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GEOLOGICAL SERIES, No. 52

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Musculature and Functions in the Ceratopsia

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HOODED HADROSAURS OF THE BELLY RIVER SERIES OF THE UPPER CRETACEOUS: A COMPARISON, WITH DESCRIPTIONS OF NEW SPECIES

By C. M. Sternberg

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Illustrations

The hooded hadrosaurs were the most diversified and perhaps the most specialized of the Upper Cretaceous duck-billed dinosaurs. Lambe was the first, in 1914, to describe a helmet-crested or hooded hadrosaur, when he figured a skull and lower jaw as *Stephanosaurus marginatus* (7). A few months later Brown described a beautifully preserved specimen of hooded hadrosaur as *Corythosaurus casuarius* (2). He believed that Lambe was not justified in referring his new skull to *Stephanosaurus marginatus* and stated that the two skulls were probably congeneric.

In 1920 Lambe proposed a reclassification of the Hadrosauridae and removed the various hooded hadrosaurs from the Saurolophinae to a new subfamily Stephanosaurinae (10). He then described and figured a well-preserved skull as *Stephanosaurus marginatus* and showed for the first time that the hood was made up of the premaxillary and nasal bones and that the narial passages lead up into the hood.

In 1923 Parks, from a study of the literature, concluded that it had not been shown that the helmet-crested skulls that Lambe described were co-specific with *Stephanosaurus (Trachodon) marginatus* and, accordingly, that they were without generic or specific name. He proposed the new name *Lambeosaurus lambei* for the skulls and, presumably, regarded the better skull, Cat. No. 2869, Geol. Surv., Canada, as the type. At the same time he proposed the new subfamily name Lambeosaurinae to replace Lambe's Stephanosaurinae (14, pages 7-8). Gilmore, after a careful study of the material on which Lamb's species *marginatus* was based and the skulls above mentioned, arrived at a conclusion similar to that reached by Parks and accepted his new nomenclature. Gilmore definitely chose the better skull, Cat. No. 2869, Geol. Surv., Canada, as the type of *Lambeosaurus lambei* Parks (5, page 34).

Although Parks proposed the new nomenclature, he states "The resemblance of both species of *Corythosaurus* (*C. casuarius* and *C. intermedius*) to the heads referred to *Stephanosaurus* by Lambe and herein provisionally named *Lambeosaurus lambei*, is sufficiently great to suggest a congeneric position for all three species" (14, page 57). In the same paper Parks refers *Parasaurolophus* to the Saurolophinae instead of the Lambeosaurinae (14, page 6).

Nopcsa went still further and suggested that the hooded and spiked hadrosaurs were the males of the flat-headed forms (11).

It is evident from these observations that students of the Hadrosauridae are not in full agreement. Since the National Museum of Canada has perhaps the best known collection of skulls of hooded hadrosaurs, the writer undertook a study of the subfamily dealing particularly with the skull characters to determine what are generic or specific characters and what should be ascribed to individual variation. Limb proportions were also compared.

Material Studied. The first move in this research was to prepare all the skulls of hooded hadrosaurs in the collections of the Geological Survey, which were still in their field wrapping. Thus eighteen skulls have been assembled for study. Some of these are incomplete and poorly preserved, but others are nearly complete and show splendid details. Among these a splendidly preserved specimen (Cat. No. 8676) of a moderately young individual adds greatly to our knowledge of *Corythosaurus*. The skull was disarticulated, but complete except for the lachrymals, quadrates, quadratojugals, articulars, and right jugal and surangular. The greater portion of the skeleton is preserved back to the sacrum but it has been only partly prepared. This specimen shows for the first time in the corythosaurs the complete narial passages, complete prevomers, and the impression of the horny beak. It is referred to *Corythosaurus excavatus* Gilmore (4).

A well-preserved skull and jaws with part of the skeleton (Cat. No. 8704) of *Corythosaurus intermedius* Parks give some additional information pertaining to the skull and fore limbs of this species. This specimen is considerably smaller than either of Parks' specimens, but it seems similar in all important details.

A nearly complete skeleton, representing an undescribed species of *Lambeosaurus* (Cat. No. 8703), gives details regarding the skeleton and skin impression in this genus. This is the first case known to the writer where skeletal parts have been found associated with a skull of *Lambeosaurus*, except for parts of the hind limbs and the ischia with specimen No. 351, Geol. Surv., Canada. Gilmore referred another specimen, in which the skeleton was preserved, No. 8503, Geol. Surv., Canada, to *Lambeosaurus* (5, page 35), but that specimen is here referred to *Corythosaurus* cf. *intermedius*.

