus is divisible into three parts: pars superficialis, medialis, and profundus. The variable superficialis may further split into several sheets (the superficial *M. levator anguli oris* and the deeper *M. adductor mandibulae externus superficialis proper*) with divergent fibers which may or may not be readily separated. Each portion of the externus normally originates in a distinct region, but frequently a common tendon, the bodenaponeurosis, supplies a single area of insertion for two or more parts of the externus mass.

#### M. LEVATOR ANGULI ORIS

The existence of the *M. levator anguli oris* has not yet been established in the members of the Hadrosauridae, although some evidence exists that seems to support its former presence. The significance of this evidence is, however, very difficult to assess; hence the author's hesitancy to accept one interpreta-

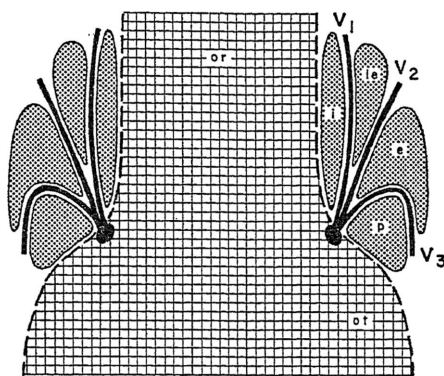


FIG. 33. Diagram of the four basic positions of the trigeminal muscles with respect to the branches of the trigeminal nerve. Abbreviations: e, external position; i, intimus position; ie, internal position; or, orbitotemporal region of the neurocranium; ot, otic region of the neurocranium; p, posterior position; V<sub>1</sub>, ramus profundus (ophthalmicus) of the trigeminal nerve; V<sub>2</sub>, ramus maxillaris of the trigeminal nerve; V<sub>3</sub>, ramus mandibularis of the trigeminal nerve. (After Säve-Söderbergh, 1945.)

tion over another. It is mentioned above that every hadrosaurian species is characterized by a pronounced ventral lobe of the inferior jugal margin. The fact that this lobe is universally characteristic of the Hadrosauridae, while it is apparently absent in all other ornithopods (with the exception of the Iguanodontidae), raises the question of the functional significance of this structure. Quite possibly the anteroventral margin of the jugal lobe served as the site of origin of the *M. levator anguli oris*, the fibers of which reached anteroventrally to the corner of the mouth in front of the coronoid process and an insertion on the quadratomaxillary ligament. If such superficial fibers existed, their attachment to the jugal lobe must have been by a tendinous sheet, for no scar or other indication of muscular attachment could be found in any of the hadrosaurian skulls.

#### M. ADDUCTOR MANDIBULAE EXTERNUS SUPERFICIALIS

The topography of the bony elements of the temporal region in the plesiotype of *Corythosaurus casuarius* offers clear evidence as to the attachments and positions of the several portions of the adductor externus. In fact good evidence indicates that the three

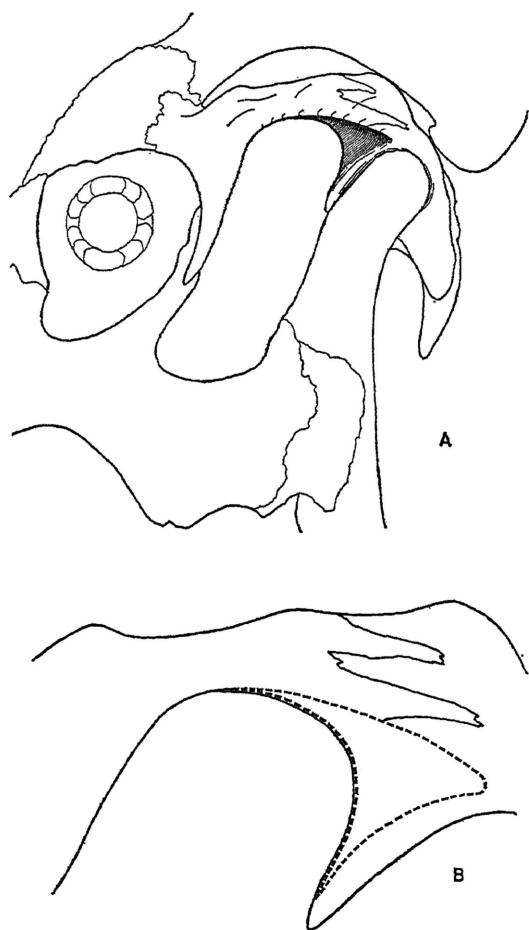


FIG. 34. The left temporal region of *Corythosaurus casuarius*, A.M.N.H. No. 5338, in lateral view. A. The origin scar of the M. adductor mandibulae externus superficialis at the dorsal border of the infratemporal fenestra on the ventrolateral surface of the temporal arch. B. Enlarged diagram of this same region, with dashed lines defining the area of origin.

major portions of the adductor externus were present and at least partially distinct. With regard to the most superficial part (here interpreted as the M. adductor mandibulae externus superficialis), at least the area of origin is distinct. The lateral surface of the squamosal, immediately above and rostral to the dorsal end of the quadrate, exhibits a small but strongly developed and well-defined depression. The lateral position of this scar on the upper temporal arch differs from the typical reptilian origin of the superficialis, which

characteristically is situated on the medial surface of this bar. Possibly this origin extended onto the lower part of the medial surface of the arch and this lateral scar provided attachment for only the more superficial fibers.

The location of this area, together with its shape, suggests that this depression is merely an incomplete extension of the infratemporal fenestra and therefore, as is the fenestra, is a reflection of the superficial temporal muscle condition. As the size and shape of the fenestrae are so closely related to the size, shape, and orientation of the temporal muscle masses, and perhaps the direct result of bone atrophy resulting from the pressures created by bulging muscle masses, this depressed area is here interpreted as the area of origin of the most superficial part of the adductor externus. Ordinarily the superficialis rarely develops such a prominent scar in recent reptiles. Why it is so prominent in *Corythosaurus*, and most of the hadrosaurs for that matter, cannot be determined, although once again it should be pointed out that the superficialis of recent forms is the most variable of the externus muscles. Another fact that may have influenced the development of such a pronounced scar is the small area involved, which would concentrate the stresses of muscular contraction and presumably cause stronger deformation of that area of bony attachment.

The insertional area is not so clearly indicated. In fact, there is no clearly defined scar to indicate the area of superficialis attachment to the mandible. The mandibular surfaces between the articulation and the tip of the coronoid process are distinctly separated into a ventrolateral and a dorsal surface, separated by a very strong and persistent dorsolateral angulation. The ventrolateral surface would seem to be eliminated as a possible insertion area because of its orientation. The broad, gently concave dorsal surface, however, appears to be logically situated in front of the articular surface to receive the fibers of the superficialis and perhaps the entire adductor externus. This surface is quite broad immediately rostral to the quadrate articulation, but it narrows rapidly near the base of the coronoid process. No distinct scars could be detected on any of the hadrosaurian mandibles examined, but all specimens ex-



hibit this well-defined dorsal surface.

It appears from this that the most likely area for the insertion of the superficialis lies on the dorsal mandibular surface between the coronoid process and the condylar facet of the articular. The width of this area may indicate that all three portions of the adductor externus attached here in one common, fleshy insertion, rather than by a bodenaponeurosis. Such, however, cannot be established. It is also possible that the insertion of these fibers extended forward onto the narrow posterior crest of the coronoid process as a tendinous insertion. This situation is commonly encountered in modern sauropsids (the more medial fibers of the adductor externus in certain Lacertilia).

The evidence for these areas of attachment of the M. adductor mandibulae externus superficialis is quite constant throughout the entire family, with only minor differences in size existing. In most hadrosaurian genera, the area of origin is deeply excavated on the lateral surface of the anterior margin of the squamosal. The only prominent deviations from this condition, in all the material examined, were found in *Corythosaurus brevicristatus* (R.O.M. No. 5856), *Parasaurolophus walkeri* (R.O.M. No. 768), *Anatosaurus annectens* (Y.P.M. No. 2182), and *Procheneosaurus erectofrons* (A.M.N.H. No. 5461). In each of the above specimens, the origin scar of the superficialis is clearly discernible, but the excavations are generally slight. In *Corytho-*

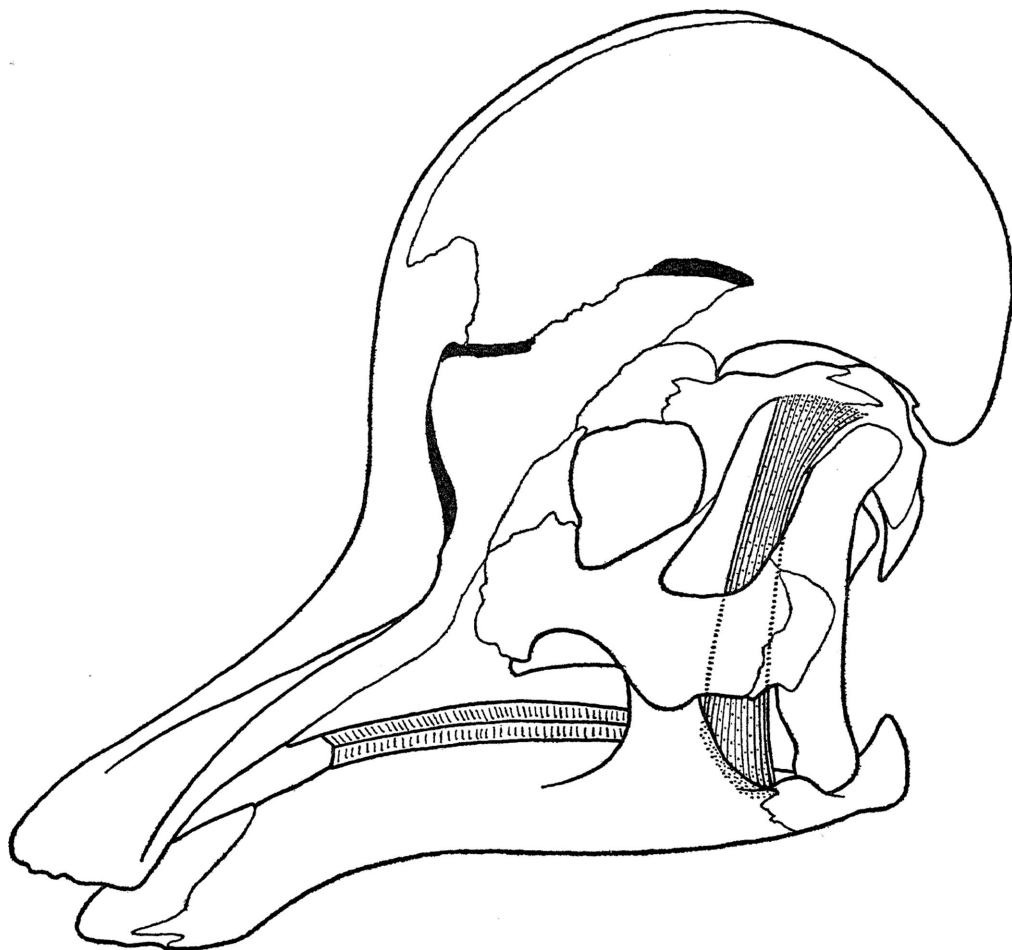


FIG. 35. Skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with the M. adductor externus superficialis reconstructed.

*saurus brevicristatus*, such a condition appears to be specific variation, although only one specimen of this species is known, because all other species of *Corythosaurus* show deeply depressed scars. The same is probably true of *Procheneosaurus erectofrons*, as specimens of other procheneosaur species possess very prominent scars. That such variation in the superficialis scar is simply ontogenetic or individual variation is possible, but cannot be established with so few specimens.

Moderate variation in the size of the superficialis scar is found throughout the family. Smaller forms, such as *Procheneosaurus*, show proportionately smaller scars. The most striking deviation, however, is found in *Edmontosaurus regalis*. The five specimens of this species all display a pronounced restriction of the upper half of the infratemporal fenestra. This opening becomes a narrow, oblique slit between the upper part of the postorbital bar and the quadrate as a result of the unique expansion of the postorbital to form the large, inflated, postorbital pouch so characteristic of this genus. With the constriction of the temporal opening, the depressed area of the squamosal at the dorsal end of the lower temporal fenestra is also restricted and is considerably smaller than in any other hadrosaurian species, which suggests that the superficialis, and perhaps the medialis also, had been greatly reduced in these forms.

The opposite condition is found in all species of *Kritosaurus*, which have experienced considerable expansion of the lateral temporal opening. Specimens of both *Kritosaurus notabilis* (R.O.M. No. 5859) and *Kritosaurus navajovius* (A.M.N.H. No. 5799) show an unusually wide (anteroposteriorly) lateral fenestra, and in these specimens there is a corresponding expansion of the excavated area of the squamosal at the upper limit of this opening.

This correlation between fenestra width and scar width seems to support the contention that temporal fenestration is influenced, if not controlled, by the size and arrangement of the temporal muscles. One can argue, of course, that the muscle arrangements and attachments shift according to the position and size of the available bony areas and that the bony elements and not the muscles are the

causal factors. In any case, there seems to be a definite correlation between muscular arrangement and temporal fenestration.

All hadrosaurian specimens were examined for indications of muscular attachments on the lower temporal arch. It is not surprising that the results were all negative (with the doubtful exception of the ventral lobe of the jugal mentioned above), because in no instance does the lower arch provide attachment for temporal muscles in modern reptiles and birds. It is the impression of the author, considering the lack of any evidence to the contrary, that such was also the case in the Hadrosauridae. The superficialis fibers probably passed freely from an origin on the lateral and ventral surface of the squamosal and postorbital ventrally and slightly forward to an insertion on the dorsal surface of the surangular between the quadrate articulation and the coronoid process, as illustrated in figure 35.

The question whether the superficialis was divided or not in the hadrosaurs cannot be answered. The *M. levator anguli oris* in recent forms is usually recognized by the discrepancy of its fiber pattern and not by a distinct origin area. Even if this slip were present in the hadrosaurs, it is not likely that it could be recognized by impressions on the bony framework because of its thin, sheet-like form.

#### M. ADDUCTOR MANDIBULAE EXTERNUS MEDIALIS

The second division of the adductor externus of modern reptiles occupies a position very similar to that of the superficialis, but medial to this last-named muscle. The presence of this division of the adductor externus in the Hadrosauridae is based on the topography of the medial surface of the upper temporal arch, the normal area of origin for the adductor medialis in most sauropsids. Only in *Sphenodon*, among recent reptiles, has this origin been reduced, with the major area of attachment shifting to occur on the dorso-lateral surface of the brain case.

The medial surface of the upper temporal arch in *Corythosaurus casuarius* forms a ventromedially directed, concave surface which is interpreted as the origin area of the *M. adductor mandibulae externus medialis*.

This surface is clearly defined ventrally by a sharp angulation which separates it from the ventral surface of the arch. Dorsally, it is equally well defined by a prominent ridge trending anteroposteriorly for nearly the entire length of the arch. This dorsal ridge separates the concave medial surface from the convex dorsal and lateral surface of the upper temporal arch. The posterior limit of the concave origin area is not clearly indicated in *C. casuarius*, but it can be located approximately in the plesiotype (A.M.N.H. No. 5338) along a very low, broad swelling that trends vertically across the medial surface of the squamosal where it forms the posterior wall of the upper temporal opening. This swelling is not easily seen on all hadrosaurian specimens, but it is usually present in the finely preserved skulls.

While the posterior border of the medialis origin area is generally quite faint, there are several specimens in which this structure is prominently developed and can be readily observed. The plesiotype of *Anatosaurus copei* (A.M.N.H. No. 5886), in the group exhibit at the American Museum, is one of these specimens which exhibits a strongly developed ridge trending obliquely dorso-ventrally across the inner surface of the posterior wall of the supratemporal fenestra. Even more striking is the degree to which this posterior limit is developed in *Lambeosaurus lambei*, in which a prominent ridge is developed in all but one specimen, N.M.C. No. 2869 being the exceptional case.

Throughout the entire family there is relatively little variation in this origin area. The size of the area in question seems to vary only slightly and usually is proportional to the size of the skull. The prominence of the limiting ridges varies moderately, apparently with variations in individual age, as there seems to be little consistency among the specimens of a single species. All hadrosaurian specimens were consistent, however, in the location of these scars.

Location of the M. adductor mandibulae externus medialis insertional area presents the same difficulties encountered in the attempts to locate the insertion of the superficialis fibers. As stated in the discussion of this latter muscle, there are no clearly defined scars on the mandibles which can safely be

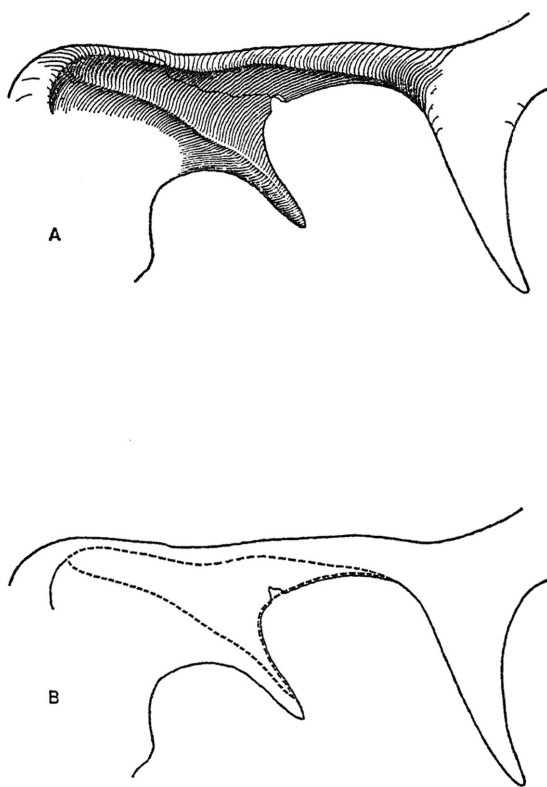


FIG. 36. Left temporal arch of *Lambeosaurus lambei*, R.O.M. No. 5131. A. Dorsomedial view of the upper arch, showing the origin scar of the M. adductor mandibulae externus medialis. B. Diagram showing the same origin area defined by dashed lines.

interpreted as an insertional area for one of the adductor externus slips. Again, the dorsal surface of the mandible between the condylar facet of the articular and the coronoid process appears to be the most probable site of the medialis mandibular attachment. If this interpretation is correct (this is a logical location in a sauropsid), it seems most likely that these fibers inserted along with the superficialis and profundus fibers as a single, undivided muscle mass.

From the evidence cited, the medialis portion of the adductor externus is interpreted as having existed as a fairly large, undivided muscle, originating over the total length and width of the medial surface of the upper temporal arch, with its fibers extending ventrally and slightly forward, passing medial to the lower arch and the fibers of the super-

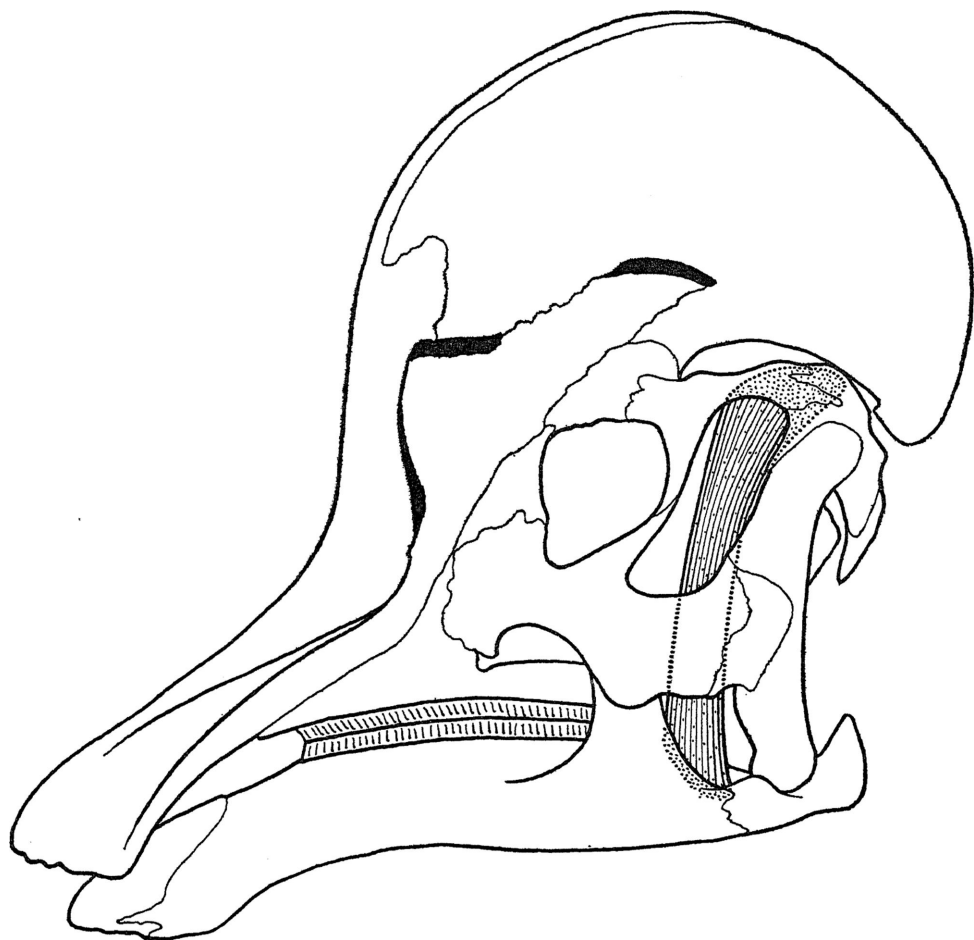


FIG. 37. Skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with the *M. adductor externus medialis* reconstructed.

ficialis, to its presumed insertion on the dorsal surface of the mandible behind the coronoid process. This pattern corresponds very well with that of other members of the Sauropsida.

**M. ADDUCTOR MANDIBULAE  
EXTERNUS PROFUNDUS**

*Corythosaurus casuarius*, as shown by the plesiotype, clearly displays osteological features that make possible the reconstruction of the position and the points of attachment of the profundus portion of the adductor externus. This deepest part of the externus in the Sauropsida characteristically is located in the temporal region filling much of the upper temporal fenestra. Examination of this area in *C. casuarius* establishes the area of attach-

ment of a relatively large muscle mass (probably the pars profundus) within the upper temporal opening. The origin area occurs largely on the lateral surface of the brain case, on the parietal and squamosal, and perhaps to a slight extent on the opisthotic. These elements form the medial and posterior walls of the supratemporal fenestra.

Posteriorly, the origin area is limited by the gentle ridge described above as defining the posterior limit of the origin of the adductor externus medialis. The location of this ridge on the anterior surface of the squamosal (posterior wall of the upper temporal opening) separates the upper fenestra into a lateral and a medial space. The lateral space, enclosed laterally by the medial surface of the

upper arch, was occupied by the medialis fibers, while the medial space in the upper fenestra, bounded by the lateral wall of the brain case medially, was filled by the fibers of the adductor profundus.

The profundus origin extends forward on the lateral surface of the parietal for nearly two-thirds of the total length of the fenestra. The anterior margin is marked by a low but prominent swelling which ascends across the lateral surface of the brain case from the vicinity of the trigeminal foramen to the dorsal surface of the brain case just behind the parietal-frontal suture. This parietal swelling is not abrupt but usually occurs as a broad, linear feature of the brain case. It is probably a reflection of the zone between the fibers of the adductor externus profundus behind and those of the pseudotemporalis in front, rather than the actual limits of the attachment areas of these two muscles. Its position agrees very well with the location of the trigeminal foramen, which generally is situated between the fibers of these two muscles in modern reptiles: at the anterior limit of the profundus fibers and the posterior limit of the pseudotemporalis fibers. Thus the position of the trigeminal foramen, at the ventral end of the parietal swelling, strengthens the above interpretation of the topography of the lateral surface of the brain case.

The dorsal boundary of the profundus origin is placed along the prominent anteroposterior-trending angulation which separates the laterally directed concave surface of the parietal from the strongly convex roof of the brain case. Ventrally, the area is marked by the strong, horizontally oriented, lateral expansion which projects out into the temporal space. This lateral swelling of the brain case extends from the postorbital across the pro-otic and the full length of the opisthotic, where it continues as the medial angle of the paroccipital process. It separates the dorsal concave area, believed to be the profundus origin, from the ventral half of the brain case wall which is marked by the cranial foramina.

These conditions proved to be quite constant in every hadrosaurian genus for which material was available. Variations in the total area involved were noticed, but in all cases were proportional to individual skull dimensions. Variations in the prominence of the

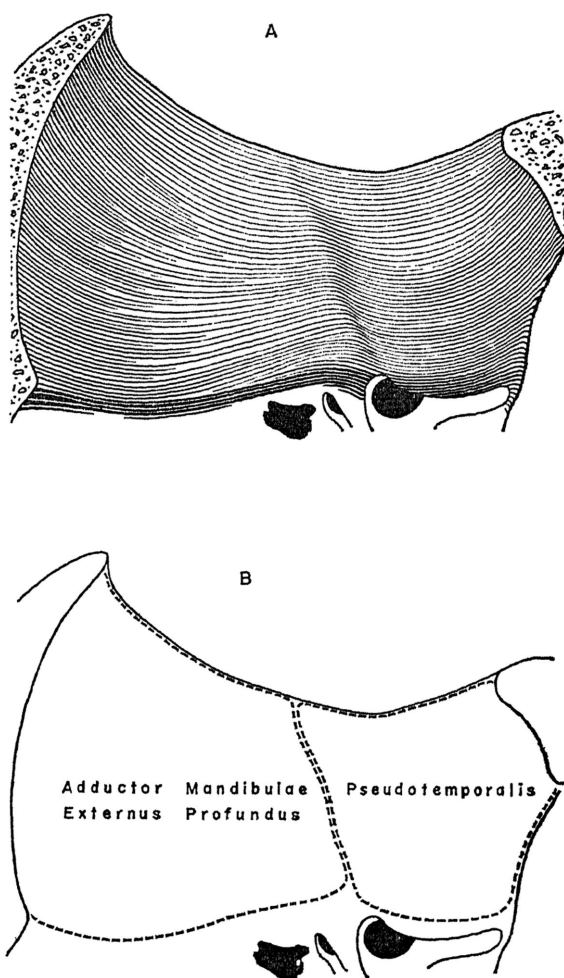


FIG. 38. Right lateral view of the brain case of *Corythosaurus casuarius*, A.M.N.H. No. 5338. A. Origin areas of the M. adductor mandibulae externus profundus and the M. pseudotemporalis of the adductor internus. B. Diagram of the same region, with the respective origin areas defined by dashed lines.

defining boundaries were slight, and no major deviations were noticed with regard to the positions of these limits. In all specimens, the large size of the origin was noted and indicated that the adductor externus profundus was by far the largest of the temporal adductors, having occupied at least twice the volume of the adjacent pseudotemporalis. The origin scar of the pars profundus can readily be seen on the specimens of *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), *Procheneosaurus cranibrevis* (N.M.C. No.

8633), *Brachylophosaurus canadensis* (N.M.C. No. 8893), *Edmontosaurus regalis* (N.M.C. No. 2288), *Lambeosaurus lambei* (A.M.N.H. No. 5353), and *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), as well as on the plesio-type of *Corythosaurus casuarius* (A.M.N.H. No. 5338).

The insertional area of the profundus fibers is interpreted as having occurred with those of the medialis and the superficialis slips, probably as a single area of attachment. As suggested above, the most logical insertional area lies between the quadrate articulation and the coronoid process on the dorsal surface of the mandible.

In a summing up of the reconstruction of the *M. adductor mandibulae externus*, sev-

eral conclusions can be stated. The hadrosaurs, as do modern reptiles, seem to have possessed a tripartite adductor externus, which not only conforms to the general sauropsid pattern but may be said to parallel closely that of certain modern representatives. Although the areas of origin have shifted and extended onto new bony elements, these locations agree, at least functionally, with the sauropsid pattern, with the superficialis arising from the ventral part of the upper temporal arch, the medialis from the medial surface of the arch, and the profundus from the lateral surface of the brain case. Normally, no portion of the externus attaches to the lower temporal arch in modern sauropsids, and the absence of any recog-

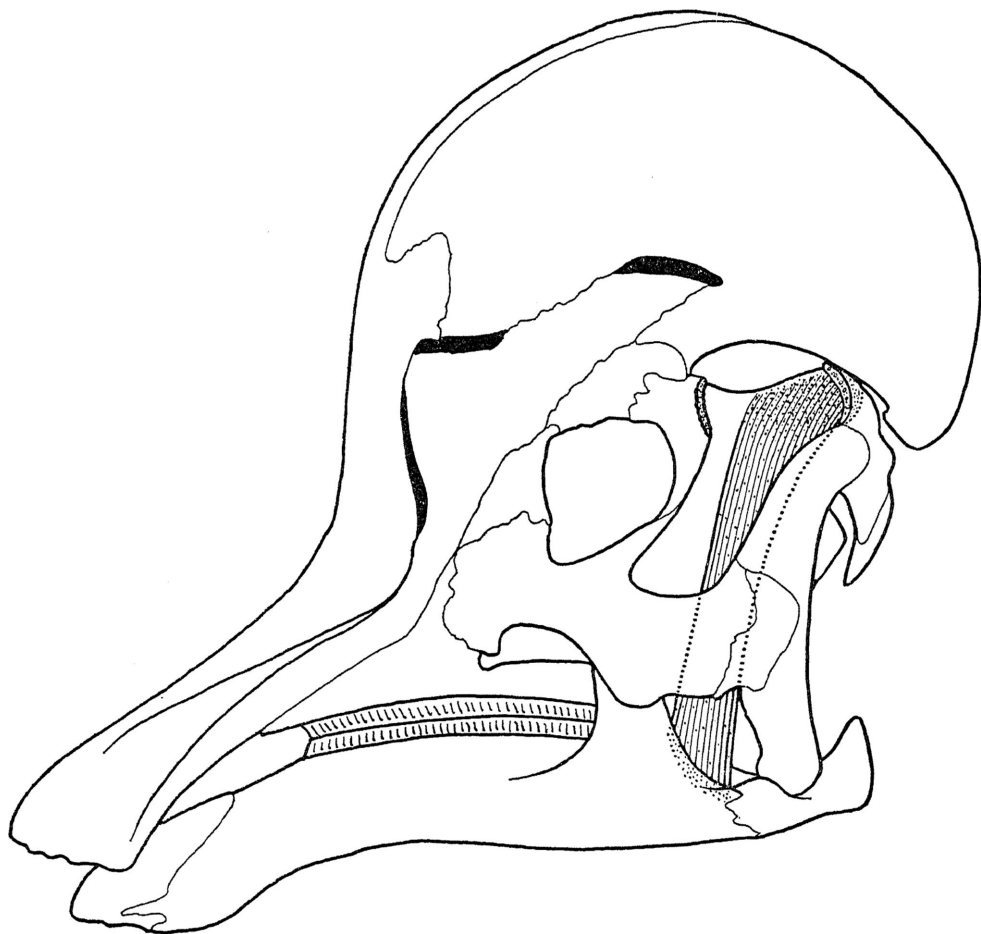


FIG. 39. Skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with the *M. adductor externus profundus* reconstructed.

nizable scar on this structure has led to the reconstruction of a similar condition in the Hadrosauridae. While the absence of any impression of muscular attachment is not conclusive, this interpretation appears quite sound in view of the general sauropsid condition. The ventral lobe of the jugal, while unique to the Hadrosauridae and Iguanodontidae, is considered insufficient evidence on which to reconstruct the *M. levator anguli oris*.

In the hadrosaurs, as in the generalized sauropsids, the walls of the upper temporal opening (the upper arch and the brain case with its lateral and posterior projections) form a bony framework for the attachment of the adductor externus. From this, it must be concluded that fenestration of the reptilian skull, at least by the upper temporal opening, is certainly related to and probably influenced by the position and development of the temporal musculature.

#### M. PSEUDOTEMPORALIS

The adductor internus, a group of muscles well defined as to position by Luther's classification (1914), is generally separable into two distinct muscles (the *M. pterygoideus* and the *M. pseudotemporalis*), differing in innervation and function, although both are basically adductors. Within various sauropsids either of these muscles may be single, double, or even tripartite. Both occupy Luther's internus position anterior or medial to the ramus maxillaris of the trigeminal nerve and lateral to the profundus branch of the same nerve. The terminology applied here is again that of Luther and Lakjer, although their term "*pterygoideus*" is an unfortunate choice, implying a homology with the mammalian muscle of the same name. Such an implication is not intended here. Hoffman's (1890) and Bradley's (1903) "*pterygomandibularis*" is more desirable and less apt to suggest such homologies, but this term is not used in the following discussion, because the consistent use of terminology of a single classification is preferable to a combination of terms from several classifications. In the author's opinion the classification of Luther and Lakjer is currently preferred by a majority of anatomists, and for this reason, among many, it has been adhered to in this paper.

The *M. pseudotemporalis* of modern reptiles normally occupies a deep position in the temporal region in the anterior part of the upper temporal opening. Its posterior limit is indicated by the position of the trigeminal foramen, because by definition it is bridged laterally by the second branch of this nerve which turns forward on its emergence from the trigeminal foramen. The precise area of the temporal vacuity occupied by this muscle varies within the sauropsids, according to the precise level of emergence of the maxillary branch, which may exist with the profundus branch, as in the Crocodilia, or with both the first and third branches, as in *Sphenodon* and most Lacertilia.

The markings on the brain case of *Corythosaurus casuarius* give a clear indication of the location of the *M. pseudotemporalis* of the adductor internus. The plesiotype of this species shows the origin scar particularly well. Here the dorsal part of the lateral brain case surface (parietal, opisthotic, and possibly the laterosphenoid and postorbital) form two dorsolaterally facing concave surfaces separated by a vertical swelling ascending across the brain case from the trigeminal foramen. The more posterior of these two areas is described above as the probable origin area of the adductor externus profundus. The anterior area forms the medial wall of the anterior third of the upper temporal opening and is here interpreted as the origin of the *M. pseudotemporalis*. (See fig. 38.) This anterior concave area, clearly defined by the bony topography, presents a fairly reliable reconstruction of the size of the *pseudotemporalis*. Posteriorly, the area is defined by the broad linear swelling, mentioned above, that separates this anterior region from the profundus origin behind, as well as by the position of the trigeminal foramen, which indicates the passage of the second trigeminal branch between the anterior *pseudotemporalis* fibers and the posterior profundus fibers. The anterior limit of the *pseudotemporalis* origin is marked by a vertically oriented ridge which traverses the posterior surface of the postorbital where it forms the anterior limit of the upper temporal opening. Dorsally, a moderately developed horizontal ridge separates this laterally directed, concave region from the more dorsally directed, convex roof of the brain case behind

the parietal-frontal suture. Ventrally the area is clearly bounded by the dorsal edge of the horizontal groove for the profundus branch of the trigeminal nerve, which is impressed in the lateral surface of the laterosphenoid-protic complex.

This area agrees perfectly with the typical sauropsid origin of the *M. pseudotemporalis*. Other hadrosaurian specimens in which these features can be seen particularly well are *Lambeosaurus lambei* (R.O.M. No. 5131), *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), *Prosaurolophus maximus* (U.S.N.M. No. 12712), *Saurolophus osborni* (A.M.N.H. No. 5221), *Procheneosaurus cranibrevis* (N.M.C. No. 8633), *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), *Hypacrosaurus altispinus* (N.M.C. No. 8501), *Corythosaurus intermedius* (R.O.M. No. 4670), *Edmontosaurus regalis* (N.M.C. No. 2288), and *Kritosaurus notabilis* (A.M.N.H. No. 5350).

The evidence for the location of the pseudotemporalis insertion on the mandible is not nearly so convincing as that related to the origin. Indeed there is no clearly defined area on the mandible to indicate a site of insertion.

However, examination of the skull of any member of the family quickly eliminates most of the possible areas. The position of the origin on the medial wall of the anterior third of the supratemporal fenestra (anterior to all other temporal adductors) suggests a correspondingly forward position for the insertion of this muscle on the mandible. The most obvious site is the stout coronoid process. The development of such a sturdy process must logically be related to the attachment of a large adductor muscle. There is, however, no distinct scar on the coronoid process. From this it would appear that any muscle attaching to this structure (most probably the pseudotemporalis) inserted by a tendinous sheet to the rather thin dorsal crest of the coronoid, a situation that is typical for the pseudotemporalis in modern sauropsids.

While all members of the Hadrosauridae display the marks of attachment described above, there is some degree of variation. In some specimens, such as *Brachylophosaurus canadensis* (N.M.C. No. 8893) and *Saurolophus osborni* (A.M.N.H. No. 5221), this origin is restricted to a relatively small surface of the brain case. Here, the *M. pseudo-*

temporalis appears to have filled a much smaller part of the upper temporal opening. In most hadrosaurian species, however, the pseudotemporalis fibers probably occupied the anterior third of the upper fenestra, the posterior two-thirds having been filled by the fibers of the pars profundus, and to a lesser degree by the medialis of the adductor externus. *Procheneosaurus*, *Corythosaurus*, and *Lambeosaurus* are characteristic of the family in having had a more expanded or bulkier pseudotemporalis.

The above reconstruction of the pseudotemporalis differs only slightly from the typical condition of modern sauropsids. In these forms, this muscle frequently is the largest of the temporal muscles, characterized by the most extensive area of origin. In the hadrosaurs, we see that the area interpreted as the pseudotemporalis origin is approximately half of the size of the origin of the adductor externus profundus. The reduced size of the pseudotemporalis is probably related to the rostral inclination of the coronoid process, which resulted in the closer proximity of this muscle to the orbital chamber. A reduction of the pseudotemporalis mass, and a corresponding enlargement of the profundus muscle of the adductor externus, may have taken place to inhibit further encroachment of the orbit by the adductor internus.

#### M. PTERYGOIDEUS

The position and general condition of the pterygoideus muscle (pterygomandibularis of Hoffman), probably the most complex of the trigeminal muscles, are by no means definitely established in this family, although the evidence cited here is believed to be quite sound.

As the insertion of the pterygoideus muscle on both the lateral and medial surfaces of the retroarticular process is quite constant in modern reptiles, it seems most logical to begin the discussion of this muscle at this point. The plesiotype of *Corythosaurus casuarius* appears to be typical of the family in the configuration of the surfaces of the retroarticular process. This process is defined by three major bone surfaces, a lateral, a medial, and a dorsal surface, each of which is triangular in shape and moderately to strongly concave. These three triangular surfaces meet in the dorsally projecting extremity of the retro-



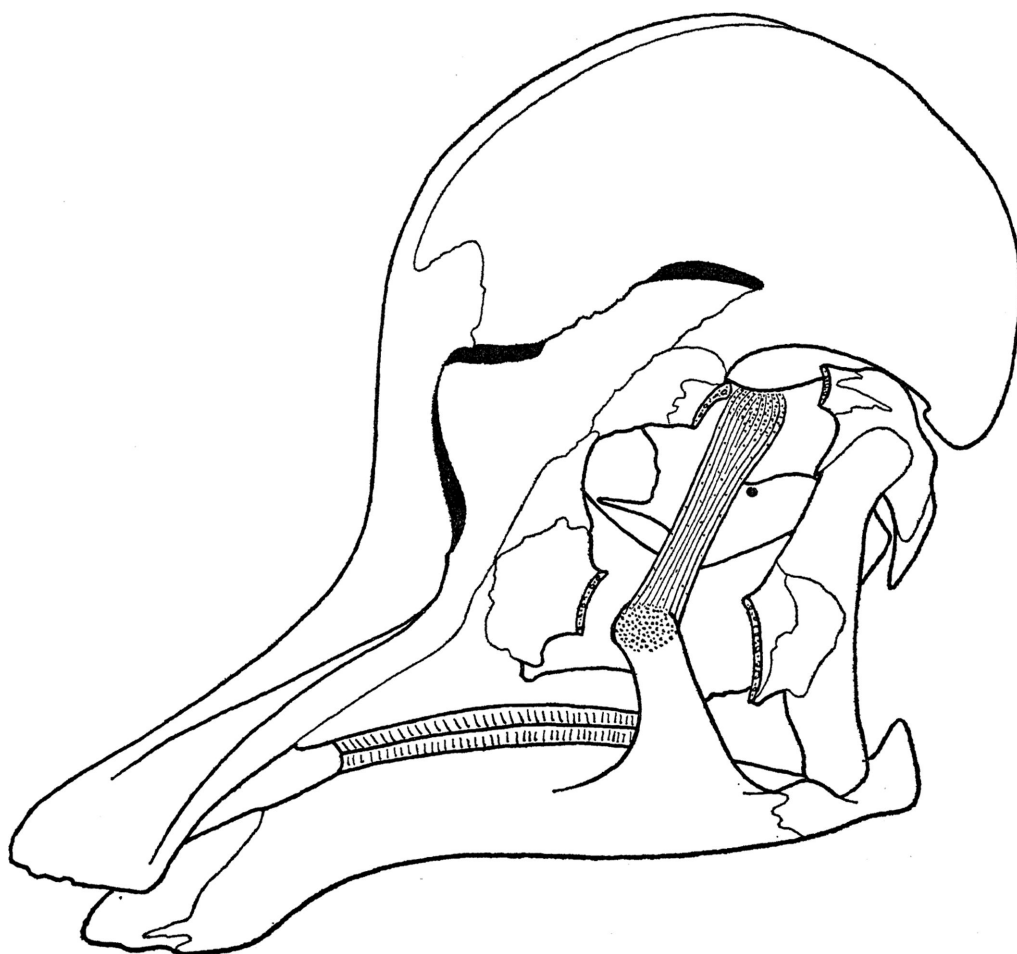


FIG. 40. Skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with the *M. pseudotemporalis* reconstructed.

articular process. The borders of the process are rather prominent ridges or angles which define or limit each triangular surface. The strongly developed lateral concavity and its more moderately developed medial counterpart are interpreted as two sites of probable insertion of the pterygoideus fibers. A double insertion is not unlikely, for such is commonly found in modern reptiles and birds.

The lateral surface of the retroarticular process in *Corythosaurus casuarius* is a strongly concave surface extending from the arcuate posterior edge of the process, diagonally forward and ventrally (see fig. 41A). Dorsally it is limited by a pronounced, laterally projecting ridge which forms the lateral edge of the concave, dorsal, postarticular sur-

face. Ventrally it is marked by the rather prominent convex angulation forming the ventral border of the process. The anterior extremity of this lateral concavity is situated immediately ventral to the articulation of the mandible with the quadrate.