A second undescribed species, represented by a skull and skeleton, is referred to the genus *Lambeosaurus.*

Another undescribed species, represented by a splendidly preserved skull (Cat. No. 8633), is here referred to *Tetragonosaurus.* This skull is much larger than the types of either *Tetragonosaurus praeceps* Parks or *T. erectofrons* Parks (15), and the hood is much higher, but the similar development of the premaxillæ and nasals suggests that it may best be placed in that genus. The larger size and more strongly developed hood could hardly be regarded as due to age development, for the open sutures seem to indicate that this head represents a less mature animal than either of those described by Parks.

Conclusions. Scarcity of juvenile specimens is a disadvantage in a study of this kind. Some of the skulls under examination have the sutures open or the bones disarticulated, showing that the animals were not old, but few very young animals have been reported. The paucity of the remains of young dinosaurs in the delta deposits of the Belly River and Edmonton formations of Alberta and the abundance of such remains in the Mongolian desert deposits seem to suggest strongly that the eggs were deposited and the young reared on the upland and that only the older animals inhabited the swamps.

Certain generic characters that seem to be dependable have been worked out and four of the genera that have been proposed for the Belly River forms appear to be justified, as will be shown later.

Nopcsa's theory (11) that the hooded hadrosaurs are the males and the flat-headed forms the females of the same species cannot be entertained, since the whole make-up of the skulls is different in the two forms. The enclosed narial passage with its complicated winding and trapping, the backward development and modification of the premaxillary and nasal bones, the great shortening of the skull, and the lengthening of the forearm among the Lambeosaurinae suggest different feeding habits from those of the flat-headed forms. These differences are too great to be included in the same subfamily, much less in the same species. Moreover, according to Nopcsa's theory the males and females are, in some cases, not found at the same horizon and during the whole of Lance time only females existed, for none but flat-headed forms have been reported from rocks of this age although they have been collected over a very wide area. In the Edmonton formation, along Red Deer river, Alberta, the writer observed that from Drumheller upstream to the northern edge of township 31 the Hadrosaurinae predominate, whereas north of this point their place is taken by members of the Lambeosaurinae.

Professor Romer, in his Vertebrate Palæontology, suggests that there may have been openings in the hood through which the animal could breathe, enabling him to remain submerged except for the top of the hood. The writer regards the openings in the hood as only lack of development or ossification of the bones.

The hood is variable within the genus, but its development is not regarded as a sexual character. The trapping of air in the elongated narial passages and subsidiary air pockets in the hood was probably an aid to feeding under water.

Through the courtesy of Dr. W. A. Parks, Director of the Royal Ontario Museum of Palæontology, and his staff, the writer was able to study the fine collections of hooded hadrosaurs in the Museum at Toronto[1]. Mr. Barnum Brown, of the American Museum of Natural History, New York, has kindly supplied measurements of the fore limbs of *Corythosaurus casuarius*. Miss Alice E. Wilson gave valuable assistance in choosing specific names. The drawings were made by Mr. J. S. H. Lefebvre.

COMPARISON OF BELLY RIVER FORMS

In comparing *Corythosaurus* and *Lambeosaurus* too much attention may have been paid to superficial resemblances, and perhaps it has not been fully realized that the premaxillæ and nasals contained ramifications of the narial passages and air reservoirs, which were different in the two genera. Parks compares the spike or process in *Corythosaurus intermedius* (14, page 9) with that of *Lambeosaurus lambei*, but in one case this is made up of nasals only and in the other of the nasals and premaxillæ. The most noticeable differences between *Lambeosaurus* and *Corythosaurus* seem to be shown in the development of the premaxillæ and nasals. These differences are linked with the development of the narial passages and no doubt had considerable influence on their feeding habits. A number of published restorations of *Corythosaurus* show the hood or helmet-like crest as a thin cockscomb rather than a fairly thick hood containing narial passages and subsidiary air reservoirs. The cheeks are much fuller and the mandible broader posteriorly than is usually shown.

The pelvic arch is quite different in the two genera. In *Lambeosaurus* the integument was made up of small scales, not differentiated into patterns and without limpet-like bosses such as are seen in *Corythosaurus*.