This lateral surface, which has been found to be quite consistent throughout the entire family and particularly well preserved in *Corythosaurus casuarius* (A.M.N.H. No. 5338), *Anatosaurus copei* (A.M.N.H. No. 5886), *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), *Procheneosaurus cranibrevis* (N.M.C. No. 8633), *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), and *Lambeosaurus lambei* (A.M.N.H. No. 5353, N.M.C. No. 2869), is interpreted as the insertional

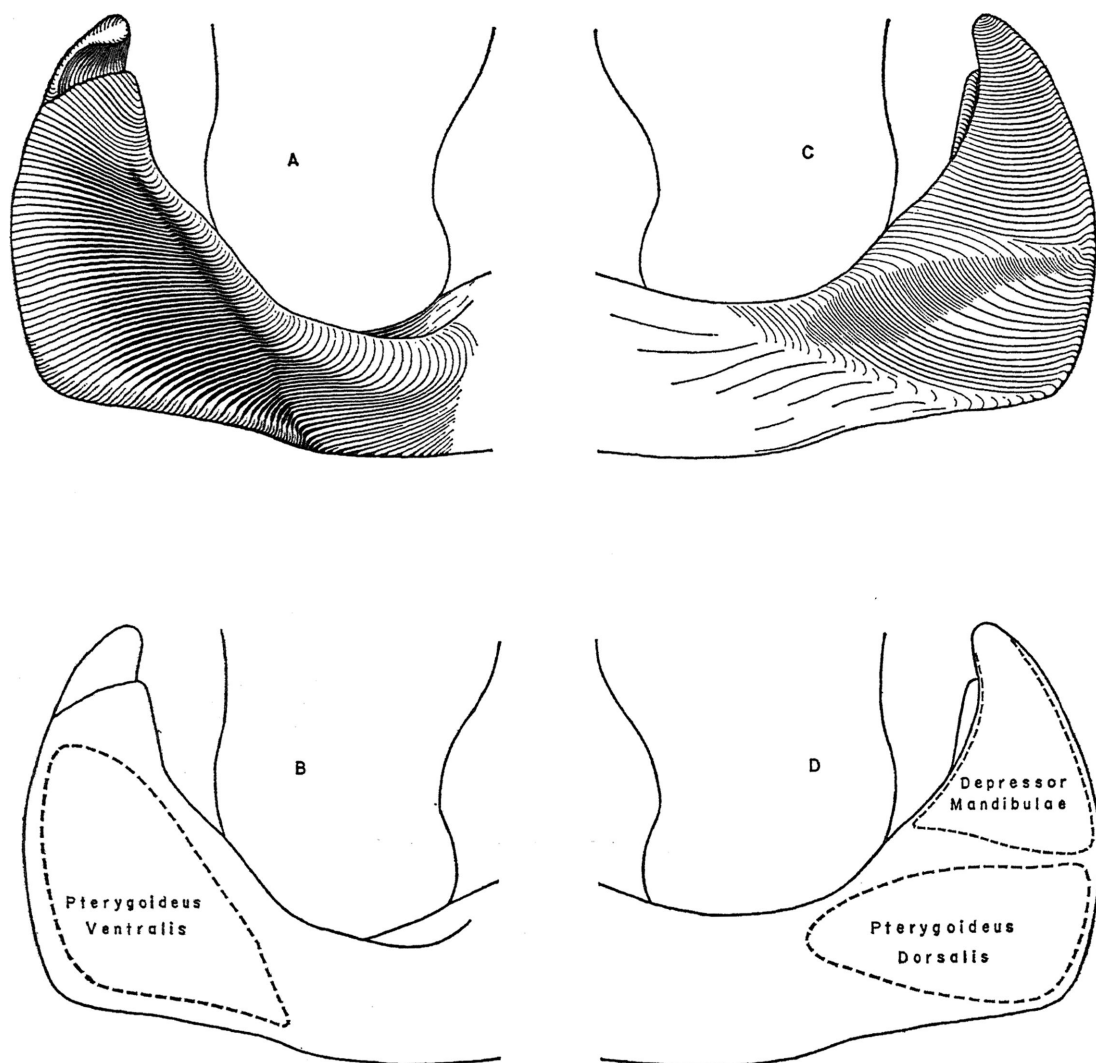


FIG. 41. Right retroarticular process of *Corythosaurus casuarius*, A.M.N.H. No. 5338. A. Lateral view, showing the insertional area of the M. pterygoideus ventralis. B. Diagram of the same region, with the pterygoideus ventralis insertion defined by a dashed line. C. Medial view of the same process, showing the probable insertional scars of the M. pterygoideus dorsalis and the M. depressor mandibulae. D. Diagram of the same region, with these insertions defined by dashed lines.

area of part of the M. pterygoideus. As this area corresponds with the insertional area of the ventral portion of the pterygoideus in lizards, birds, and crocodiles, the hadrosaurian muscle is hereafter referred to as the M. pterygoideus ventralis.

The medial surface of the retroarticular process, while very similar to the lateral surface in size and shape, is more moderate in

its degree of concavity (see fig. 41C). As does the lateral surface, it descends diagonally forward from the posterior margin of the retroarticular process. It is defined ventrally by the same ventral border of the process and dorsally by the less prominent convex medial margin of the dorsal surface. *Corythosaurus casuarius* (A.M.N.H. No. 5338) and *Lambeosaurus lambei* (A.M.N.H. No. 5353) display

this area particularly well, although its presence may be readily observed on many other hadrosaurian specimens.

This medial surface is proposed as a second area of insertion for pterygoideus fibers, corresponding with the dorsalis portion of the pterygoideus muscle so characteristic of the Squamata and certain birds. Although there are only two distinct areas for the insertion of pterygoideus fibers, it must be kept in mind that one or both of these areas may have provided attachment for more than one slip of the pterygoideus, because the pars ventralis and dorsalis may have split in their passage forward to the maxillary segment of the skull. Examination of the pterygoid-ectopterygoid-maxillary complex does not

completely solve this problem, as the reader will discover, for there is good evidence of at least two distinct origins and possibly a third in this region of the skull. These areas are located and described first; then an attempt is made to relate these areas to possible pterygoideus conditions.

*Corythosaurus casuarius*, as may be seen in the plesiotype, together with several other hadrosaurian species, illustrates the two distinct areas that are believed to have served as the sites of origin of portions of the pterygoideus fibers. The first of these areas may be seen on the ventromedial part of the posterior surface of the pterygoid, close to the midline and immediately ventral to the pterygoid process of the basisphenoid. The

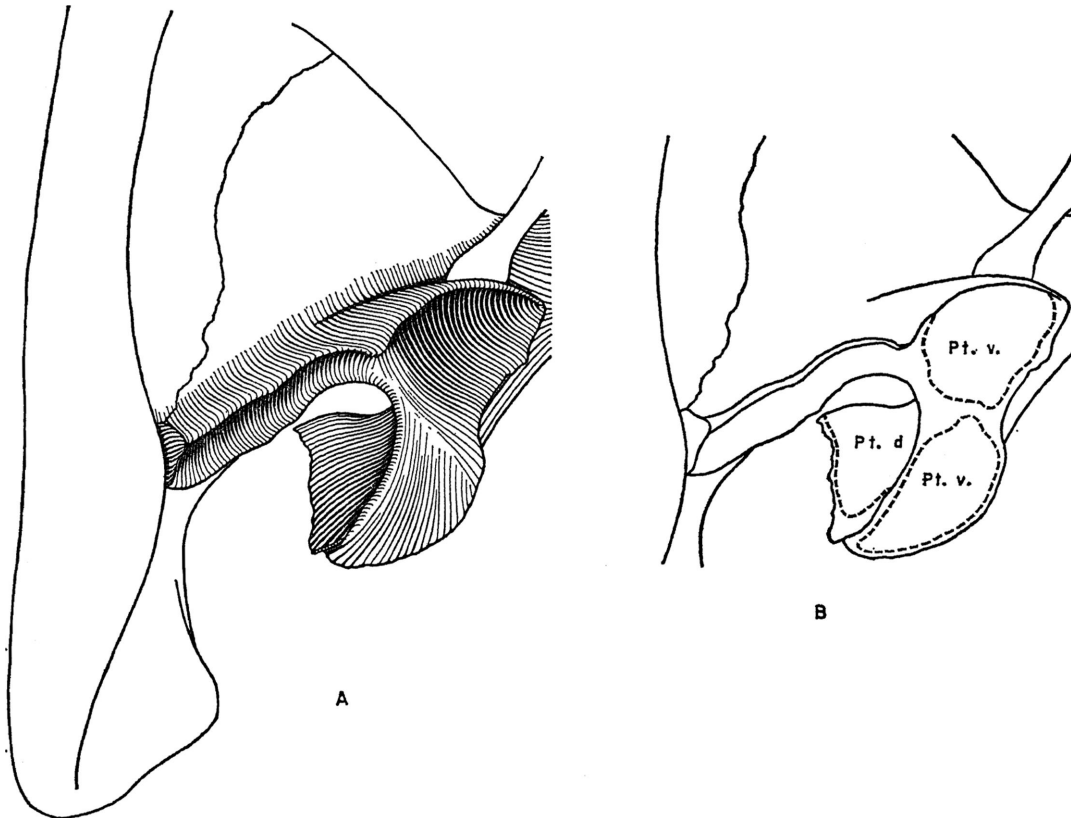


FIG. 42. Left pterygoid, ectopterygoid, and quadrate of *Brachylophosaurus canadensis*, N.M.C. No. 8893. A. Posterior view, showing the scars interpreted as the origin areas of the M. pterygoideus ventralis and dorsalis. B. Outline diagram of this same region, with these origin areas defined by dashed lines. The ventral area suggests a bipartite condition for the pars ventralis. Abbreviations: Pt. d., origin of the M. pterygoideus dorsalis; Pt. v., possible origins of the M. pterygoideus ventralis.

typical hadrosaurian skull, when viewed from behind, displays a very deeply depressed, caudally directed surface in this area. This "pocket" lies immediately ventral to the anterior extremity of the pterygoid ridge (see fig. 42). The prominence of this depressed scar and the total area involved vary moderately within the family, but it is strongly developed in every hadrosaurian specimen in which this region of the skull is preserved. In no case are the precise limits of the area clearly discernible, because the marginal areas grade imperceptibly into the adjacent convex surfaces. Being located near the midline, it is correlated with the lateral insertion area of the retroarticular process and the pars ventralis of the *M. pterygoideus*.

The second area, here interpreted as the probable site of origin of the pars dorsalis of the pterygoideus, is the prominent maxillary "shelf" situated ventral and medial to the jugal, above the posterior half of the maxillary dental battery. This shelf is strongly developed in the posterior part of the lateral maxillary surface in all members of the family. Lull and Wright (1942) interpreted the lateral, ridge-like extremity of this shelf as the origin area of a reptilian analogue of the mammalian buccinator muscle, the fibers of which passed ventrally to insert on what is described by Lull and Wright as "a distinct rounded ridge" of the dentary.

To the best of the author's knowledge, the buccinator is a purely mammalian muscle, and no corresponding muscle is known in any modern reptile. The author, in his dissections of *Ctenosaura*, *Amblyrhynchus*, *Varanus*, *Iguana*, *Sphenodon*, and *Alligator*, found no muscular fibers linking the lateral surfaces of the mandible with the lateral maxillary surfaces or those of the lower temporal arch, as the buccinator does in mammals. Furthermore, the "distinct rounded ridge" mentioned by Lull and Wright as the insertional area could not be located by the present author. In fact, the lateral surface of the dentary, in all hadrosaur specimens examined, is a smooth and gently convex surface which, in the author's opinion, shows no indication that it ever served as an area of muscular attachment.

While the length and breadth of the maxillary shelf vary slightly in the family, the

position is quite constant. It is partially exposed laterally in most of the crested hadrosaurs but is nearly completely concealed by the overlapping jugal in the flat-headed forms. The shelf, as typified by the plesiotype of *C. casuarius*, is an elongate surface about 150 mm. in length, which slopes slightly outward. It is formed largely by the anterior portion of the ectopterygoid, with only the lateral, medial, and anterior margins formed by the maxilla. A pronounced lateral ridge extending caudally from the maxillary-jugal suture separates this shelf from the lateral maxillary surface. Anteriorly and medially the shelf is limited by the steeply inclined surfaces of the maxilla, which ascend to their unions with the jugal and palatine, respectively. (See fig. 43.)

This recessed maxillary shelf is correlated with the medial concave scar of the retroarticular process. Fibers that attached to the

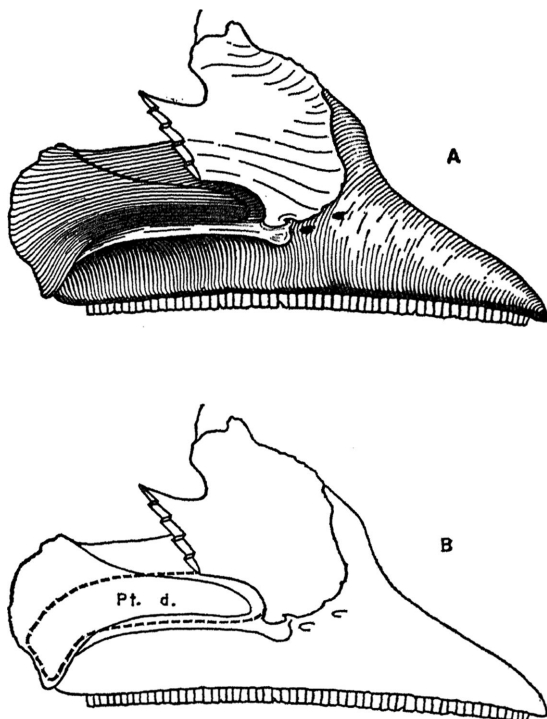


FIG. 43. Right maxilla and ectopterygoid of *Corythosaurus casuarius*, A.M.N.H. No. 5338. A. The maxillary shelf which is interpreted as the origin site of the *M. pterygoideus dorsalis*. B. Diagram of the same region, with the origin area defined by a dashed line. Abbreviation: Pt. d., origin of the *M. pterygoideus dorsalis*.

medial mandibular surface would have passed forward lateral to the previously described pars ventralis to a more laterally placed origin on the maxillary shelf. These fibers are hereafter referred to as the *M. pterygoideus dorsalis* and are presumed to be homologous with the same fibers of modern sauropsids.

A third area on the maxillary segment is so prominent and logically situated that it requires at least a brief mention as a possible area of attachment for pterygoideus fibers. The ventral process of the pterygoid, medial to the ectopterygoid as illustrated in figure 42, forms a distinct, caudally facing flange at the posterior end of the maxillary battery. Its medial position, along with its caudally directed surface, offers an ideal area of origin

for some of the pterygoideus fibers, but whether such was the case, or whether such attachment was in the form of a separate muscle slip or just the ventral fibers of the pars ventralis, cannot be determined. There is no indication in the nature of the flange surfaces to substantiate or eliminate this area as one of muscular attachment, but the possibility of a tripartite pterygoideus in the hadrosaurs exists.

In summary, the pterygoideus is interpreted as having been a double muscle in the Hadrosauridae. The *M. pterygoideus ventralis* (or *superficialis*) is believed to have originated on the posterior surface of the pterygoid near the midline, with a possible second slip attaching to the ventrocaudal flange of

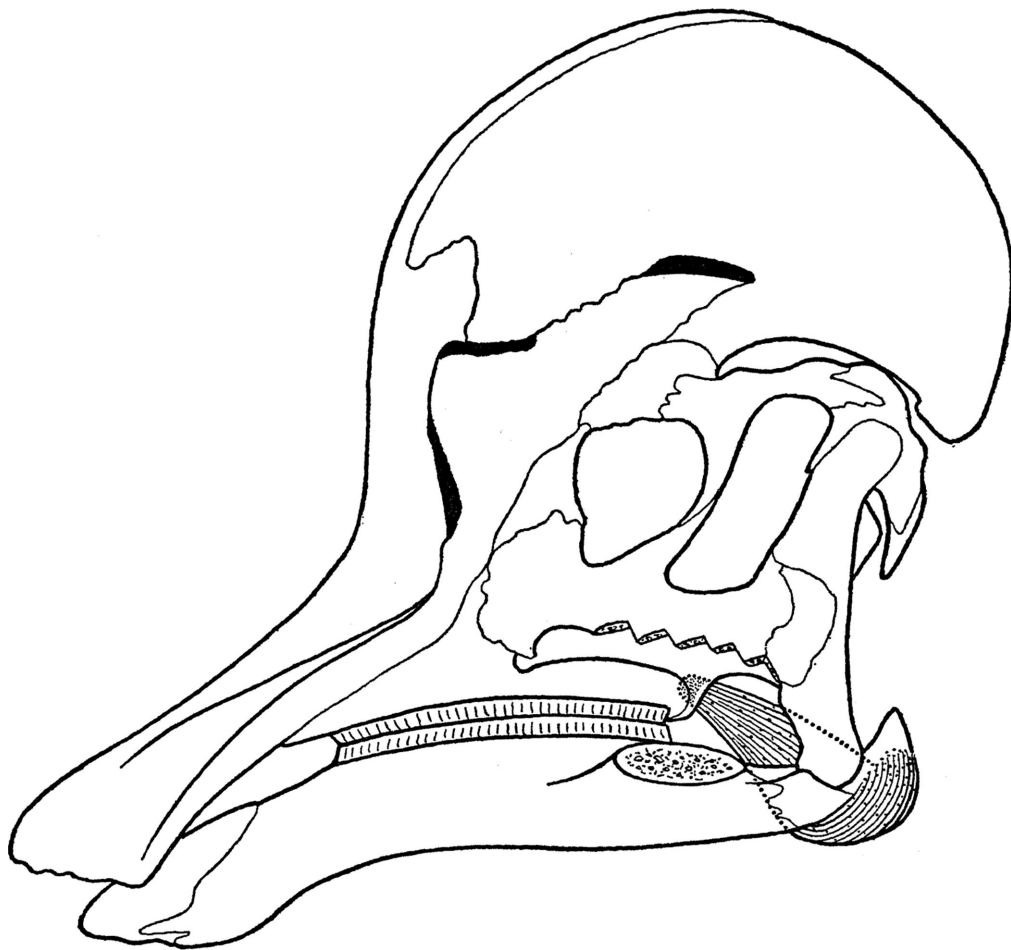


FIG. 44. Skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with a reconstruction of the *M. pterygoideus ventralis*.

this bone. The ventralis fibers passed caudally and ventrally to the posterior end of the mandible, where they wrapped around the ventral border of the retroarticular process to insert on the lateral surface of this process, after the modern sauropsid plan. The *M. pterygoideus dorsalis* (profundus) is believed to have originated on the dorsolateral surface (shelf) of the ectopterygoid and maxilla. These fibers passed caudoventrally to their insertion on the medial surface of the retroarticular process. As indicated in the description of these areas, these conditions appear to have been constant for the entire family, with only minor variations in the size of the attachment areas noted.

It appears that the basic sauropsid pterygoideus plan is repeated in the hadrosaurs, that is, linkage through this muscle group of the posterior portions of the mandibles with the caudal surfaces of the maxillary segment of the skull. It further appears that this muscle was separated into at least two divisions, a superficial part believed to correspond with Lakjer's *M. pterygoideus ventralis* and a deeper part that is correlated with Lakjer's pterygoideus dorsalis. Except for the possible bifurcation of the pars ventralis, there apparently was no extreme differentiation of the pterygoideus as in crocodiles and birds, although, as is demonstrated below in the discussion of functional morphology, there

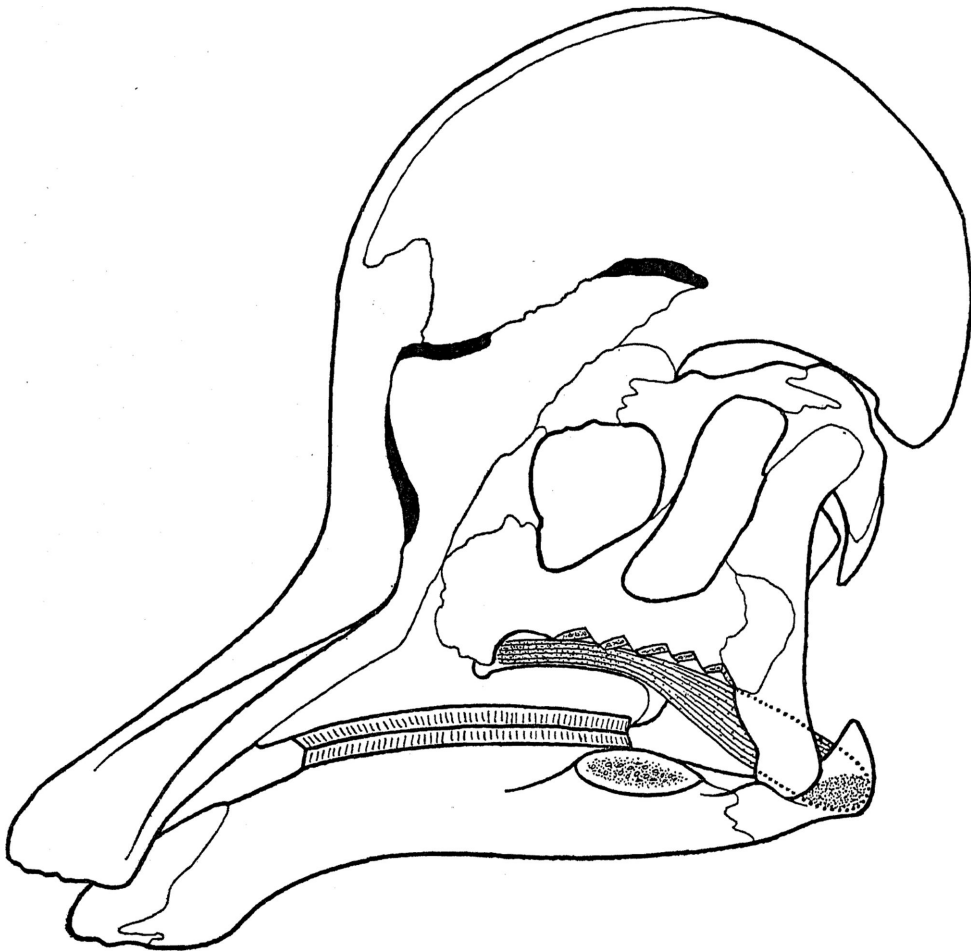


FIG. 45. Skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with the *M. pterygoideus dorsalis* reconstructed.

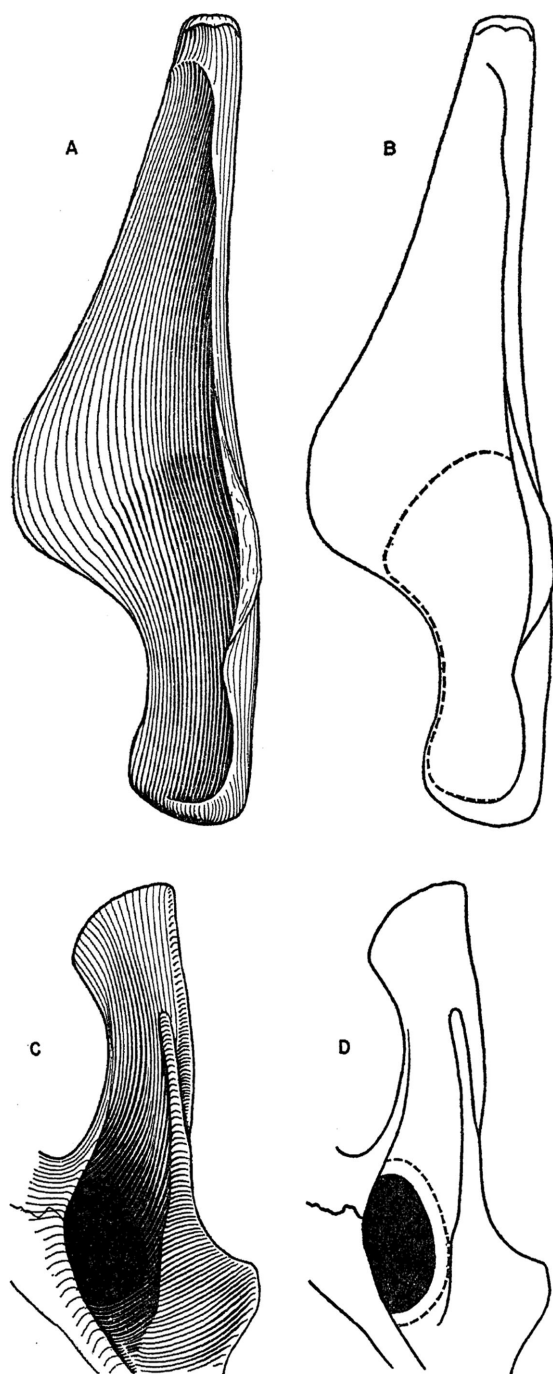


FIG. 46. Hadrosaurian quadrate and mandibular fossa. A. Left quadrate of *Edmontosaurus regalis*, N.M.C. No. 2289, in anterolateral view. B. Outline of this same bone with the origin area of the M. adductor mandibulae posterior outlined by the

has been a modification of fiber attachment and orientation which resulted in a significant change of function.

#### M. ADDUCTOR MANDIBULAE POSTERIOR

According to Luther's classification (1914), which is used here, the M. adductor mandibulae posterior is separated from the other adductor muscles by its position medial and posterior to the ramus mandibularis of the trigeminal nerve. In modern reptiles this muscle is typically found in the posterior and ventral corner of the temporal region, linking the quadrate with the posterior part of the inframandibular fossa. While some degree of splitting may occur as a result of the intercalation of the pseudotemporalis fibers into the adductor posterior insertional area, it is generally a single muscle.

The bony elements in the inferior temporal region of the hadrosaurian skull suggest that the adductor posterior was one of the larger adductor muscles and was situated in a typical sauropsid position. The quadrate of *Edmontosaurus regalis* (N.M.C. No. 2288), described by Lambe (1920) as a transversely compressed bar with a rostromedially directed flange (pterygoid process), clearly demonstrates the area of origin of the adductor posterior fibers. The anterior face of the quadrate forms a very deeply depressed surface which extends nearly the full length of the quadrate. This elongate depression is believed to have served as the site of a large fleshy origin of the M. adductor mandibulae posterior. The area in question suggests a formidable bulk for the adductor posterior, but it is the author's opinion that this is not extreme in view of the large size of the hadrosaurian mandible. The topography of the quadrate anterior surface is generally quite smooth and offers little evidence as to the exact limits of attachment. A similar depression is prominently developed in all members of the family, varying only in size as the size

dashed line. C. Coronoid process and mandibular fossa of *Lambeosaurus lambei*, N.M.C. No. 2869, in dorsoposterior view. D. Outline diagram of the same region, with the insertional area of the adductor posterior defined by the broken line.

of the quadrate varies. *Corythosaurus casuarius* (A.M.N.H. No. 5338) and *Anatosaurus saskatchewanensis* (N.M.C. No. 8509) are two other specimens in which this depression can be seen particularly well.

From this anterior quadrate surface, the fibers of the adductor posterior probably descended rostroventrally to the mandible where they inserted in the large inframandibular fossa. Examination of any hadrosaurian mandible will reveal this large cavity, but it is particularly well preserved in *Edmontosaurus regalis* (N.M.C. No. 2289). The large, caudodorsally directed entrance to the fossa is bounded laterally by the surangular and the stout coronoid process, medially by the dentary, splenial, and the angular, anteriorly by the base of the coronoid process (dentary), and posteriorly by the surangular. The inframandibular fossa extends forward as a large cavity within the dentary and beneath the posterior part of the dental battery to a point beneath the anterior limit of the coronoid process. At this point it narrows quite abruptly to continue as the narrow Meckelian groove which is usually exposed medially between the dentary and splenial above and the angular below.

While this fossa is not so long as that found in the Crocodilia, it is certainly similar to that cavity and most likely served a similar function. The broad entrance supports the previous conclusion that the adductor posterior was of considerable size. It is possible, however, that the fibers of one or more of the other adductors also attached within the limits of this fossa. It cannot be determined whether or not the mandibular cavity housed an intramandibular muscle as in the crocodiles, but the relatively smaller volume of this fossa, together with the massive size of the hadrosaurian mandible and non-predaceous habits of these ornithopods, suggests that such was not the case and that the ventral fibers of the temporal adductors alone filled this cavity.

In summary, the evidence of the hadrosaurian quadrate and inframandibular fossa points to the presence of a large adductor posterior, probably not unlike that seen in modern lacertilians and *Sphenodon*. While there is no evidence as to the single or multiple nature of this muscle, it appears safe to

assume an undivided condition for the adductor posterior in the hadrosaurs, as subdivision of the adductor posterior is associated with streptostylic or kinetic conditions, which, as is shown below, did not exist in the Hadrosauridae. Figure 47 illustrates the author's reconstruction of the adductor posterior.

#### CONSTRUCTOR DORSALIS GROUP

Lakjer (1926) recognized three distinct muscles in the sauropsids which he placed in the constrictor dorsalis division: the M. protractor pterygoidei, the M. levator pterygoidei, and the controversial M. levator bulbi. The sauropsid constrictor dorsalis pattern can be described as a simplified product of the complex muscle system of the more mobile fish skull. With the decrease in skull mobility of the tetrapods, a general reduction in the number and complexity of the constrictor dorsalis muscles followed.

While deviations occur in the precise position of the constrictor dorsalis muscles, Sæve-Søderbergh (1945) points out that Luther's principles of adductor mandibulae classification (1914), based on the three positions of the muscles relative to the trigeminal nerve branches, may be applied to the muscles of the constrictor dorsalis division. Sæve-Søderbergh describes a fourth position, which he refers to as the intimus position (see fig. 33), located anterior and medial to the profundus (and maxillaris) branch of the trigeminal nerve, a position that is typically occupied by the constrictor dorsalis muscles. Sæve-Søderbergh is quick to point out, however, that "transitional" cases do occur, and "in this division the position mentioned seems to be less suitable as a basis of classification" (1945, p. 8).

The muscles of the constrictor dorsalis group, with the exception of the M. levator bulbi, are concerned with the movements of the palatoquadrate (maxillary segment of De Beer and others) with relation to the brain case (neurocranial segment). As is shown below, there is no evidence of kineticism in the hadrosaurian skull, nor, for that matter, is there any sound evidence of a streptostylic quadrate. In view of the conditions found in modern akinetic skulls, such as those of the Crocodilia, Chelonina, and mammals, there is no reason to assume the existence in the



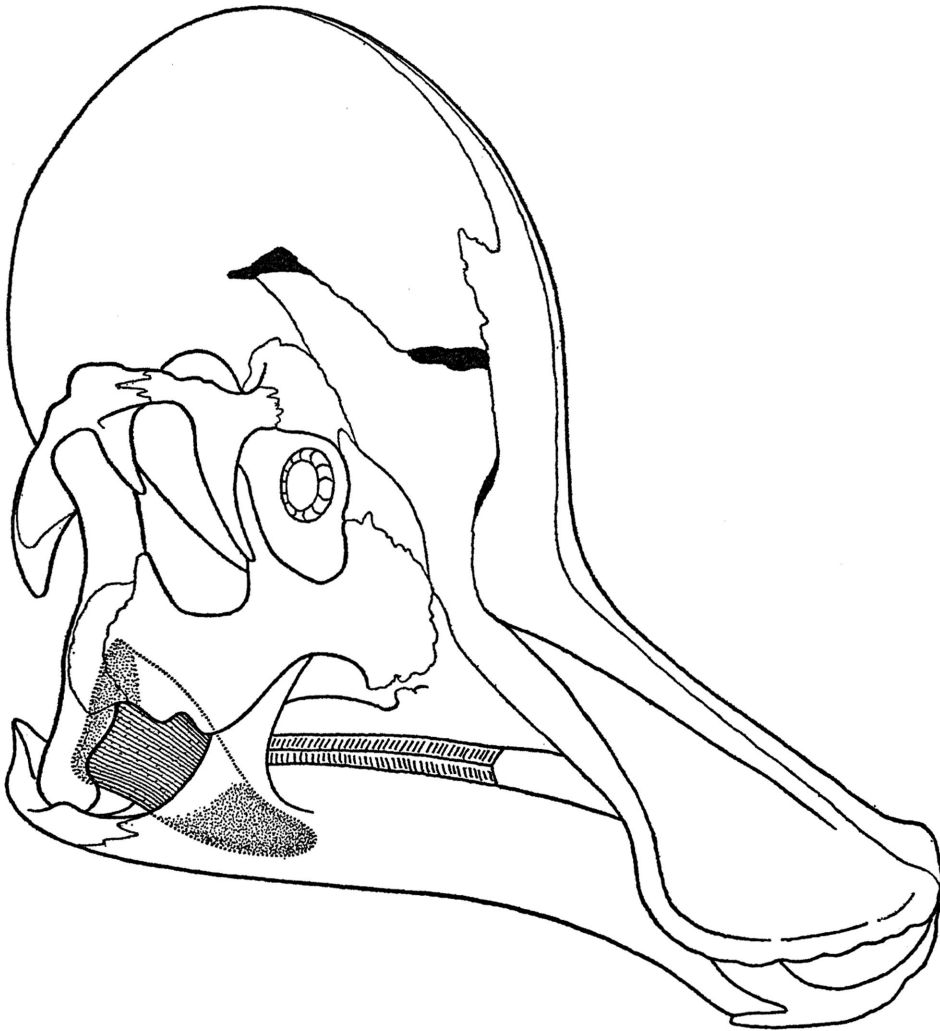


FIG. 47. Anterolateral view of the skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with a reconstruction of the *M. adductor mandibulae posterior*.

Hadrosauridae of muscles concerned with the movement of the maxillary segment. With the loss of kineticism, these muscles may have undergone migration and transformation of function, or may have been lost altogether. Certainly they would not persist in the "primitive" position in a secondarily akinetic skull.

In spite of the unquestionably akinetic character of the hadrosaurian skull, the author examined each skull carefully for evidence that might indicate the existence of one or more parts of the constrictor dorsalis division. With regard to the protractor and

levator pterygoidei, the results were completely negative. Indications were found, however, that seem best correlated with the *M. levator bulbi*; this evidence is presented below.

#### M. LEVATOR BULBI

The frequently discussed (Lakjer, 1926; Säve-Söderbergh, 1945; Luther, 1914; Edgeworth, 1911, 1925, 1935; Jarvik, 1942) and still problematical *M. levator bulbi* occurs in all modern sauropsids, save the Chelonia. As pointed out by Lakjer (1926, p. 25), and later by Ivo Poglayen-Neuwall (1953b, p. 279),

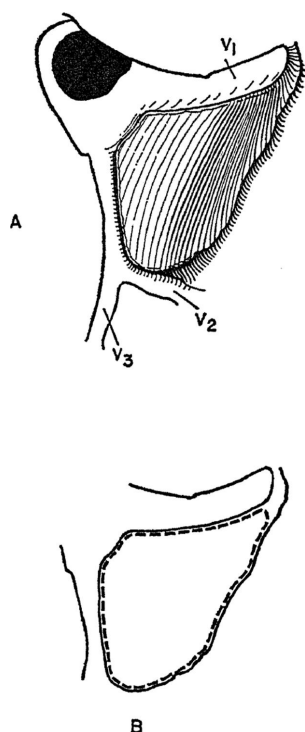


FIG. 48. The right trigeminal foramen and a portion of the laterosphenoid of *Corythosaurus casuarius*, A.M.N.H. No. 5338. A. The lateral cranial wall adjacent to the trigeminal foramen, partially bordered by the bony channels of the trigeminal rami, which may be the origin site of the M. levator bulbi. B. Diagram of this same region with this possible origin area defined by a broken line. Abbreviations: V<sub>1</sub>, channel for the profundus branch of the trigeminal nerve; V<sub>2</sub>, channel of the maxillary branch of the trigeminal nerve; V<sub>3</sub>, channel of the mandibular branch of the trigeminal nerve.

only *Dermochelys* retains a remnant of the levator bulbi in the adult stage. All other turtles apparently have lost this, as well as the other constrictor dorsalis muscles.

In view of the fact that all other modern sauropsids possess a well-developed M. levator bulbi, it may be expected that the hadrosaurs also possessed this muscle. The levator bulbi may be double, as in *Sphenodon* and most Lacertilia, or single, as in birds and crocodiles. While the evidence found in the hadrosaurs cannot be considered conclusive, it indicates the presence of a M. levator bulbi and suggests that this muscle may have been single, as in the akinetic Crocodilia.

The plesiotype of *C. casuarius*, as well as a number of other specimens, shows a surface that may be considered as the origin area of this muscle. Anterior and ventral to the trigeminal foramen, located on the laterosphenoid between the bony grooves for the profundus and maxillary branches of the trigeminal nerve, is situated a moderately concave, anterolaterally facing, triangular surface which may have served as the origin site of the M. levator bulbi. While this surface may be considered rather large, it is not excessive considering the large size of the orbital opening towards which this surface is directed and also the large size of the bulbus oculi, as reconstructed from the ring of sclerotic plates preserved in this specimen. The two facts that stand out in support of such an interpretation are the position of the area, immediately in front of the trigeminal foramen on the anterior part of the lateral brain case wall, and the direction in which this surface faces, directly at the orbit. Possibly this interpretation is in error, but it must be stated that no other surface was detected in any of the numerous skulls examined by the author that corresponded to the probable position of attachment of a levator bulbi. The akinetic nature of the hadrosaurian skull rules out the possibility that this was the origin of either a levator or a protractor pterygoidei. If the interpretation presented here is correct, we may then correlate this laterosphenoid scar with the pars dorsalis of Lakjer. No evidence was found suggesting the presence of a second part, a pars ventralis, as is typically developed in *Sphenodon* and the Lacertilia.

#### CONSTRUCTOR VENTRALIS GROUP

The constrictor ventralis group (intermandibularis muscles) is the third of the three mandibular groups of cranial muscles. These muscles generally occur as superficial sheets of fibers extending between the mandibular rami and innervated by several branches of the mandibularis branch of the trigeminal nerve.

#### M. MYLOHYOIDEUS

All modern sauropsids possess, in varying degrees of development, a mylohyoideus muscle, which normally occurs as a thin, superficial sheet of transverse fibers extending from the region of the symphysis back close

to the posterior extremities of the mandibles. The fibers may originate on the ventrolateral, ventral, or ventromedial surface of the mandible over the greater portion of mandibular length. The transverse fibers pass medially to insert in a midline raphe with the opposing fibers of the opposite side. The *M. mylohyoideus* may be a single sheet, as in the crocodiles, or it may separate into anterior and posterior sheets, as in *Sphenodon* and certain lizards.

Within the hadrosaurs, a general absence of mandibular scars was noted. Only one specimen (A.M.N.H. No. 5799), the right mandible of *Kritosaurus navajovius*, possesses a surface that could be considered as the site of some muscular attachment. This surface occurs as an elongate, horizontally oriented, very gentle concavity on the ventromedial surface of the mandible. Extending from a point near the midlength of the lower jaw, back to the level of the articular cotylus, it is located entirely on the medial surface of the angular just beneath the Meckelian groove. While the area in question is ideally located for this muscle, the evidence of a single specimen is considered insufficient, and the presence and location of a mylohyoideus in the Hadrosauridae are considered to be indeterminable. (See fig. 49.)

#### BRANCHIAL AND HYOIDAL MUSCULATURE

The musculature included here is discussed under two headings, separated primarily according to their position but also on a functional basis. First to be discussed are the superficial branchial fibers of the *M. depressor mandibulae*. Following this, the hyoidal and glosseal musculature is discussed very briefly. The terminology used in this section is that of Edgeworth (1935).

##### BRANCHIAL MUSCULATURE *M. DEPRESSOR MANDIBULAE*

Nearly every adequately preserved hadrosaurian specimen demonstrates some evidence for the location of this muscle. As in previous discussions, the conditions found in the plesiotype of *Corythosaurus casuarius* (A.M.N.H. No. 5338) are described as being generally characteristic of the entire family.

As in all modern reptiles, the depressor mandibulae of the hadrosaurs is presumed to

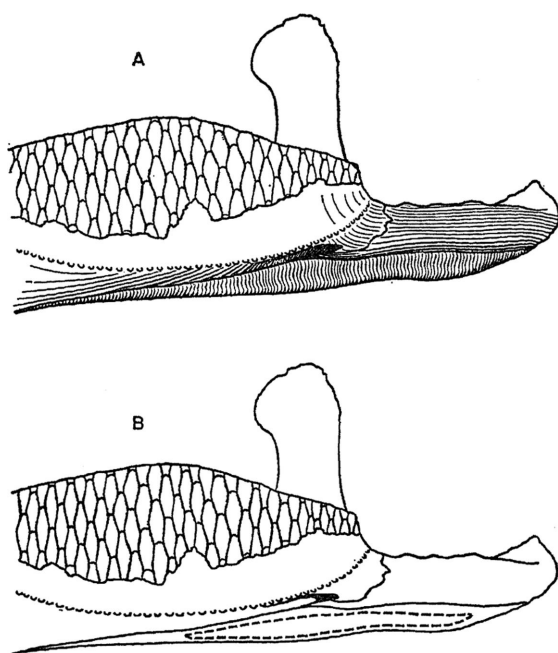


FIG. 49. Posterior half of the right mandible of *Kritosaurus navajovius*, A.M.N.H. No. 5799. A. Medial view, showing the shallow depression on the angular which may represent the origin scar of the *M. mylohyoideus*. B. Outline diagram of the same area, with this scar defined by a broken line.

have linked the retroarticular process of the mandible with the dorsal occipital surfaces of the skull. No other diductor system seems possible after consideration of the skull, the mandibular architecture, and the probable position of the axial muscles, although the surprisingly short retroarticular process may raise some initial doubts. This aspect of the mandible is discussed elsewhere from the functional standpoint.

Location of the depressor attachment areas is restricted considerably with the acceptance of the customary position of the depressor mechanism. Of the two areas, the insertion is the easier to locate and can be restricted to the retroarticular process. This structure is unique, among reptiles, in that it is deflected strongly upward, posterior to the articular cotylus, into a stout and rather abruptly tapering projection. The degree of dorsal deflection varies slightly within the family, but it is remarkably persistent in all specimens examined and is believed to represent bony deformation resulting from the

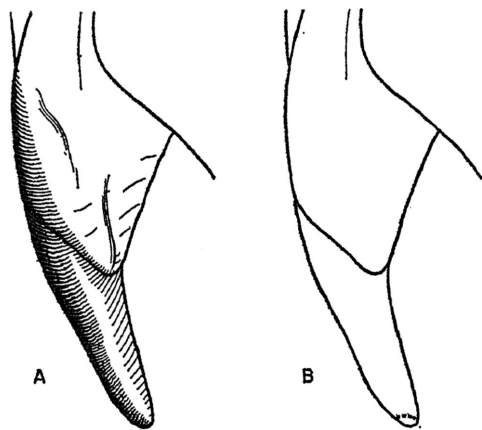


FIG. 50. A. Right paroccipital process of *Corythosaurus casuarius*, A.M.N.H. No. 5338. B. Outline sketch of the same structure, with the probable origin site of the M. depressor mandibulae defined by the broken line.

tensional stresses of depressor fiber contraction at right angles to the mandibular axis, and therefore it is considered to indicate the trend of the depressor fibers. This deflection is most pronounced in the plesiotype of *C. casuarius* in which the dorsal tip of the retroarticular process rises approximately 100 mm. above the articular cotylus. It is equally prominent in the smaller holotype of *Procheneosaurus erectofrons* (R.O.M. No. 3578).

Such a strongly deflected process suggests a very strong tendinous insertion of the depressor fibers on the very tip of this structure. The insertion of these fibers may have extended ventrally from the extremity on to the dorsal part of the medial surface of the retroarticular process, for several specimens, among them *Lambeosaurus lambei* (A.M.N.H. No. 5353) and *Kritosaurus navajovius* (A.M.N.H. No. 5799), show a slight excavation in the region below the process extremity. A similar impression has been illustrated (fig. 41C) in *C. casuarius*. In spite of the apparent sculpturing of this surface, it appears unlikely that the depressor fibers were concentrated anywhere other than the retroarticular extremity.

The attachment of the depressor fibers to the skull is not quite so easily located, but study of the posterior cranial surfaces and a reconstruction of the axial cervical muscles (discussed in a following section) allow a

sound reconstruction to be made. The ventrally deflected paroccipital process of the hadrosaurian skull undoubtedly closely paralleled the fibers of the depressor mandibulae and perhaps was also molded to some extent by the stresses created by this muscle. Keeping in mind the fact that the depressor mandibulae of modern reptiles occupies a superficial position, the paroccipital process offers the most logical site of origin. An examination of the posterior and lateral surfaces of the paroccipital process (the ventral and medial surfaces having been eliminated because of their deep position) shows a prominent rugose area at the dorsal and lateral edge of the posterior surface. This narrow, arcuate rugosity may mark a zone of muscular attachment, but the shape of the paroccipital process and its position with respect to the retroarticular process beneath suggest that the origin of the depressor fibers was largely restricted to the ventral extremity of the paroccipital process. This seems to be the only available superficial origin site for this muscle.

#### HYOIDAL MUSCULATURE

The hyoidal muscular plan is quite uniform in modern sauropsids and can be separated into anterior muscles that link the hyoid apparatus with the anterior portions of the mandibles and posterior muscles that connect the hyoid apparatus with the anterior elements of the pectoral girdle. The anterior hyoid muscles include the normally bipartite M. geniohyoideus, the M. mandibulohyoideus, and the intrahyoidal M. branchiohyoideus. These function to depress the hyoid and draw it forward. Behind the hyoid apparatus, the posterior muscles include the laterally placed M. omohyoideus and the more medial M. episternohyoideus which, aided by the branchiohyoideus, tend to elevate and retract the hyoid structures.

Also attached to the hyoid apparatus, but situated deep to the anterior hyoid muscles, is the M. hyoglossus which, together with the more anterior M. genioglossus (originating in the symphyseal region of the mandibles), extends and retracts the tongue. These two muscles may also aid in the depression of the hyoid.

A number of hadrosaurian specimens, representing four genera, possess partially or

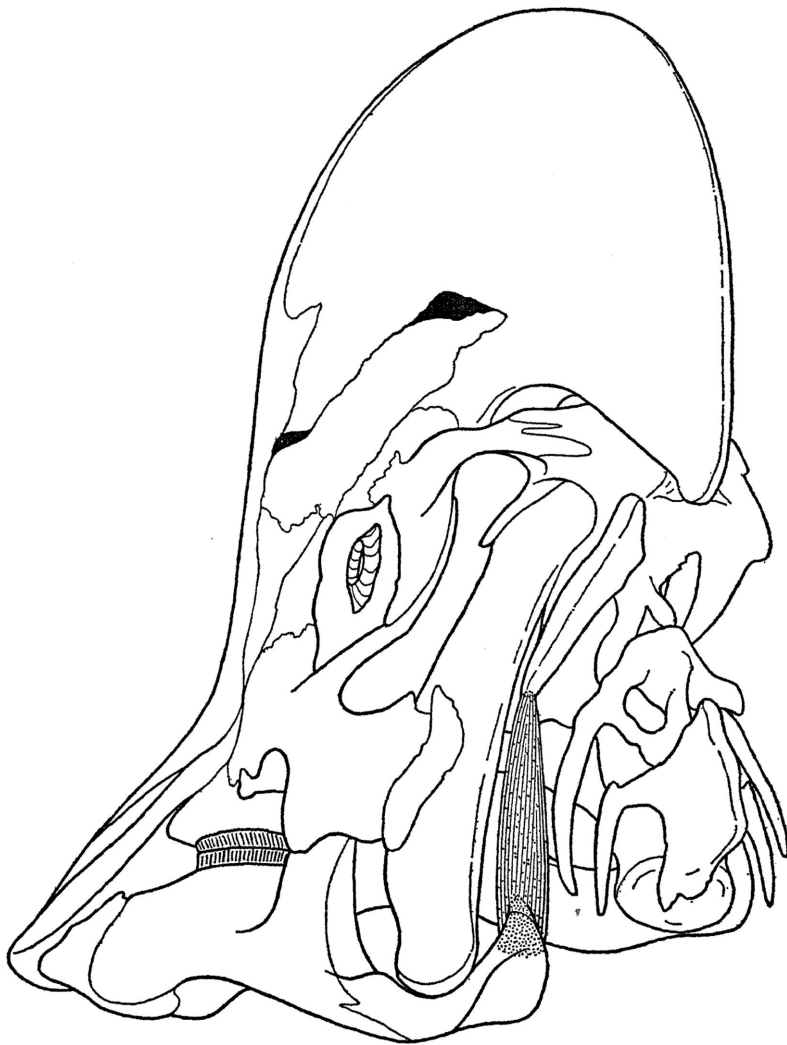


FIG. 51. Posterolateral view of the skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with the *M. depressor mandibulae* reconstructed.

completely preserved hyoid elements. In none of these instances, however, is the complete hyoid apparatus preserved. These elements are described in detail in the section on cranial osteology, so are not described here. The hyoid material of *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), *Saurolophus osborni* (A.M.N.H. No. 5220), *Lambeosaurus lambei* (A.M.N.H. Nos. 5353 and 5373), and *Corythosaurus casuarius* (A.M.N.H. Nos. 5240 and 5338) was examined carefully with the hope that some evidence might be discovered indicating the plan of the hadrosaurian hyoidal

and glosseal musculature. However, in even the best material, in which one or both of the first ceratobranchials were completely preserved, no consistent topography was seen on their surfaces that could be interpreted as sound evidence of muscular attachment. Although the hyoidal muscle pattern and the location of muscular attachments cannot be determined, it should be noted that the broad and slightly concave anterolateral and posteromedial surfaces of the first ceratobranchials offer large areas for the attachment of both the prehyoidal and posthyoidal muscles.

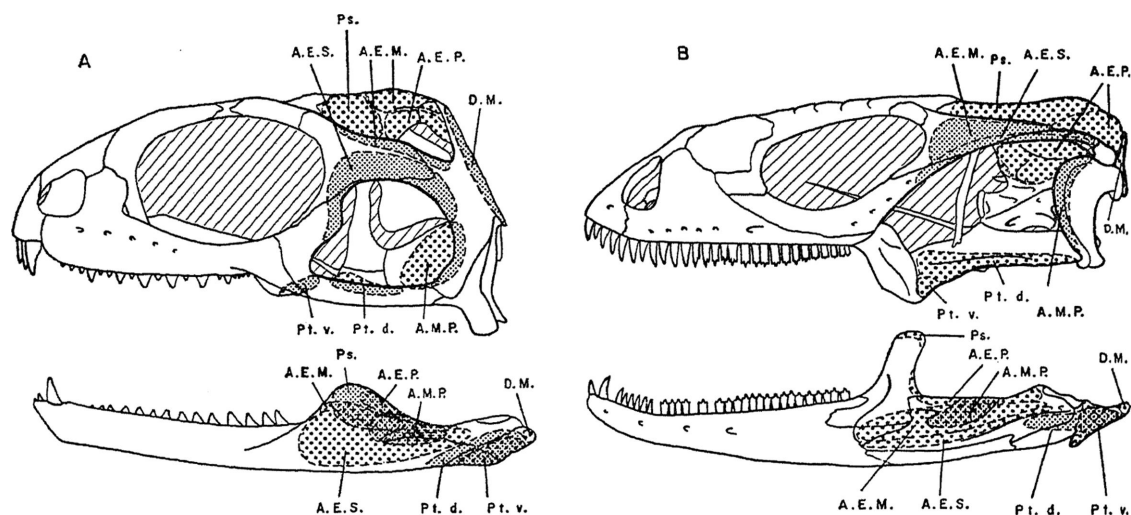


FIG. 52. The skulls and mandibles of two modern sauropsids, showing the origin and insertion areas of certain cranial muscles for comparison with the preceding hadrosaurian muscular reconstructions. The constrictor dorsalis muscle scars have been omitted, because these are believed to have been absent in the hadrosaurs. A. Lateral view of the skull and mandible of *Sphenodon punctatum*. B. Lateral view of the skull and mandible of *Ctenosaura pectinata*. The coarse stippling indicates those attachment areas that are visible in lateral view. The fine stippling marks those attachment areas that are concealed in lateral view either because of intervening superficial bones or of its position on a medial surface of cranial or mandibular bones. Abbreviations: A.E.M., M. adductor mandibulae externus medialis; A.E.P., M. adductor mandibulae externus profundus; A.E.S., M. adductor mandibulae externus superficialis; A.M.P., M. adductor mandibulae posterior; D.M., M. depressor mandibulae; Ps., M. pseudotemporalis; Pt.d., M. pterygoideus dorsalis; Pt.v., M. pterygoideus ventralis.

### AXIAL MUSCULATURE

The following discussion attempts to describe the evidence for, and the reconstruction of, the occipital axial musculature of the hadrosaurs. This treatment is restricted to those axial muscles that insert on the occipital surfaces of the skull. No attempt is made here to reconstruct the purely cervical or post-cervical axial muscles, as this study has been limited to cranial morphology. While the neck musculature may not be considered a part of the cranial anatomy, the influence of the occipital axial muscles, through their cranial attachments, on the shape and topography of the posterior skull elements cannot be denied. Any cranial morphological study would be incomplete if it failed to consider the arrangement, attachments, and effects of these muscles on the occipital surfaces. The terminology used in the following discussions is that of Nishi (1916).

#### M. SPINALIS CAPITIS

Of all the hadrosaurian axial muscles, the *M. spinalis capitis* seems to be one of the

most constant and easiest to recognize. Nearly every specimen examined demonstrates essentially similar development of the supraoccipital region of the skull, which is here interpreted as its site of cranial attachment. As mentioned in the osteological section, the supraoccipital is a small median element of the occiput, which is excluded from the dorsal margin of the foramen magnum by the medial expansions of the exoccipitals. Typically the supraoccipital is depressed (very strongly in some specimens), or its dorsal part is depressed to form a caudally facing, triangular, or elliptical pocket. This depression has been interpreted by Lull and Wright (1942) as the attachment area of the ligamentum nuchae. In view of its constant position in the midline close to the dorsal limit of the occiput, such an interpretation appears quite sound. The large size of the typical hadrosaurian skull undoubtedly accounts for the size and prominence of this scar, yet several specimens indicate that this area may also have provided for the attachment of the *M. spinalis capitis*.

The spinalis capitis in modern reptiles, such as *Sphenodon*, the lizards, and crocodiles, occupies a superficial position very close to the midline. If we can assume a similar position in the hadrosaurs, the lateral portions of this supraoccipital depression are ideally situated for the insertion of spinalis capitis fibers. A dorsal (superficial) position of insertion is mandatory for this muscle, if we assume that its fibers extended caudally to an origin on the neural spines of the posterior cervical and anterior thoracic vertebrae, as they do in modern reptiles, in order that the shorter occipital muscles, linking the occiput with the atlas-axis complex may have unrestricted passage.

In both type specimens of *Corythosaurus casuarius*, this depressed area is shaped like an inverted T, with a deep, narrow depression in the midline ascending from the supraoccipital on to the posterior parietal surfaces. The entire supraoccipital forms the depressed horizontal bar of this T and is defined by the posterior projections or convexities of the surrounding exoccipitals below, opisthotics laterally, and parietals above. This latter feature is believed to be the insertional area of the paired M. spinalis capitis. The vertical groove, which rises from this cross bar, probably represents the ligamentum nuchae attachment area.

A similar situation may be seen in a fine specimen of *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), which is illustrated in figure 53. Here the areas are not so strongly depressed (not a surprising situation in the much smaller *Procheneosaurus*), but they are still quite discernible. The ligamentum nuchae area is restricted to an oval concavity at the dorsal margin of the triangular supraoccipital, although it appears to extend upward as a very narrow and short groove along the midline suture of the parietals. The M. spinalis capitis insertion areas occur as very slight concavities on the lateral extremities of the supraoccipital.

The plesiotype of *Corythosaurus excavatus* (N.M.C. No. 8676) displays a slight variation of the condition described above. In this specimen, three distinct oval depressions, oriented vertically, are visible on the dorsal part of the supraoccipital. The medial depression is the largest of the three and is most likely the attachment area of the ligament.

The smaller, lateral depressions may be the insertional sites of the spinalis capitis fibers. This condition is unlike that found in other hadrosaurian species. In all other forms in which the spinalis scars are preserved, these scars are oriented with the greatest dimension in a horizontal plane. Only *Corythosaurus excavatus* was noted to have the reverse situation. In most cases, the M. spinalis capitis scar is a single, horizontal depression extending the full width of the supraoccipital. A few specimens, *Hypacrosaurus altispinus* (N.M.C. No. 8501), *Kritosaurus notabilis* (A.M.N.H. No. 5350), and perhaps *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), however, show this as a paired feature.

#### M. LONGISSIMUS CAPITIS

The longissimus capitis, the only longissimus muscle that attaches to the skull, is somewhat more variable than the spinalis capitis. In modern reptiles, for instance, it may separate into two or three distinct muscles, the insertions of which are quite variable. All portions of the longissimus capitis of modern reptiles are constant in their origins: on the prezygapophyses of the fourth cervical vertebra. From these attachments, the longissimus fibers may split as they pass forward, into a pars transversalis capitis, a pars transversalis cervicis, and in some cases (*Sphenodon*, *Iguana*) into a third part, the pars articulo-parietalis. The first and last of these generally occupy positions well lateral to the midline, in keeping with their function, which is the rotation and abduction of the head.

It is assumed that the M. longissimus capitis was represented among the axial muscles of the Hadrosauridae, although no distinct scars were found on any of the hadrosaurian skulls to prove the presence of any of the three parts mentioned above. If a pars articulo-parietalis were present, it can be assumed that it occupied a position similar to that of modern reptiles and inserted near the dorso-lateral margin of the posterior skull surface, which would place the insertion on the dorsal part of the exoccipital-opisthotic complex, just beneath the squamosal at the dorsal edge of the paroccipital process. Some specimens (*Procheneosaurus erectofrons*, A.M.N.H. No. 5461, and *Corythosaurus casuarius*, A.M.N.H. No. 5338) show a broad, shallow

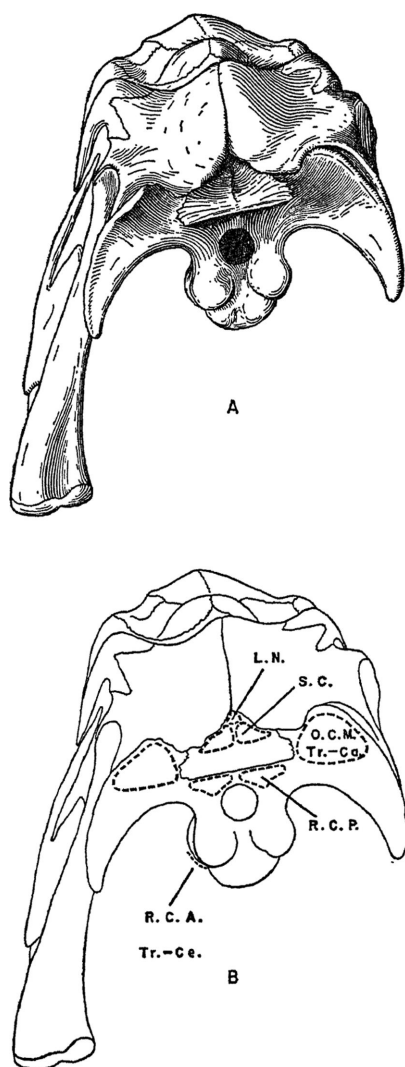


FIG. 53. A. Posterior view of the skull of *Procheneosaurus erectofrons*, A.M.N.H. No. 5461, showing the insertion scars of the axial cervical muscles. B. Outline sketch of the same, with each of the axial muscle insertion areas defined by broken lines. Abbreviations: L.N., attachment area of the ligamentum nuchae; O.C.M., insertion of the *M. obliquus capitis magnus*; R.C.A., insertion of the *M. rectus capitis anterior*; R.C.P., insertion of the *M. rectus capitis posterior*; S.C., insertion of the *M. spinalis capitis*; Tr. Ca., insertion of the *M. transversalis capitis*; Tr. Ce., insertion of the *M. transversalis cervicis*.

concavity in this vicinity, but the area appears too large to be the insertional scar of the articulo-parietalis and elsewhere is interpreted

as the insertion of the normally much larger *M. obliquus capitis magnus* and possibly the *pars transversalis capitis*. Possibly this large scar was the attachment area for more than two axial muscles, especially those that typically insert lateral to the condyle. Such a possibility is important, because the hadrosaurian skull is definitely limited with respect to occipital areas that are feasible for such lateral attachments. However, no evidence supports the possibility of the attachment of more than two muscles nor are there indisputable muscle scars on the occipital surfaces to support even a *pars articulo-parietalis* of the *M. longissimus capitis*.

A similar situation was found with regard to the reconstruction of the *pars transversalis capitis*. This muscle functions primarily to rotate and abduct the head, and therefore, according to the situation found in modern reptiles, its cranial attachment should be located far lateral to the midline. In both *Sphenodon* and the *Lacertilia*, its insertion is closely associated with that of the *M. obliquus capitis magnus*, which has a similar function, near the lateral extremity of the paroccipital process, slightly above and well lateral to the occipital condyle.

Again, the corresponding area of the hadrosaurian occipital surface is in the dorso-lateral portion of the posterior surface of the exoccipital-opisthotic complex, at the dorsal extremity of the paroccipital process. The large concavity in this area (*Procheneosaurus erectofrons*, A.M.N.H. No. 5461, and *Corythosaurus casuarius*, A.M.N.H. No. 5338) is believed to have served as the attachment site of the *M. obliquus capitis magnus*. However, in view of the similar function of these two muscles and their frequent proximity in modern reptiles, it is quite possible that this gentle and rather large concavity provided for the insertion of both the *obliquus capitis* and the *pars transversalis capitis*. Again, as with the *pars articulo-parietalis*, the evidence offered by the hadrosaurian occipital surfaces is insufficient to support any conclusions concerning the *pars transversalis capitis*. It may or may not have been present as a distinct muscle.

The *pars transversalis cervicis* of the hadrosaurs presents a problem similar to the prob-



lems regarding the other portions of the longissimus capitis. *Sphenodon* and most lacertilians possess a distinct transversalis cervicis which inserts on a prominent speno-occipital tubercle on the ventral surface of the brain case. Nearly every hadrosaurian skull examined possessed a comparable feature in the form of a rather bulbous speno-occipital swelling or prominence, which exists as a ventrolateral expansion of the brain case ventral and anterior to the occipital condyle. In modern reptiles, the speno-occipital process provides for the attachment of both the pars transversalis cervicis of the M. longissimus capitis and the M. rectus capitis anterior. Whether or not a similar condition existed in the hadrosaurs cannot be established, but it seems very likely if these muscles were concerned with the same functions as in modern forms, which is flexion of the head. The roughened surface of the hadrosaurian speno-occipital prominence gives no indication of whether one or two muscles inserted here. It appears to be a safe assumption that flexion of the head was a definite necessity in the hadrosaurs, and therefore a reasonable interpretation is that at least one, or possibly both, of these flexors attached on this, the only visible ventral scar on the cranium.

#### M. ILIO-COSTALIS CAPITIS

The ilio-costalis system of modern reptiles is a laterally situated muscle system that connects the pelvis and the lateral rib surfaces. In the cervical region there is generally an anterior extension of this system which links the cervical ribs and the atlas-axis complex with the basioccipital of the skull.

In the hadrosaurs, this anterior extension of the M. ilio-costalis dorsi may have been present, but no distinct scar indicating its presence was detected in any of the skulls examined. Possibly these fibers did exist and inserted in the same area of the speno-occipital prominence at the ventro-anterior margin of the basioccipital along with the M. rectus capitis anterior and possibly the pars transversalis cervicis.

The development of the speno-occipital process in the Hadrosauridae indicates that one or more of these muscles attached on the ventral surface of the brain case. This structure typically appears as a broad, rugose ex-

pansion, projecting ventrolaterally from the base of the brain case. The large roughened surface of this prominence is both large enough and appropriately situated to have provided attachment for any or all of these muscles, but, as is pointed out above, no reliable division of this surface into two or three distinct scars is possible on a basis of the topography in currently known specimens.

#### M. RECTUS CAPITIS POSTERIOR

The suboccipital muscles include the most powerful of the neck muscles—those that form the very short muscular link between the occipital surfaces of the skull and the atlas-axis complex. Aside from their primary function of supporting the head, these muscles are concerned with the extension, rotation, and abduction of the head. Two muscles, the M. rectus capitis posterior and the M. obliquus capitis magnus, both of which may be either single or double, make up the suboccipital muscle system.

The M. rectus capitis posterior of modern reptiles is frequently separated into a pars superficialis and a pars profundus. The evidence for a large undivided rectus capitis posterior is very good in the hadrosaurs, for every hadrosaurian skull that was studied possesses the prominent scar of this muscle. The insertion scar of the rectus capitis posterior may be seen particularly well in the following specimens: *Procheneosaurus erectofrons* (A.M.N.H. No. 5461), *Kritosaurus notabilis* (A.M.N.H. No. 5350), *Corythosaurus casuarius* (A.M.N.H. No. 5338), *Edmontosaurus regalis* (N.M.C. No. 2289), *Brachylophosaurus canadensis* (N.M.C. No. 8893), and *Anatosaurus saskatchewanensis* (N.M.C. No. 8509).

The M. rectus capitis posterior scars consistently appear as two very prominent oval to subcircular depressions situated on the posterior surface of the exoccipitals on each side of the upper limits of the foramen magnum, or just above this foramen. These two areas are usually equal in size and occupy corresponding positions on each side of and close to the midline, a condition in keeping with the function of this extensor muscle. These depressions are most strongly developed in the specimens mentioned above, but they exist as strong to moderate depressions

in all of the hadrosaurs. The position varies slightly, being above or on a level with the upper part of the foramen magnum, according to the skull height. In low-vaulted forms, such as *Edmontosaurus regalis*, *Kritosaurus notabilis*, and *Anatosaurus copei*, these depressions occupy a low position on each side of the foramen magnum. In higher-vaulted forms, such as *Corythosaurus casuarius*, *Anatosaurus saskatchewanensis*, and *Brachylophosaurus canadensis*, they occur above the foramen. This muscle was apparently undivided in the hadrosaurs, or at least any second portion was relatively small and left no visible scar.

#### M. OBLIQUUS CAPITIS MAGNUS

Much has already been said here about the obliquus capitis muscle, but it should be stated that it is something of a problem in the Hadrosauridae, as some doubt exists as to whether or not this muscle was present and, if it was, where it was located. Normally this is the largest of the reptilian abductor muscles (those muscles that produce a lateral deflection of the head), but, as discussed below, such a muscle may have been relatively small and thus left no prominent scar or other indication of its existence. Because this muscle typically connects the skull with the atlas-axis complex, the reduction of this muscle is entirely possible, for lateral displacement of the head can be effected just as well, indeed more effectively, by a lateral bending of the neck, thereby reducing the degree of deflection between the skull and the atlas-axis complex and also reducing the need of large occipital abductor muscles. A long neck, like that of the hadrosaurs, is most advantageous in increasing the range of the lateral, as well as the vertical, deflection of the head.

The rather limited occipital surfaces lateral to the condyle diminish considerably the possible regions on which the obliquus capitis could have inserted. Such a limitation at first appears to support the suggestion made above. The most likely area of insertion on the hadrosaurian skull is on some portion of the posterior surface of the paroccipital process. The ventral extremity of this process appears rather delicate for the attachment of a large muscle, the fibers of which would

have extended caudally at nearly right angles to the axis of the process. Therefore it seems most likely that the *M. obliquus capitis magnus* attached to the much stouter upper part of the paroccipital process on an area better capable of resisting the stresses created by muscular contraction. Several specimens (*Corythosaurus casuarius*, A.M.N.H. No. 5338; *Procheneosaurus erectofrons*, A.M.N.H. No. 5461; and *Hypacrosaurus altispinus*, N.M.C. No. 8501) exhibit areas that may have been the site of insertion of this muscle. Even in these specimens, however, the evidence is quite doubtful, but these areas are described here as the only functionally logical points of attachment.

The caudal surface of the exoccipital-opisthotic complex extends laterally and upward from the foramen magnum. Laterally this surface expands dorsally to meet the overlying squamosal and ventrally to form the paroccipital process. In the specimens listed above, the dorsal expansion is marked by a very gentle concavity. So slight is this depression that its borders cannot be precisely outlined, but it appears to have been excluded from the paroccipital process below. This broad, gentle depression, which can be seen on both sides in the above specimens, may mark the insertion of the *M. obliquus capitis magnus*. Because of their almost obscure nature and the lack of similar topography on most of the other hadrosaurian specimens, these features would not have been considered except for the fact that there is no other occipital surface that functionally, at least, could have served as the cranial site of attachment of the obliquus capitis.

In *Edmontosaurus regalis* (N.M.C. Nos. 2288 and 2289) a moderately well-defined, rugose area, lateral to the supra-occipital at the upper margin of the exoccipital-opisthotic complex, may represent a different insertion for the obliquus capitis. The fact that this feature occurs on both sides of the occiput in both the holotype and the paratype of *E. regalis* seems to rule out any possibility that this rugosity was the result of an osteological abnormality or an accident of preservation. The dorsal part of the exoccipital-opisthotic complex in *Edmontosaurus* projects caudally, with the rugose areas situated at the lateral extremities of this strong occipital overhang.

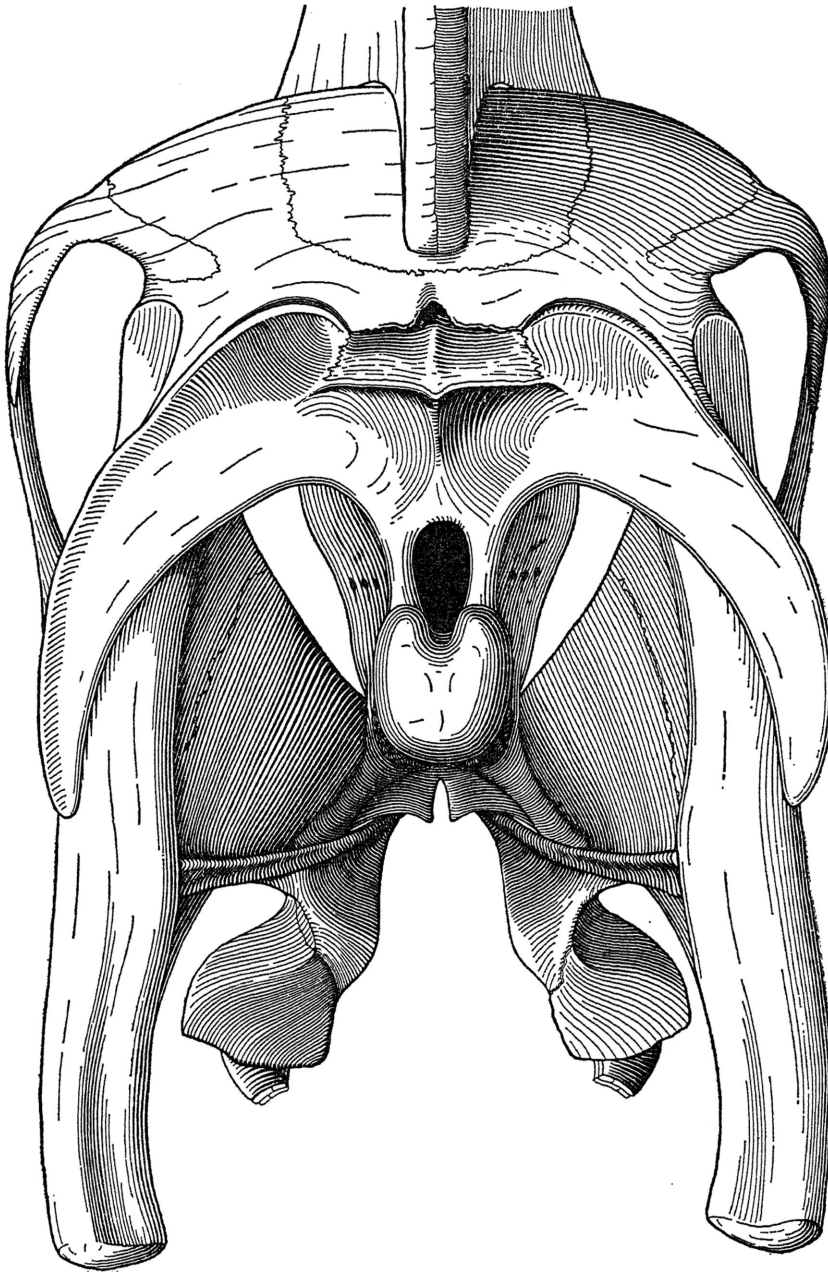


FIG. 54. Posterior view of the restored skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338. This specimen exhibits some of the insertional scars of the axial cervical muscles which are similar to those illustrated in figure 53 for *Procheneosaurus erectofrons* (for the location and identification of these, compare with fig. 53).

This horizontally oriented, posterior projection on the upper occipital surfaces is much more prominent (partly as a result of crushing) than in other members of the family. Typically, a slight overhang exists above the foramen magnum and beneath the supraoccipital, but this is generally not so strongly developed, nor does it extend beyond the lateral extremities of the supraoccipital in other hadrosaurian species.

The more prominent development of these "scars" in *Edmontosaurus* suggests that the muscles concerned were much larger in this species than in any other member of the family. Their prominence may, on the other hand, be a reflection of a restricted tendinous insertion along the crest of the strong, caudally projecting ridge of the occiput, as opposed to a fleshy attachment on the broader, nearly flat upper part of the exoccipital-opisthotic complex in *Corythosaurus*.

While the evidence seen on various hadrosaurian skulls is far from conclusive with regard to the presence and location of an obliquus capitis, the existence of an abductor muscle system is quite obvious. Whether abduction of the head was effected largely by articulation between the occipital condyle and the atlas-axis complex or largely by articulation between the cervical vertebrae cannot be established. The articulation surfaces of the condyle and the atlas-axis complex appear to have provided considerable freedom of lateral movement. Therefore, it is believed that abduction was promoted, at least partly, by condylar articulation, which would imply the existence of a hadrosaurian *M. obliquus capitis magnus*. Undoubtedly abduction was also effected in part by lateral bending in the cervical region.

#### M. RECTUS CAPITIS ANTERIOR

The presence of this muscle appears almost certain in the hadrosaurs, in spite of deficient evidence for its cranial attachments. The *M. rectus capitis anterior*, along with the *pars transversalis cervicis* of the *M. longissimus capitis*, functions to lower or flex the head in modern reptiles, which is accomplished by both condylar, atlas-axis movement and articulation between the cervical vertebrae.

The ventral surfaces of the hadrosaurian crania do not offer many areas of attachment for the ventral axial muscles, but the large spheno-occipital swellings on the lateroventral surfaces of the brain case, characteristic of most hadrosaurian species, appear to provide ample insertion area. This is the only inferior cranial feature that can reliably be correlated with muscular attachment. None of the skulls examined displays any other topographic depression or prominence that is functionally possible as a muscular insertion area.

As indicated above, this spheno-occipital prominence most probably served as the point of attachment for both the *pars transversalis cervicis* and the *M. rectus capitis anterior* (and perhaps also the *M. ilio-costalis capitis*) as the corresponding process does in recent reptiles. No proof could be found in the surface texture of this process, which is usually imperfectly preserved. The reconstruction of the *M. rectus capitis anterior* is based solely on the general similarity of the hadrosaurian spheno-occipital prominence to that of modern forms, such as *Sphenodon* and the lizards, and the belief that ventrally situated flexors are necessary to effect flexion of the head, an important movement in herbivorous animals.

### NEUROLOGY

Various authors have contributed to the rather meager knowledge of hadrosaurian neuro-anatomy. Included among these contributions are those of Marsh (1893, 1896), Brown (1914a), Lambe (1920), Gilmore (1924b), and Lull and Wright (1942). Only three hadrosaurian genera are included in these several works: *Anatosaurus*, *Edmontosaurus*, and *Lambeosaurus*. The last-named is, however, only very superficially described

by Gilmore. Although a number of partial or complete crania are known, only a few of these are adequately preserved or prepared for detailed endocranial studies. The best of these specimens are *Anatosaurus annectens* (U.S.N.M. No. 4737), *Anatosaurus* ("Trachodon") sp. (A.M.N.H. No. 5236), *Anatosaurus* sp. (Y.P.M. No. 618), *Edmontosaurus regalis* (N.M.C. No. 2289), and *Kritosaurus notabilis* (A.M.N.H. No. 5350). The discussion

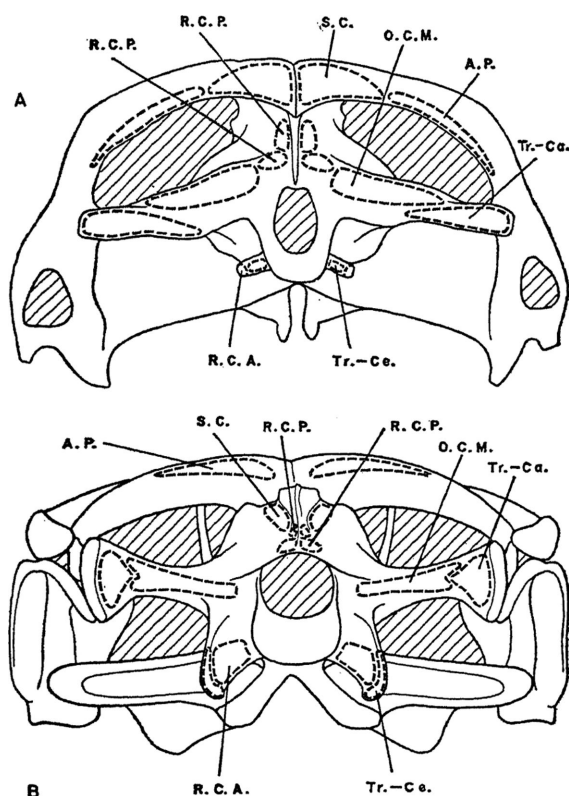


FIG. 55. Posterior views of two modern sauropod skulls, showing the insertional areas of the axial cervical muscles. A. *Sphenodon punctatum*. B. *Ctenosaura pectinata*. Abbreviations: A.P., insertion of the pars articulo-parietalis; O.C.M., insertion of the M. obliquus capitis magnus; R.C.A., insertion of the M. rectus capitis anterior; R.C.P., insertion of the M. rectus capitis posterior; S.C., insertion of the M. spinalis capitis; Tr. Ca., insertion of the pars transversalis capitis; Tr. Ce., insertion of the pars transversalis cervicis.

that follows is based primarily on these crania (particularly those of *Kritosaurus* and *Edmontosaurus*) and their endocranial casts, although an occasional reference is made to other specimens.

Considerable discussion has centered about the reliability of endocranial casts of fossil vertebrates and the degree of accuracy with which the original brain size and form are reproduced. Dendy (1910) was one of the first to note that the reptilian brain may not fill the entire endocranial cavity. In his study of *Sphenodon* he noted that the brain was suspended within the brain cavity by in-

numerable thin strands of connective tissue extending radially across the subdural space. Dendy emphasized the great disparity between the size of the brain and that of the cranial cavity and suggested that this condition was probably also true of many fossil reptiles. Papez (1929) notes that this condition is also true of turtles, but adds that in the Squamata the brain more nearly fills the cranial cavity. Dissections by the present author of *Ctenosaura*, *Amblyrhynchus*, and *Varanus*, as well as *Sphenodon*, verified these conditions. Additional dissections of *Alligator* crania established that the dura mater occupies a major portion of the endocranial cavity here also. Consequently, endocranial casts do not faithfully reproduce the details or true form of most modern reptilian brains.

In his study of *Tyrannosaurus* and *Allosaurus*, Osborn (1912a), influenced by Dendy's work, assumed that the brain of *Tyrannosaurus* occupied approximately half of the total cranial volume, comparable to the condition found in *Sphenodon*. Romer (1956), while recognizing that the reptilian brain case typically does not fit closely about the brain in all areas, believes the internal contours of the brain case are generally molded by the brain, because embryonic development of the brain is quite rapid and usually far advanced before the skull development even begins. It should also be pointed out that the brain size apparently diminishes slightly with age in modern reptiles, so that, even with considerable discrepancy in size, the brain cavity most probably reflects the approximate size and form of the brain at an earlier stage of development.

The topography of the internal brain case surfaces, in the hadrosaurian crania mentioned above, suggests that these elements were not very closely applied to the brain surfaces. Therefore we may assume that the hadrosaurian brain, at least in relatively mature individuals, did not completely fill the endocranial cavity. Indications of this can be seen in the general absence of delicate impressions, such as those that might be left by superficial vascular tracts, on the medial cranial surfaces. Furthermore, the generally subdued relief of these surfaces fails to demonstrate the pronounced boundaries between certain brain divisions or between

paired lobes, which otherwise might be expected in view of their frequency and prominence in modern reptilian brains. In spite of this situation, endocranial casts are still valuable sources of information concerning the anterior central nervous system and provide us with data concerning the general shape of the brain, its major divisions and their relative degree of development, and the number, size, and approximate location of the cranial nerves. Some approximation of brain volume can also be determined, but this of course is subject to significant error. Obviously, small superficial details may be lost as a result of a relatively thick dura mater envelope.

### THE BRAIN

While the hadrosaurian brain was very small in proportion to the skull size, on examination of endocranial casts it is apparent that the brain was quite highly developed and typically reptilian in form. The major divisions are usually distinct, although their precise limits are not generally discernible in the endocranial casts. The brain casts of three hadrosaurian genera (*Anatosaurus*, *Edmontosaurus*, and *Kritosaurus*) reveal an elongate brain which is slightly flexed at the midbrain and strongly expanded locally. In its anterior portions it is considerably larger than the spinal cord of the cervical region.

Both the prosencephalon, or forebrain, and rhombencephalon, or hind brain, are more or less clearly indicated in the endocranial casts studied. The midbrain (mesencephalon), however, as is so typical of modern reptiles, is more difficult to define. These hadrosaurian casts indicate three major constrictions of the endocranial cavity and two prominent zones of expansion. These are believed to reflect similar constrictions and expansions of the hadrosaurian brain, although the relief and definition undoubtedly have been suppressed by a more or less thick envelope of dura mater which surrounded the brain. The anterior constriction, which is the most abrupt, marks the anterior termination of the cerebral hemispheres and separates this part of the brain from the more anterior olfactory segments. Behind the anterior constriction, the cerebral expansion is oval in cross section, with a width about twice the height. A second con-

striction, which is somewhat broader and less sharply defined than the anterior constriction, indicates the posterior limit of the cerebral expansion as well as the anterior margin of the cerebellum. This constriction is correlated with the mesencephalon, the smallest of the three major brain divisions. Even in modern reptiles the midbrain is somewhat obscure because of its position between two prominent neural expansions. The situation was no different in the hadrosaurian brain. The midbrain constriction of the endocranial cavity is the most critical feature displayed by the various casts, aside from certain cranial nerve passages, for on this feature rest the reconstructions of all three major brain divisions. Behind the midbrain region, the large cerebellar expansion is triangular in section. The last commissure or zone of constriction occurs approximately at the midlength of the rhombencephalon where it impressed both the lateral and dorsal surfaces of the brain behind the cerebellum, establishing an arbitrary boundary marking the subdivision of the hind brain.

### RHOMBENCEPHALON

The endocranial cast of *Kritosaurus notabilis* (A.M.N.H. No. 5350) indicates a rather distinct hind brain which is marked at midlength by a prominent posterior constriction or commissure. This feature, which lies posterior to the cerebellar expansion, has been selected as the arbitrary boundary between the myelencephalon and the adjacent metencephalon. The hind brain, as indicated by the cast, measured approximately 125 mm. in length, with a maximum height and width of 75 mm. and 40 mm., respectively. These dimensions compare very well with those of the endocranial cast of *Edmontosaurus regalis* (N.M.C. No. 2289): 140 mm., 76 mm., and 42 mm. Similar dimensions hold true for the brain casts of *Anatosaurus* sp. (Y.P.M. No. 618) and *Anatosaurus* ("Trachodon") sp. (A.M.N.H. No. 5236), although in the latter specimen the cerebellum is somewhat more inflated.

### MYELENCEPHALON

The myelencephalon or posterior portion of the *Kritosaurus* cast between the foramen magnum and the level of the ninth cranial

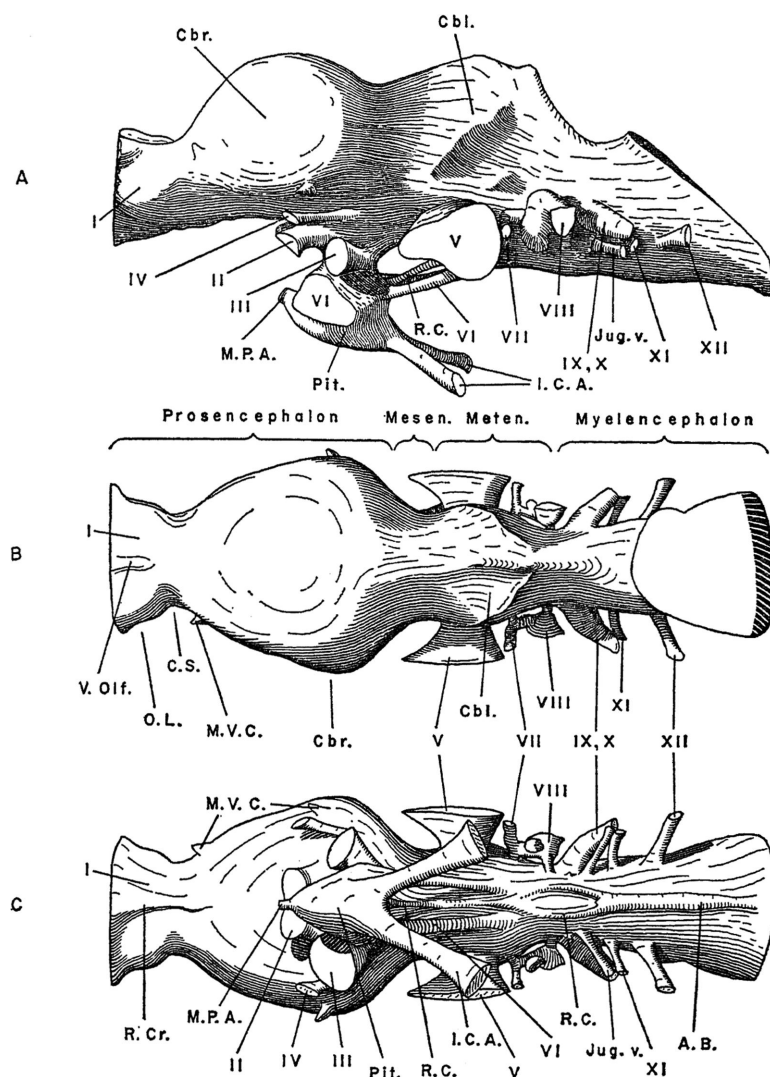


FIG. 56. Endocranial cast of *Kritosaurus notabilis*, A.M.N.H. No. 5350. A. Left lateral view. B. Dorsal view. C. Ventral view. *Abbreviations:* A.B., arteria basilaris; Cbl., cerebellum; Cbr., cerebrum; C.S., coronal sulcus; I.C.A., internal carotid artery; Jug. v., jugular vein; Mesen., mesencephalon; Meten., metencephalon; M.P.A., median palatine artery; M.V.C., minor vascular canals; O.L., olfactory lobe; Pit., pituitary body; R.C., ramus caudialis; R.Cr., ramus cranialis; V. Olf., vena olfactoria; I, olfactory nerve; II, optic nerve; III, oculomotor nerve; IV, trochlear nerve; V, trigeminal nerve; VI, abducens nerve; VII, facialis nerve; VIII, auditory nerve; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve. Approximately  $\times \frac{1}{3}$ .