The narial passage in *Tetragonosaurus* seems to be similar to that of *Corythosaurus*. In *Hypacrosaurus* from the Edmonton formation, as will be described later, the narial passage follows a totally different course. No specimen of *Parasaurolophus* is available for study, so this genus is not considered here, but there seems to be no question that it should be placed with the *Lambeosaurinae*.

Family, **Hadrosauridae**

Subfamily, LAMBEOSAURINAE PARKS

Genus, *Corythosaurus* Brown

Corythosaurus excavatus Gilmore

Can. Field-Nat., vol. 37, pp. 46-7, March, 1923

Plesiotype. No. 8676, Geol. Surv., Canada, consists of nearly complete skull and skeleton back to sacrum (skeleton only partly prepared). Collected by the writer in 1919.

Horizon. Pale Beds, Belly River series, Upper Cretaceous.

Locality. About 3 miles south of the mouth of Little Sandhill creek, 225 feet (aneroid) above the level of Red Deer river, Alberta.

Generic Characters (emended). Hood or helmet-like crest variable; facial slope variable; lower limb of premaxilla extending backward and

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[1]Since this paper was prepared Dr. Parks has described three new species of hooded hadrosaurs (Univ. of Toronto Studies No. 37, 1935).

not separating upper limb and nasal; nasals strongly developed, forming much of superior, and all of posterior, portion of hood and separating upper and lower limbs of premaxilla posteriorly; narial passage running from lower to upper limb of premaxilla through S-like passage and surrounded posteriorly by subsidiary air chamber; cranium narrow; prefrontal well developed; maxilla slender anterior to jugal overlap; teeth more numerous in maxilla than in dentary; humerus much shorter than radius, radial crest strongly developed; ilium decurved anteriorly; pubis with anterior blade short and broadly expanded; ischium long, with foot-like terminal expansion; skin-impression with raised limpet-like bosses.

Specific Characters. Facial slope uniformly steep; nasals short and high, excavated behind; narial passage open superiorly back to division of premaxilla; lower limb of premaxillæ not reaching nasal postero-superiorly; upper limb of premaxilla extending to superior tip of crest; diagonal groove across lower limb of premaxilla strongly developed and running into air chamber; 39 rows of teeth in maxilla; 36 rows in dentary; dental magazine shallow; edentulous portion of dentary short; predentary and horny beak broad in front; scapula slender, rounded posteriorly; radius 25 per cent longer than humerus, radial crest strongly developed; metatarsals large.

The shorter nasal, open narial passage, slight contact between the nasal and lower limb of premaxilla, and fewer teeth might be regarded as juvenile characters were it not for the fact that these characters seem to go together in both large and small skulls; several specimens that are smaller than the type *C. excavatus* show the typical *C. casuarius* development. Among the skulls being studied is one considerably smaller than Gilmore's type or than the types of *C. intermedius* Parks (14), but it shows the typical *C. intermedius* development. It would, therefore, seem that the above-mentioned characters are real specific differences. It is recognized, however, that there is considerable variation within the species, in the development of the hood and the closing of certain openings. It is quite to be expected that the hood would not be so well developed in younger animals or primitive species.

SKULL

When viewed from the side the facial slope is uniformly steep and the hood is moderately high and short.

Premaxilla, Nasal and Narial Passage. In this species, as well as in other members of the Lambeosaurinae, the premaxilla was much folded and extended posteriorly and served the important function of enclosing the greater part of the narial passage.

The premaxilla is somewhat pointed in front, but the horny sheath must have been broad to conform to the squarish lower beak. It divides into upper and lower limbs above the middle of the maxilla and just behind a well-defined groove that runs diagonally upward and backward and enters the hood under the anterior edge of the lower limb. The function of this groove is not known, but it may have carried some special blood supply. The lower end of this groove is almost directly above the large infraorbital foramen. In its anterior portion the thin lower edge of the premaxilla is developed upward and inward to cover the narial passage.

The upper part of the bone, anterior to its division into upper and lower limbs, is thickened and folding is less pronounced. The upper and lower parts do not meet, but there is a narrow slit above the narial passage back to the diagonal groove. In *C. casuarius* and *C. intermedius* and in *Lambeosaurus* these edges meet in their posterior portion and in *Cheneosaurus* and *Hypacrosaurus* they are well united from near the anterior end. The floor and that part of the bone that is folded to surround the narial passage are very thin throughout, but the narial passage is completely enclosed in bone except for the narrow slit above referred to.