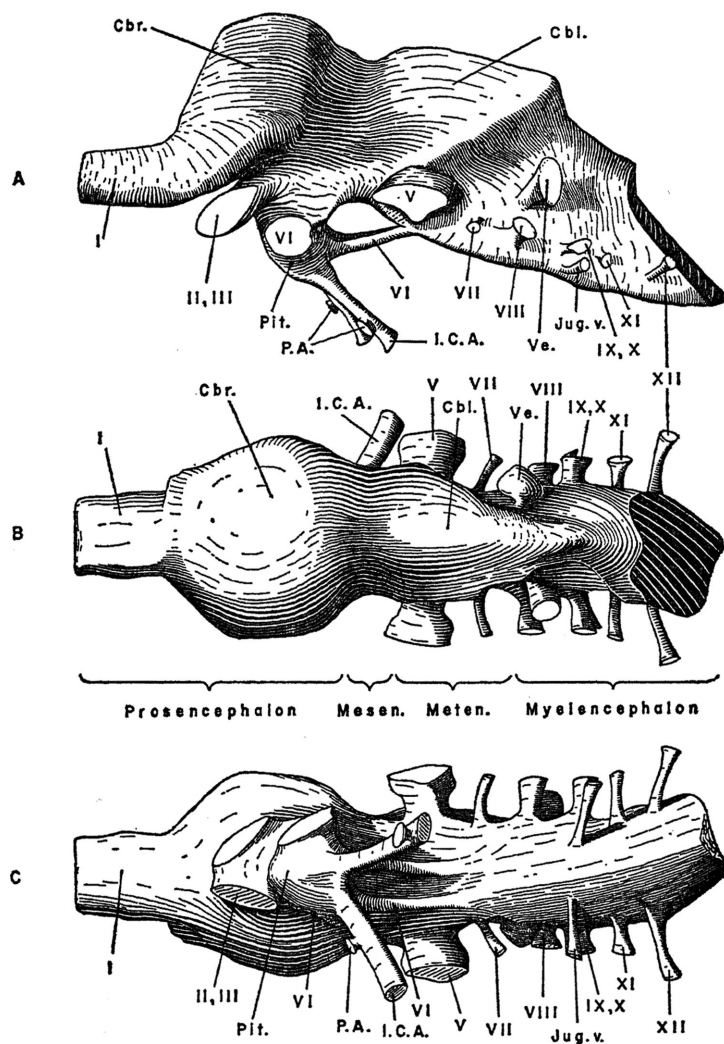


FIG. 57. Endocranial cast of *Edmontosaurus regalis*, N.M.C. No. 2289. A. Left lateral view. B. Dorsal view. C. Ventral view. *Abbreviations:* Cbl., cerebellum; Cbr., cerebrum; I.C.A., internal carotid artery; Jug. v., jugular vein; Mesen., mesencephalon; Meten., metencephalon; P.A., palatine artery; Pit., pituitary body; Ve., vestibulum of cavum capsularis; I, olfactory nerve; II, optic nerve; III, oculomotor nerve; IV, trochlear nerve; V, trigeminal nerve; VI, abducens nerve; VII, facialis nerve; VIII, auditory nerve; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve. Approximately  $\times \frac{1}{3}$ .



nerve is moderately inflated but quite constant in size. The ventral margin is straight in lateral aspect but is marked by a narrow midline ridge which indicates an elongate midline depression or groove in the floor of the brain case. The dorsal limit is slightly convex anteroposteriorly, ascending from the foramen magnum to its maximum height in the region of the eleventh cranial nerve. From this high point, the myelencephalon dorsal surface descends to the prominent posterior constriction. The lateral surfaces of the myelencephalon are gently convex dorso-ventrally but are nearly straight anteroposteriorly.

Most prominent of the features in the myelencephalic region are the indications of several passages through the lateral wall of the brain case. These indicate the sites of emergence of the last four cranial nerves, as well as the passages of certain vascular elements. As illustrated in figure 56, these cranial nerves arise from the inferior lateral surface of the anterior half of the myelencephalon. Approximately 34 mm. anterior to the foramen magnum, the stout hypoglossal (XII) nerve emerges from the lateral surface of the hind brain, passing laterally and slightly caudally through the posterior portion of the exoccipital. The smaller accessory (XI) nerve is located about 13 mm. in front of and slightly below the hypoglossal and extends through a much smaller canal in the exoccipital-opisthotic complex. The passage of the accessory nerve is very nearly parallel to that of the hypoglossal. A much larger protuberance approximately 16 mm. in front of and above that of the accessory nerve in the *Kritosaurus* cast represents the large, laterocaudally directed canal which pierces the opisthotic region of the cranium. This feature indicates the emergence of a significantly large mass of neural fibers from the brain cavity, a mass that must have been considerably larger than either the vagus or the glossopharyngeal nerves. In view of the large size of this passage, it is quite probable that it provided a route for both the vagus (X), which is usually large in reptiles, and the somewhat smaller glossopharyngeal (IX) nerves. Still a fourth passage can be seen penetrating the opisthotic region of the brain case in most hadrosaurian specimens, and

this is represented in the *Kritosaurus* endocranial cast by a small, narrow process which extends in a posterocaudal direction from its origin immediately below that of the combined passage of the ninth and tenth cranial nerves. This is believed to mark the passage of the jugular vein from the myelencephalon out through the lateral wall of the brain case. A very small process, just anterior to this last feature of the cast, probably represents the position of a smaller subsidiary vascular element.

As might be expected, this endocranial cast fails to indicate or differentiate between the medulla and the more dorsally situated choroid plexus. It is assumed that the cranial nerves emerged from the medulla oblongata, as in modern reptiles, so the choroid plexus, as a result, is assumed to have occupied a position above the cranial nerve level.

The endocranial cast of *Edmontosaurus regalis* (N.M.C. No. 2289), described by Lambe (1920), illustrates a hind brain that was remarkably similar to that just described for *Kritosaurus*. Not only is the rhombencephalon similar in size, but the same general proportions and features can be seen. The brain as a whole, although showing a greater degree of flexing at the midbrain, has the same general form, with the inflated cerebral and cerebellar regions and the three more or less prominent constrictions. The anterior constriction again is the most abrupt, but the midbrain constriction behind the cerebrum is the most prominent. The less obvious posterior constriction separates the rhombencephalon into the posterior myelencephalon and the anterior metencephalon, as in *Kritosaurus*.

The myelencephalon of *Edmontosaurus*, similar to that of *Kritosaurus*, is rather large but is more uniform in size than is that of *Kritosaurus*. Emerging from its lower lateral surface are the roots of the last four cranial nerves arranged in a pattern almost identical with that described above for *Kritosaurus*. Lambe's interpretation of these features differs markedly, however, from that which is expressed here.

The hypoglossal nerve, as indicated in the endocranial cast, was of the same order of magnitude as that of *Kritosaurus*, and it occupied a like position near the posterior

limit of the hind brain. This most caudal passage was similarly identified by Lambe as the emergent passage of the hypoglossal nerve. Immediately in front of this passage, a second canal is indicated in the cast which is believed to mark the path of the smaller accessory nerve. Lambe, however, interpreted this as the passage of the anterior condyloid artery. The emergence of the vagus and glossopharyngeal nerves is again indicated by the cast of a single canal just anterior and dorsal to that of the accessory nerve. Lambe (1920) included the accessory nerve with these last two nerves, suggesting that all three emerged from the cranium through a common canal. As in *Kritosaurus*, a fourth passage has left its impression on the endocranial cast just beneath that interpreted here as the vagus-glossopharyngeal canal. This fourth opening in the brain case is presumed to have been occupied by the jugular vein.

Three endocranial casts of *Anatosaurus* have been described in the literature: *Anatosaurus annectens* described by Marsh (1893, 1896); *Anatosaurus* ("Trachodon") sp., by Brown (1914a); and *Anatosaurus* sp., by Lull and Wright (1942). Except for the missing midbrain and forebrain sections of the "Trachodon" cast, the first two of these casts are very similar. The cast described by Lull and Wright is somewhat less perfect, but otherwise it compares closely with the other casts. With the exception of Brown's more thorough investigation of the otic capsule and his remarkable cast of the semicircular canals, the hind brains of these two casts are basically like those of *Kritosaurus* and *Edmontosaurus*. Both demonstrate the prominent, broad, mid-brain constriction anterior to the cerebellum which marks the anterior margin of the rhombencephalon. The posterior constriction is much less pronounced but is still clearly recognizable. Behind this posterior constriction the somewhat shorter myelencephalon is expanded laterally, rather than dorsally and ventrally as in the specimens discussed above. The solitary passages of the hypoglossal and accessory nerves are indicated by two distinct processes low on the lateral surfaces of the casts. The larger, common passage of the vagus and glossopharyngeal nerves occurs immediately anterior to these and slightly above them. These interpretations all corre-

spond with the reconstructions of *Kritosaurus* and *Edmontosaurus*. Neither cast, however, offers any evidence of a fourth canal through the lateral wall of the brain case in this region, which might correspond with that which was interpreted as the route of the jugular vein in the two preceding genera.

Brown (1914a) suggests that the jugular vein emerged from the endocranial cavity together with the ninth, tenth, and eleventh cranial nerves through the largest of the canals in the myelencephalic region of the cranium. The passage immediately anterior to the twelfth or hypoglossal canal was also interpreted by Brown as the canal of the anterior condyloid artery. These interpretations may be correct, but further consideration suggests a different interpretation.

It is a generally accepted fact that the cranial nerves, particularly the major trunks, are remarkably constant, whereas vascular elements are notoriously variable. In view of the variation seen in certain cranial foramina, these variable openings, when present, appear more reasonably interpreted as vascular passages. On the other hand, those foramina that are consistently located in closely related forms probably represent neural canals. Therefore the conclusion is reached that the three foramina that are indicated in the "Trachodon" cast, so closely paralleling the three openings of the *Kritosaurus* and *Edmontosaurus* crania, probably mark the routes of the last four cranial nerves. The relative sizes and positions of these canals further suggest that Brown's anterior condyloid canal was the route of the small accessory nerve. The absence of the fourth canal, as in "Trachodon," suggests that, when present, as in *Edmontosaurus* and *Kritosaurus*, it contained a blood vessel, presumably the jugular vein. In "Trachodon" this vessel must have passed out of the brain case through one of the neural canals, as was suggested by Brown. Indeed, the internal surface of the "Trachodon" cranium supports this theory quite strongly, for there is a small canal ventral to the large vagus-glossopharyngeal canal which appears to be continuous with that passage. This subsidiary passage quite possibly conducted the jugular vein from the ventral part of the brain cavity to the vagus-glossopharyngeal canal and finally out of the cranium. The

three canals in the myelencephalic region in "*Trachodon*" therefore appear to have conveyed the hypoglossal and the accessory nerves independently and the vagus and glossopharyngeal nerves together with the jugular vein via a single canal.

Marsh's cast of *Anatosaurus* agrees very well with that of "*Trachodon*," with the exception that the fourth foramen is present in the myelencephalic region. This opening, located beneath that of the vagus and glossopharyngeal nerves, again is interpreted as having conveyed the jugular vein from the endocranial cavity. Whether or not this passage communicated with the vagus-glossopharyngeal canal distally, as in "*Trachodon*," could not be determined.

The endocranial cast of the Yale *Anatosaurus* is not so perfect in the finer details as are the above-described casts. The hind brain exhibits the same general form as the former specimens, with a slightly expanded myelencephalon marked by what appear to be individual exits of the hypoglossal and accessory nerves. The vagus and glossopharyngeal nerves apparently emerged from the cranium through a common canal, as suggested for the specimens discussed above.

#### METENCEPHALON

The metencephalon or anterior portion of the hindbrain, measuring approximately 55 mm. long in the *Kritosaurus* cast, is expanded both laterally and vertically between the posterior and midbrain constrictions. Its lower surface is marked by a slight ventral expansion, from which the abducens (VI) nerves emerge in their passage forward out of the brain cavity. The lateral surfaces are moderately convex. The maximum width of this segment (42 mm.) occurs at the level of the trigeminal foramen. The dorsal margin is strongly convex, rising steeply from the posterior constriction behind to its maximum height 76 mm. above the floor of the brain case. This dorsal expansion indicates a moderate-sized cerebellum in the Hadrosauridae. Its shape further suggests that the cerebellar inflation was directed upward and caudally, thus overlapping the choroid plexus and the anterior portion of the hind brain as in the modern Crocodilia, Chelonina, and some lizards. The cerebellar region of the endocranial

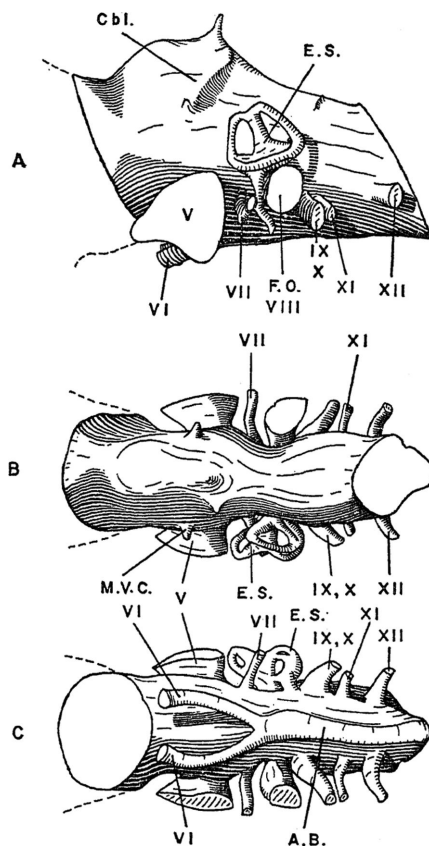


FIG. 58. Incomplete endocranial cast of *Anatosaurus* ("*Trachodon*") sp., A.M.N.H. No. 5236. A. Left lateral view. B. Dorsal view. C. Ventral view. Abbreviations: A.B., arteria basilaris; Cbl., cerebellum; E.S., endolymphatic system; F.O., fenestra ovalis; M.V.C., minor vascular canals; V, trigeminal nerve; VI, abducens nerve; VII, facialis nerve; VIII, auditory nerve; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve. Approximately  $\times \frac{1}{3}$ .

cast is triangular in transverse section, with the apex rising high into the cranial roof.

The lateral surfaces of the cerebellum are marked by gentle but moderate-sized expansions situated well above the trigeminal nerve. These are linear features oriented obliquely with respect to the brain axis. The endocranial cast of *Edmontosaurus* shows very similar features on the cerebellar lateral surfaces. Here, however, these features are less prominent, although of greater length. Presumably these local expansions mark the positions of paired endolymphatic sacs be-

tween the cerebellum and the roof of the brain case. A number of other smaller but sharper projections on most of these hadrosaurian brain casts may represent other endolymphatic features, but some of these undoubtedly were vascular structures. Comparison of Brown's cast with the "*Trachodon*" cranium demonstrates that the small process on the lateral cerebellar surface of the cast is actually an impression of the proximal end of a small canal which pierces the skull roof and emerges high on the lateral parietal surface. This is obviously a minor vascular canal and not a neural passage. Presumably most of the similar features of this and other casts are vascular in origin also, but an endolymphatic origin is suggested here for the broader, more subdued and irregular, surficial endocranial impressions.

Four cranial nerves emerge from the metencephalon region of the hind brain. The most caudal of these is the auditory (VIII) or acoustic nerve, located ventrolaterally in the posterior or rhombencephalic constriction. This nerve passed laterally into the large otic capsule located in the greatly thickened lateral wall (opisthotic and pro-otic) of the brain case. The *Kritosaurus* cast clearly indicates the size and position of the inferior otic cavity just lateral to this constricted region of the brain. The auditory nerve, as in modern reptiles, did not emerge from the brain case but terminated at the cochlear and endolymphatic systems within the otic capsule.

Nearly 20 mm. in front of the auditory nerve, the rather small facialis (VII) nerve emerged from the lower lateral surface of the metencephalon. The endocranial cast of *Kritosaurus* suggests that the passage of the facialis was continuous with the otic chamber. The significance of this narrow communicating canal is not known, as no similar passage has been observed in other hadrosaurian or modern reptilian crania. This canal may have been occupied by the hyomandibular ramus of the facialis nerve, but such a situation would be unique among reptiles, for modern forms, such as *Ctenosaura*, *Varanus*, and *Sphenodon*, are characterized by an external bifurcation of the facialis nerve. Typically the hyomandibular ramus of the facialis nerve passes caudally, superficial to the pro-otic, through the middle ear cavity, rather

than through the inner ear as the *Kritosaurus* cast suggests.

The trigeminal (V) nerve, the largest of the cranial nerves arising from the hind brain, emerged from the metencephalon directly beneath the cerebellum and close to the anterior limit of the rhombencephalon. The size of the trigeminal passage, as indicated by the *Kritosaurus* cast, is exceptionally large, which may be at least partially accounted for by the presence of a large trigeminal ganglion within the bony passage.

The abducens (VI) nerve, in contrast to the trigeminal nerve, is very small. The *Kritosaurus* brain cast very clearly illustrates the passage of this nerve from its origin in the slight ventral expansion of the metencephalon, posterior and ventral to the fifth cranial nerve, forward to the pituitary fossa.

As might be expected, the endocranial cast of *Edmontosaurus* is very similar to that just described for *Kritosaurus*. The most important difference between these two casts is in the more prominent nature of the posterior constriction of the latter cast. The dimensions of the metencephalon are otherwise similar, with this region of the *Edmontosaurus* cast measuring approximately 65 mm. in length, 54 mm. in width, and 74 mm. in height. The form of the metencephalon in this cast closely parallels that of *Kritosaurus*, with the moderately convex lateral surfaces, the slight inflation of the ventral surface, and the prominent wedge-shaped expansion of the metencephalon roof. As mentioned above, the lateral surfaces of the cerebellar region are marked by slight, obliquely oriented, elongate swellings which have been interpreted as evidence of endolymphatic sacs lying between the cerebellum and the brain case.

The auditory nerve is located in the ventrolateral portion of the posterior constriction, between the two segments of the hind brain, as in *Kritosaurus*. Associated with this, but occupying a more dorsal position on the cast, is a second feature which apparently indicates a second passage between the otic capsule and the endocranial cavity. As no similar passage is known in modern reptiles, this feature of the cast is believed to have resulted from damage to the bony wall between the endocranial cavity and the vestibule of the cavum capsularis which in life was occupied by the

sacculus and utriculus. It should be pointed out here that the *Kritosaurus* cast displays a feature situated medial and dorsal to the trigeminal foramen, which very probably is a partial cast of the vestibule of the cavum capsularis. Thus this second canal between the otic and cranial cavities is interpreted as an abnormal condition, probably a result of poor preservation or damage during preparation. Reexamination of this specimen should verify this interpretation.

The brain cast of *Edmontosaurus* illustrates a small facialis nerve canal just anterior to the canal of the auditory nerve. The large trigeminal nerve occupies its typical position on the ventrolateral surface of the metencephalon at its anterior limit. The abducens nerve again appears to have been relatively small. Its passage can be traced in the cast, from the ventral surface of the metencephalon forward and down to the posterior region of the hypophyseal cavity. While the cast suggests that this nerve originated at a point directly beneath the trunk of the trigeminal nerve, it appears more likely that the abducens fibers originated more caudally in the floor of the metencephalon, probably passing forward beneath the medulla within the endocranial cavity before entering the narrow canal through the basisphenoid at the level of the trigeminal nerve. This interpretation appears reasonable in the light of similar conditions found in modern lizards, such as *Ctenosaura* and *Amblyrhynchus*.

Brown's remarkable reconstruction of the semicircular canals in the partial "*Trachodon*" cranium has provided us with our only knowledge of this system within the Hadrosauridae.<sup>1</sup> Brown's description of these canals follows (Brown, 1914a, p. 546): "These canals have the normal reptilian position and open freely from one to the other with distinct ampullae at the origin, but the horizontal is much shorter and smaller than either the anterior or posterior divisions." Figure 59 is a restoration of the hadrosaurian endolymphatic system based on Brown's cast of the semicircular canals and the vestibule of the cavum capsularis.

<sup>1</sup> A recent analysis of an additional hadrosaurian endolymphatic system, published in 1960 by Langston, was received too late for inclusion in the present study.

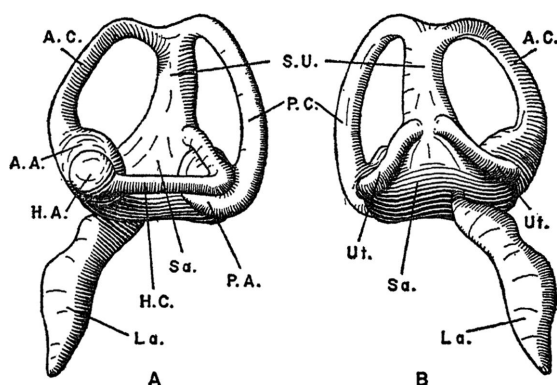


FIG. 59. Reconstruction of the left endolymphatic system of *Anatosaurus* ("*Trachodon*"), A.M.N.H. No. 5236. A. Lateral view. B. Medial view. Abbreviations: A.A., anterior ampulla; A.C., anterior semicircular canal; H.A., horizontal ampulla; H.C., horizontal semicircular canal; L.a., lagena; P.A., posterior ampulla; P.C., posterior semicircular canal; Sa., saccule; S.U., superior utricle; Ut., utricle. Approximately  $\times 1$ .

The remaining portions of the otic region of this well-preserved cranium also require mention here. The external surface of the "*Trachodon*" cranium is marked by a large, rectangular depression just behind the facialis foramen. Situated in the ventral part of the depression is the opening of a canal of moderate size, which undoubtedly provided for the emergence of the auditory nerve from the endocranial cavity into the cavum capsularis. Extending upward and inward from the upper part of this depression is a large, expanding cavity, which is interpreted as the vestibule of the cavum capsularis, originally occupied by the sacculus, utricle, and the semicircular canals. Although the lower portion of the recess is not so clearly defined as the upper part, it presumably represents the lagenar recess. This lower chamber must have communicated with the middle ear cavity, the fenestra ovalis and received the foot plate of the stapes and therefore probably also contained, in addition to the lagena, the cochlea.

The remaining metencephalic nerves of "*Trachodon*" or of *Anatosaurus* require no further comment. In all three casts, in spite of the fact that these are not so complete or perfectly preserved as are the casts of *Kritosaurus* and *Edmontosaurus*, the neural passages indicate cranial nerve conditions which

are essentially identical with the condition described for these latter genera.

#### MESENCEPHALON

Although the mesencephalon or midbrain is usually easily defined in the lower vertebrates, it is quite obscure and difficult to define in currently existing hadrosaurian endocranial casts. Only four relatively complete casts are known, and none of these reveals much about the actual size, the shape, or the limits of the hadrosaurian midbrain—undoubtedly a result of the relatively large size of the cerebral hemispheres in front and the somewhat lesser inflation of the cerebellum behind, as well as the failure of the midbrain section of the brain case to adhere to this region of the brain.

The endocranial cast of *Kritosaurus* is characterized by a large constriction behind the cerebral hemispheres. This region is incapable of precise definition, as the cast does not reflect the smaller features which might mark the midbrain boundaries. There can be little doubt, however, that this was the shortest of the brain segments. In *Kritosaurus*, the mesencephalon did not exceed 20 mm. in length, and in all probability it was somewhat shorter. The only prominent midbrain features that could be expected to be visible in an endocranial cast are the optic lobes (tectum). This center, however, left no visible impression on the endocranial walls and therefore can only be inferred in brain reconstructions. Apparently the optic lobes, which are not exclusively visual centers in the Reptilia, were not greatly expanded, at least with respect to the adjacent regions of the brain. There is ample space within the midbrain region of the endocranial cavity for a relatively large optic center. It is possible, therefore, that the tectum was quite highly developed but failed to impress its imprint on the cranial walls between the cerebellar and cerebral inflations.

Commonly the only cranial nerves arising from the mesencephalon are the relatively small trochlear (IV) and oculomotor (III) nerves. The brain cast of *Kritosaurus* indicates the level at which these nerves entered their respective bony canals, but in both instances these appear to be located anterior to the mesencephalon. The trochlear nerve root occurs on the lower lateral surface of the

brain cast at the level of the hypophysis, extending forward along the lateral surface of the diencephalon. This nerve undoubtedly originated at a more caudal level and passed forward within the brain cavity before entering its bony passage in the diencephalic region. Indeed, the rostral, rather than lateral, passage of the trochlear canal through the cranial wall strongly supports such a conclusion.

The oculomotor nerve appears to have been much larger than the nerve just mentioned; at least the cast of its canal so suggests. As seen in the *Kritosaurus* cast, the oculomotor nerve appears to emerge from the stalk of the hypophysis and extend forward towards the orbital region. Such an "origin" is definitely atypical. It seems safe to assume that the oculomotor nerve emerged from the ventral or ventrolateral surface of the mesencephalon, as it does in modern reptiles. Its passage forward along the ventrolateral wall of the brain cavity may have been masked by a thick dura mater envelope. Consequently, only the inner opening of its bony passage through the brain case can be recognized in the cast.

The endocranial cast of *Edmontosaurus* provides no additional information about the mesencephalon, except that here, too, the midbrain is considerably smaller than the adjacent brain divisions. That the midbrain constriction in *Edmontosaurus* is not so pronounced as that of *Kritosaurus* may or may not indicate the existence of larger optic lobes in *Edmontosaurus*.

Lambe's (1920) interpretation of the trochlear and oculomotor nerves in the brain cast of *Edmontosaurus* is at variance with that given above for *Kritosaurus*. Lambe visualized these two nerves as emerging from the brain case through a common foramen at the level of the hypophysis, a condition in disagreement with that typically found in modern reptiles in which the trochlear nerve commonly arises from the ventral part of the midbrain, with the fibers ascending within the mesencephalon to emerge finally high on the lateral midbrain surface. Upon emergence, the trochlear fibers pass over the brain, posterior to the optic lobes, to extend slightly downward and forward on the opposite side of the brain in their passage to the orbital region. The trochlear foramen is typically situ-

ated high on the wall of the brain case, anterior to the midbrain, as seen in the *Kritosaurus* cast. No such evidence is found on the *Edmontosaurus* cast, and Lambe, recognizing the trochlear nerve as a ventral motor nerve, believed it emerged together with the oculomotor nerve. More than likely the trochlear nerve passage was not preserved or prepared, hence the resulting interpretation. It is assumed, however, that the route of this nerve was like that reconstructed in *Kritosaurus*.

The oculomotor nerve of *Edmontosaurus*, as in *Kritosaurus*, probably originated in the floor of the midbrain, from which point it passed forward within the brain cavity lateral to the diencephalon to its bony passage just lateral to the stalk of the hypophysis. Such an opening is present in the *Edmontosaurus* cranium, and its impression is clearly visible at the base of the infundibulum in the brain cast.

The endocranial cast of *Anatosaurus* studied by Marsh (1893, 1896) and that described by Lull and Wright (1942) are similar in the form of the midbrain region. Both are marked by the prominent midbrain constriction. Only faint impressions of the trochlear and oculomotor nerves are visible in Marsh's specimen, but these appear to correlate closely with the conditions seen in *Kritosaurus*. No indication of these nerve outlets is detectable in the Yale *Anatosaurus* cranium or its brain cast.

#### PROSENCEPHALON

The prosencephalon of *Kritosaurus* constitutes the most conspicuous portion of the endocranial cast, with its greatly expanded cerebral hemispheres and the rather prominent, ventrally suspended hypophyseal cast. Its total length is 100 mm., of which more than 70 mm. is that of the anterior telencephalon. The respective lengths of the two forebrain divisions can only be estimated according to the locations of the hypophysis and the optic stalks, because no other superficial features of the brain are indicated in the cast to allow location of the precise boundary position between the diencephalon and the telencephalon.

#### DIENCEPHALON

This segment of the forebrain, together with the mesencephalon behind, forms the

centrally located, constricted brain region. Dorsally and laterally the diencephalon is indistinct and cannot be differentiated from the telencephalon, probably owing to its concealment beneath the large, overlapping, cerebral hemispheres. Ventrally, however, the diencephalon is more or less definable as a result of the rather large infundibulum or stalk of the pituitary and the cast of the optic tracts situated anterior to the infundibulum.

The relatively large optic tracts beneath the ventral surface of the cerebrum are undivided in the endocranial cast of *Kritosaurus*, indicating a common passage for at least the posterior part of the optic nerves. No indication of the optic chiasma is visible in this brain cast, nor can the exact level of the optic nerve origin from the diencephalon be determined.

The infundibulum of *Kritosaurus*, judging from its cast, was quite short and massive (less than 30 mm. in length and approximately 25 mm. in maximum diameter). This structure extended directly downward from the ventral surface of the forebrain beneath the posterior portion of the cerebrum. Distally the infundibulum communicated with the larger, bulbous-shaped pituitary body, as shown by the cast of the hypophyseal cavity. This cast implies a pituitary body of approximately 40 mm. in length and nearly 30 mm. in height and width. These figures obviously represent only the maximum possible dimensions, as, quite probably, the pituitary did not completely fill its cavity.

Several other features of this brain cast should be mentioned here. The sixth cranial nerve, which is believed to have originated in the floor of the metencephalon, descends rostrally through the basisphenoid and enters the posterior part of the pituitary fossa. The exit of the abducens nerve from the pituitary cavity is clearly indicated on the anterolateral surface of the pituitary cast. The opening, however, is at least four times the size of the posterior abducens canal, indicating that this enlarged opening in the pituitary fossa probably served as a multiple passage.

Brown, in an unpublished study of this endocranial cast, suggested that the ophthalmic branch of the internal carotid artery passed anteriorly through this opening together with the anterior portion of the abducens nerve. Such a hypothesis appears

quite reasonable, although it hardly accounts for the excessive size of this opening.

Complete casts of the Vidian canals in the endocranial cast of *Kritosaurus* clearly illustrate the location of these canals and the passage of the internal carotid arteries. These structures are described in greater detail in the section dealing with portions of the hadrosaurian cranial circulatory system. Discussion of the median parasphenoid canal, which is so well preserved in *Kritosaurus*, is also deferred to this section.

The forebrain cast of *Edmontosaurus* is essentially like that of *Kritosaurus*, both in size (110 mm. in length) and in form. As in the latter specimen, there is no visible separation between the diencephalon and the telencephalon. Only the location of the infundibulum indicates the region of the diencephalon ventrally, while the lateral and dorsal surfaces lack any diagnostic markings.

The emergence of the optic nerves is indicated by the rather large cast of the diverging optic canals beneath the cerebrum and anterior to the pituitary stalk. In this cast, however, there is at least a faint impression of the optic chiasma where the large optic tracts meet in front of the infundibulum and then pass back lateral to this structure as very faint lateral ridges on the endocranial cast surface between the overlying cerebrum and the pituitary body below. The passage of the oculomotor nerve is not indicated on the *Edmontosaurus* cast, but probably it emerged from the cranial cavity between the second and sixth cranial nerves.

Again the hypophysis appears as a rather bulbous body at the ventral extremity of a short and massive infundibulum. Entering the hypophyseal cavity from behind are the paired abducens canals which transmitted the sixth cranial nerves from their origin in the ventral medullar wall. Emergence of the sixth nerve from the hypophyseal cavity was through the large anterolateral foramen, probably together with the ophthalmic branch of the internal carotid artery, as suggested in *Kritosaurus*.

This endocranial cast does not show the median parasphenoid canal leading from the anterior margin of the pituitary cavity to the interorbital region as was seen in the previous cast. The anterior portion of this canal, how-

ever, is preserved in the *Edmontosaurus* cranium (N.M.C. No. 2289), extending back from the interorbital region between the parasphenoid and the presphenoid, and is interpreted as the anterior passage of the median palatine artery, as is discussed in a section below.

Although the dimensions are somewhat less, the endocranial casts of the *Anatosaurus* crania (Y.P.M. No. 618 and U.S.N.M. No. 4737) are basically similar to those of *Kritosaurus* and *Edmontosaurus*. These casts differ most conspicuously from those of the latter specimens in the degree of detail reproduced on the casts, a reflection of incomplete preservation or preparation of the *Anatosaurus* crania. Except for the less sharply defined superficial features, these casts agree very well with those described above.

The Yale cranium, as well as its cast, shows a feature very similar to the median parasphenoid canal noted in *Kritosaurus* and *Edmontosaurus*. In this cranium, however, there appear to have been two closely spaced canals which led forward from the pituitary cavity. The endocranial cast clearly reflects the paired nature of the contained structure, but whether these canals were in part coalesced, forming a common medial canal as in *Kritosaurus*, or were completely divided by a thin, bony, cartilaginous, or membranous wall could not be determined and can only be speculated upon. The cranium of *Anatosaurus*, however, definitely establishes the fact that this canal, single or paired, was occupied by a paired structure and thereby eliminates the possibility of a single, median, neural or vascular element.

#### TELENCEPHALON

The anterior portion of the forebrain, referred to as the telencephalon, is the most conspicuous part of the *Kritosaurus* endocranial cast, with its greatly inflated cerebral hemispheres. The cerebral region of the cast has a maximum width of approximately 80 mm. and rises nearly 60 mm. above the floor of the endocranial cavity. The dorsal and lateral surfaces are strongly convex, and, with the exception of a few minor impressions of several lateral diverticulae, the entire cerebral surface is quite smooth. Anteriorly, the dorsal cerebral outline descends very abruptly to the



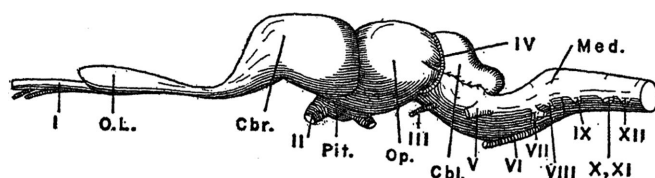


FIG. 60. Left lateral view of the brain of *Varanus bivittatus*. Abbreviations: Cbl., cerebellum; Cbr., cerebrum; Med., medulla; O. L. olfactory lobe; Op., optic lobe; Pit., pituitary body; I, olfactory nerve; II, optic nerve; III, oculomotor nerve; IV, trochlear nerve; V, trigeminal nerve; VI, abducens nerve; VII, facialis nerve; VIII, auditory nerve; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve. (Modified from Watkinson, 1906.)  $\times 1$ .

coronal sulcus and the relatively small, unseparated, olfactory lobes. This pronounced constriction of the anterior portion of the endocranial cavity, which is so sharply reflected in the cast, is believed to represent a similar constriction of the brain, the coronal sulcus or union of the cerebral and olfactory lobes. The total length of the olfactory lobes is probably less than 20 mm., although this portion of the brain cast is incomplete.

The great snout length of the skull in *Kritosaurus* suggests that the olfactory stalks were of considerable length. Another indication is the rather large diameter (40–50 mm.) of the olfactory centers at the rostral extremity of the brain case. The anterior cranial walls bear no evidence that would indicate the partial or complete separation of the olfactory lobes, but it seems reasonable to assume a completely separated condition for the olfactory stalks, even though they may have occupied a common canal.

The telencephalon of *Edmontosaurus* is very conspicuous, with its greatly expanded cerebrum. The cerebral section of the cast has a maximum width of 77 mm. and rises to a height of nearly 60 mm. The dorsal outline rises abruptly from the midbrain constriction to the high point of the cerebral expansion and then descends steeply to the coronal sulcus anteriorly. Both the lateral and dorsal surfaces are smooth and strongly convex as in *Kritosaurus*.

Again the olfactory lobes are short and apparently undivided, forming a compressed cylinder, with a height that is approximately half of the width. This region is more uniform

throughout its rather short length than is that of *Kritosaurus*, which is slightly more convex and diminishes slightly in its diameter towards the anterior extremity. Thus the olfactory lobes appear to have extended nearly undiminished to their emergence from the endocranial cavity. This nearly constant, untapering form again suggests a length of considerable magnitude for the olfactory stalks, a logical condition in view of the great snout length of *Edmontosaurus*.

The Yale *Anatosaurus* cranium reflects a similar development of the telencephalon, with a strongly inflated cerebral expansion measuring 86 mm. in breadth and 46 mm. in height. This strongly convex region of the cast tapers abruptly in its anterior part where it joins the much narrower and more uniform olfactory section. The latter portion of the cast is considerably longer, nearly 70 mm. over all, than that of the other endocranial casts, but again it has the form of an undivided, dorsoventrally compressed cylinder, which suggests paired olfactory lobes or stalks that occupied a common canal.

The remaining endocranial cast, that of *Anatosaurus* (U.S.N.M. No. 4737), is similar to that made from the Yale cranium except that it is much smaller in most dimensions.

#### THE CRANIAL NERVES

The following discussions of the cranial nerves, as a result of the superficial information available, are rather general and brief. The few endocranial casts demonstrate the relative nerve size and the approximate location with respect to the brain segments. Their

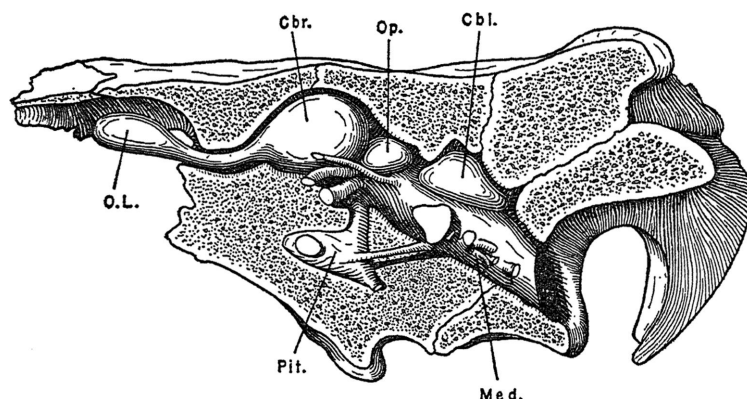


FIG. 61. The sectioned cranium of *Anatosaurus* sp., Y.P.M. No. 618, with the brain restored in the endocranial cavity. Abbreviations: Cbl., cerebellum; Cbr., cerebrum; Med., medulla; O.L., olfactory lobe; Op., optic lobe; Pit., pituitary body.

points of emergence from the cranial cavity are, of course, more precisely known, but information about their extracranial paths and locations is, in most cases, hypothetical.

#### OLFACTORY NERVE (I)

This, the largest of the cranial nerves, is quite obvious in all of the complete endocranial casts, although it is likely that only the proximal segment of the lobes are reflected in any of these casts. In the flat-headed hadrosaurs there is no information about the size, length, or position of the anterior olfactory tracts or the rostral position of the bulbs. It seems reasonable, however, in view of the relatively long olfactory tracts and the distal position of the olfactory bulbs in modern Crocodilia and lizards, that the hadrosaurian olfactory bulbs may have been situated at the end of long olfactory stalks which extended well anterior to the orbits. The great snout length of members of the Hadrosaurinae would seem to require a rather elongate olfactory apparatus, although such a consequence is not absolute. Figure 62 illustrates the anterior position of the olfactory bulbs as they may have existed in the flat-headed hadrosaurs.

Unfortunately no complete endocranial casts of a crested hadrosaur are available, for the olfactory system probably was very different from that of the non-crested hadrosaurs. A number of lambeosaurian skulls demonstrate a rather remarkable condition

which is considered to be a significant clue concerning the function of the cranial crests. *Corythosaurus casuarinus* (R.O.M. No. 1933), *Corythosaurus excavatus* (N.M.C. No. 8676), *Lambeosaurus lambei* (N.M.C. No. 2869), and *Lambeosaurus claviventris* (Y.P.M. No. 3222) show varying portions of the narial chambers and passages within the crest. More significant here, however, is that each of these specimens shows the exit of the narial passage (as a single opening) from the base of the crest into the interorbital region of the skull. The size of this opening varies slightly in these specimens, but its position is quite constant—from 20 to 40 mm. anterior to and immediately above the anterior opening of the brain cavity. Considering the size of the olfactory opening, that the olfactory stalks terminated abruptly only 20 mm. anterior to their emergence from the endocranial cavity appears to be unlikely. In view of the close proximity of these two openings to each other and the moderately large size of the narial exit from the crest, it is concluded that the primary function of the hadrosaurian crest was the housing of the olfactory bulbs and expanded sensory tissues and therefore related to increased olfaction.

It is presumed that the olfactory stalks turned dorsad just anterior to their emergence from the brain cavity and passed upward into the crestal cavity, adjacent to the actual narial passage, as illustrated in figure 63. The complex pattern of the crestal pas-

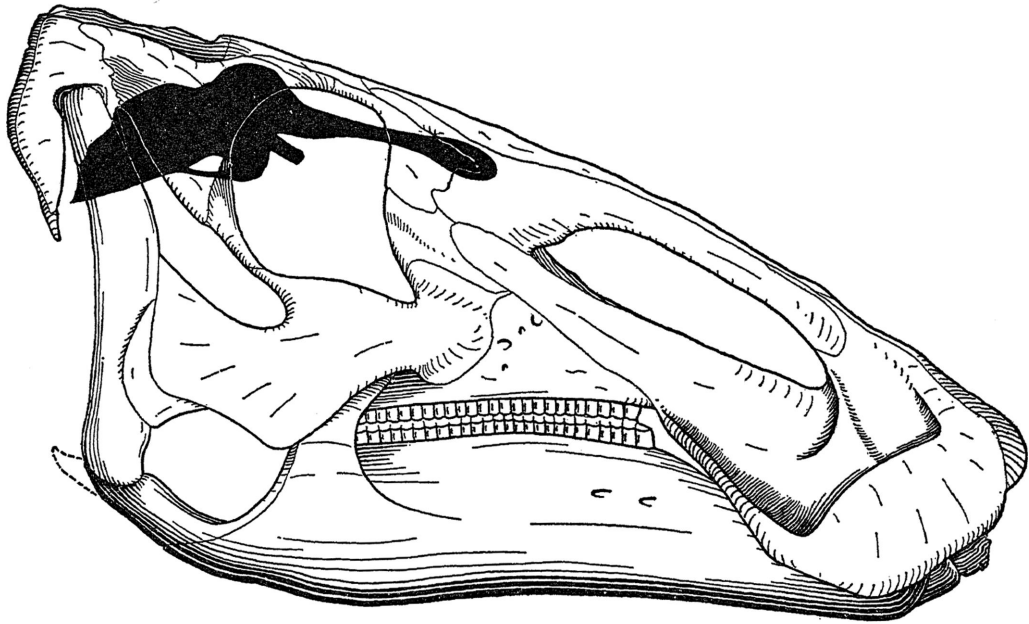


FIG. 62. Skull of *Edmontosaurus regalis*, N.M.C. No. 2288, with the endocranial cavity shown in silhouette. Notice the hypothetical position of the olfactory stalks and bulbs as reconstructed in this non-crested species. Approximately  $\times \frac{1}{3}$ .

sages and chambers is interpreted as a primitive, but undoubtedly effective, mechanism for increasing the surface area of the olfactory mucous membrane, paralleling the turbinal and ethmoidal systems of the macrosmatic mammals. The multiple narial pockets within the crest, communicating with the narial passages, would have provided a significant increase in mucous membrane area and thereby increased olfactory sensitivity.

#### OPTIC NERVE (II)

The optic nerves, which are indicated in all the endocranial casts at their point of emergence from the cranium, undoubtedly arose from the diencephalon in the typical vertebrate manner. From their origin, they must have passed forward beneath the diencephalon, passing lateral to the infundibulum to the optic chiasma above and in front of the pituitary. The *Kritosaurus* cast does not show the anterior divergence of these tracts beyond the chiasma, but those of *Edmontosaurus* and *Anatosaurus* do. From the chiasma, the optic nerve extended forward and slightly downward beneath the cerebrum to enter the optic foramen in the orbitosphenoid, an opening of

approximately 10 mm. in diameter in *Kritosaurus*. Upon emergence, the optic nerve undoubtedly passed forward adjacent to the lateral surface of the orbitosphenoid into the orbital region and a medioposterior innervation of the eye.

#### OCULOMOTOR NERVE (III)

This much smaller nerve, arising from the inferior lateral surface of the mesencephalon, passed forward lateral to the hypophyseal stalk, as can be seen in the *Kritosaurus* cast, to emerge from the brain case via the large (13 mm.) foramen situated between the orbitosphenoid, presphenoid, and pro-otic in the anterolateral part of the brain case. This foramen is not always preserved as a separate opening, owing to damage to the narrow bony bridge separating the oculomotor foramen from the larger abducens foramen below, but it is finely preserved in the cranium of *Kritosaurus notabilis* (A.M.N.H. No. 5350) on the anterior surface of the vertical pro-otic ridge. From this emergence, the oculomotor nerve presumably passed forward into the orbit, where it innervated some of the eye muscles and perhaps several accessory orbital

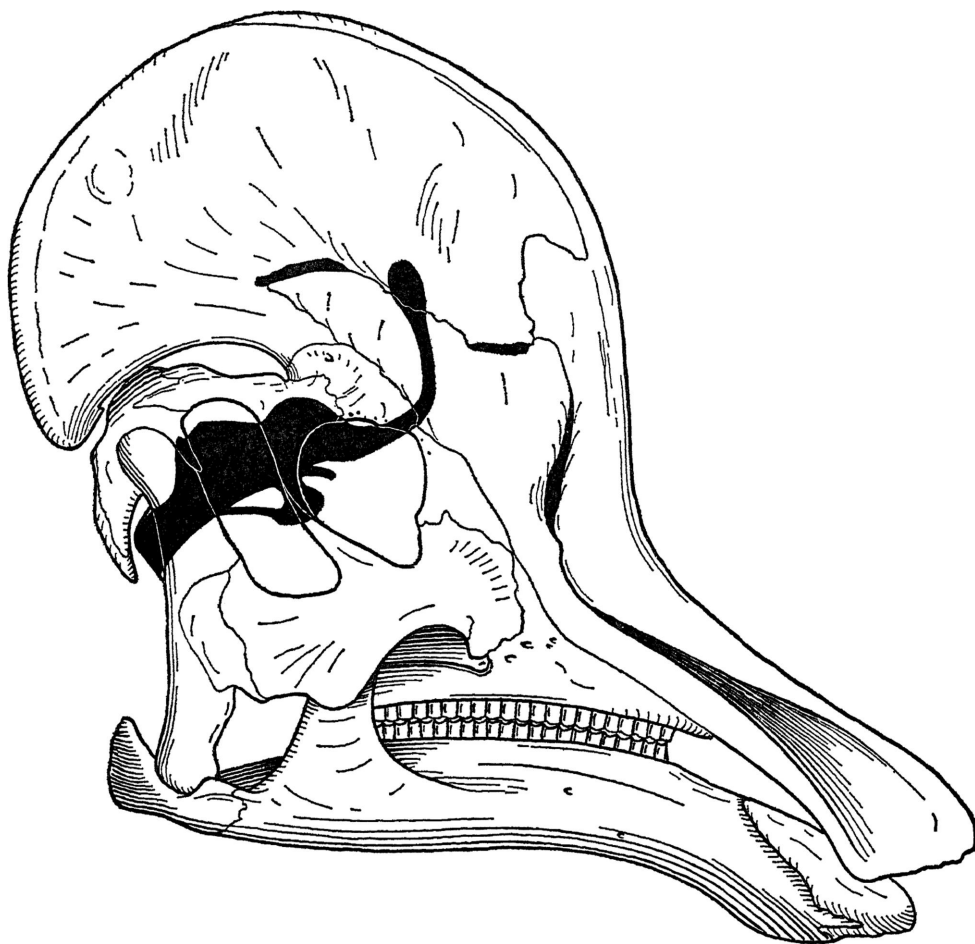


FIG. 63. Skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with the endocranial cavity shown in silhouette. Notice the reconstructed position of the olfactory stalks and bulbs in this crested species, as contrasted with that suggested in figure 62 for the Hadrosaurinae. Approximately  $\times \frac{1}{6}$ .

muscles. Of course it is not possible to determine which of the orbital muscles were innervated by the oculomotor nerve, but it seems unlikely that these differed markedly from the modern lacertilian condition as exemplified by *Varanus*. There is no indication in any of these casts or crania of the distal bifurcation of the oculomotor nerve into a ramus superior and a ramus inferior, as in *Varanus* (Watkinson, 1906) and *Ctenosaura* (Oelrich, 1956).

#### TROCHLEAR NERVE (IV)

The trochlear nerve, although probably arising from the ventral surface of the mesen-

cephalon as in modern Reptilia, emerged from the endocranial cavity through its own small canal in the lateral wall of the brain case anterior to the midbrain. The canal, which measures 4 mm. in maximum diameter, pierces the orbitosphenoid in its upper part, opening to the exterior slightly dorsal to the optic tracts. The trochlear canal is infrequently preserved or prepared, but it is well displayed in the crania of *Kritosaurus notabilis* (A.M.N.H. No. 5350), *Hypacrosaurus altispinus* (R.O.M. No. 702), and possibly *Corythosaurus casuarius* (A.M.N.H. No. 5338). The orbitosphenoid region is typically poorly preserved or completely missing,

thus accounting for the relatively few specimens that show this feature. In modern reptiles the trochlear nerve arises from one side of the mesencephalon and passes over the brain to emerge from the brain cavity on the opposite side. In all probability such was the case in the Hadrosauridae, but this is pure speculation. The anterior passage of this nerve into the orbital region, as indicated by the cast of the trochlear canal, suggests a function similar to that of modern reptiles, which is the innervation of a single eye muscle, the M. superior obliquus.

#### TRIGEMINAL NERVE (V)

This nerve, second only to the olfactory nerve in size, is readily located in any reasonably well-preserved cranium. It is conspicuous in each of the currently available endocranial casts, situated as the most anterior of the cranial nerves arising from the hind brain. The trigeminal foramen is very large and may exceed 30 mm. in maximum diameter in some cases. It is particularly well displayed at the anterior margin of the pro-otic on the lateral cranial wall in *Corythosaurus casuarius* (A.M.N.H. No. 5338), *Procheneosaurus erect-*

*tofrons* (A.M.N.H. No. 5461), and *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), to name only a few of the better specimens. In most specimens, the trigeminal foramen occurs as a single, large, oval opening (as large as 30 by 39 mm. in diameter).

The superficial cranial surface in the trigeminal region is marked by two moderate to deep grooves, one leading forward from the trigeminal foramen and the other reaching ventrally. The former indicates the almost immediate branching off and forward passage of the deep ramus ophthalmicus ( $V_1$ ), a sensory branch of the snout. The ventrally directed groove indicates the passage of the third trigeminal branch, the ramus mandibularis ( $V_3$ ), which presumably transmitted sensory impulses from the mandible as well as having innervated the mandibular muscles. Most specimens do not indicate the position or path of the ramus maxillaris ( $V_2$ ), but *Corythosaurus casuarius* (A.M.N.H. No. 5338 and R.O.M. No. 1933), *Hypacrosaurus altispinus* (R.O.M. No. 702), *Corythosaurus intermedius* (R.O.M. No. 4670), *Edmontosaurus regalis* (N.M.C. No. 2289), and *Lambeosaurus lambei* (R.O.M. No. 5131) all show

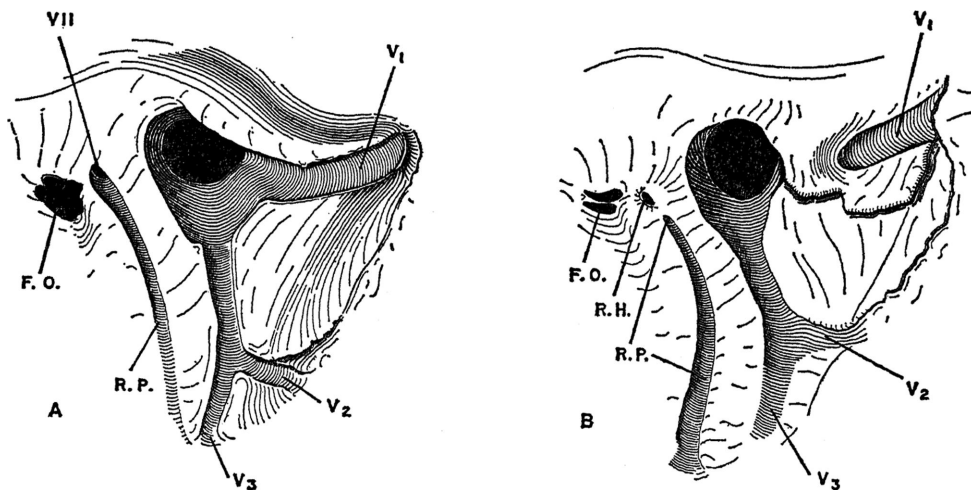


FIG. 64. The right trigeminal foramen and the surrounding region. A. *Corythosaurus casuarius*, A.M.N.H. No. 5338. B. *Lambeosaurus lambei*, N.M.C. No. 2869. Notice the canal of the profundus branch ( $V_1$ ) in *Lambeosaurus* as contrasted with the more typical open channel demonstrated by *Corythosaurus*, also the double foramina for the facialis nerve in *Lambeosaurus*. Abbreviations: F.O., fenestra ovalis; R.H., foramen for the ramus hyomandibularis of the facialis nerve; R.P., channel for the ramus palatinus of the facialis nerve;  $V_1$ , channel for the ramus profundus (ophthalmicus) of the trigeminal nerve;  $V_2$ , channel for the ramus maxillaris of the trigeminal nerve;  $V_3$ , channel for the ramus mandibularis of the trigeminal nerve; VII, foramen facialis.

the descending groove as a forked feature, with one branch continuing ventrally, while the other slightly smaller groove veers anteriorly (see fig. 64A), which indicates that the ventral groove actually was occupied in its upper part by both the mandibular and maxillary branches of the trigeminal nerve. The anterior extension of the ventral groove is therefore indicative of the proximal position of the ramus maxillaris. This branch is assumed to have innervated the major mandibular muscles as well as having acted as a sensory transmission route from the upper jaw. Three specimens of *Lambeosaurus* (*L. lambei*, N.M.C. No. 2869 and R.O.M. No. 5131, and *L. clavinitalis*, Y.P.M. No. 3222) deviate slightly from the condition described above. Here the ramus ophthalmicus passed forward from the trigeminal foramen through a concealed canal in the laterosphenoid instead of lying exposed within a superficially open groove. This canal opens to the exterior by a separate foramen anterior to the trigeminal foramen (see fig. 64B).

#### ABDUCENS NERVE (VI)

In modern reptiles this nerve, which innervates the M. posterior rectus, generally arises from the floor of the metencephalon. As illustrated particularly well in the endocranial casts of *Kritosaurus* and *Edmontosaurus*, such an origin was true also of the hadrosaurs. In *Kritosaurus*, this small nerve passed ventro-anteriorly through a narrow (4 mm.) but long (67 mm.) canal which penetrated the basisphenoid between the brain cavity and the pituitary fossa. After passing through this last cavity, lateral to the pituitary body, the abducens nerve emerged to the exterior through the large fenestra at the junction of the orbitosphenoid, presphenoid, pro-otic, and basisphenoid. Undoubtedly other structures, probably vascular, also emerged through this large opening. This foramen is visible in most hadrosaurian crania, although it is usually poorly defined because of the thin, delicate nature of the anterior cranial elements. The anterior route of this neural passage, directly towards the orbit, certainly suggests a relationship similar to that of modern reptiles. In *Ctenosaura*, for example, the M. posterior rectus, the M. bursalis, and

the M. retractor bulbi are all innervated by the abducens nerve (Oelrich, 1956).

#### FACIALIS NERVE (VII)

The emergence of the facialis nerve from the brain case is clearly indicated behind the trigeminal foramen in numerous hadrosaurian crania, such as *Corythosaurus casuarius* (A.M.N.H. No. 5338), *Corythosaurus excavatus* (N.M.C. No. 8676), *Hypacrosaurus altispinus* (R.O.M. No. 702), *Lambeosaurus lambei* (N.M.C. No. 2869), *Brachylophosaurus canadensis* (N.M.C. No. 8893), and *Anatosaurus saskatchewanensis* (N.M.C. No. 8509). The endocranial casts of both *Kritosaurus* and *Edmontosaurus* also indicate the emergence of this nerve immediately posterior to the trigeminal nerve. In the *Kritosaurus* cast, this canal measures 5 mm. in maximum diameter.

The facialis nerve of *Varanus* typically divides into anterior (ramus palatinus) and posterior (ramus hyomandibularis) branches (Watkinson, 1906), and Oelrich (1956) describes a similar pattern in *Ctenosaura*. The palatine ramus passes ventral to the basipterygoid process and then forward to the palate, where it receives sensory impulses from the roof of the mouth. The hyomandibular branch passes directly caudad from the fenestra rotunda, passing over the stapes and the fenestra ovalis to innervate the M. depressor mandibulae, M. constrictor colli, and possibly the M. mylohyoideus. The chorda tympani usually branches off from the ramus hyomandibularis and descends along the quadrate to enter the Meckelian fossa of the mandible, where it extends forward chiefly as a sensory branch.

Most hadrosaurian specimens, and particularly those mentioned above, display a condition that at least suggests a facialis pattern quite similar to that found in modern lizards. In *Anatosaurus saskatchewanensis* (N.M.C. No. 8509), a well-defined narrow groove descends ventrally from the facial foramen. This groove extends behind the caudal process of the pro-otic and the basisphenoid flange beneath the trigeminal foramen, to the Vidian canal of the internal carotid artery on the posterior basal surface of the basipterygoid process. At this point the groove be-

comes indistinct, but in at least one specimen (*Corythosaurus excavatus*, N.M.C. No. 8676) a very faint groove appears to lead around behind the basipterygoid process. Such a passage corresponds with the modern one of the ramus palatinus of the facialis nerve, except that, with the increased height of the ornithopod cranium, this branch descended much farther below the facial foramen before swinging forward beneath the basipterygoid process in its passage forward to the roof of the mouth.

The ramus hyomandibularis emerged from the same foramen in *Anatosaurus saskatchewanensis* and probably in most members of the family. Presumably this branch passed caudally over the stapes and then down to its innervation of certain neck muscles and the M. depressor mandibulae. No indication of such a route can, however, be seen in any of the crania examined. A few specimens [*Corythosaurus excavatus*, N.M.C. No. 8676; *Lambeosaurus lambei*, N.M.C. No. 2869; and *Anatosaurus* ("Trachodon") sp., A.M.N.H. No. 5236] possess two separate foramina for these two branches of the facialis nerve (see fig. 64B). The lower foramen is marked superficially by the descending groove described above. Apparently continuous with this foramen, by a short bony canal, is a second smaller, upper opening which is interpreted as the passage of the ramus hyomandibularis. This upper opening lies slightly behind the lower one and is marked by a short groove which extends dorsocaudally across the surface of the pro-otic. In no specimen was any indication found of the chorda tympani, the descending branch of the ramus hyomandibularis.

A second, although not necessarily contradictory, interpretation is suggested by this surficial groove extending from the facial foramen to the vicinity of the Vidian canal. In modern reptiles the carotid artery normally gives off a small branch, the stapedial artery, just prior to entering the Vidian canal. Possibly the stapedial artery occupied the lower part of this groove, which does not, however, explain the relationship of the groove to the facial foramen. It may be, although it seems unlikely, that this sharply defined groove in the lateral surface of the basisphenoid was occupied in part by both

the ascending stapedial artery and the descending palatine ramus of the facialis nerve.

#### AUDITORY NERVE (VIII)

This nerve, sometimes termed the acoustic, is unique among the cranial nerves in that it fails to emerge from the brain case. It extends from its origin in the lateral surface of the metencephalon into the otic capsule where it divides into anterior and posterior rami which receive sensory impulses from the perilymphatic and endolymphatic systems. Its position with respect to the brain segments is well marked in all hadrosaurian endocranial casts. In *Kritosaurus*, the auditory canal measures approximately 7 mm. in diameter and nearly 5 mm. in length between the endocranial and otic cavities. In well-preserved crania, such as that of *Anatosaurus* ("Trachodon") (A.M.N.H. No. 5236), the auditory region is characterized by two foramina separated by a very thin bridge of bone. The lower opening is the fenestra rotunda which penetrates the cranium to the brain cavity and doubtlessly housed the posterior ramus and the cochlea (Watkinson, 1906). The upper opening, which extends upward within the cranial wall into the otic capsule, does not extend into the brain cavity. This is the fenestra ovalis and undoubtedly provided for the passage of sensory fibers, the ramus anterior of Watkinson (1906), from the semicircular canals within the otic capsule to the auditory canal and the metencephalon. Brown's (1914a) reconstruction<sup>1</sup> of the semicircular canals, together with the recent discovery of a hadrosaurian stapes (Colbert and Ostrom, 1958), certainly indicates the existence of well-developed perilymphatic and endolymphatic systems in the Hadrosauridae.

#### GLOSSOPHARYNGEAL NERVE (IX)

Characteristically one of the smallest cranial nerves, the glossopharyngeal nerve arises from the lateral surface of the myelencephalon at its anterior limit in modern lizards such as *Varanus* and *Ctenosaura*. Frequently it passes through the cranial wall together with the vagus nerve, but in some reptiles it occupies a separate canal. Hadro-

<sup>1</sup> See also Langston (1960).

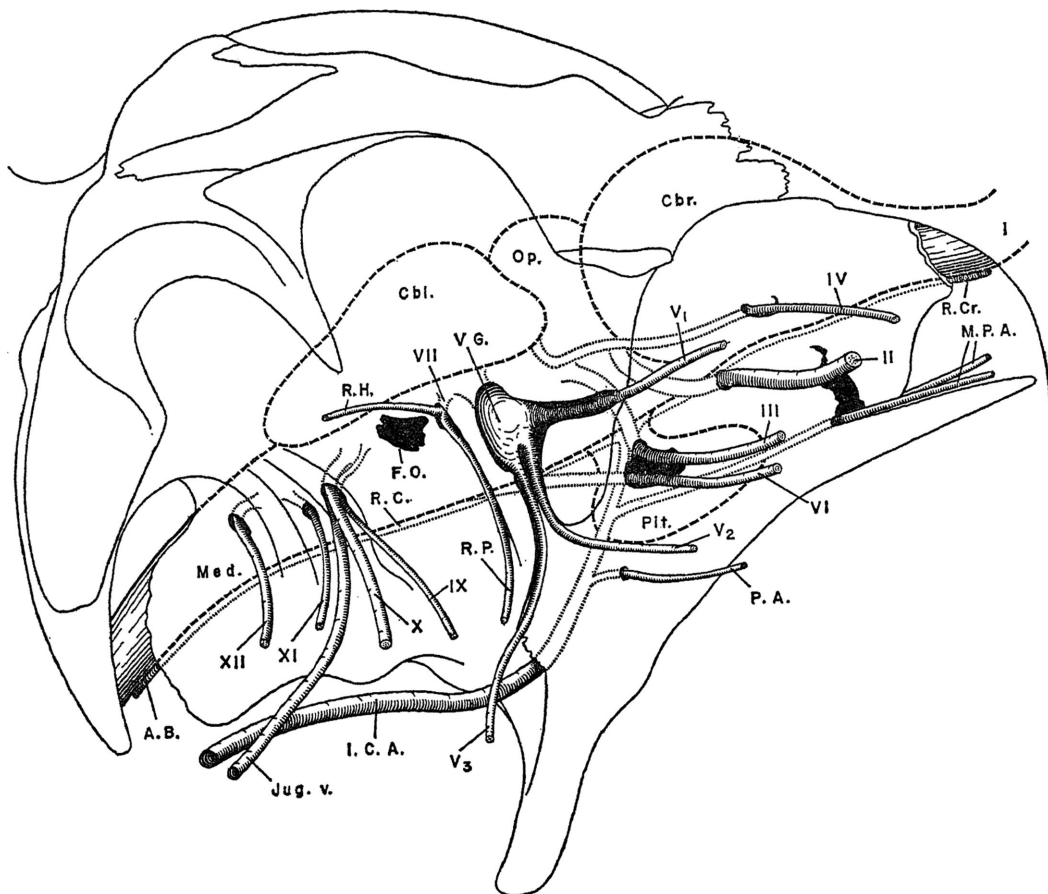


FIG. 65. Outline sketch of the cranium of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with the brain restored (broken lines) in outline, together with the cranial nerves and certain vascular elements. The dotted lines indicate the probable positions of the cranial nerves and certain vascular elements within the cranium. *Abbreviations:* A.B., arteria basilaris; Cbl., cerebellum; Cbr., cerebrum; F.O., fenestra ovalis; I.C.A., internal carotid artery; Jug. v., jugular vein; Med., medulla; M.P.A., median palatine artery; Op., optic lobe; P.A., palatine artery; Pit., pituitary body; R.C., ramus caudalis of the internal carotid artery; R. Cr., ramus cranialis of the internal carotid artery; R.H., ramus hyomandibularis of the facialis nerve; R.P., ramus palatinus of the facialis nerve; V.G., trigeminal ganglion; I, olfactory nerve; II, optic nerve; III, oculomotor nerve; IV, trochlear nerve; V, trigeminal nerve; V<sub>1</sub>, ramus profundus (ophthalmicus) of the trigeminal nerve; V<sub>2</sub>, ramus maxillaris of the trigeminal nerve; V<sub>3</sub>, ramus mandibularis of the trigeminal nerve; VI, abducens nerve; VII, facialis nerve; VIII, auditory nerve; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve.

saurian crania all seem to be characterized by a common canal for the emergence of the ninth and tenth cranial nerves, for in the most perfectly preserved crania, and in all the complete endocranial casts, the canal immediately posterior to the auditory canal is quite large (13 by 9 mm.), unusually so for the typically small glossopharyngeal nerve. The vagus nerve, on the other hand, is usu-

ally quite large and, in view of the small size of the adjacent foramina, it appears reasonable to reconstruct a common passage for these two cranial nerves in the Hadrosauridae. Nearly all well-preserved crania suggest such a condition.

Modern reptiles demonstrate a complex and multiple branching pattern in the extracranial portions of the glossopharyngeal



nerve. Typically many major rami exist, including several rami communicantes, which connect this nerve with various branches of the facialis and vagus nerves, the ramus sympathicus and the ramus pharyngolaryngeus. In the hadrosaurs, nothing is known of the extracranial pattern of this nerve or of its particular function. The conservative interpretation, of course, is that its over-all pattern and primary functions were not very different from those of the Lacertilia or Crocodilia of today.

#### VAGUS NERVE (X)

As mentioned above, the vagus nerve is believed to have emerged from the hadrosaurian brain case together with the ninth cranial nerve. Typically this nerve is very large, considerably larger than either the glossopharyngeal nerve or the accessory nerve. The foramen immediately behind the otic capsule is by far the largest opening behind the trigeminal foramen and therefore appears to have been occupied by the largest of the posterior cranial nerves, which in living reptiles would be the vagus nerve.

The extracranial passage of the vagus nerve is unknown. As a result, little can be concluded about its function in the hadrosaurs, although, considering the evidence of modern reptilian neurology, cardiac, pleural and visceral innervations seem the most probable. In some lizards (*Varanus*), this nerve also supplies fibers to the pharynx and the hyoid musculature (Watkinson, 1906).

#### ACCESSORY NERVE (XI)

This is a very small nerve in modern reptiles, believed by some to be part of the vagus nerve. Its primary function is the innervation of the M. episternocleidomastoideus. In *Varanus*, this nerve consists of a number of fibers from the anterior part of the spinal cord. These unite and enter the cranial cavity through the foramen magnum. After passing forward within the cranium, the accessory fibers join the root of the vagus nerve and enter the vagus canal. In many lacertilians, the accessory nerve passes only part way through the cranial wall within the vagus canal, separating from the vagus nerve and emerging from its own foramen posterior to that of the vagus.

The accessory nerve of *Kritosaurus*, as interpreted from the endocranial cast, appears to have passed through the cranial wall completely independently of the vagus nerve. Other hadrosaurian crania, particularly the cranium of *Anatosaurus* ("*Trachodon*") (A.M.N.H. No. 5236), indicate a similar condition for this nerve, although the evidence is not conclusive. The endocranial casts of *Kritosaurus* and *Edmontosaurus* clearly indicate the presence of four separate passages behind the otic capsule, which penetrate the lateral cranial wall. From the rear forward, Lambe (1920) interpreted these as the hypoglossal canal, the anterior condyloid foramen, the common canal of the accessory, vagus, and glossopharyngeal nerves, and finally the jugular vein canal below the last-named neural passage. Almost identical in pattern, these same passages in *Kritosaurus* are here interpreted as the hypoglossal canal, the accessory canal, the common canal of the vagus and glossopharyngeal nerves, and beneath the latter the jugular vein passage. There is little evidence to support one interpretation over the other, but the consistency with which the first three of these cranial openings occur in the Hadrosauridae suggests these were primarily neural rather than vascular passages.

#### HYPOGLOSSAL NERVE (XII)

According to Watkinson (1906) and others, this nerve consists of cranial fibers and elements from the cervical region of the spinal cord. These meet outside the cranium following the origin of three separate roots from the lateral wall of the myelencephalon. In *Varanus*, the cranial elements of the hypoglossal nerve emerge together with the vagus trunk, whereupon they separate from the vagus and unite with the cervical fibers of the hypoglossal nerve (Watkinson, 1906). In other forms, the hypoglossal nerve may emerge from the cranial cavity via one, two, or three foramina independent of the vagus nerve. Typically this nerve extends laterally away from the brain case and then veers caudad and ventrally where it innervates the hyoid and glosseal musculature in the throat region.

There is no evidence on the inner surface of hadrosaurian crania as to the origin of the hypoglossal fibers, nor is any conclusion possible regarding their extracranial paths. The

passage through the cranial wall, however, is well marked in a number of hadrosaurian crania and is clearly demonstrated in the endocranial casts of *Kritosaurus*, *Edmontosaurus*, and *Anatosaurus*. The *Kritosaurus* cast indicates a minimum dimension of 5 mm.

for this canal, while that of "*Trachodon*" is slightly smaller. In the absence of any significant evidence, the hadrosaurian hypoglossal nerve is presumed to have been similar in function and in pattern to that of modern reptiles.

### SOME ASPECTS OF CRANIAL CIRCULATION

In a study of this type, it seems desirable to include some discussion of the vascular system of the head. For obvious reasons, however, it is not possible to reconstruct the entire cephalic circulation or, for that matter, even a significant portion of this system. Therefore, the discussion that follows is simply an interpretation of certain cranial features that appear to be related to vascular structures. Reconstructions of only those portions of the vascular system that have left an impression on the cranium itself are included in this section, and no serious attempt is made to reconstruct the remaining elements of the system.

#### ARTERIES

With the exception of small branches to the throat region, the reptilian cephalic arterial system is usually composed entirely of branches from the carotid arches. These branches stem from one of two major rami of the carotid arch, the external and internal carotid arteries. This pattern is so constant within modern tetrapods that there can be little doubt of its existence in the Hadrosauridae and the dinosaurs in general.

As might be expected, owing probably to its superficial position in the tracheal, hyoid, and intermandibular musculature, there is no indication of any portion of the external carotid system in any of the hadrosaurian cranial material examined. Similarly, much of the internal carotid system is unknown as a result of its superficial position. Certain deeper elements, however, may be reconstructed with reasonable certainty.

#### MANDIBULAR ARTERY

The reptilian stapedia artery, the first branch of the internal carotid artery, bifurcates into two major vessels, the temporal artery and the mandibular artery. The latter usually descends along the medial sur-

face of the quadrate in modern lizards (*Ctenosaura*, *Varanus*) to enter the mandibular canal together with the fibers of the M. adductor posterior. This condition cannot be verified in any members of the Hadrosauridae, except that some analogous vascular element must have supplied the mandible. Within the lacertilian Meckelian canal, the mandibular artery separates into two branches, the internal mandibular artery which continues forward within the mandible, and the external mandibular artery which emerges to the lateral surface of the lower jaw through the anterior supra-angular foramen. Although structural differences between the hadrosaurian and lacertilian mandibles are extreme, a condition illustrated by several hadrosaurian mandibles seems to suggest a parallel vascular plan. Situated at midlength in the lateral dentary surface of *Corythosaurus casuarius* (A.M.N.H. Nos. 5240 and 5338) is a relatively large, anteriorly directed foramen which appears to be continuous with the mandibular canal. This may very well represent the emergence of an "external mandibular artery." If correctly interpreted, this opening differs markedly from the modern reptilian condition with respect to its location well anterior to the coronoid process and the surangular. This is not a serious problem, however, in view of the mandibular structure of the hadrosaurs in which the mandible is composed largely of the dentary. The surangular is greatly reduced, while the coronoid is completely lacking (the coronoid process being formed almost entirely by the dentary) in the hadrosaurian mandible.

Presumably a mandibular artery extending forward within the hadrosaurian Meckelian canal divided into two branches, one of which continued forward within the mandible while the other emerged through the lateral dentary wall, analogous to the modern internal and external mandibular arteries. Several smaller

foramina in the lateral dentary surface probably represent the passages of finer twigs from the "internal mandibular artery." These, together with branches from the "external mandibular artery," may have supplied the labial glands and the skin of the lower jaw and lips.

#### INTERNAL CAROTID ARTERY

Following the separation of the stapedial artery, the internal carotid artery of modern reptiles (*Ctenosaura*, *Varanus*, *Sphenodon*) extends forward through the tympanic cavity and along the lateral surface of the basioccipital and basisphenoid to the entrance of the Vidian canal. In its passage through the basisphenoid, the internal carotid artery gives off a single branch, the palatine artery. On entering the hypophyseal cavity through the carotid foramen, the carotid ascends together with the infundibulum into the cranial cavity. Here, beneath the midbrain, the internal carotid branches into two rami which pass in opposite directions beneath the brain. Extending anteriorly beneath the prosencephalon and supplying branches to the cerebral hemispheres, optic chiasma, and olfactory stalks is the ramus cranialis. Reaching caudally beneath the rhombencephalon and supplying the optic lobes, cerebellum, choroid plexus, and medulla is the ramus caudalis.

Portions of the internal carotid artery and its branches are very clearly indicated in several hadrosaurian crania. Numerous crania are marked by the entrance of the Vidian canal in the lateral surface of the basisphenoid directly beneath the trigeminal foramen ("*Trachodon*," A.M.N.H. No. 5236; *Anatosaurus saskatchewanensis*, N.M.C. No. 8509; *Corythosaurus intermedius*, R.O.M. No. 4670; *Corythosaurus excavatus*, N.M.C. No. 8676; *Edmontosaurus regalis*, N.M.C. No. 2289; *Procheneosaurus erectofrons*, A.M.N.H. No. 5461; *Lambeosaurus lambei*, R.O.M. No. 5131 and N.M.C. No. 2869). The passage of the Vidian canal through the basisphenoid is well illustrated in the crania and endocranial casts of *Kritosaurus notabilis* (A.M.N.H. No. 5350) and *Edmontosaurus regalis* (N.M.C. No. 2289). This canal rises anteriorly to open in the ventroposterior wall of the pituitary cavity. It appears to be a simple straight canal in *Kritosaurus*, but the cast of *Edmonto-*

*saurus* shows the craniad divergence of a smaller subsidiary canal from the Vidian canal. This smaller passage undoubtedly represents the canal of the palatine artery, which passed forward through the basisphenoid, much as it does in modern lizards (*Ctenosaura*, Oelrich, 1956), to emerge from the anterolateral surface in front of the basisphenoid flange.

The parasphenoid canal mentioned above, which is well preserved in the crania of *Kritosaurus notabilis* and *Edmontosaurus regalis*, as well as in the Yale cranium of *Anatosaurus* sp. (Y.P.M. No. 618), leads forward from the hypophyseal cavity between the parasphenoid and the presphenoid. This feature is interpreted as the common canal of the paired median palatine arteries, which branch from the internal carotid arteries. The median palatine artery is believed to have separated from the internal carotid within the pituitary cavity. From this region it passed forward out of the pituitary cavity by way of the midline parasphenoid canal into the interorbital region. In *Kritosaurus* this canal is oval in cross section and is unpaired. In *Anatosaurus* and *Edmontosaurus*, the incomplete development of a median septum indicates the paired nature of the transmitted structure.

Although none of the other crania does so, the cranium and endocranial cast of *Kritosaurus* clearly reflect portions of the intracranial extremities of the hadrosaurian internal carotid system. The ventral surface of the hind-brain region of the *Kritosaurus* cast is marked by a pronounced midline ridge, which appears to fork both anteriorly beneath the auditory nerve and posteriorly near the foramen magnum. The paired anterior extremities certainly reflect the existence of the paired rami caudalis of the internal carotids. As in *Sphenodon* (Dendy, 1909) and in several lizards (*Varanus*, *Ctenosaura*), these branches passed back beneath the hind brain in *Kritosaurus*, finally joining to form the single median arteria basilaris. In the region of the foramen magnum, this midline ridge of the *Kritosaurus* cast again separates into a double ridge, indicating a redivision of the basal artery at this level. The posterior bifurcation is interpreted as the anterior half of the *circus arteriosus spinalis*. Unfortunately the region immediately behind this feature is not

known, as it was situated outside the cranial cavity, but this incomplete pattern is so remarkably similar to that found in modern reptiles, particularly *Sphenodon*, that at the very least it raises the question whether other major hadrosaurian arterial patterns were equally similar to those of *Sphenodon* and modern lizards.

Unfortunately none of the hadrosaurian crania or casts reveals any reliable information about the rami cranialis, the anterior intracranial branches of the internal carotid arteries. There is a slight midline groove in the floor of the brain cavity underlying the olfactory tract in *Kritosaurus*, but, while it occupies the expected position and in fact may represent an impression of the ramus cranialis, there is some doubt as to whether or not this feature is natural. Brown (1914a), however, reports that the cranium of *Anchiceratops* reflects the passage of the ophthalmic rami, presumably a branch of the ramus cranialis, between the pituitary body and the optic nerves. The position of this vascular element suggests the existence of the rami cranialis, as any arterial elements at this level of the cranial cavity probably branched from the extremity of the internal carotid artery. However, the evidence is insufficient on which to establish the presence or position of the rami cranialis in the Hadrosauridae. Figures 56, 57, and 58 illustrate the features mentioned above that form the bases of these arterial reconstructions.

### VEINS

As in the case of the arteries, the superficial portions of the cephalic venal system are unknown in the hadrosaurs. The limited evidence seen in several hadrosaurian skulls is related exclusively to the intracranial system and even this is exceedingly fragmentary. It has been assumed that, as in modern tetrapods, the endocranial structures were drained largely by a median dorsal sinus, the sinus longitudinalis of Dendy (1909), which drained into the internal jugular vein by way of the posterior cephalic vein. A second drainage route may have existed in the form of a vena spinalis. The evidence for such a dorsal sinus within the hadrosaurian cranial cavity is, at best, very poor, but it is deemed worthy of brief mention here.

### OLFACTORY VEIN

Dendy (1909), in his study of the intracranial vascular system of *Sphenodon*, describes a large median sinus situated immediately beneath the cranial roof. This sinus longitudinalis receives venous branches from nearly all portions of the brain, including the superior cerebral veins from the cerebral hemispheres and the superior bigeminalis veins from the optic lobes. The median olfactory vein, which drains the olfactory centers of the nervous system, joins this median sinus anteriorly.

The ventral surface of the frontal region of the cranium of *Kritosaurus notabilis* (A.M.N.H. No. 5350) is marked by a slight midline groove just anterior to the cerebral chamber. The endocranial cast reflects this linear depression in the form of a rounded ridge situated in the midline above the olfactory lobes. The anterior extremity, beyond the rostral limits of the cranial cavity, is unknown, but the posterior extremity extends into the center of the steep anterior surface of the cerebral cast, as if the original structure had passed between the large cerebral hemispheres.

Conceivably the median structure here described represents a median intracranial vascular element, probably venous, which passed caudally, dorsal to the olfactory lobes and between the cerebral hemispheres, to enter a superior intracranial sinus. Such a pattern corresponds closely to that of modern reptilian intracranial patterns exemplified by the vena olfactoria and the sinus longitudinalis.

### INTERNAL JUGULAR VEIN

This element is presumed to have emerged from the posterior part of the cranial cavity, as in modern reptiles, most probably in the postotic region. Of the four prominent foramina that penetrate the medial surface of the opisthotic-exoccipital complex of *Kritosaurus notabilis* (A.M.N.H. No. 5350) and *Edmontosaurus regalis* (N.M.C. No. 2289), none can be established exclusively as vascular canals. These four passages seem to have conveyed the last four cranial nerves through the brain case wall independently. Examination of other crania, however, established the fact that three postotic canals are more typical of

the hadrosaurs ("Trachodon" sp., A.M.N.H. No. 5236; *Anatosaurus saskatchewanensis*, N.M.C. No. 8509; *Procheneosaurus erectifrons*, A.M.N.H. No. 5461; *Anatosaurus* sp., Y.P.M. No. 618; *Corythosaurus casuarius*, A.M.N.H. No. 5338).

The "extra," or fourth, passage seen in the first two specimens, because of its inconsistency within the family, is believed to have been purely vascular, rather than neural, in function. In both *Kritosaurus* and *Edmontosaurus*, this "extra" canal is situated immediately behind and somewhat below the otic capsule, beneath the much larger foramen lacerum posterius, which transmitted the ninth and tenth cranial nerves. Following Lambe's (1920) interpretation, this "extra" canal is believed to mark the emergence of the internal jugular vein.

It would appear from the preceding discussion that the jugular vein of other hadrosaurian species emerged from the endocranial cavity through one of the three remaining "neural" canals that are more constant in this family. While quantitative comparisons could not be made, apparently the foramen lacerum posterius is appreciably smaller in *Kritosaurus* and *Edmontosaurus* than it is in other forms in which only three postotic foramina exist. The smaller size of this opening in these specimens suggests that either fewer or smaller structures passed through this canal than in other species that possess only three postotic foramina. The larger size of the foramen lacerum posterius then suggests the emergence of an additional structure, such as the internal jugular vein, together with the trunks of the glossopharyngeal and vagus nerves, in such hadrosaurs as *Corythosaurus casuarius*.

None of the crania examined offered any further evidence of the position or pattern of the internal jugular vein.

#### VENAL SINUSES

A curious structure peculiar to two hadrosaurian genera deserves some attention in this discussion of the cephalic vascular system, although the suggestion that follows borders on pure speculation.

The skulls of *Edmontosaurus regalis* (N.M.C. Nos. 2288 and 2289, U.S.N.M. No. 12711, C.N.H.M. No. P15003) are character-

ized by strongly inflated postorbitals which form large, pouch-like cavities in the rear orbital wall. The expansion of the postorbital is so extreme in this genus that the upper part of the infratemporal fenestra behind has been reduced to a narrow slit one-half to one-fifth of the width of the lower fenestral margin. To a far less degree, the prefrontal is similarly inflated to form a bony pouch in the anterior orbital wall.

These orbital pockets in the superficial skull elements are most strongly developed in *Edmontosaurus*, but they also exist in more moderate form in all adequately known species of *Anatosaurus* (*A. annectens*, U.S.N.M. No. 2414, Y.P.M. No. 2182; *A. copei*, A.M.N.H. Nos. 5730, 5886; *A. saskatchewanensis*, N.M.C. No. 8509; and *A. edmontoni*, N.M.C. No. 8399). The degree of postorbital inflation in these species is greatest in *A. copei*, intermediate in *A. saskatchewanensis* and *A. edmontoni*, and least prominent in *A. annectens*. Curiously, only one other species (*Corythosaurus excavatus*, N.M.C. No. 8676) shows a similar development of the

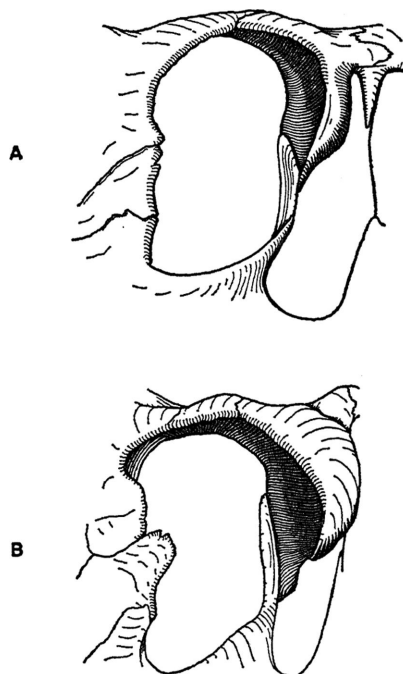


FIG. 66. The orbit and adjacent postorbital pouches. A. *Anatosaurus saskatchewanensis*, N.M.C. No. 8509. B. *Edmontosaurus regalis*, N.M.C. No. 2288.

postorbitals, but the corythosaurian postorbital cavities are very slight by comparison.

Most prominent among modern reptilian venous structures are the several large sinuses that collect blood from adjacent cephalic structures and transmit it to the vena jugularis interna. Of these, the very large sinus orbitalis is the most conspicuous. Orbital sinuses with varying degrees of development are present in *Sphenodon*, most lizards and snakes, and to a less extent in the Crocodilia and Chelonia. In *Sphenodon* and the Squamata, the orbital sinus plays a dominant role in cephalic intumescence and particularly in the protrusion of the eye. Intumescence is a common trait of modern reptiles, particularly of lizards and snakes. This swelling, generated by the gorging of vascular sinuses or highly vascularized tissues, varies in degree and in function from one species to another, as well as from one region to another within a single individual.

To correlate the orbital pouches of *Edmontosaurus* and *Anatosaurus* with the orbital sinuses of modern lizards may seem unwarranted but is not so improbable as it first

appears. The high variability of reptilian vascular sinuses may very well account for the diverse development, and even lack of development, of the orbital pouches in hadrosaurian genera. Whatever the genesis of these structures, their extreme development in *Edmontosaurus* certainly indicates a significant degree of encroachment into the temporal region and the mandibular musculature.

If Murray's (1936) and Bernhard's (1924) thesis (that tension stimulates growth while compression causes atrophy of bony tissues) can be relied on, these postorbital (and prefrontal) cavities can be explained as bony response in areas of high pressure. When the stresses that must have been created within the infratemporal fossa by the bulging adductor muscles are considered, the orbital pouches must have been molded by rather excessive opposing forces to encroach so on the active muscle area. Such forces in the orbital area could have been created by intumescence of large orbital sinuses. The function of such orbital intumescence, as conjectured here, is unknown.

## FUNCTIONAL MORPHOLOGY

THE FOLLOWING TREATMENT attempts to interpret the cranial adaptations and to reconstruct the cranial dynamics in relation to the various systems that have been reviewed above in the present paper. In addition, an attempt is made to evaluate the influence

that cranial functions have had on cranial morphology. This discussion is arbitrarily organized according to the type of activity or process involved, that is, sensory processes or responsive activities.

### SENSORY FUNCTIONS

#### FUNCTIONS ASSOCIATED WITH THE BRAIN

Foremost among the many varied functions of the head and all its components are those that required the expansion and differentiation of the anterior parts of the nervous system. These are the many activities of the brain, both sensory and motor. Very generally these may be classified as the reception and transmission of neural impulses and the generation of responsive neural impulses. As described in a preceding section, the hadrosaurian brain was a highly developed yet typically reptilian structure. Endocranial casts have established the existence of relatively large olfactory centers, very prominent cerebral hemispheres, a cerebellum of moderate size, and a large medulla. Although impossible of verification, it seems safe to correlate the major divisions of the hadrosaurian brain with functional centers known in modern reptilian brains. These very briefly are: for the medulla, control of involuntary activities such as respiration, heart activity, and metabolic rates, together with transmission of neural stimuli and responses; for the cerebellum, equilibration and orientation; for the cerebrum and midbrain, coordination of muscular response and certain sensory activities; and for the telencephalon, olfaction.

Very little can be inferred, except by direct observation of behavioral traits, about the relative levels or intensities of various neural activities. The relative sizes of different brain segments, however, may suggest something along these lines. For example, as is typical in the lower tetrapods, the hadrosaurian cerebellum appears to have been the least expanded segment of the brain, with the possible exception of the midbrain, which suggests that equilibration was not a highly developed

activity and was not of critical importance in the hadrosaurs. The relatively larger size of the cerebrum, on the other hand, implies a relatively high level of sensory perception or coordination of muscular response. Accordingly, the stout telencephalon suggests a high level of olfactory sensitivity. Other than these very general comments, it is obvious that very little can be determined about the specific activities of the hadrosaurian brain.

The brain case, of course, is very closely related to the central nervous system, which is particularly well shown in a consideration of brain case functions. The hadrosaurian brain case, which is described in detail elsewhere, has been referred to as the neurocranial segment of the skull (occipital segment of some authors). Although immovably united with the maxillary segment, it may still be considered as a distinct functional unit which served primarily to support and protect the axial portions of the cephalic nervous system. Its massive construction, with all components joined by firm sutural or fused unions, has formed a rigid, thick-walled, elongate shell which very nearly enclosed the entire brain. Figure 61 illustrates this almost complete encasement of the brain by the thick and firmly united cranial elements. In addition to this heavy, protective shell, the neural mass was quite probably still further protected through its suspension within the cranial cavity on strands of connective tissue. Certainly there can be little doubt that the hadrosaurian brain was well supported and effectively protected against injury by this massive bony shell. Although superficially disguised by secondary cranial features, the general shape of the brain case conforms to the gross form of the brain, demonstrating how strongly the neural elements and their

sensory functions have influenced the development of the neurocranial segment.

While the neurocranial segment has been strongly influenced by the neurological activities of the brain, and molded by the brain for its support and protection, certain aspects of the maxillary segment also show their domination by these neurological activities. Such structural adaptations of the maxillary segment are most obvious where they are clearly related to sensory apparatus, such as the olfactory, optic, and auditory structures.

### VISION

The orbital region of the maxillary segment is one of these superficial regions that have been strongly influenced by the location, size, and perhaps by the sensitivity of the neural structures: in this case the bulbus oculi. Although the orbital dimensions vary considerably within the family, all species are characterized by unusually large, circular to slightly oval, orbital cavities situated high on the lateral cranial surface. The unusually large size of the orbits indicates a very large size for the eye. Sclerotic rings, which have been preserved in several specimens, substantiate this implication and give much more accurate indications of the original dimensions of the hadrosaurian eyeball. Although Edinger (1929b) has expressed some doubts about the accuracy of these measurements, the eyeball certainly could have been no smaller in diameter than the sclerotic ring. In *Corythosaurus casuarius* (A.M.N.H. No. 5338) the sclerotic ring measures approximately 70 mm. in external diameter, while the minimum orbital diameter is slightly less than 100 mm. In *Lambeosaurus lambei* (R.O.M. No. 1218) the outside diameter of the sclerotic ring is approximately 60 mm. Brown (1912b), in restoring a partial sclerotic ring in *Saurolophus*, estimated the external diameter of this structure at 88 mm.

If an analogy can be drawn with the birds and primates, these large orbital dimensions, together with the large size of the hadrosaurian optic nerve and the expanded cerebral hemispheres, which among other functions is concerned with vision, seem to indicate a relatively, if not extremely, high degree of visual perception in these ornithopods.

The chief function of the circumorbital elements of the maxillary segment is clearly one of protection and support of the visual apparatus. Unquestionably the location and size of these visual receptors have determined the form of this part of the superficial cranium. Thus the development of accurate light sensitive receptors, which provided the possessor with certain information about its environment, has had a significant, if only local, influence on the form of the maxillary segment.

### HEARING

Auditory perception has been a doubtful factor in hadrosaurs, and in dinosaurs in general, in spite of Versluys' (1923) and von Huene's (1926) reports of dinosaurian stapes. Versluys very briefly mentioned the presence of a columella auris in the Senckenberg "*Trachodon*." The presence of a nearly complete stapes *in situ* in a second hadrosaur (*Corythosaurus casuarius*, A.M.N.H. No. 5338) certainly seems to eliminate any doubt about hadrosaurian hearing ability.

The presence of a functional tympanic membrane located superficially in the notch between the paroccipital process and the quadrate is strongly indicated by the stapes position found in *Corythosaurus*. (See fig. 24 and pl. 6.) As noted by Colbert and Ostrom (1958), the tympanic cavity must have extended between this post-quadratic notch and the fenestra ovalis in the lateral wall of the brain case. Although it is difficult, if not impossible, to determine the extent of their influence on the development of the adjacent elements of the maxillary segment, it is obvious that the tympanic membrane and the membranous walls of the tympanic cavity were all supported by the paroccipital process, the quadrate, and the lateral wall of the brain case. The modification of the neurocranial segment, on the other hand, is more easily recognized. Here the lateral wall of the brain case, specifically the pro-otic and opisthotic, have been greatly thickened to house and support the cochlea. The inner ear structures are very poorly known in these forms, but it is apparent that the thickening of the adjacent bony elements insured maximum protection of this most delicate structure of the auditory apparatus.



### EQUILIBRATION

Brown's preparation of the endolymphatic cavities and his description of the semicircular canals in *Anatosaurus* ("Trachodon") (Brown, 1914a) represent our total knowledge of this system in the hadrosaurs.<sup>1</sup> Brown's cast of the endolymphatic cavities (fig. 59) reveals that a common chamber existed for the utriculus and sacculus which was nearly conical in form, with a broadly inflated base. Two vertical semicircular canals existed at nearly right angles to each other. These ascended from a common origin at the apex of the utricular cavity and descended in a sharp curve to reënter this same cavity at its basal posterior and anterior lateral extremities. A third canal, the external or horizontal canal, emerged from the lower anterolateral region of the utricular cavity and swung laterally and posteriorly to reënter at the lower rear extremity of the same cavity. Brown's cast further indicates that ampullae were situated at the lower extremities of both vertical canals and also at the anterior origin of the horizontal canal. This pattern conforms almost precisely with that of modern tetrapods and certainly establishes equilibration as an active function in the hadrosaurs.

As in all vertebrates, the hadrosaurian equilibrating apparatus was completely enclosed in the thickened lateral wall of the neurocranial segment. This condition then, as now, quite certainly was a protective adaptation, to prevent damage or injury to the delicate membranous labyrinth. Again it is apparent that a small neurological structure has locally modified the surrounding elements of the skull to insure its protection and support.

### OLFACTION

The Lambeosaurinae have provoked much inquiry and considerable disagreement among vertebrate paleontologists concerning the function of the rather bizarre and diverse cranial crests ever since Lambe described and figured the first hooded hadrosaur, *Lambeosaurus lambei* (*Stephanosaurus marginatus*) in 1914. Now the cranial crests of *Lambeosaurus*, *Corythosaurus*, *Hypacrosaurus*, and

*Parasaurolophus* are well known, but their function has remained elusive. With Lambe's discovery in 1920 that the crest was made up of the premaxillaries and nasals, rather than the frontals and prefrontals, and that it was penetrated by the complicated narial passages, new insight was gained regarding crest functions. Since that time, most students of the Hadrosauridae have associated the narial crests with respiration, generally relating these strange structures in some way to the now generally accepted semi-aquatic habits of these creatures.

Among the several theories that have been offered in explanation of the crest, Nopcsa's (1929) is certainly one of the most extreme. Nopcsa suggested that these crests were an example of sexual dimorphism, with the crested forms representing the males. Other structural differences between the crested "males" and the non-crested "females," which can hardly be explained by sexual variation, seem to argue against such a theory. The fatal blow to Nopcsa's hypothesis, however, is found in the stratigraphic distribution of the "males" and "females." With the exception of *Parasaurolophus tubicen*, only non-crested forms have been recovered from the Lance and equivalent stratigraphic units, thus indicating a much earlier extinction of the "males" than of the "females." Abel's (1924) suggestion that these crests were used as defensive weapons, and Wiman's (1931) resonating chamber theory, may also be discarded as equally improbable.

Parks (1922) argued very strongly that the crest of *Parasaurolophus* was joined by a strong muscular or ligamentous connection with the dorsal vertebrae, perhaps to facilitate the movement of the rather large and unwieldy head. Other forms, however, such as *Edmontosaurus* and *Kritosaurus*, possessed far larger heads, which apparently did not require such additional support or leverage. Furthermore, the crest itself is largely responsible for the unwieldy form of the head and therefore can hardly be seriously considered as an adaptation to compensate for its own disadvantageous affects. Also, this theory does not account for the narial passages within the crest, and, finally, there are no recognizable muscle or ligament scars on any of the hadrosaurian crests.

<sup>1</sup> See also Langston's (1960) recent study.

Wilfarth (1938) suggested that the hadrosaurian hood or crest, together with the expanded beak, provided areas for the attachment of muscles controlling a proboscis. This theory, however, is not confirmed by the cranial structures of modern proboscis-bearing animals in which the nasals are usually greatly reduced rather than expanded. It also seems unlikely, as pointed out by Charles M. Sternberg (1939), that an expanded beak, which almost certainly existed in all hadrosaurs, and a proboscis would both be functionally advantageous in a single individual. Furthermore, there is no evidence in any of the hooded hadrosaurs that indicates muscular attachments on any part of the crest or beak.

Because the hadrosaurian crest is very definitely related to the nasal apparatus and respiration (see figs. 25-29), it is desirable to consider the various functions of the tetrapod nasal system. First, the nasal apparatus is concerned with the passage of air to the lungs. At the same time the nasal apparatus performs other functions in addition to air conduction. These are the preparation of the inhaled air for exposure to the delicate lung tissues, and olfaction. The former specifically involves the cleansing, humidifying, and temperature regulation of the inspired air. It is necessary, therefore, in any attempt to solve the riddle of the hadrosaurian crest, to consider each of these broad functions: inhalation, preparation of inhaled air, and olfaction. That the first of these activities applies to the hadrosaurian crest there can be no doubt, for it is now well established that the narial passages traversed these structures. However, the passage of air to the lungs does not solve the problem of the peculiar crest development. For what reason was the inhaled air passed over this longer and more complex route? The answer would seem to rest with one of the two remaining activities.

Most of the theories proposed so far have related this structure to a respiratory or breathing adaptation for a semi-aquatic mode of life. Romer (1933) suggested that there may have been narial openings high on these crests, through which the animal could have breathed while almost completely submerged. However, no such openings have been preserved in complete and nearly perfect speci-

mens. Colbert (1945b, 1955), Romer (1945), and others have attempted to explain these crests as air storage chambers which would have allowed the animal to remain submerged for longer periods of time. Two points argue strongly against such a function. First, the volume of the hadrosaurian crest appears quite insignificant in comparison with the probable lung capacity. A very conservative estimate of the lung capacity of *Corythosaurus casuarius*, for example, is approximately 65,000 cc., or less than one-fifth of the total volume of the rib cage. If it be assumed that the entire crest of this species could have been utilized as storage space, the total crest volume did not exceed 2500 cc. Thus the crest volume in this species probably did not represent more than 4 per cent of the total lung capacity, and it more likely represented a much smaller fraction. Such a small reservoir of air appears not to have been very effective, even if the effective lung capacity (eliminating residual air volume) were half as great, especially in view of the rather extreme structural modifications involved. In smaller hadrosaurian crests, the reservoir volume would have been even less significant. It also seems somewhat anomalous that a semi-aquatic form should have undergone such extreme modification for such purposes, when purely aquatic air-breathing vertebrates have been so conservative with regard to such adaptations. Furthermore, and probably most conclusive of all, it must be assumed that, for the utilization of such a reservoir of air, highly undesirable or even impossible consequences would have been required. In order to withdraw this reserve air supply from the crest cavities and into the lungs, something (either air or water) must have displaced it. Water does not seem a likely agent, in view of its adverse effects and the effective precautions against just such circumstances that have been repeatedly developed in most semi-aquatic and aquatic tetrapods. Air, as a displacing substance, obviously was available only in an emerged state, in which case such an air reserve was unnecessary. If narial sphincter muscles or vascularized valves prevented the entrance of water into these narial passages, as seems most probable, these very same valves obviously must have prevented air withdrawal

from the crest during submergence.

Charles M. Sternberg (1935, 1939, 1942, and 1953) also visualized the hadrosaurian crest as an adaptation to breathing in an aquatic habit. He considered the crest as a trapping mechanism to prevent water from entering the narial passages and lungs during under-water feeding activities. Russell (1946) also vigorously supported a trapping function for these crests, maintaining that *Parasaurolophus* represented the functional summit of this adaptation. The implications here are that the narial loop within the hadrosaurian crest is analogous to an inverted U tube. This theory is unsatisfactory on several counts. First, the mere presence of an inverted loop in the narial passage could not, in itself, prevent water from moving up into the narial passages and even into the lungs. Even at shallow depths, the hydrostatic pressure would have been far greater than the air pressure within the crest and lungs, thus producing compression of the crest and lung gases and the entrance of water into the narial passages, even in an upward path against the force of gravity. Only a lung pressure greater than the hydrostatic pressure could have prevented water from rising into the narial loop, and no modern animals, aquatic or semi-aquatic, rely solely on lung pressure to prevent drowning. It therefore seems quite unlikely that the

hadrosaurian crest was developed exclusively to prevent the passage of water into the narial passages and lungs, especially when one considers that another highly effective and far simpler mechanism has been developed repeatedly by many different (and distantly related) creatures for exactly the same purpose. Sphincter valves, or highly vascularized narial tissues, have effectively performed this function in such diverse forms as cetaceans, sirenians, pinnepeds, rodents, crocodiles, lizards, snakes, and amphibians. In light of the more conservative valve mechanisms that have been developed in these forms, the extreme modifications of the hadrosaurian crest appear quite superfluous as a trapping mechanism.

As accepted above, the relationship of the hadrosaurian crest to the narial passages, and its construction from the nasals and premaxillaries, certainly suggest some crestal function associated with breathing. So far, the prominent theories have considered this structure as a breathing adaptation for a semi-aquatic habit. These are all shown to be impossible or highly improbable. Therefore, the two remaining nasal functions, air preparation and olfaction, which have not yet been considered, must now be reviewed.

Stebbins (1943, 1948) has demonstrated the degree to which nasal structures have

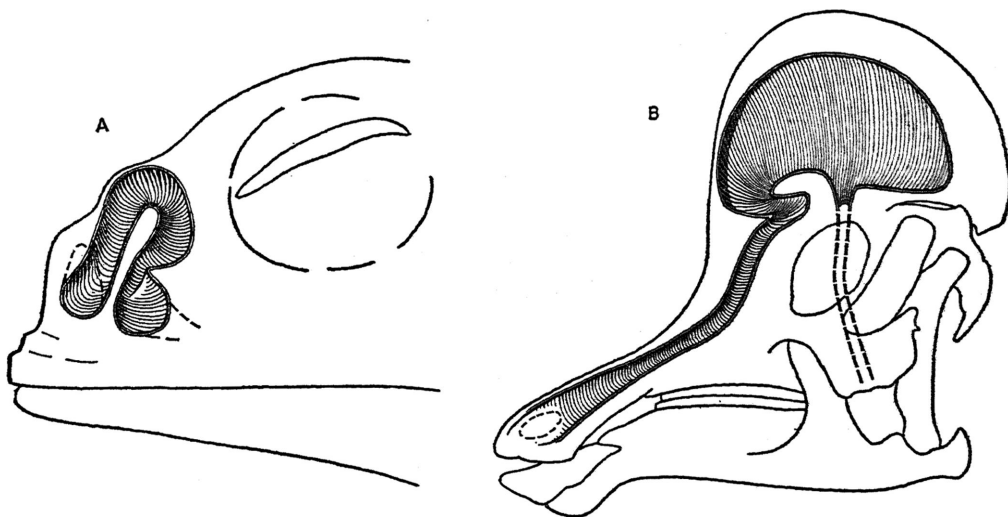


FIG. 67. Diagram showing comparison of the narial passages. A. *Phrynosoma coronatum*. (After Stebbins, 1948).  $\times 5$ . B. Generalized narial passages as reconstructed in *Corythosaurus casuarius*.  $\times \frac{1}{12}$ .

been modified in certain lizards for more effective preparation of inspired air. At first glance, a striking parallel exists between the inverted loops of the narial tracts in the crested hadrosaurs and those exhibited by certain sand-burrowing lizards such as *Uma*, *Callisaurus*, and particularly *Phrynosoma* (see fig. 67). In these forms, the narial passage ascends posteriorly at a relatively steep angle, as in the Lambeosaurinae, then turns and descends behind and beneath the anterior limb of the narial loop. This arrangement forms an effective trap for sand particles and prevents these solid particles from entering the lungs. The inspiration of air is insufficient to lift these particles against the force of gravity. It is pointed out above that this loop structure alone could not have prevented the admission of fluids into the bronchial and lung cavities of the hadrosaurs, if the water pressure exceeded the lung pressure. It is equally doubtful that the hadrosaurian loop functioned as a trap for solid particles, because they probably neither occupied arid regions nor buried themselves in loose sand as does *Phrynosoma*. Thus it would seem that the hadrosaurian nasal complex did not serve as an air cleansing mechanism.

Two preparatory activities remain, humidification and the thermoregulation of the inhaled air, which certainly were as important during the Cretaceous as they are at the present time. Humidification seems not to arouse much support, for these creatures certainly were semi-aquatic and presumably, therefore, occupied relatively humid regions. Such extreme adaptations for insuring an adequate moisture content of the inhaled air during occasional periods of drought hardly seems an adequate explanation either. Thermoregulation, the adjustment of air temperature to approximate body temperature as the air passes over highly vascularized nasal tissues, appears to be a more plausible solution, although in this respect, too, the extreme modifications of the Lambeosaurinae hardly seem necessary in view of those hadrosaurs that survived without such a thermoregulating adaptation. Because both crested and non-crested hadrosaurs occurred together (geographically and stratigraphically), any suggestion that these two types were adapted for markedly different climatic con-

ditions must be ruled out. It is possible, of course, that the Lambeosaurinae perfected the adaptation for adverse temperature ranges, while the non-crested species developed some other completely different structure for temperature adjustment of inhaled air. Such a theory seems very improbable, and the author is inclined to support a completely different hypothesis.

It is surprising that one of the fundamental activities of the tetrapod nasal apparatus, olfaction, has received so little consideration. Only Abel (1924) and Wiman (1931) considered this at all and then only briefly. Within the tetrapods, the sense of smell is largely associated with the respiratory process and is therefore involved with the narial structures. Vertebrates, particularly certain mammals, with an acute sense of smell are characterized by a complex and highly developed turbinal and ethmoid system. Not all of the turbinal complex of macrosmatic mammals is concerned with olfaction, but, where the turbinal system has been expanded, the sensory epithelium has also been expanded, and increased olfactory sensitivity is characteristic. Secondarily aquatic or semi-aquatic tetrapods usually exhibit reduced olfactory sensitivity, but the hadrosaurs, while certainly semi-aquatic, undoubtedly were active terrestrial foragers as well and therefore may well have required an intensification of their olfactory powers.

The expanded and complex narial cavities of the lambeosaurian crest may very well have been an adaptation for such a function, which appears even more certain when it is realized that most, if not all, olfactory receptors must have been situated within the crestal cavities, as the "choanal" position in the crested hadrosaurs so conclusively demonstrates. As mentioned above, the olfactory foramen of the endocranial cavity is located not more than 40 mm. posterior to the narial orifice at the base of the crest, which very definitely limits the possible locations of the olfactory epithelia. The greatly expanded and pocketed narial cavities of *Corythosaurus*, *Lambeosaurus*, and *Hypacrosaurus* could very well have housed greatly expanded olfactory and mucous membranes, similar to the turbinal system of mammals, for increased olfactory sensitivity. The elongate and simpler

tube-like crest of *Parasaurolophus* (and also *Tsintaosaurus* of China; see Young, 1957) represents a simple elongation of the narial passage, without the development of extensive subsidiary cavities. The lengthening of this narial tract also would have resulted in an increase in the surface area of the olfactory epithelium.

If improved olfaction is the real function behind the hadrosaurian crest, as seems reasonable at the present stage of our hadrosaurian knowledge, this structure illustrates a very striking example of extreme cranial modification associated with neurological activities. In this case, it should be noted that this sensory-initiated transformation has affected only elements of the maxillary or superficial segment of the skull, as there is little if any basic difference between the neurocranial segments of crested and those of non-crested species. The failure of the non-crested hadrosaurs to develop any similar olfactory adaptation remains a mystery, although possibly an analogous structure resided in the large excavation of the snout in the non-crested forms. Different levels of olfactory sensitivity are not uncommon in modern mammals and may represent a modern parallel to the hadrosaurian condition.

Some comment pertaining to the function

of the pseudo-narial crests of the Saurolophinae is pertinent here, in spite of the fact that these features seem not to be related to the narial passages or to olfaction. As noted above, the present evidence indicates that the pseudo-narial crests are not perforated by narial passages. Such a condition makes it obvious that the two structures involved were quite independently developed for completely different functions. There is, of course, the possibility that the pseudo-narial crest represents an incipient or rudimentary narial crest, an explanation that seems not to be supported by the morphological evidence. On the other hand the narial crest of the lambeosaurs may have possessed some ornamental value, and the pseudo-narial crest of the Saurolophinae might represent an example of mimicry. The close relationship between the Saurolophinae and the Lambeosaurinae may support the first explanation, but this would imply that the saurolophine crest was merely a genetic accident rather than a functional adaptation, an implication that is certainly contradicted by the stratigraphic and geographic evidence. From the functional standpoint, therefore, it would appear that the pseudo-narial crest of the Saurolophinae was simply an inaccurate imitation of the true narial crest of the Lambeosaurinae.

## RESPONSIVE FUNCTIONS

Of the possible responsive functions of the hadrosaurian head, only a few seem to be of any real significance here. Inhalation and the passage of air to the bronchial and lung cavities are discussed above. Defensive structures are not known to be related to the cranial features, as the hadrosaurian defensive tactics most probably were of a retreating rather than an aggressive nature, probably involving a return to the relative security of an aquatic environment where terrestrial predators could not follow and where aquatic enemies were few, if present at all. Thus there are no cranial defensive adaptations, unless the crests of the Lambeosaurinae can be considered as fright or warning mechanisms. Vocalization within the hadrosaurs can only be inferred from the presence of a highly developed auditory system which may have aided in species recognition as well as in

the warning of approaching danger. Morphological features related to these activities are not known.

Vastly more significant, however, particularly in terms of hadrosaurian cranial morphology, are those activities associated with the ingestion of food. When it is considered that these activities have probably had a far greater influence on the cranial development than any other cranial function, it is surprising indeed that so little attention has been directed towards feeding and mastication. Only Versluys (1922, 1923) and Kripp (1933) have considered these activities in detail. In view of the extreme specialization of the hadrosaurian dental apparatus, this deficiency is critical. The discussion that follows centers about the mechanical operation of a most unusual reptilian masticatory apparatus.

Before this discussion is begun, however, it seems desirable to enumerate the many cranial modifications characteristic of the hadrosaurs that have been developed in response to their chewing and feeding activities. Very briefly these are: the spoon-like expansion of the prementary and premaxillaries; the multiplication and close packing of the "cheek" teeth to form the large dental "mills"; the loss of the anterior dentition; the increased height of the skull; the enlargement, lateral position, and forward and medial inclination of the coronoid process; the lateral inclination of the occlusal surfaces; the oblique, rather than vertical, alignment of opposing batteries; the lengthening and buttressing of the quadrate; the depression of the quadrate-mandibular articulation; and the rearrangement of the mandibular musculature.

### FEEDING

The existence of a very broad, edentulous, spatulate beak in the hadrosaurs has long been accepted, ever since Cope (1883) and Versluys (1923) described remnants of this structure in two species of *Anatosaurus* (*A. annectens*, S.M. No. R4036, and *A. copei*, A.M.N.H. No. 5730). The expanded and somewhat thickened anterior margins of the premaxillaries and prementary undoubtedly served as broad areas of attachment for these superficial horny beaks.

Versluys (1923), in describing the impression of this horny beak in the Senckenberg specimen (*A. annectens*), noted that the anterior margin of the premaxillaries was overlapped for a distance of 80 mm. by the poorly preserved remains of this beak. He described this structure as being situated nearly vertically, with its superficial surface undulating regularly anteriorly but with decreasing amplitude laterally. Versluys failed to discover any impression of a similar structure attached to the lower jaw. Cope (1883), however, described beak impressions at the anterior extremities of both the upper and lower jaws in a specimen of *A. copei* (*Diclonius mirabilis*). Further evidence of a lower beak has been found in a third specimen (*Corythosaurus excavatus*, N.M.C. No. 8676), described by Charles M. Sternberg (1935), in the form of an impression of an incomplete

horny beak in front of and along the left side of the prementary. This specimen indicates the presence of small, tooth-like projections on the inner surface of the beak, which probably contributed to a firm union of this structure with the lower jaw.

Although Versluys did not find any impression of the lower beak, he very definitely indicated that the upper beak, because of its form, could not have met the lower margin of its counterpart in the manner characteristic of modern ducks. He believed that the lower beak must have fitted up inside the upper beak, with the free margin of the former coming in contact with the concave ventral surface rather than the free lower margin of the latter. In accepting this reconstruction, Versluys objected strongly to the frequent comparisons made between the beaks of hadrosaurs and those of ducks. Furthermore, he did not believe that the hadrosaurs gathered their food by groveling about in muddy swamp bottoms with these beaks, as was proposed by Abel in 1912, but suggested that the free overlapping margin of the upper beak was better suited for the scraping of bark and leaves from small branches or the uprooting of small, herb-like plants from the ground.

Kräusel's studies (1922) of the preserved stomach contents of a hadrosaur specimen seem to support this opinion of Versluys. These contents contained, along with other unrecognizable material, the needles of a Cretaceous conifer (*Cunninghamites elegans*) and the remains of other land plants. As pointed out by Kräusel, however, these merely indicate that these creatures could feed on land plants. They do not eliminate the possibility that they fed on aquatic vegetation as well. Indeed, the harsher fibers of land plants might be more readily preserved than the softer materials of aquatic plants.

The general similarity in size and form of the opposing prementary and premaxillary anterior margins suggests a more conformable opposition of the upper and lower beaks than Versluys was willing to accept. Also, the probability of considerable fore and aft motion of the mandible, as is elaborated below, would have allowed considerably more freedom of beak action than was visualized by Versluys. With fore and aft mobility of the mandibles, opposition of the beaks could

have ranged from perfect alignment of opposing margins to that proposed by Versluys, in which the lower beak fitted within the concave lower surface of the upper beak, permitting both a plucking or nipping action of perfectly aligned beak margins and a scraping or gouging (hoe fashion) of misaligned beaks. The former activity, considering Kräusel's evidence again, seems quite well suited for terrestrial browsing, while the latter appears better designed for under-water feeding in the gouging up of bottom mosses and reeds.

The relative lack of evidence pertaining to the actual size and shape of the hadrosaurian beak makes any definite conclusions concerning its operation somewhat premature. But, with the slight amount of information now available, any consideration of this problem must include the potential mandibular movements, for, regardless of the precise beak form, these actions ultimately determine the operation of distal mouth parts. Versluys failed to take these into consideration and therefore failed to realize the full flexibility of the hadrosaurian food-gathering apparatus.

Several authors (Abel, 1912; Versluys, 1922, 1923; and Lull and Wright, 1942) have considered the possible existence of a prehensile tongue which may have aided in feeding activities. The rather highly developed hyoid apparatus, described above, would seem to imply an active, if not prehensile, tongue. However, as Lull and Wright (1942, p. 43) have pointed out, "the effectiveness of the cropping beak would seem to preclude the necessity of such a protrusile tongue." While a prehensile or grasping tongue seems improbable, there is considerable evidence for accepting the existence of a highly active hadrosaurian tongue. The use of the tongue for manipulation of food during mastication and swallowing is well known in modern tetrapods, particularly mammals. Even in predaceous lizards that do not chew their food, the tongue aids in food manipulation preparatory to ingestion, a process that is readily observable in common American lizards such as *Sceloporus* and *Crotaphytus*. In animals that masticate the food before swallowing it, the tongue plays a very active role in moving the food material about in the mouth to insure its complete

disintegration. The position of the hadrosaurian dental "mills" in the posterior part of the mouth would certainly seem to have required a mobile but not necessarily prehensile tongue to shift the food backward in the mouth, where it could be prepared by the action of the dental batteries. Such would, at least in part, explain the highly ossified character of the preserved portions of the hadrosaurian hyoid apparatus. Because of the long, narrow space between the hadrosaurian mandibles, the tongue must have been similarly quite long and narrow, but probably it was highly muscularized and flexible.

### MASTICATION

Only Versluys (1922, 1923) and Kripp (1933) have made detailed studies of the masticatory movements in members of the Hadrosauridae. However, their rather complex interpretations, based on *Anatosaurus annectens* (*Trachodon*) and *Edmontosaurus*, have not generally been noted or accepted by American paleontologists, for most students of this family still consider mastication to have been characterized by vertical shearing (Lull and Wright, 1942, pp. 43, 69). The evidence and interpretations presented here refute the currently accepted vertical shear action, as well as many of Versluys' and Kripp's less well-known conclusions.

The opposing dental batteries, as is well known, are composed of dozens of lozenge-shaped teeth arranged in closely spaced vertical rows. Each vertical row, of which there may be 40 or 50 in each battery, consists of four to six teeth arranged in succession. The two or three superficial teeth of each row, which are transected obliquely by the occlusal surface, are the functional teeth and are underlain by several non-functional replacement teeth. The diamond-shaped crowns are inclined at an angle of about 60 degrees from the tooth axis and, in the case of the lower batteries, as a result of the close spacing of vertical rows and of successional teeth in each row, collectively form a medially facing, enameled mosaic or pavement. In the case of the upper batteries, the enameled crown is concealed by the root of the preceding tooth, so that only the crowns of the oldest or most advanced teeth are exposed by the wearing of the grinding surface. But here, too, the

tightly spaced vertical rows, with their successional tooth series, form a solid block of interlocking teeth. These batteries range in length from 105 mm. in *Procheneosaurus erectofrons* to 436 mm. in *Edmontosaurus regalis*, but they rarely exceed 25 mm. in width.

The occlusal surfaces, which are aligned parallel to each other and to the long axis of the head, are steeply inclined at about 40 to 55 degrees from the horizontal, so that the lower grinding surface faces outward, while that of the upper battery faces medially. Opposing surfaces are almost always conformable, so that in most specimens they meet almost perfectly on elevation of the lower jaw. Usually, although variably, the occlusal surfaces deviate slightly from a perfect plane. In most specimens these exhibit a slight but distinct warp in a longitudinal direction, with the result that the lower surface is usually convex upward, while the upper surface tends to be concave downward. With somewhat less frequency, these occlusal surfaces often exhibit the opposite curvature transverse to the battery axis. In such instances, the lower surface tends to be concave upward, and its opposite is convex downward; thus the grinding surface of the lower battery tends to have the appearance of a shallow, inclined groove which arches up slightly from front to back. Conversely, the opposing surface of the upper battery presents just the opposite form.

The massive mandible, which is described in detail elsewhere for *Corythosaurus casuarius*, forms a stout supporting frame for the very large and heavy mandibular battery. The anterior third of the lower jaw is completely devoid of teeth and, together with its mate, is greatly expanded anteriorly to form a spatula-like foundation for the horny beak noted above. The battery, which usually approaches half of the total mandibular length, is typically situated close to the middle of the lower jaw length, extending caudally almost to the rear margin of the coronoid process. The latter feature rises as a very stout limb from the lateral surface of the mandible at a position nearly three-fourths of the mandibular length behind the beak. In all species, the coronoid process bends medially and rostrally in its ascent, so that its dorsal

extremity lies anterior and medial to its base, lying above the lateral portion of the maxilla, in or close to the vertical plane of the dental batteries. Thus the posterior extremities of the batteries actually lie medial to the shaft of the coronoid process and ventral to its dorsal tip.

Considering the great bulk of the mandible, one can see a strange paradox in the very small retroarticular process. On the average, the hadrosaurian retroarticular process constitutes about 5 per cent of the total mandible length. This process turns inward and upward behind the quadrate articulation. Although not clearly defined on most specimens, the articular surface of the mandible appears to be considerably larger than the head of the quadrate, being at least 50 to 60 mm. in length in *Corythosaurus casuarius* (A.M.N.H. No. 5338). In nearly every specimen this surface slopes slightly to the side, except at its anterolateral margin where it is limited by a rather prominent, dorsolaterally projecting ledge of the surangular. In no instance was a socket-like surface even suggested. Close examination of this articular surface in dozens of hadrosaurian mandibles has established this as a rather broad and elongate, slightly concave surface which slopes laterally at a shallow angle. In all hadrosaurs, the articulation of the mandible with the quadrate is located well below the occlusal plane of the batteries. In *Corythosaurus casuarius* (A.M.N.H. No. 5338) it is approximately 65 mm. below these grinding surfaces.

The maxillary segment, as is the mandibular, is greatly expanded in its ventral portions to provide a firm foundation for the upper battery, which occupies nearly the entire ventral length of the maxilla. Again, the anterior portion of the maxillary segment is devoid of teeth and is greatly expanded anteriorly for the attachment of a horny beak. From the lateral maxillary surface, the thin but broad jugal arch bows out laterally in its passage back to the latero-anterior margin of the quadrate. The stout and very long (280 mm. in *Corythosaurus casuarius*, A.M.N.H. No. 5338) quadrate stands nearly vertically. Dorsally it fits closely into the socket-like "cotylus" of the squamosal. Its lower lateral margin butts against and is slightly overlapped anteriorly by the quadratojugal of the



lower temporal arch. Medially the pterygoid process of the quadrate unites in a squamose union with the broad alar process of the pterygoid.

The mandibular muscles, which are described in detail in a preceding section, are typically sauropsid in pattern, although certain functional variations have been developed. The adductor mandibulae group consisted of three major muscles, as in modern reptiles: the *M. adductor mandibulae externus*, the *M. adductor mandibulae internus* (including the *M. pseudotemporalis* and *M. pterygoideus*), and the *M. adductor mandibulae posterior*. The fibers of the adductor externus extended dorsocaudally in a nearly vertical pattern from an insertional area on the dorsal mandibular surfaces to multiple origins on the lateral, ventral, and medial surfaces of the upper temporal arch and on the medial and posterior walls of the supratemporal fossa. The position and orientation of the long, narrow, infratemporal fenestra almost exactly mark the position and orientation of the adductor externus fibers. In fact, this lateral fenestra quite probably resulted from the expansion of the underlying adductor externus belly.

Oriented almost parallel to these fibers were those of the *M. pseudotemporalis*, extending dorsocaudally from the dorsal tip of the coronoid process to an origin on the anteromedial wall of the supratemporal fossa just anterior to the origin of the deep fibers of the adductor externus. To some extent the postorbital bar defines the position and attitude of the pseudotemporalis muscle. Together, these two muscles formed a rather powerful adducting apparatus. The orientation of these two muscle masses (see fig. 72)

clearly establishes their function as one of adduction, and their rather remarkable length (ranging from 250 mm. to nearly 350 mm. in *Corythosaurus casuarius*) and bulk indicate considerable power for the generation of high grinding pressures.

The hadrosaurian jaw, as in all vertebrates, operated as a class-III lever, with the force applied at a point between the fulcrum (articulation) and the resistance (dentition). As any point farther from the fulcrum than the point of force application (muscle insertion) receives less force than is exerted by muscle contraction, there is no mechanical increase in the effective grinding pressure. Speed of adduction is the only advantage of a class-III lever. When the base of the coronoid process is considered as the average point of force application, it is apparent that the grinding force diminishes anteriorly. The grinding force that resulted at the posterior extremities of the batteries, medial to the coronoid process, must have been approximately equal to the force exerted by the adductor muscles, while the anterior extremities of the batteries, which are approximately four times as far from the fulcrum, received one-fourth as much grinding force. Such reduction of the grinding force away from the fulcrum was probably responsible, in part at least, for the edentulous anterior portions of the jaws and the apparent posterior shifting of the dental batteries. Rostrally placed teeth could not have been effective crushers.

The adductor posterior, extending from the mandibular fossa upward and caudally to a formidable origin in the large, forward-facing excavation of the quadrate formed a second large adductor mass. These fibers, however, were less steeply inclined, with the largest

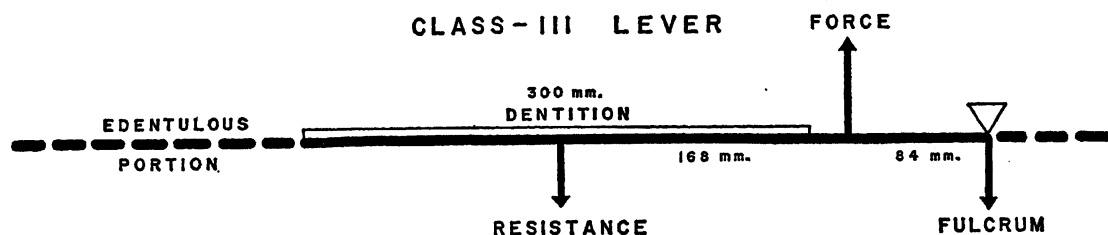


FIG. 68. Lever diagram of the hadrosaurian mandible based on measurements taken from *Corythosaurus casuarius*, A.M.N.H. No. 5338. The point of force application is illustrated at the geometric center of the reconstructed mandibular muscle attachments. The resistance is illustrated at the mid-point of the battery.

portion running more nearly parallel to the axis of the elevated mandible. (See fig. 72.) The action of the adductor posterior was also one of adduction or elevation of the mandible, but, in addition, the anterior-posterior orientation of these fibers, with their origin located posteriorly on the anterior quadrate surface, indicates a more important function of mandible retraction for this muscle.

The second division of the adductor internus group, the *M. pterygoideus*, inserted on the lateral and medial surfaces of the retroarticular process and immediately adjacent surfaces of the mandible. From these areas, the pterygoideus passed medially beneath the mandible, swinging forward and slightly upward to multiple origins on the ventroposterior surfaces of the ectopterygoid and maxilla and the posterolateral surface of the maxilla medial to the jugal and above the dental battery. The position of the pterygoideus insertions, concentrated about the mandibular articulation and the retroarticular process, precludes adduction as a significant function of this muscle, when the excessive mass of the mandibles and their batteries is considered. The leverage possessed by this muscle arrangement, with respect to jaw adduction, was very slight. The slightly inclined, fore and aft orientation of this long muscle complex (as is illustrated in fig. 72) immediately restricts the contraction of these fibers to an essentially anterior-posterior direction, and the anteriorly placed origins establish the pterygoideus as a protractor of the mandible. Thus a fore and aft movement of the lower jaws must be considered as an important action in the hadrosaurs, generated largely by the powerful retractive action of the adductor posterior and the equally powerful, but opposing, protractive action of the pterygoideus. (See fig. 70.)

The very short retroarticular process, together with the relatively small origin scars preserved on the occipital surfaces of a few specimens, indicates a relatively small depressor mandibulae. This muscle, owing to the very short retroarticular process with its correspondingly reduced advantage as a lever, may have been almost non-functional. Depression of the great mandibular mass probably did not require much muscular contraction.

Nopcsa (1900) was the first to suggest a forward and backward motion of the hadrosaurian mandibles. However, he related this to a streptostylic condition of the skull, in which the fore and aft displacement of the mandibles was effected by a similar movement of the quadrates. Versluys (1910) considered the problem of hadrosaurian streptostylism in his review of dinosaurian streptostylism. He was unable to arrive at a conclusion at that time, but in later discussions (1923) he accepted the existence of a streptostylic quadrate in the hadrosaurs and related it to the protraction and retraction of the lower jaws.

Other students of the hadrosaurs, beginning with Lambe (1920, pp. 55, 56), and most recently Lull and Wright (1942, p. 43), have persistently adhered to a vertical shearing type of chewing movement in this family. Lull and Wright refer to "vertical striations" (presumably on the occlusal surfaces) "which imply a chopping and no discernible fore and aft motion." Although dozens of hadrosaurian specimens were examined by the present author, none of these exhibited any vertical or transverse striations whatever. Other evidence has been observed, however, that establishes beyond doubt not only that horizontal mandibular movement was possible but that it must have been the principal chewing action.

A comparison of the two excellent specimens of *Corythosaurus casuarius* on display at the present time in the American Museum of Natural History will verify the longitudinal mobility of the hadrosaurian mandibles. The forward position of the lower jaws, most easily seen by the forward position of the coronoid process, is displayed in the holotype (A.M.N.H. No. 5240) of this species, while a more retracted mandible position is illustrated by the plesiotype (A.M.N.H. No. 5338). While these examples can hardly be accepted as proof of such jaw action, they demonstrate clearly that it is a mechanical possibility. Also, while the mandibles are displaced in these specimens relative to the skull, the quadrates are not displaced at all (see pls. 1, 2).

The conclusive evidence of protraction and retraction of the mandibles is found in a difference in the lengths of opposing occlusal

surfaces in three hadrosaurian specimens. In *Brachylophosaurus canadensis* (N.M.C. No. 8893), the lengths of both upper grinding surfaces exceed those of the lower surfaces by 11 mm. All four batteries are complete, and in each instance the worn grinding surface extends the full length of the battery. In another specimen, *Lambeosaurus lambei* (N.M.C. No. 2869), the worn surfaces of the mandibular batteries measure 10 mm. longer than those of the complete maxillary batteries. In a second specimen of *Lambeosaurus lambei* (A.M.N.H. No. 5353), the lower left occlusal surface exceeds the length of the upper left surface by 15 mm. Here, too, the batteries in question are complete, and the worn surfaces extend the full length of the batteries. These are not significant dimensions, when compared with the total battery lengths, but such discrepancies in the lengths of opposing abraded surfaces could have resulted only from a forward and backward grinding action of the dental apparatus. Undoubtedly other specimens originally possessed similar discrepancies, but perfect preservation of complete grinding surfaces on opposing batteries is very rare.

Further evidence in the form of very slight longitudinal striations, which extend over much of the length of the occlusal surface, can be seen in the fine skull of *Anatosaurus annectens* (U.S.N.M. No. 3814). This cannot be considered as absolute proof of mandibular retraction and protraction, but it is most suggestive. Unfortunately, no other specimens exhibit similar longitudinal striations on the grinding surfaces in support of this single specimen.

Still another feature that seems to support a fore and aft mandibular movement and appears to rule out any significant degree of vertical shearing is the frequent shallow groove (described above) that runs the entire length of many lower occlusal surfaces. Such a groove can be explained only as a result of abrasion created by fore and aft motion (parallel to the groove) or by some type of rotational movement of the individual mandibles about longitudinal axes. Versluys (1922, 1923) strongly supported such a rotation of the mandible, primarily as an accessory movement to the depression and elevation of the lower jaws, although he also considered it

to be a helpful masticatory process.

Versluys suggested that each lower jaw rotated independently about the long axis of the mandible. He emphasized that such a rotational axis was situated below the occlusal surface. Such a position, however, would have resulted in a transverse convexity of the lower occlusal surface, as this surface would in effect move through the rotational arc or parallel to it, and the resulting abrasion must conform to the path of rotation. Instead, we find that most lower batteries show transversely concave occlusal surfaces, which indicates that any rotational axis must have been situated above, not below, the grinding surface. Such a position requires that either the upper jaws rotated on a longitudinal axis, which was mechanically quite impossible, or the lower jaw, instead of rotating on its own axis, swung from side to side about a longitudinal axis situated well above the mandible (as illustrated in fig. 69), an equally impossible condition. Versluys' rotational movement could not have created the transverse concavity of the lower dental surface, and the alternative rotational movements that might



FIG. 69. Cross-sectional diagram of the hadrosaurian dental apparatus (modified from Kripp, 1933), illustrating the erroneous mandibular rotation, similar to that suggested by Versluys, which would be required to create the known abrasion pattern of the hadrosaurian occlusal surfaces. The broken lines indicate the extreme mandibular positions, relative to the maxillary battery, as the mandible rotates about the upper battery (the rotational axis). The arrow indicates the arc of rotation required by this theory.

explain this abrasion feature are mechanically impossible. Therefore, it is concluded that only a fore and aft grinding action of the lower jaw could have created this longitudinal groove of the lower occlusal surface. The final evidence supporting this fore and aft motion of the lower jaws is found in the arrangement of the mandibular muscles, as is described above.

Mastication in the hadrosaurs is believed to have been chiefly by forward and backward displacement of the lower batteries against those of the maxillaries. Adduction or elevation of the mandibles, by contraction of the nearly vertical fibers of the large adductor externus and pseudotemporalis and to a lesser extent by the adductor posterior, brought the grinding surfaces of the opposing dental batteries together, while alternate contraction of the adductor posterior and pterygoideus muscles initiated the forward and backward grinding action.

While Versluys (1922, 1923) also proposed a similar fore and aft motion of the lower jaws (associated with a movable quadrate), he also strongly argued for a complex rotational

movement of each mandible about its long axis, as is noted above. Apparently, the chief basis for his argument was the unique form of the coronoid process and the nature of the symphysis, which he felt formed a relatively flexible union. The strong medial curvature of the coronoid process, with the resultant overhang of this process above the maxilla, led Versluys to conclude that this overhanging coronoid process prevented effective depression of the mandible. A lowering of the coronoid process, in his opinion, would have been obstructed by the lateral bulge of the maxilla. For this reason, he believed that the mouth could not have been opened wide enough for feeding unless some outward rotation of the jaws occurred, displacing the coronoid process laterally so that it was no longer impeded by the maxilla beneath. He suggested that the depressor mandibulae, together with the mylohyoideus and intermandibular muscles, brought about this outward rotation of the mandible when the mouth was opened. During the elevation of the mandibles, the pseudotemporalis initiated the reverse inward rotation of the lower jaw.

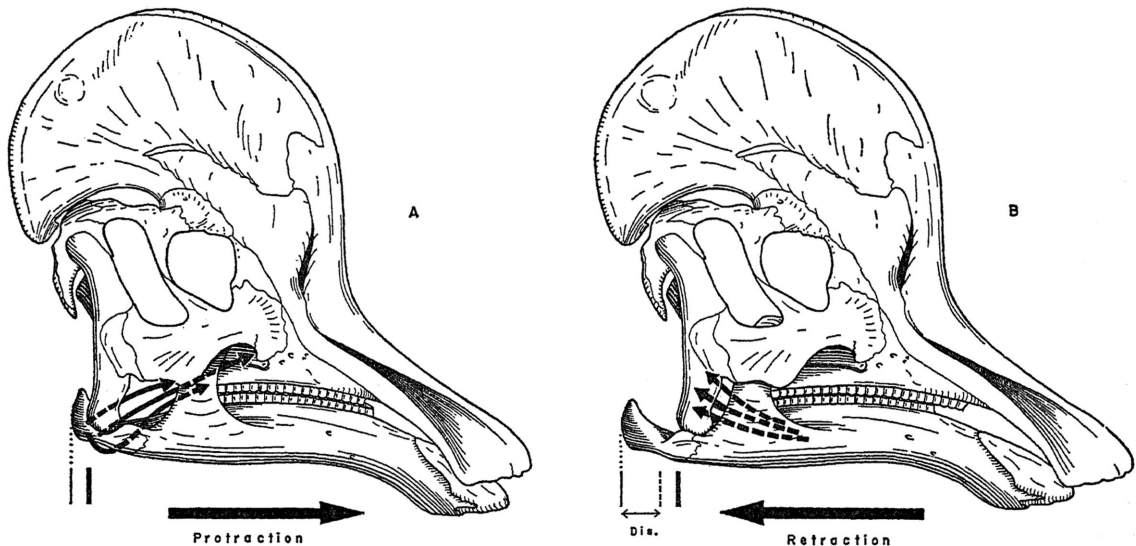


FIG. 70. Profile sketches of *Corythosaurus casuarius*, illustrating the author's concept of hadrosaurian mandibular movement. It is suggested that this was the primary masticating motion in this family. A. Protraction of the mandible. B. Retraction of the mandible. The heavy vertical lines indicate the position of the quadrate with respect to the extremity of the retroarticular process (the light vertical lines). In B the dashed vertical line indicates the position of the protracted retroarticular process. The short arrow (Dis.) indicates the approximate displacement of the mandible that was mechanically possible. The multiple arrows show the position and action of the protracting and retracting muscles, the pterygoideus and adductor posterior.

Versluys' solution pertains, however, to a non-existent mechanical problem. He failed to realize that the proximity of the coronoid process to the fulcrum (quadrate articulation) of the mandible meant that a slight depression of the lower jaws at the level of the coronoid process resulted in a much greater depression at the mandibular extremity. Using the mandibular dimensions of *Corythosaurus casuarius*, the present author proved that a displacement of 20 mm. at the level of the coronoid process, which appears to be a very conservative estimate of the vertical freedom at this point, created a gape of more than 135 mm. between the prementary and the premaxillaries. An even wider gape of the mouth is probable, although an extreme gape is not necessary in a herbivorous animal. Thus it appears that a rotation of the mandibles was not at all necessary in order to create an adequate gape of the hadrosaurian mouth.

The symphyseal region appears to have been far from firm, as Versluys has pointed out, but the enclosing prementary, together with its superficial horny beak, certainly added to the strength, if not also to the rigidity, of this union. It does not seem reasonable to assume any significant degree of rotational freedom between the mandibles and the enclosing prementary, in spite of Versluys' attempts to minimize the necessary degree of freedom here. Rotation of the mandibles was not necessary, as Versluys thought, and, except for the possibility of a slightly flexible symphyseal union, no evidence has been found which supports such mandibular rotation. In fact, as is noted above, the form of the abraded occlusal surfaces stands in opposition to this type of mandibular motion.

Kripp (1933), basing his interpretations on a mechanical analysis of *Edmontosaurus*, presented an excessively complicated hypothesis of hadrosaurian mastication, which also must be considered here. Kripp suggested that the hadrosaurian mandible rotated inward (rather than outward as Versluys maintained) about a longitudinal axis. At the same time the posterior portions of the rami were displaced laterally in order that the overhanging coronoid process could clear the maxilla during depression of the mandibles. Such simultaneous medial rotation and lateral displacement of the mandibles, ac-

cording to Kripp, were facilitated by peculiar motions of the quadrate, which involved a rotation of this bone about its long axis while apparently swinging in a transverse arc: pivoting laterally and medially while twisting in the squamosal "socket."

Kripp maintained that these motions were permitted by the lack of a strong symphyseal union of the rami and what he and Versluys describe as articular facets between the dentaries and the prementary, together with the "ball and socket" joint of the quadrate and squamosal, the "articular facets" between the quadrate and the jugal arch, the sloping articular surfaces of the mandibles, and the "weak junction" between the jugal and the postorbital which would have allowed the jugal arch to be pushed outward. Kripp also maintained that a pure fore and aft motion of the quadrate was impossible, with which the present author is in complete agreement. However, the author cannot agree with the theory of either mandibular rotation or lateral displacement of the quadrate and mandible proposed by Kripp.

The inward rotation of the mandible is opposed here on the same grounds that Versluys' outward rotation is opposed. The necessary freedom, particularly medial to the jugal arch, seems not to have existed, and the form of the abraded occlusal surfaces is inconsistent with this type of mandibular motion. The lateral displacement and rotation of the quadrate, if not obstructed by the jugal arch, which was in firm sutural union with the maxilla at least, would have been obstructed by the extensive squamous union with the pterygoid. The hadrosaurian quadrate and pterygoid are rarely displaced or separated from each other, a strong indication that a firm union probably existed between these two bones. Furthermore, the present author is not aware of any musculature that could have produced either the mandibular rotation or the complex quadrate motions as presented by Kripp.

The multiplication of teeth and the close spacing of adjacent tooth rows are obviously adaptations for more effective pulverizing or grinding of plant fibers. The grinding surface has been enlarged and united by the closer spacing of teeth to form a single, continuous, and elongate "milling" surface. Rapid attri-

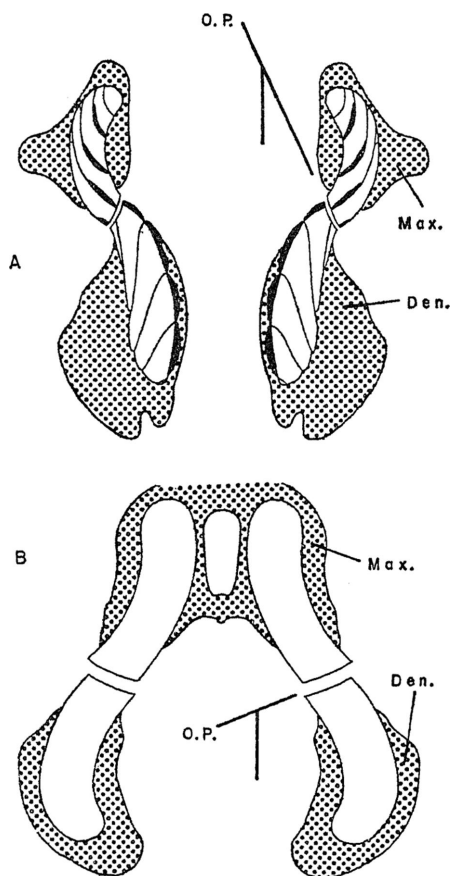


FIG. 71. Cross-sectional diagrams comparing the hadrosaurian upper and lower jaw relationship with that of a modern rodent. A. A hadrosaur. B. *Castor*. In addition to the pattern of tooth succession, notice the steep outward inclination of the occlusal plane in the hadrosaurs. In contrast, *Castor* (and many other herbivorous mammals) display an occlusal plane which slopes gently inward. Regardless of the alignment of opposing dentitions, the occlusal surfaces are directed at the opposing teeth. The steep outward inclination of the hadrosaurian occlusal surface is largely the result of the lateral position of the maxillary teeth as related to the mandibular dentition. The opposite is true of *Castor* and most mammalian herbivores. Abbreviations: Den., dentary; Max., maxilla; O.P., occlusal plane.

tion of the dentition by harsh substances has been compensated for by the highly effective replacement series, which incidentally has also broadened the functional grinding surface. Further widening of the occlusal surface was created by the inclined attitude of this

surface, which is oblique rather than perpendicular to the battery axis. This inclination of the grinding surfaces has resulted in a significant increase in the total grinding area of the dental batteries.

The inclination of the occlusal surfaces has resulted not from longitudinal rotation of the mandibles, as suggested by Versluys, but from the misalignment of opposing batteries and the differential wearing of the exposed teeth. The position of the enameled crowns of the mandibular teeth, forming the medial margin of the occlusal surface, resulted in the slower attrition of this inner margin, while more rapid abrasion occurred on the more lateral areas. This, together with the lateral position of the upper battery with respect to the lower dentition, further inhibited level or horizontal wear, because the abrasion of opposing surfaces tends to form a plane nearly perpendicular to the applied force or grinding pressure. Thus, with the upper batteries situated outside (as well as above) the mandibular batteries, the lower grinding surfaces were worn so they faced dorsolaterally towards the opposing teeth, as illustrated in figure 71A.

Examination of the dental apparatus of numerous herbivorous mammals, particularly rodents which are capable of a fore and aft grinding motion like that proposed for the hadrosaurs, demonstrates that most grinding surfaces are inclined to some degree. Horizontal occlusal surfaces are all characterized by vertical dental planes, i.e., the upper dentition lies vertically above the lower dentition. In every instance in which significant inclination of the occlusal plane exists, the opposing dentitions do not occupy a vertical plane. In rodents (*Castor* is a good example), the lower grinding surfaces are usually inclined medially, i.e., inward towards the upper dentition which lies medial to it. This condition, which is common in herbivorous mammals, provides an interesting and highly suggestive parallel to the hadrosaurian condition. The chief differences are that the lower surfaces of the latter are inclined outward towards the more laterally situated upper dentition, while in most mammalian herbivores the inclination is inward towards the more medially placed upper dentition. Also the angle of inclination is much steeper in the hadrosaurs, probably a

result of the extreme lateral position of the upper battery plus the greater resistance to abrasion of the medial margin of the mandibular battery and the lateral margin of the maxillary battery.

Thus the inclined hadrosaurian grinding surfaces are believed to have resulted from two separate conditions: the misalignment of the opposing batteries and the differential attrition of the dentition. The inclined occlusal plane probably was a functional adaptation, as similar conditions occur frequently in modern herbivores. In addition to expanding the total grinding area of the dentition and exposing successive replacement teeth before loss of the older functional teeth, the inclined occlusal surface also forms a relatively sharp medial edge on the lower battery (and a similar feature on the lateral margin of the upper battery). As these edges are oriented parallel to the principal grinding motion, they undoubtedly served as significant cutting edges and further increased the efficiency of the hadrosaurian dental apparatus.

The anterior third of the long upper and lower jaws became edentulous for two reasons. First, the development of a specialized beak for the gathering of food eliminated any need for marginal cropping teeth. Second, the great length of the jaws, with the adductor muscles inserted far back near the articulation, reduced the effectiveness of anteriorly placed grinding surfaces. The greatest adduction force, and therefore the most effective grinding pressures, was located towards the rear of the mouth near the fulcrum and the areas of attachment of the adductor muscles, as is pointed out above in the discussion of the mandibular lever. With increased leverage towards the rear of the mouth, a shift in the position of the dentition resulted. The grinding "mills" enlarged posteriorly, where the grinding forces were concentrated, and conversely became reduced and finally lost anteriorly, where grinding pressures were quite inadequate.

The posterior extension of the dental batteries resulted in still further modifications of the mandibles in the displacement of the coronoid process. In most instances, the reptilian coronoid process rises from the posterior dorsal margin of the mandible, usually

behind and in line with the tooth row. The caudal progression of the hadrosaurian batteries, however, required some displacement of this process from the normal position. A caudal displacement, behind the encroaching dental blocks, would have required extreme modification and increase in the size of the adductor muscles, for any shift of the coronoid process closer to the fulcrum would have decreased the leverage of the adductor muscles and thus their mechanical advantage. Therefore, a lateral displacement of the coronoid, the only other possibility, resulted, with the final development of the stout coronoid base rising from the lateral surface of the mandible, lateral to the posterior portion of the batteries. The strong medial curvature of the coronoid process simply relocated the dorsal tip of this process, with its insertions of the pseudotemporalis, back in the dental plane, maintaining the nearly vertical longitudinal plane of the adductor muscles and reducing any lateral component, and thus any rotational vector, of the pseudotemporalis. If rotation of the lower jaw had been important, as maintained by Versluys (1922, 1923), such a medial deflection of the coronoid process most certainly would not have developed, as a more laterally placed point of insertion of the "rotators" would have provided maximum leverage for the contracting fibers of the pseudotemporalis to act on, and thereby generate an inward rotation of, the lower jaw. The more medial position of the coronoid dorsal extremity has therefore reduced, not increased, the rotational leverage of the pseudotemporalis, which means that the rotational stability of the mandible has been increased. This medial deflection of the coronoid has accomplished just the opposite effect of that interpreted by Versluys.

The heavy form of the coronoid process is a necessary consequence of the great mandibular mass. Upon this process, with its lateral position, the greatest stresses were concentrated, and its large size and broad base insured maximum strength for the adductor attachments. The forward deflection of the coronoid is interpreted as an adaptation to increase the angle of force application during adduction. With the mandible in the depressed state, and the rostral inclination of the coronoid thereby increased, the angle

between the pseudotemporalis fibers and the coronoid shaft more closely approached a right angle, the angle of maximum leverage, which resulted in an increased adduction leverage for the *M. pseudotemporalis*, as in a bent lever.

The increased demands for efficient grinding of plant materials initiated still further modifications of the hadrosaurian skull in the form of a pronounced lengthening of the quadrate and an over-all increase in the height of the temporal region of the skull. This marked increase in skull height generated a significant lengthening of the adductor muscles, principally the adductor externus and the pseudotemporalis. Such increased

fiber length permitted a greater total amount of contraction and therefore a greater total displacement of the mandible during depression and elevation. The greater fiber length, and therefore the larger muscle mass, must have resulted in increased grinding pressures between the upper and lower batteries. Generally speaking, short muscular fibers exert greater stresses than do long fibers, but, where displacement must be great, an increase in the muscle mass as the fiber length is increased will maintain or even increase the contractile forces. The increased height of the temporal region may therefore be correlated with increased mandibular displacement and perhaps with increased adductive pressure.

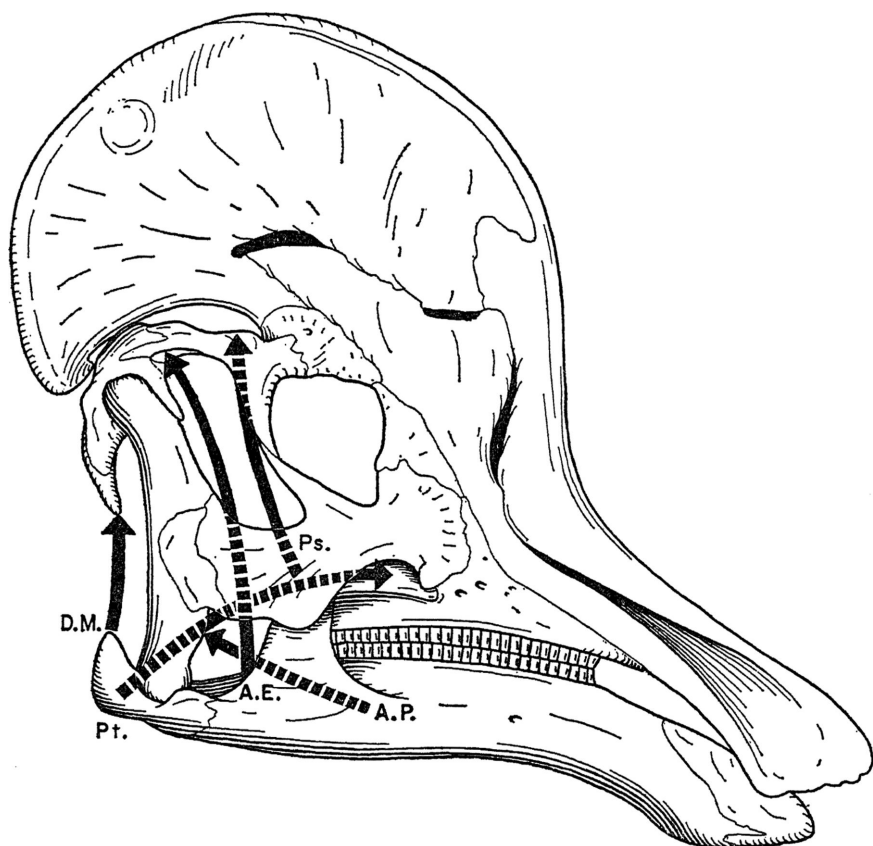


FIG. 72. Diagrammatic profile of *Corythosaurus casuarius*, illustrating the location and action of the major cranial muscles (arrows). Segmented portions of the arrows indicate the passage of these muscles beneath superficial bones of the skull. Abbreviations: A.E., *M. adductor mandibulae externus*; A.P., *M. adductor mandibulae posterior*; D.M., *M. depressor mandibulae*; Ps., *M. pseudotemporalis* of the *M. adductor mandibulae internus*; Pt., *M. pterygoideus* of the *M. adductor mandibulae internus*.



Also associated with increased grinding efficiency was the lowered position of the quadrate-mandibular articulation well below the occlusal plane. This lowering of the fulcrum allowed the opposing grinding surfaces to approach each other in a more nearly parallel fashion, so that anterior and posterior segments of one grinding surface met those of the opposing surface almost simultaneously, thereby insuring the maximum possible area of simultaneously functional grinding surface. With this adaptation the entire grinding surface length became functional. Similar adaptations are well known in numerous herbivorous animals. This adaptation is quite distinct from the usual carnivorous one in which shearing is important and simultaneous occlusion of all points along the dentition is undesirable. In this case, the fulcrum lies within the occlusal plane, creating a scissors type of occlusion and maximum shearing action on adduction of the lower jaw.

### INTRACRANIAL MOBILITY

#### KINETICISM

An examination of the hadrosaurian skull material demonstrates quite conclusively that these forms were akinetic. At every junction of the neurocranial and maxillary segments, there exists a completely coalesced or very strong sutural union which appears to have been completely or very largely inflexible. The skull roof is firmly united at every juncture from the supraoccipital to the premaxillaries, forming an inflexible connection between the neurocranial and maxillary segments. A posterior union of these segments is established by the squamosals, which lie cap-like over the posterior part of the neurocranial segment. While most specimens display a relatively loose connection between this bone and the underlying exoccipital and paroccipital process, ventromedially it appears to be firmly united by complex digitate sutures with the supraoccipital and parietals, and laterally the squamosal joins the rear process of the postorbital in a strong squamous union.

Gilmore (1937), however, has described a strange, double, condylar articulation between the squamosals and the supraoccipital which deserves some attention here. (See

Finally, maximum grinding efficiency and full utilization of the dental "mills" were effected by a shifting of the mandibular muscle pattern. (See fig. 72.) First, the levators, or adductor muscles, in addition to increasing their length, assumed a more steeply inclined orientation, by which maximum leverage could be exerted almost perpendicular to the grinding surfaces. Second, the adductor posterior was expanded and depressed somewhat in its inclination to act as a powerful mandibular retractor. Third, the pterygoideus was greatly lengthened, through a more forward location of the origin, expanded, and oriented nearly horizontally to provide powerful protractive stresses against the mandible. These adaptations have all contributed to the formation of a most highly effective herbivorous grinding mechanism in the hadrosaurs, a condition that is quite unusual among reptiles.

fig. 73.) His comments (1937, p. 483), "this is a most unusual cranial articulation that gives every indication of being a movable union, although the other articulating surfaces of both the squamosal and supraoccipital are through the medium of roughened sutural contacts," fail to establish either the mobility or immobility of this junction, but his succeeding statement suggests that he favored its immobility, at least in the adult stage. He notes that through coalescence no trace of this ball and socket union has been observed before in members of the Hadrosauridae. The fact that most well-preserved crania appear to be firmly united at this point and that no other similar articulations are exposed in existing hadrosaur material suggests that any mobility of this articulation probably existed only in the juvenile stages, which implies that a meta-kinetic condition existed early in hadrosaurian ontogeny, with a subsequent fusion and loss of mobility with the continued growth of the individual. Such an implication is not at all improbable, in view of the high degree of cranial mobility exhibited in the juvenile forms of certain modern akinetic reptiles (i.e., the Crocodilia). The possibility supports

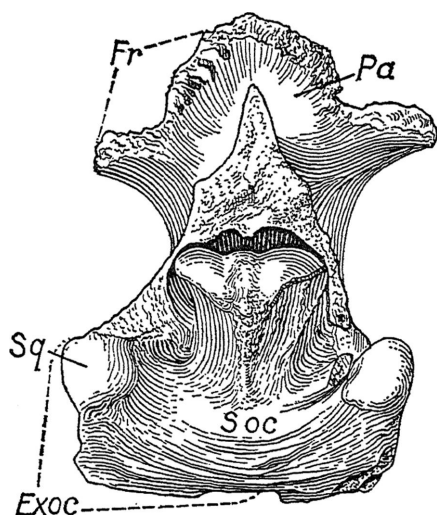


FIG. 73. Posterior view of the parietal (lacking the posterior end) and supraoccipital of a fragmentary hadrosaurian cranium, U.S.N.M. No. 11893. (From Gilmore, 1937, fig. 29.) Notice the peculiar posterolateral condyles which appear to have articulated with the ventromedial surfaces of the squamosals. *Abbreviations:* Exoc., sutural border for the exoccipital; Fr., sutural border for the frontal; Pa., parietal; Soc., supraoccipital; Sq., articular condyle for articulation with the squamosal.

Versluys' position (1910, 1912) that the kinetic (metakinetic) condition is primitive and that the akinetic state is a secondary condition.

More anteriorly, another union between the neurocranial and maxillary segments occurs between the postorbital and frontal and between the prefrontal and frontal and nasal. Each union here is marked by a strongly digitate or squamous contact, which appears to be completely immobile. The postorbitals, therefore, which are firmly and immovably joined with the squamosals behind, are also immovably united with the frontals, or frontals and prefrontals, anteriorly. These conditions appear to preclude any mobility of the squamosal with respect to the brain case, at least in the adult stage, and therefore eliminate the possibility of kinetic mobility between the neurocranial and maxillary segments at these points.

Although very few specimens illustrate adequately the nature of the internal con-

tacts between the neurocranial and maxillary segments, the maxilla, palatine, ectopterygoid, and vomer all appear to have been firmly united with the premaxillaries and nasals, which in turn are firmly united with the solid and inflexible skull roof. Aside from these superficial and indirect contacts with the neurocranial segment, the pterygoids provided more medial and ventral contacts between the two cranial segments. The complexly shaped pterygoid articulates with the basisphenoid process of the neurocranial segment ventromedially, and the palatine, maxilla, ectopterygoid, and possibly the vomer of the maxillary segment anteriorly, as well as with the quadrate posteriorly. Thus the pterygoid occupies a very strategic position intermediate between the two segments, and its mobility is a critical factor in permitting or obstructing cranial kineticism.

With the exception of the pterygoid-quadrate contact, none of the contacts mentioned above is very extensive, nor could they be described as unquestionably firm sutural unions. In the disarticulated skull of *Edmontosaurus regalis* (N.M.C. No. 2289) these have the form of relatively small, roughened surfaces which probably were united by cartilage and connective tissue. Some movement very well may have been possible at one time, at one or more of these points, but the few specimens in which these contacts are visible do not indicate any extensive motion. The pterygoid-quadrate contact, on the other hand, is formed by the junction of very broad and somewhat roughened surfaces. Some sliding movement may have occurred between these two broad processes but appears most improbable. No distinct articular facets are known here or elsewhere in the hadrosaurian skull, with the exception of the head of the quadrate and Gilmore's peculiar supraoccipital condyles. From the very inadequate material available, it appears probable that the hadrosaurs were entirely akinetic. The skull appears incapable of elevation or depression of the maxillary segment with respect to the neurocranium, certainly not an unexpected condition in such highly specialized herbivorous animals as the hadrosaurs, for kineticism is almost exclusively characteristic of highly predaceous varieties, as Versluys (1910, 1912) so clearly demonstrated.

## STREPTOSTYLISM

Streptostylism or quadrate mobility, on the other hand, is quite another problem in the hadrosaurs. Stannius (1856) first noted that the quadrate may be movable relative to neighboring bones, particularly with respect to the squamosal. The term "streptostylism," which he applied to this phenomenon, usually involves an additional mobility relative to the brain case, of the whole upper jaw or maxillary segment, this motion being imparted to it by the movable quadrate. Such additional movement is considered above and determined to be absent in the hadrosaurs. The streptostylic or monimostylic condition of the hadrosaurian quadrate, however, has not as yet been resolved.

Marsh (1893, pp. 84, 85) described the quadrate of *Claosaurus* as follows: "It is firmly supported above by the squamosal, but its distinct rounded head indicates the possibility of some motion." Nopcsa (1900), in his discussion of *Orthomerus* (*Telmatosaurus*), also noted the condylar nature of the quadrate-squamosal junction and concluded that the quadrate was quite free to move with a forward and backward motion. He considered the other contacts between the quadrate and the pterygoid and the quadrate and the lower temporal arch as loose contacts that failed to inhibit quadrate movement. Versluys (1910) was of the opinion that all hadrosaurs were akinetic and monimostylic, although he apparently accepted Nopcsa's conclusions about *Orthomerus* as an exceptional case of hadrosaurian streptostylism. In 1923, however, Versluys strongly supported a streptostylic condition for the hadrosaurian quadrate. This, he believed, under the influence of Nopcsa's works, was a major factor in the fore and aft motion of the lower jaws.

Among the leading opponents of hadrosaurian streptostylism was Lambe. In his detailed study of *Edmontosaurus* (1920), he noted that the head of the quadrate fitted immovably into the pit of the squamosal. "There can be no doubt that it was firmly fixed in position and immovable in the genus now under description. The fact that a heavy process from the squamosal descended for some distance on and suturally united with the anterior border of the quadrate below its head is sufficient to prove that the quadrate

was stable at its upper end. The very extensive lapping contact, between the quadrate and the pterygoid would in itself be sufficient to prevent any movement of the former element" (Lambe, 1920, p. 32). Kripp (1933) believed that fore and aft quadrate mobility was restricted, but he accepted a lateral or transverse mobility as well as a rotational movement of the quadrate about its long axis. The most recent comments on this subject were expressed by Lull and Wright (1942, pp. 57-59), but, while they have acknowledged some evidence of quadrate movement, they failed to come to any conclusion.

From all these remarks, the hadrosaurian quadrate presents all appearances of being quite mobile. The smooth, rounded cotylus of the squamosal and the rounded head of the quadrate are very suggestive of a diarthrodial joint. However, detailed examinations of this junction, of the mechanical relationships between the quadrate and other adjacent bones, and of the dynamics of a movable quadrate have led the author to conclude that the hadrosaurian quadrate was quite stable and immovable.

If it be accepted for the moment that the quadrate-squamosal contact could have permitted movement of the former, before such movement can be accepted as fact it is imperative that the other bony contacts with the quadrate be very closely examined, for the adjacent elements determine the degree, if any, of quadrate mobility. First, the pre-quadratic process of the squamosal projects ventrally from the anterior margin of the squamosal cavity. It is closely applied in nearly all specimens to the upper anterior surface of the quadrate over a considerable distance (approximately 60 mm. in *Edmontosaurus regalis*, N.M.C. No. 2289, and nearly 50 mm. in *Corythosaurus casuarius*, A.M.N.H. No. 5338). Lambe (1920) noted a sutural union between this squamosal process and the quadrate, as is noted above. A post-quadratic process of the squamosal is also present in all hadrosaurs, but normally this is closely applied against the ventro-anterior margin of the paroccipital process and appears not to have restricted the quadrate posteriorly in any significant way. Here, then, we find a restricting contact anteriorly but not posteriorly.

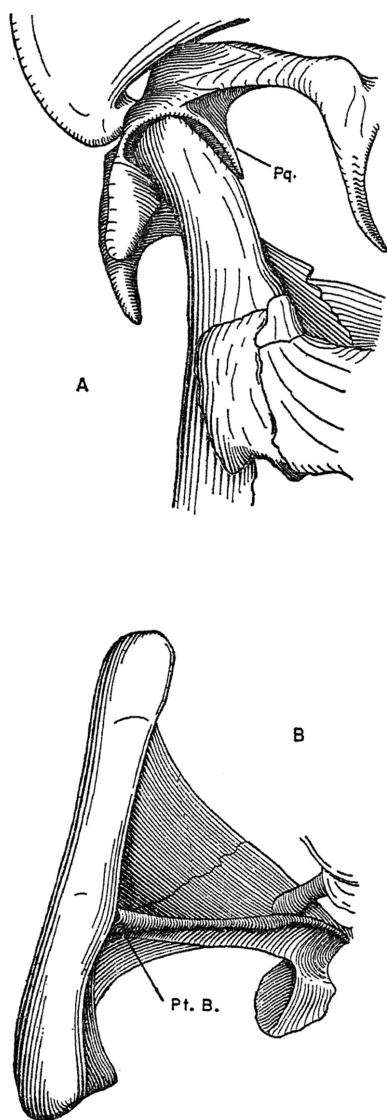


FIG. 74. Cranial structures that promoted monimostyly of the hadrosaurian quadrate. A. The right quadrate of *Corythosaurus casuarius*, A.M.N.H. No. 5338, showing the anterior contact with the jugal arch and the close proximity of the prequadratic process (Pq) of the squamosal. B. The left quadrate and pterygoid of *Procheneosaurus erectofrons*, A.M.N.H. No. 5461, viewed from behind. This specimen shows the pterygoid buttress (Pt. B.) which butted against the medial flange of the quadrate shaft.

More obvious is the superficial junction of the quadrate and the elements of the lower temporal arch: specifically the quadratojugal

and jugal. Much has been said about this structure, usually to the effect that for such large animals it is a relatively weak arch. No firm sutural union has been found between the quadrate and the quadratojugal, although the latter seems to be solidly joined with the jugal. Certainly the union of the jugal with the maxilla permitted no movement. Nopcsa (1900) suggested that some bending of this arch took place, thus absorbing any forward displacement of the quadrate. As noted by Lull and Wright (1942), the quadrate meets the lower arch in an end to end contact, with only slight lateral overlap. This, together with the thin but solid nature of the arch, again seems to preclude any forward displacement of the quadrate, as well as any transverse displacement as suggested by Kripp (1933).

Quite different are the rather complex contacts of the pterygoid with the quadrate. The thin but very broad pterygoid process of the quadrate extends forward and medially. Its posteromedial surface is extensively overlapped and quite firmly united with the equally broad quadrate process of the pterygoid. It appears impossible that this overlapping contact allowed any sliding movement. Lambe (1920) was quite firm in his belief that this union was solid and immovable. In addition, a unique feature associated with this contact has been developed in the hadrosaurs apparently for the sole purpose of restricting any quadrate movement. The thin alar process of the pterygoid is strengthened by a thickened ridge extending posteriorly along its medial surface. As a stout bar of this quadrate process, it projects caudally and laterally to an enlarged terminus which butts against the medially projecting flange of the posteromedial surface of the quadrate shaft (see fig. 74B). Had any sliding been possible between the alar processes of the quadrate and pterygoid, this buttressing of the quadrate shaft posteriorly would have restricted the amount of forward displacement. To the best of my knowledge, this feature is unique to the hadrosaurs. Its form suggests that it functioned as a stabilizing element, to insure the stability of the quadrate.

In spite of the diarthrodial appearance of the quadrate-squamosal junction, it is evident that the contacts between the quadrate and

adjacent bony elements were of a restricting or stabilizing nature, particularly with respect to forward displacement of the quadrate. Functionally, such a condition is the only acceptable one. Conclusive evidence is presented above for a fore and aft motion of the lower jaw, which certainly was accomplished in the main by a sliding of the mandibular articular surface past the distal head of the quadrate, not by a fore and aft pivoting of the quadrate.

While Versluys (1923) has argued that this fore and aft motion of the lower jaw was initiated by or related to a fore and aft pivoting of the quadrate in the squamosal cavity, such a condition appears quite improbable and most ineffective, in spite of the fact that pivoting of the quadrate in a longitudinal plane would have increased the total amount of fore and aft mandibular movement. No evidence has been found of a muscle arrangement that could have generated such a motion of the quadrate and the longitudinal movement of the mandible which presumably resulted. On the contrary, however, evidence exists of the necessary muscle patterns for protraction and retraction of the mandible against a stationary quadrate. This muscle pattern, which is reconstructed above, provides a powerful and efficient system for longitudinal mandibular movement *only* if the quadrate remained fixed.

A retraction of the mandible, effected by the contraction of the adductor posterior, required that the quadrate should not be displaced. Had quadrate mobility been possible, contraction of these fibers would have pulled the quadrate forward, rather than have retracted the lower jaw. Thus the fore and aft motion of the lower batteries against the maxillary batteries would have been minimized and the effectiveness of this grinding mechanism greatly reduced. Mandible protraction would not have been so seriously affected by a movable quadrate, although the contraction of the large pterygoideus certainly would have created some frictional stresses against the distal end of the quadrate. Such stresses undoubtedly would have tended to displace the quadrate forward along with the mandible.

The inhibiting structures associated with the quadrate, the prequadratic process, the

lower temporal arch, the extensive quadrate-ptyergoid union, and the posterior buttress or shaft of the pterygoid all seem to have restricted anterior displacement of the quadrate. Furthermore, the efficient operation of mandibular protraction and retraction required the prevention of forward displacement of the quadrate. Complete consideration of hadrosaurian streptostylism, however, requires the reconsideration of two facts mentioned, or implied, above. The first, that quadrate mobility could have increased the total distance of horizontal mandible displacement, need not be considered at length, for it is already obvious that mandibular displacement was possible without quadrate mobility. Also, a great displacement is not necessary, because even a relatively short fore and aft movement is quite effective, and increasing the total amount of displacement would not increase the efficiency of the grinding action, particularly in the hadrosaurs, in which the quadrate provided the leverage for the retracting fibers. The second point is that while significant structures existed to prevent or restrict forward displacement of the quadrate, none appears to have existed for the purpose of preventing a caudal displacement of this bone. If complete rigidity of the quadrate was advantageous, such a deficiency seems quite critical to the soundness of the monimostylic condition here proposed. The question arises, Could the quadrate move backward away from the lower arch, perhaps to increase the ultimate retraction of the mandible? If so, how was this movement generated?

None of the other adductor muscles, neither the adductor externus nor the adductor internus, could have initiated this movement. Nor does it seem likely that the depressor mandibulae, acting against the retroarticular process, could have accomplished it. The only possibility seems to rest with the constrictor dorsalis muscles, of which no evidence could be found. Mechanically it seems possible that a retractor pterygoidei, acting on the pterygoid, could have forced the hadrosaurian quadrate back away from the lower temporal arch against the contraction of the adductor posterior fibers. But for what purpose? Greater mandibular retraction was not necessary.

If such activities occurred in the hadrosaurs, they are certainly unique among herbivorous tetrapods. The adaptation of the constrictor dorsalis series for the protraction and retraction of the lower jaw, rather than the elevation and depression of the upper jaw, is completely new. At present, the problem cannot be completely solved, but certain evidence seems to rule against hadrosaurian streptostylism. First, the contacts between the pterygoid and adjacent bones seem to have permitted no significant movement of the pterygoid. In fact, the pterygoid appears to have been immobile, although the typical reptilian basipterygoid process still exists. Second, no evidence has been observed that indicates the presence of a powerful retractor pterygoidei. Third, except for the cotylus of the squamosal, the contacts of the quadrate with adjacent bones appear to have restricted rather than promoted quadrate mobility. Finally, the most efficient operation of the mandibular protractors (the pterygoideus) and retractors (the adductor posterior) required the complete immobility of the hadrosaurian quadrate.

It seems very probable that a streptostylic condition existed within the hadrosaurian ancestry, but with the cranial modifications that accompanied the adaptive shift to a herbivorous habit, and especially to the hadrosaurian type of mastication, the quadrate became quite immovable and thus monostylic. To insure this immobility, the quadrate became buttressed effectively by its contacts with adjacent bones, but only to prevent any forward movements of the quadrate. It was not necessary for it to be buttressed against posterior displacement, for with the loss of the kinetic condition, together with the constrictor dorsalis muscles, no posterior displacement could be achieved. Both protraction and retraction of the mandible tended to move the quadrate forward but not backward. The stresses created by this grinding action always acted to displace the quadrate anteriorly. Thus the quadrate became reënforced against such displacement, because its prevention was critical for the effective retraction and protraction of the hadrosaurian mandible.

## PHYLOGENY

THE IMMEDIATE ANCESTRAL STOCK of the hadrosaurs is not known, although, for a number of years, that they were probably derived from a camptosaurus-like ornithomimid has been generally accepted. Evidently the iguanodonts of the Morrison and Wealdon are rather closely related to these late Cretaceous ornithomimids. Unfortunately the early Cretaceous has as yet produced no evidence that substantiates such an opinion, but possibly light will be shed on the problem by future explorations of the non-marine facies of the Kootenai, Cloverly, Thermopolis, Bear River, and Frontier formations of Montana and Wyoming. *Camptosaurus*, while definitely more primitive than the typical hadrosaurs, exhibits many features that appear to be precursors of the more advanced hadrosaurian conditions. The scope of the present study does not permit a detailed comparison of camptosaurian and hadrosaurian characteristics, but a brief résumé of the more salient features seems advisable.

As were the hadrosaurs, *Camptosaurus* was a bipedal, herbivorous ornithomimid, but unlike the Cretaceous forms, it was not characterized by special adaptations for feeding and aquatic activities. The camptosaurian skull is long and low, almost rectangular in lateral aspect, and is quite similar in its organization to the general hadrosaurian plan (see fig. 75A). The chief differences lie in the nearly horizontal snout, the wedge-shaped muzzle, the shorter edentulous portions of the jaws, the lower occiput, and the incipient dental batteries of *Camptosaurus*, as contrasted with the steeply sloping snout, the laterally inflated muzzle, the long edentulous portions of the jaws, the high occiput, and the highly developed dental batteries of the hadrosaurs. In addition, of course, some hadrosaurs display the highly varied supracranial modifications involving the premaxillaries and nasals. The camptosaurid dental apparatus is particularly suggestive of the hadrosaurian condition and forms an ideal structural prototype. Although not arranged in true dental batteries, the camptosaurid teeth are arranged in a number of transverse rows, each of which is composed of several

teeth of which more than one may be functional. The superficial or oldest teeth of every alternate row are the principal functional teeth, and these are arranged in a single longitudinal row flanked by the replacement teeth medially. Adjacent non-functional rows acted as reserves which became functional with the loss of the functional teeth in adjacent series. Other similarities are found in the postcranial skeleton in which the vertebral column (except for the shorter neural spines and the somewhat shorter hemapophyses of the caudals) and the forelimbs and hind limbs are very hadrosaur-like. In the pelvis, the longer postpubis and the slightly greater curvature of the ischium are the only significant deviations from the typical hadrosaurian condition.

When these and the many other structural similarities involved are considered, that *Camptosaurus*, or some very similar mid-Mesozoic iguanodont was the original ornithomimid progenitor of the Hadrosauridae is probable. Paleontologic proof is so far lacking from the Mesozoic sequence of North America, but the earliest known hadrosaur, *Claosaurus* from the Niobrara chalk, provides additional evidence of such relationship. First, only *Claosaurus*, of all the hadrosaurs, retains a vestige of the first metatarsal as does *Camptosaurus*. Most interesting of all, however, is the very strong resemblance between the teeth of *Claosaurus* and those of *Camptosaurus*, as illustrated in figure 76. In both genera the enameled crown is restricted to one side of the tooth (the lateral side of the maxillary teeth and the lingual side of the dentary teeth), as in all hadrosaurs. In both forms, the crowns are leaf-shaped, with rounded apices and strongly serrated margins. The crowns are also sculptured by a strong vertical ridge which nearly bisects the crown, as in typical hadrosaurian teeth. But unlike the hadrosaurs, additional secondary ridges are also developed on both sides of the primary ridge in the teeth of *Camptosaurus*. Although *Claosaurus* is definitely a hadrosaur, the teeth, with their serrated margins, more closely resemble camptosaurian teeth than they do hadrosaurian teeth. These

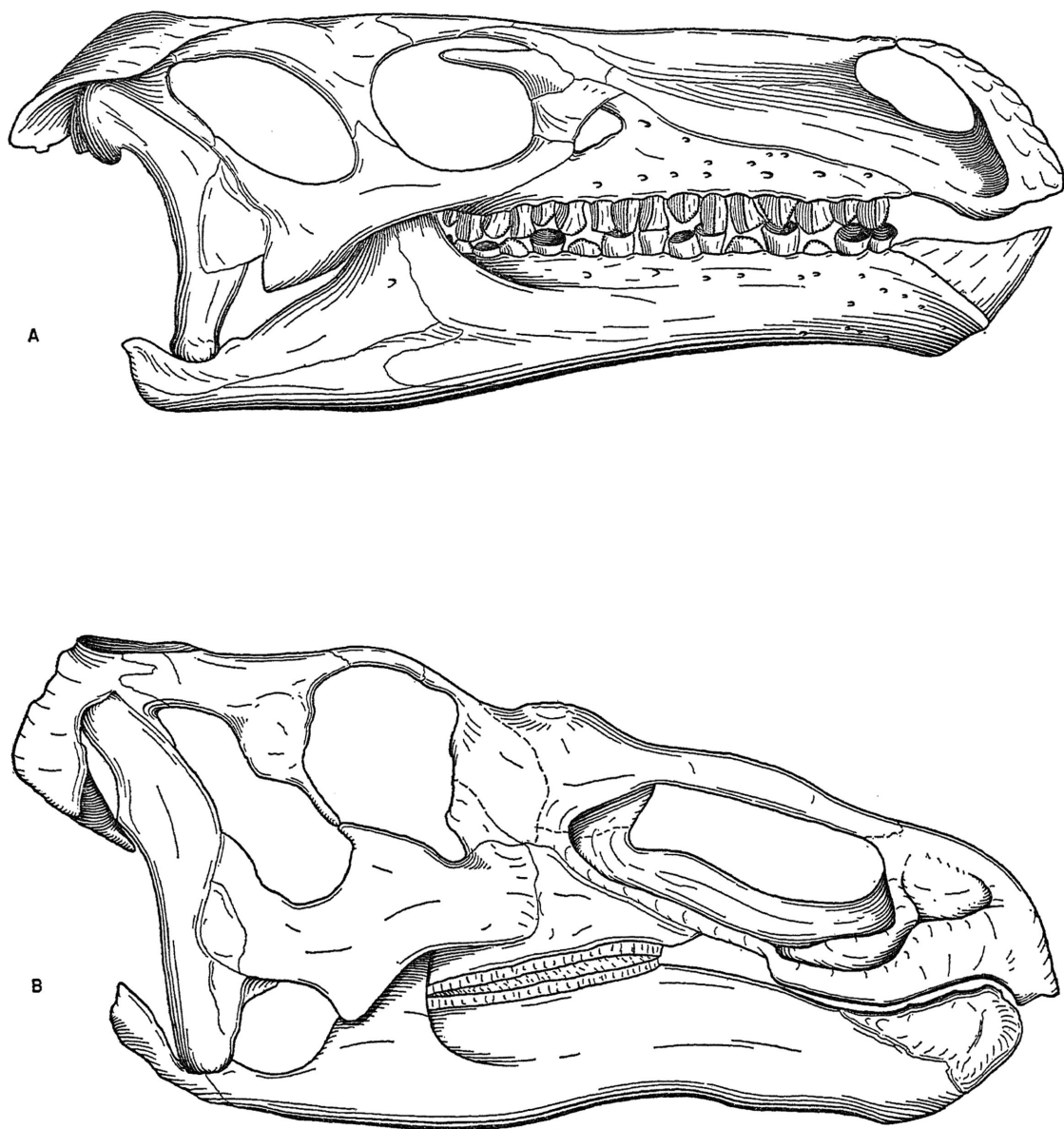


FIG. 75. A. *Camptosaurus* skull in lateral view. (Composite restoration from Gilmore, 1909.)  $\times \frac{1}{3}$ . This may represent the ancestral form that gave rise to the hadrosaurs. B. Lateral view of the skull of *Anatosaurus edmontoni*, N.M.C. No. 8399, which as an unspecialized hadrosaur may represent a conservative descendant from camptosaurian stock.  $\times \frac{1}{3}$ .

similarities between *Camptosaurus* and *Clasaurus* are suggestive, in view of the general camptosaurid-like morphology of the hadrosaurs, and appear to substantiate a close relationship between these two genera.

The precise phylogenetic position of *Clasaurus* cannot be determined in the absence

of significant cranial material, but its stratigraphic position, its postcranial anatomy, and its camptosaurid-like dentition indicate that it may be the most primitive representative of the Hadrosauridae and perhaps represents a transitional form derived from *Camptosaurus*.



By Belly River time, the earliest interval from which we have adequate hadrosaurian remains, the hadrosaurian stem had already split into at least three distinct phyla: the conservative Hadrosaurinae, the intermediate Saurolophinae, and the highly varied and specialized Lambeosaurinae. The paucity of the pre-Belly River hadrosaurian record prohibits an accurate evaluation of this early hadrosaurian divergence, but for many years the flat-headed Hadrosaurinae have been considered the conservative, centralized, hadrosaurian line, with the bizarre Lambeosaurinae and Saurolophinae recognized as early divergents from the central stock. Without more information about the "proto-hadrosaurian" varieties, the question can hardly be settled and is still open to debate.

If only the cranial morphology be considered (there is relatively little significant variation in the postcranial anatomy), three distinct evolutionary trends are apparent within the Hadrosauridae: (1) the development of normal (non-crested) skulls; (2) the development of true narial crests; and (3) the development of pseudo-narial crests.

The normal or non-crested line, classically considered as the most primitive trend and presumed to represent the continuation of the conservative characteristics of the campylosaurid condition, involves the three hadrosaurine genera. This lineage is first recog-

nized with the occurrence of *Kritosaurus* (*K. notabilis*) in the Belly River, although *Claosaurus agilis* may represent an older, more primitive member of this line, and is terminated by the four species of *Anatosaurus* (*A. annectens*, *A. copei*, *A. saskatchewanensis*, and *A. longiceps*). *Kritosaurus navajovius*, *Edmontosaurus regalis*, and *Anatosaurus edmontoni* are the only reliably flat-headed species currently known from the intervening Edmontonian interval. While not so spectacular and not nearly so diversified as the lambeosaurs, the non-crested hadrosaurian line had the longest duration of any hadrosaurian trend, from Belly River to Lance times.

As noted elsewhere, the most characteristic hadrosaurian trend is illustrated by the Lambeosaurinae with their highly developed narial crests. The various members of this line are characterized by varying degrees of posterior prolongation of the premaxillaries and recession of the nasals. These elements formed a variety of supracranial crests which enclosed either simple or complex narial passages, and for this reason have been referred to throughout this report as the true narial crests. The evolutionary trend that resulted in the development of these narial crests enjoyed its greatest success during the Belly River interval when lambeosaurian species greatly outnumbered all other hadrosaurian varieties (13 lambeosaurian species are cur-

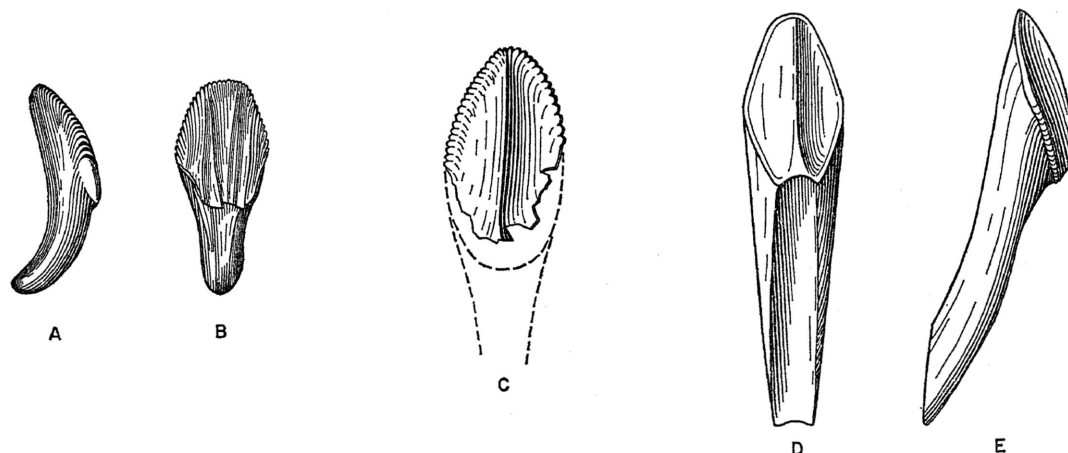


FIG. 76. Individual dentary teeth. A, B. *Camptosaurus medius*, Y.P.M. No. 1880.  $\times 1$ . C. *Claosaurus agilis*, Y.P.M. No. 1190.  $\times 2$ . D, E. *Anatosaurus annectens*, U.S.N.M. No. 2414.  $\times 1$ . A and E, anterior views; B, C, and D, lingual views. The *Claosaurus* tooth, while hadrosaurian, is strongly campylosaurid-like.

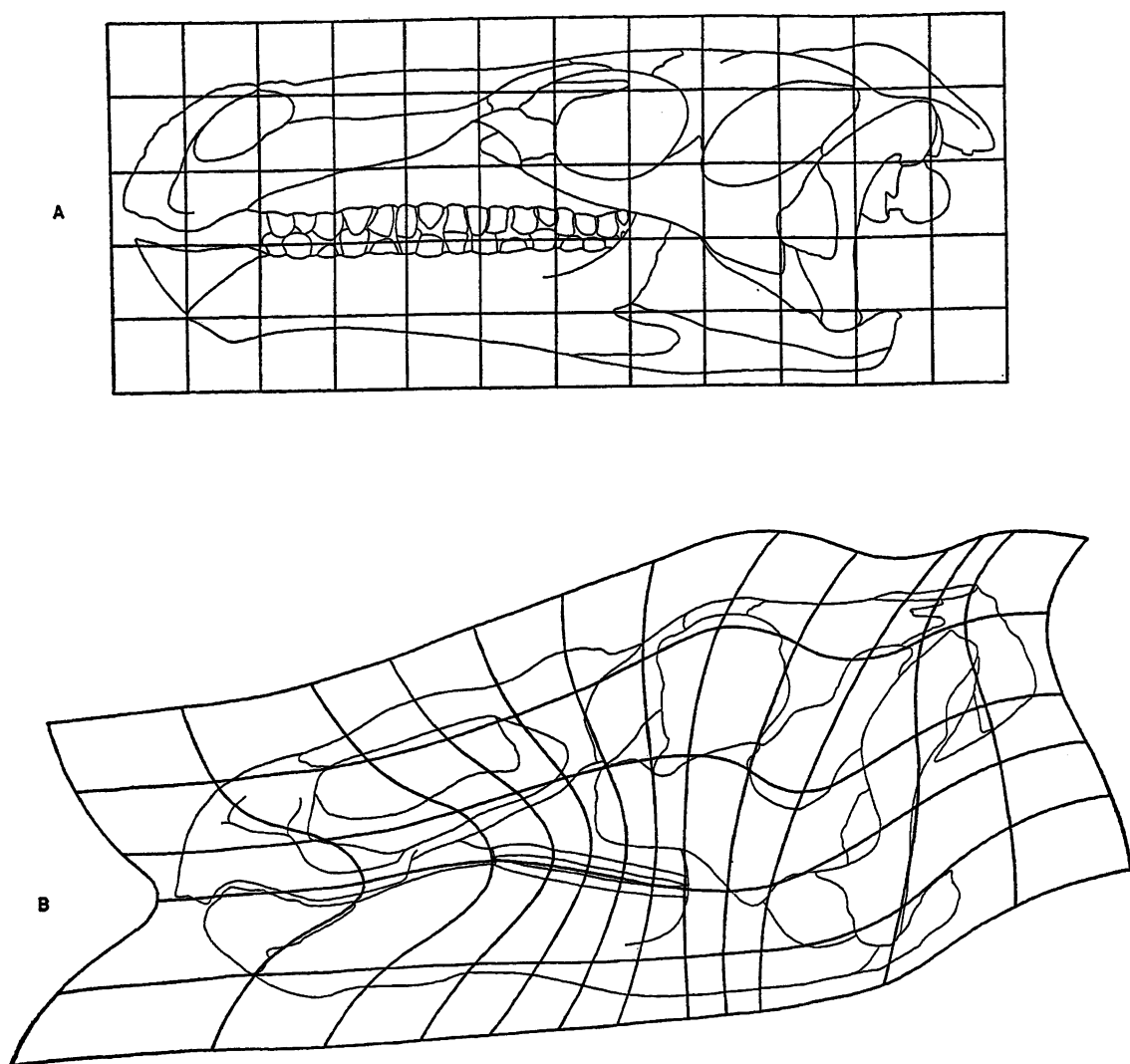


FIG. 77. Cartesian coordinate diagram for *Anatosaurus edmontoni* (B) based on *Camptosaurus* (A). *Anatosaurus edmontoni*, N.M.C. No. 8399, was used in this diagram as a conservative member of the Hadrosauridae, in the absence of any adequate cranial material of *Claosaurus*.

rently recognized from the Belly River and its equivalents, as compared with a total of four or five species of the Hadrosaurinae and Saurolophinae). The Edmonton interval, on the other hand, saw an almost complete reduction of this lineage, and the Lambeosaurinae appear to have been close to extinction by the beginning of the Lance interval.

The central lambeosaurian stock appears to have been represented by the numerous species of *Lambeosaurus* and *Corythosaurus*. In both genera, the premaxillaries are prolonged dorsocaudally and, together with the

posteriorly displaced nasals, form a high and frequently long, thin, blade-like crest overlying the postorbital region of the skull. Enclosed within this structure are the looped and pocketed narial tracts. While no Edmonton derivative of *Lambeosaurus* has been recognized as yet, *Hypacrosaurus* appears to have been derived from some corythosaurian species, probably *C. casuarius*.

The *Procheneosaurus-Cheneosaurus* line seems to represent the most conservative of the lambeosaurian trends, although it may constitute a relict lineage of the Lambeosau-

rinae ancestral stock. *Procheneosaurus*, represented by three species from the Belly River, and its successor *Cheneosaurus tolmanensis* from the Edmonton, are characterized by relatively small and perhaps incipient crests, which undoubtedly would be considered as the ancestral lambeosaurian prototypes if they occurred in pre-Belly River strata. As they are contemporaneous with the *Corythosaurus-Hypacrosaurus* sequence, they can be considered only as a slightly divergent lambeosaurian lineage.

The most extreme of the lambeosaurian trends is formed by the several species of

*Parasaurolophus*. *Parasaurolophus walkeri* of the Belly River and *P. tubicen* of the Ojo Alamo constitute the opposite end members of this lineage, with a third species, *P. cyrtocristatus*, characterized by a much shorter and more strongly recurved crest, occurring in the intermediate Fruitland formation of New Mexico. In this lineage, the narial crest is formed almost entirely of the premaxillaries, and the nasals contribute only slightly to the posterior half of the crest base immediately anterior to the frontals. These very long, arc-shaped premaxillaries completely enclose the tightly looped narial pas-

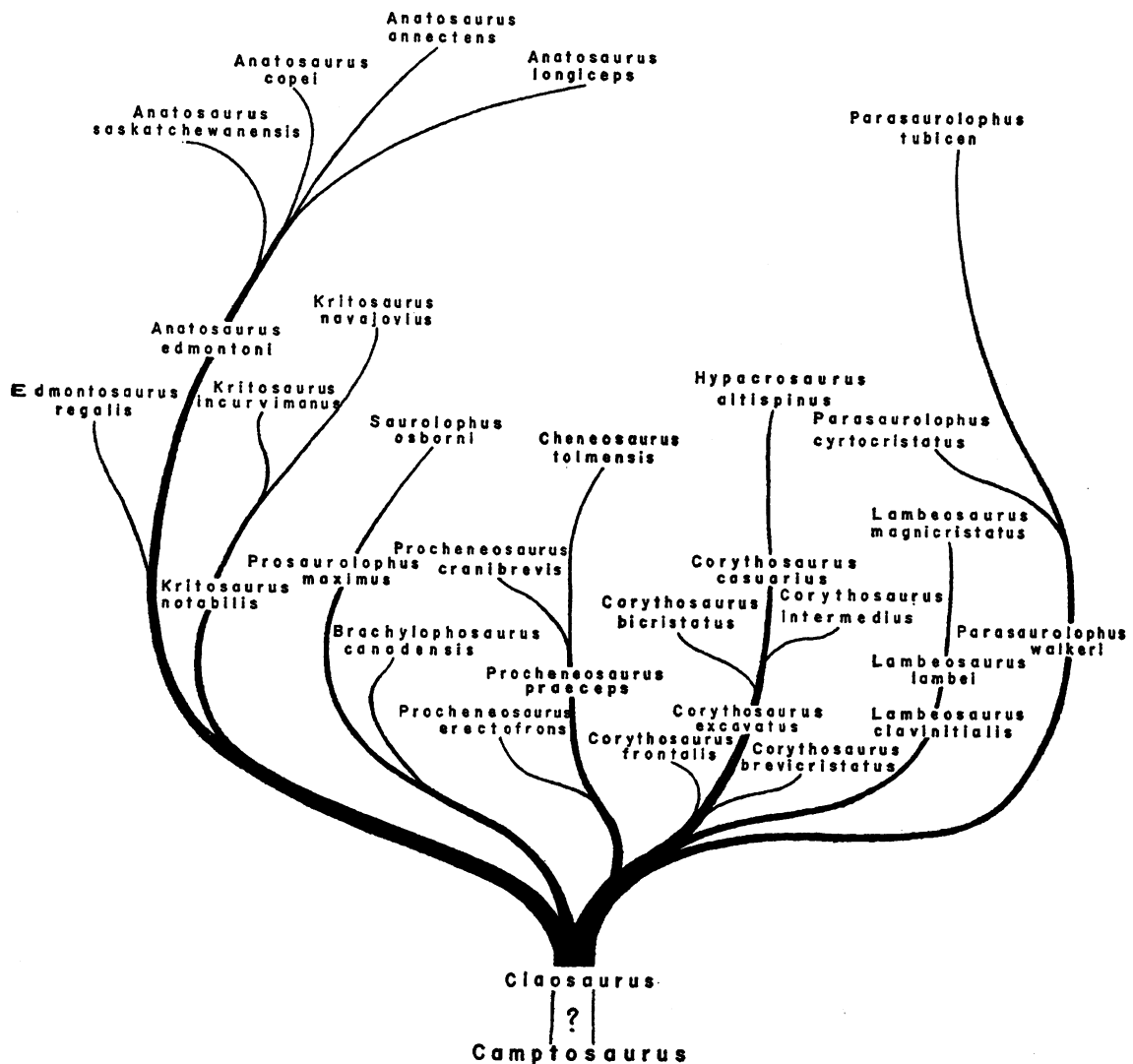


FIG. 78. Suggested phylogeny of the Hadrosauridae.

sages, as in other lambeosaurs, but in this case the narial tracts are not complicated by extensive subsidiary narial cavities, as are those of the corythosaurian and lambeosaurian species.

The third principal evolutionary trend of the hadrosaurs is typified by the members of the Saurolophinae. Here, a crest-like structure, which rises caudally from the supra-orbital region, is formed exclusively by the prolonged nasals, quite unlike the lambeosaurian crest. Some of these crests resemble those of the lambeosaurs in general appearance, but they are quite distinct in that they do not enclose any part of the narial passages and therefore are referred to here as pseudo-narial crests. *Prosaurolophus maximus* and *Brachylophosaurus canadensis*, both from the Belly River series, are the earliest known members of this lineage. *Saurolophus osborni*, from the Edmonton, presumably represents the terminal member of this trend. Unfortunately, these three species constitute our total knowledge of this relatively small intermediate subfamily. In view of the insufficient material presently available, it is impossible to determine the significance or specific affinities of the Saurolophinae, or the origin of the pseudo-narial trend, but these genera apparently represent the persistence of an intermediate stage between the flat-headed and lambeosaurian lineages.

One point that is perhaps significant and may offer a clue to the relationships between the three principal hadrosaurian subfamilies is that only one genus (*Saurolophus*) has been recovered from the late Cretaceous of both the North American and Eurasian continents. (No hadrosaurs have been discovered in either South America or Africa.) As both crested and non-crested hadrosaurs are known by abundant remains in both continents, it is surprising that a genus of the much less abundant Saurolophinae should be the common element. It seems much more likely that either a lambeosaurian or hadrosaurian (flat-headed) genus should be common to both regions, but each continent apparently had its own unique lambeosaurian and hadrosaurian faunas. The presence of unique examples of the two major phyletic trends of the Hadrosauridae in these two separate regions of the world suggests that these two lineages

were introduced into both areas prior to the Belly River interval, with the subsequent independent development of both lines in the two regions. Any subsequent migrations between these regions could not have been significant, according to our present paleontologic evidence.

The presence of *Saurolophus* in both North America and Asia presents a very interesting zoogeographical problem. At first glance, it appears that this represents a hadrosaurian migration during the Edmonton interval. But if such were the case, why were no other members of the family able to make similar migrations? Is it possible that this genus is a relic of an earlier dispersal? When the more or less intermediate nature of the saurolophine cranial structures is considered, is it possible that *Saurolophus*, and perhaps the Saurolophinae in general, represent the conservative survivors of a primitive ancestral stock which gave rise to both the flat-headed and crested species independently in both the Asiatic and North American continents? It seems possible, although perhaps improbable, that the saurolophine hadrosaurs were the derivatives of a primitive, central, hadrosaurian stock and were dispersed throughout the Cretaceous world prior to Belly River time, carrying the genetic potential for producing both the crested and non-crested hadrosaurian varieties.

These comments are purely speculative, of course, but they may provide the answers to several questions of considerable import. First, what is the origin of the two extreme hadrosaurian types that are represented by unique examples in both the North American and Eurasian continents? Second, what is the relationship between the Saurolophinae and the two principal hadrosaurian subfamilies? Third, what is the significance of the pseudo-narial crest? Is it not possible that what appears to be a purely decorative or imitative supracranial crest in the Saurolophinae gave rise to a physiologically functional structure, such as the lambeosaurian crest appears to be? Without a great deal more information, these questions obviously cannot be answered, and the possibility that the Saurolophinae represent relics of a primitive hadrosaurian line cannot be determined one way or the other.

In summary, it appears that the Hadrosauridae probably evolved from a camptosaur-like structural type no later than Neocomian or earliest Comanchian. It further appears probable that the hadrosaurian divergence was initiated no later than early Gulfian. This divergence was quite complete by Belly River time, the peak of lambeosaurian radiation. The Hadrosaurinae and the Saurolophinae, although quite distinct by

this time, endured as relatively minor groups until Edmonton time, when the former, perhaps in response to the lambeosaurian decline, underwent a minor expansion prior to their final radiation during the Lance interval. The intermediate Saurolophinae tapered off during the Edmonton, having never achieved prominence, and finally became extinct before the Lance interval began.

## SUMMARY

CRANIAL STUDIES indicate the development of three distinct hadrosaurian phyletic trends, which were derived from an unknown camptosaur-like ancestor. These trends are given systematic recognition in three subfamilies of the Hadrosauridae. The non-crested species (Hadrosaurinae) apparently represent a conservative line, which first appeared during the Belly River interval, but which did not achieve its maximum radiation until Lance time after the decline of the crested hadrosaurs. The species of the subfamily Lambeosaurinae, characterized by true narial crests, achieved their greatest abundance and diversity during the Belly River interval, after which time this dominant hadrosaurian line suffered a severe decline. The Saurolophinae, which include all species bearing pseudo-narial crests, appear to represent an intermediate group of only minor importance.

The narial crests of the Lambeosaurinae are correlated with olfaction, not with air storage or with the exclusion of water from the narial system. The large size of the olfactory foramen and its proximity to the narial orifice at the base of the crest are interpreted as evidence that the olfactory stalks extended up into the crestal sinuses. The crest cavities are considered to be an adaptation for the expansion of olfactory epithelia, an ancient parallel to the expansion of the turbinal-ethmoid complex of modern macrosmatic mammals.

The saurolophine pseudo-narial crest, on the other hand, is not related to the narial apparatus and is considered to have been an ornamental imitation of the true narial crest, which implies that the lambeosaurian crest had a decorative as well as a physiological function.

The hadrosaurian skull is a large, moderately massive, and completely akinetic unit. The maxillary and neurocranial segments are firmly united at nearly every junction by overlapping or digitate sutures, some of which may be fused. A monimostylic or immobile quadrate is very probable, as effective mastication apparently depended on quadrate stability. Several features, particularly the overlapping contact with the pterygoid and the pterygoid buttress, have been developed to insure a monimostylic quadrate.

Well-preserved cranial muscle scars make possible a nearly complete reconstruction of the mandibular musculature. The hadrosaurian muscle pattern was sauropsid in plan, with well-developed adductor externus, adductor internus, and adductor posterior muscles. The constrictor dorsalis, with the possible exception of the levator bulbi, apparently was absent. The pterygoideus of the adductor internus was modified to function as a protractor mandibulae, while the adductor posterior functioned as a mandible retractor. The cervical axial muscles are partially reconstructed. The presence of the spinalis capitis, rectus capitis anterior, rectus capitis posterior, and the obliquus capitis magnus is indicated, but the existence of the other axial muscles of the neck could not be determined.

In general, the hadrosaurian skull reflects a high degree of adaptation for both sensory and responsive activities. In addition to the olfactory acuity concluded for the lambeosaurs (in connection with the narial crests) the visual, auditory, and balance senses also appear to have been highly developed. Such development is indicated by the expanded cerebral chamber, the large size of the respective cranial nerves, the extreme size of the bulbus oculi, and the presence of a stapes and a well-developed membranous labyrinth. Such high sensory perception is entirely in keeping with the non-aggressive, retreating habits that must have been characteristic of the hadrosaurs.

The hadrosaurian brain was typically reptilian in form, with all three major brain divisions clearly recognizable in the several endocranial casts. Distinct cerebellar and cerebral expansions are prominent, but little, if any, evidence points to the existence of enlarged optic lobes. Although somewhat different in its proportions, the gross brain form was not unlike that of modern lizards. Collectively, the hadrosaurian crania reveal the approximate size and location of all cranial nerves and in some instances additional evidence pertaining to the extra-cranial patterns of certain cranial nerves. In all cases, these nerve locations, and partial patterns where known, closely parallel modern lacertilian conditions.

Most significant among the hadrosaurian cranial adaptations are those that contributed to the unique and highly effective masticatory activities. The large dental batteries, constructed of hundreds of tightly packed teeth, constitute highly specialized "milling" structures which were utilized in a simple fore and aft grinding motion of the mandibles. This protraction and retraction of the lower jaws are well established as the principal mastication process in the hadrosaurs by several independent lines of evidence. Most con-

clusive is the discrepancy in the lengths of unbroken worn surfaces of opposing dental batteries. The *M. adductor posterior* and the *M. pterygoideus* have been slightly modified from the typical sauropsid pattern to function as mandibular retractors and protractors, respectively. Such adaptation, which is comparable to that of modern ruminants and rodents, is considered to be remarkable, for no other reptile, ancient or modern, has approached the highly specialized and efficient chewing mechanism of the hadrosaurs

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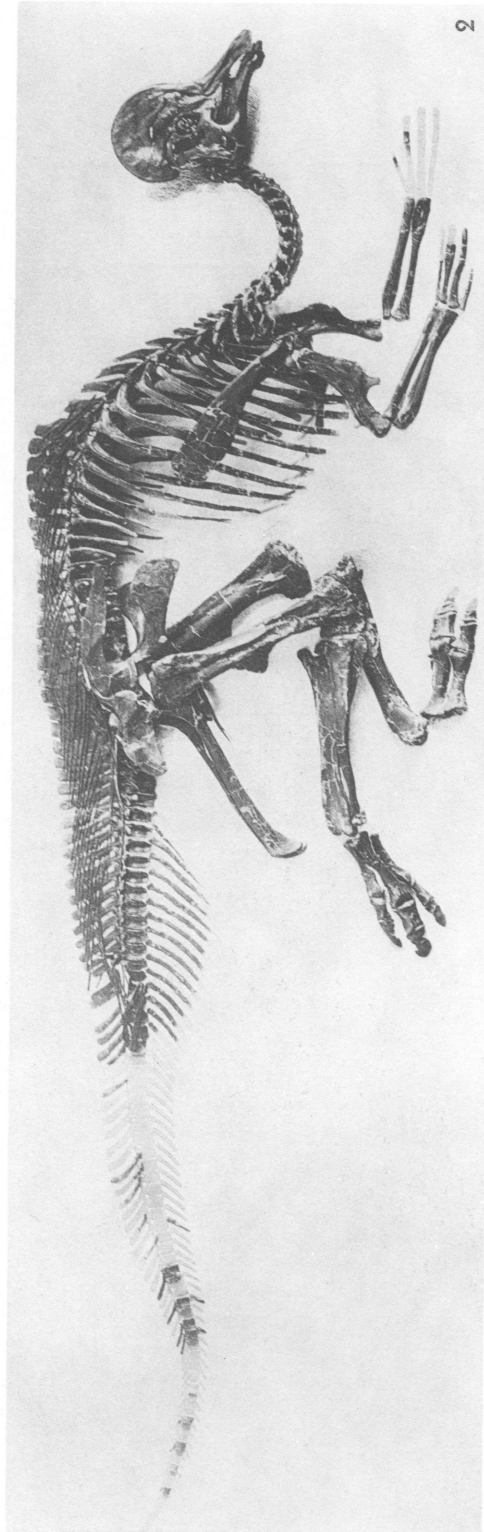
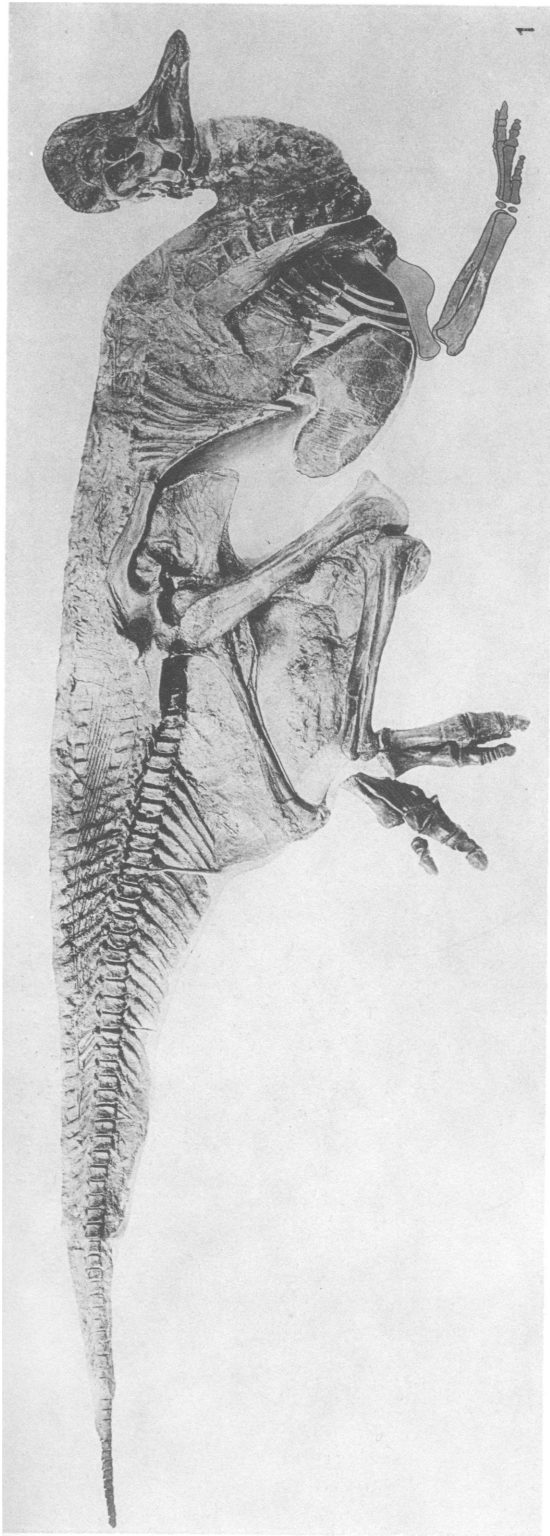
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Lateral views of skeletons of *Corythosaurus casuarius*. 1. Holotype, A.M.N.H. No. 5240. 2. Plesiotype, A.M.N.H. No. 5338.  $\times 1/45$

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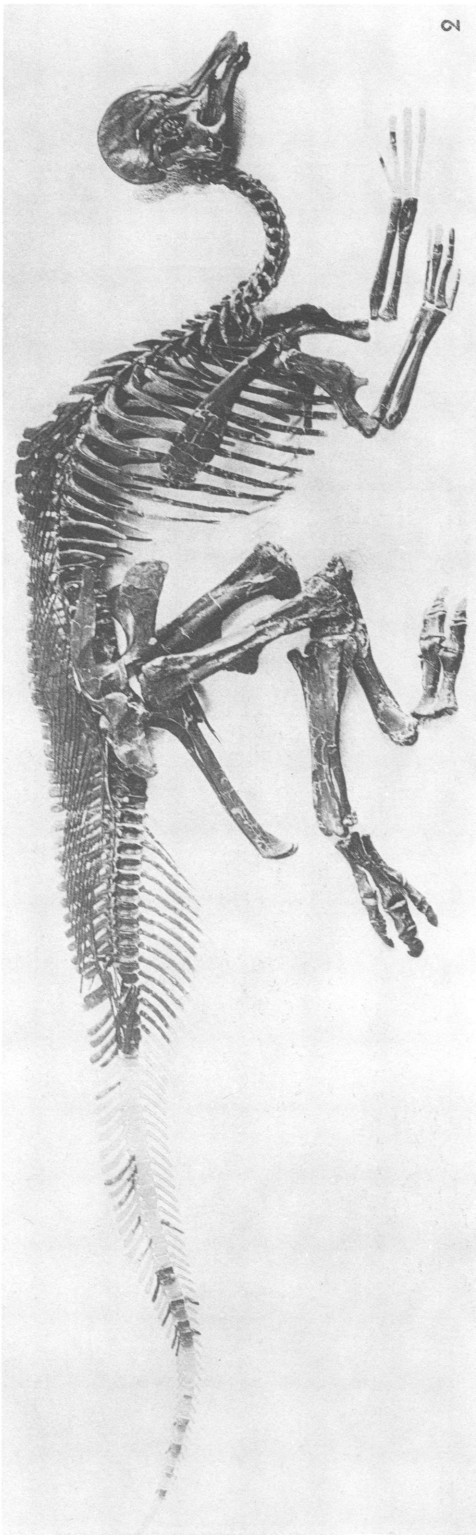
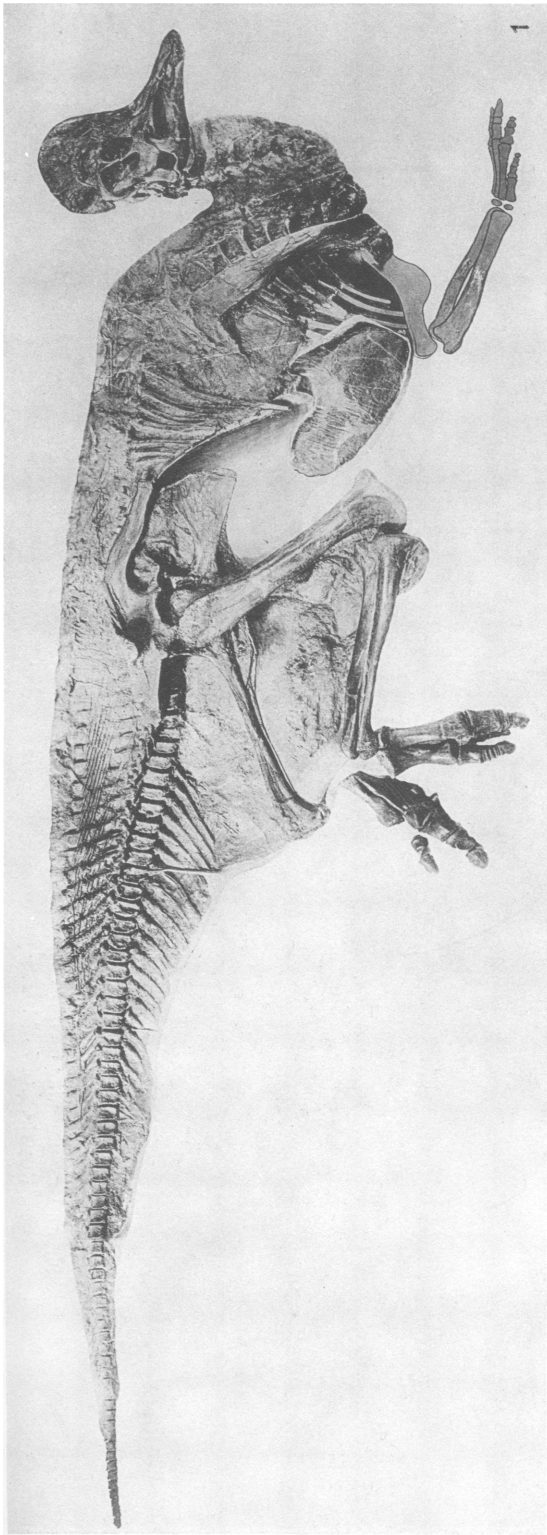
**PLATES 1-6**



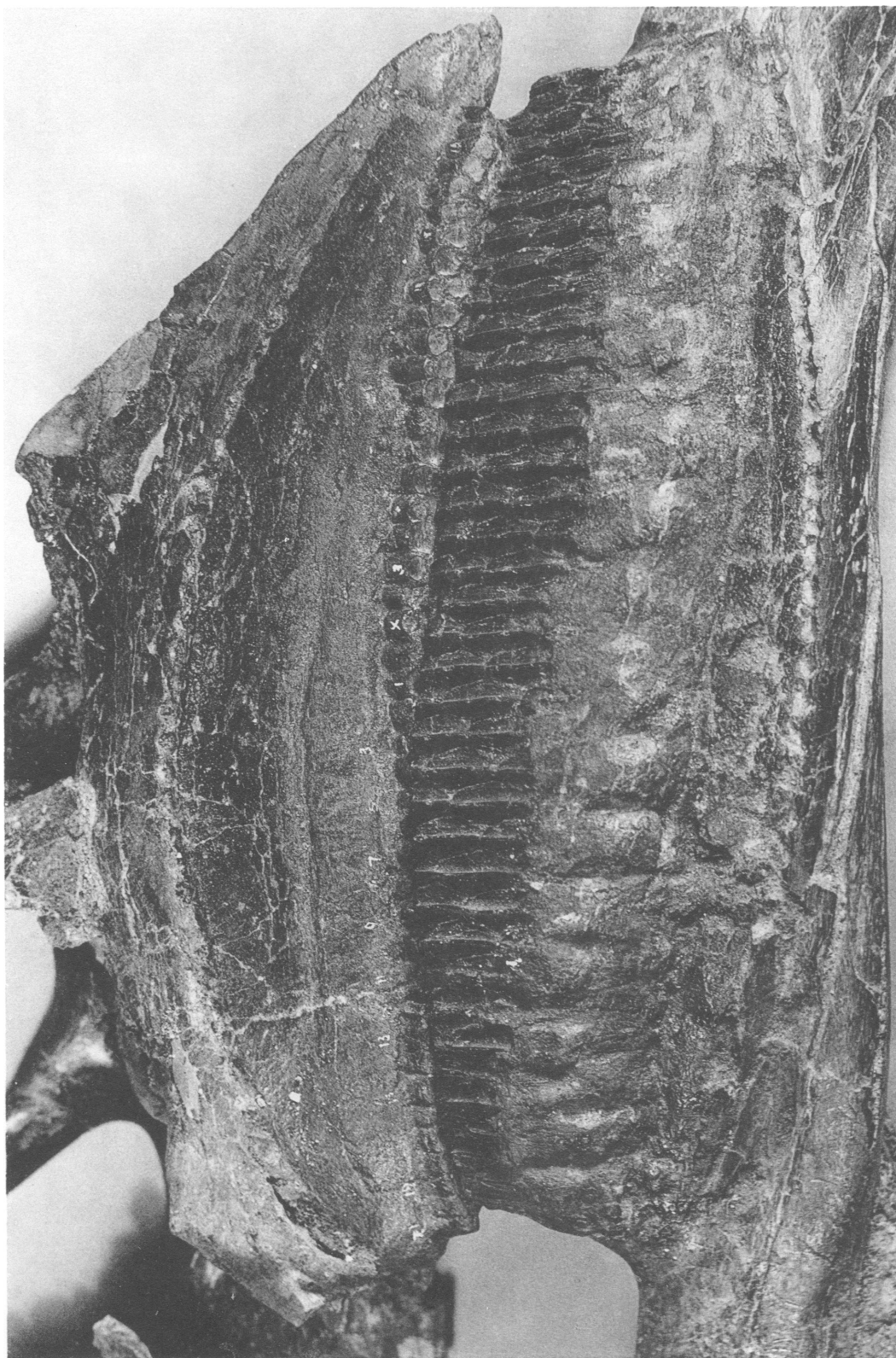
Lateral view of the holotype skull of *Corythosaurus casuarius*, A.M.N.H. No. 5240.  $\times 1/5$



Lateral view of the plesiotype skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338.  $\times 1/5$



Lateral views of skeletons of *Corythosaurus casuarius*. 1. Holotype, A.M.N.H. No. 5240. 2. Plesiotype, A.M.N.H. No. 5338.  $\times 1/45$

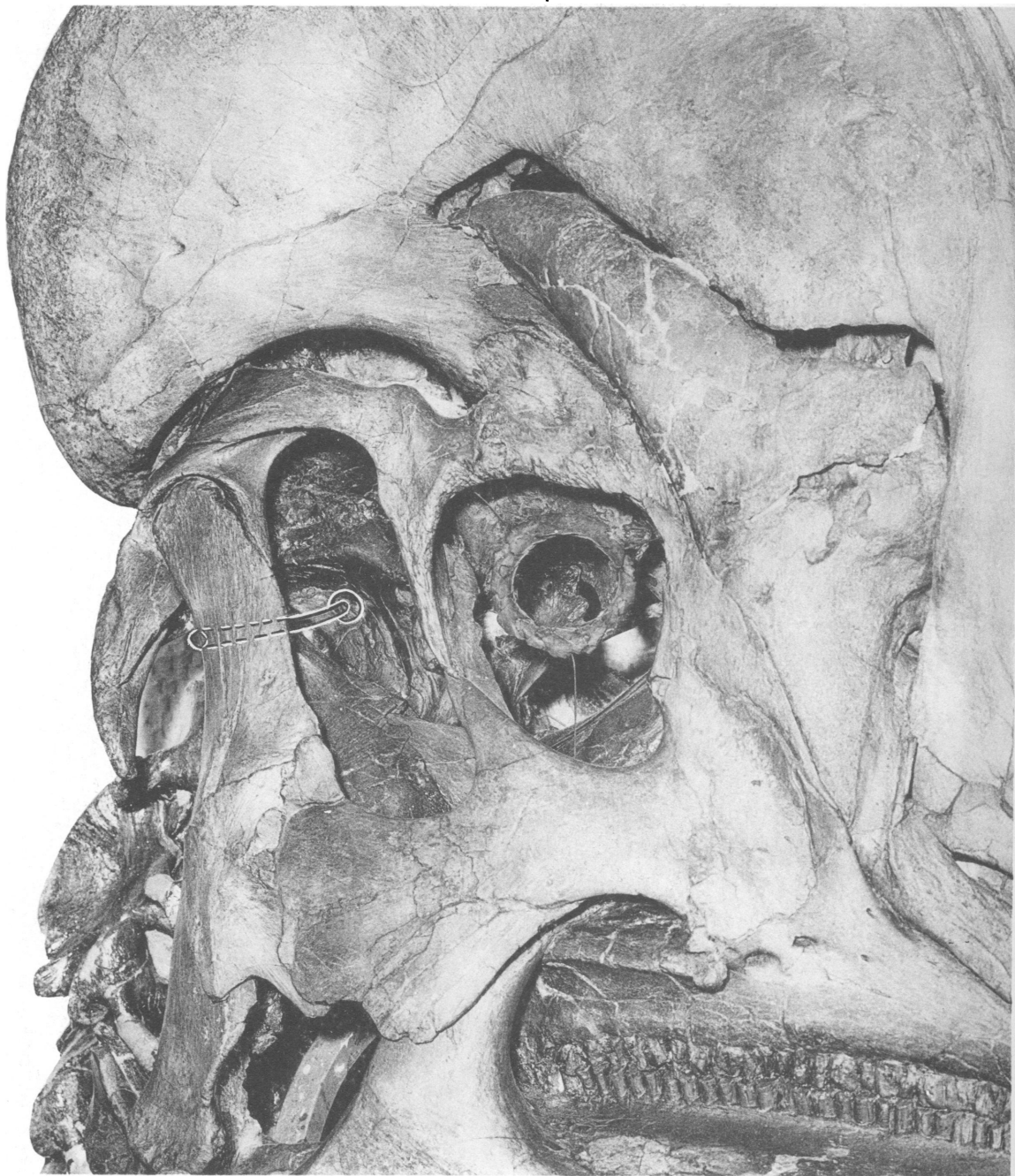


Medial view of the maxillary and mandibular dental batteries of *Corythosaurus casuarius*, R.O.M. No. 1933. Photograph furnished by Dr. Gordon Edmund, Curator of Fossil Reptiles, Royal Ontario Museum, Toronto, Canada.  $\times 3/5$





Occipital view of the plesiotype skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, showing the left stapes *in situ* immediately behind and medial to the upper end of the quadrate. (This photograph is reversed, because it was taken with the aid of a mirror.)  $\times 2/5$



Oblique lateral view of the orbital and temporal regions of the plesiotype skull of *Corythosaurus casuarius*, A.M.N.H. No. 5338, with the stapes restored.  $\times 1/3$