From where the premaxilla divides the lower limb broadens and continues backward and upward at about the same angle as the anterior portion. Its anterior edge rises somewhat steeply, and is in contact with the posterior edge of the upper limb for some distance, then turns sharply backward and presents a free edge to its posterior extremity. Throughout most of its length the lower limb is in contact infero-internally with a forward development of the nasal. Postero-inferiorly it meets the antero-external tip of the nasal. It is in contact infero-externally with the lachrymal and prefrontal and is well removed from the orbital rim. This lower limb, with the nasal, covers the large air reservoir within the hood, but not the direct narial passage.

The upper limb turns upward with a moderate angle and continues backward to the superior tip of the crest. It is thin internally where it meets its fellow on the mid-line of the skull. The internal face is quite deep back to opposite the anterior point of the nasal (*See* Plate I, figure 1). From here it continues back as a thin process about 50 mm. high. This process is flanked by the very thin superior portion of the nasal and, with it, makes up the thin superior part of the hood. Antero-externally the upper limb folds outward and downward to form the gently rounded anterior edge of the hood and cover the central portion of the narial passage.

A cross-section of the left premaxilla (Figure 1) taken at the posterior extremity of the open slit, or just about where the bone divides into upper and lower limbs, shows the upper and lower air passages. On the external side the groove that runs diagonally upward and backward across the lower limb is seen. The lower air passage (L.P.) is roughly oval and higher than wide. Behind this point it becomes slightly enlarged, then turns sharply forward and enters the upper air passage (U.P.). The section intersects the upper air passage near its anterior extremity and shows it much smaller than it is farther back. A short distance behind the break one could see the bone dividing the upper air passage proper and the entrance to it into which the lower air passage extended. If the section had been a little farther back the S-shaped tube would have been shown, but the bone is too delicate to attempt sectioning except at a break.

The nasal is far removed from the anterior naris, but surrounds the narial passage posteriorly. It is situated directly above the orbit and rests on the frontal, which is developed forward and downward to give greater sutural contact. It unites with its fellow on the mid-line, but they are separated superiorly by the thin flanges of the upper limbs of the premaxillæ. It makes up much of the side and all of the back of the hood, and is flanked infero-laterally by the prefontal and posterior end of the lower limb of the premaxilla.

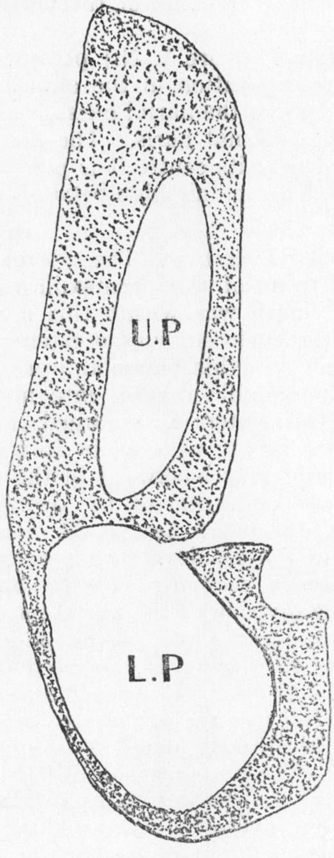

Figure 1. Cross-section (natural size) of left premaxilla of No. 8676 taken through the back of the open slit. L.P. = lower air passage; U.P. = anterior part of upper air passage.

When viewed from the side the disarticulated nasal (Plate III, figure 1) is roughly triangular, with the apex posterior and the anterior edge deeply notched. This notch is carried far back on the external surface and receives the posterior development of the lower limb of the premaxilla. The main body of the bone has thin outer and inner walls with a large cavity between. These walls unite inferiorly, and give the appearance of a thick lower surface, but the bone wall is very thin. The mid portion of this inferior surface shows striation for sutural union with the frontal and prefrontal, and posterior to this is a rugose area. Anterior to the sutural surface a long, decurved, convex process runs forward and downward to flank the posterior part of the narial passage. Externally it shows sutural surface for union with the prefrontal and lachrymal. Superiorly the outer and inner walls of the nasal unite and extend upward, as a very thin sheet of bone, to flank the posterior process of the upper limb of the premaxilla and form the outer portion of the postero-superior part of the hood.

The inner view (Plate I, figure 1, N.) presents a smooth, flat surface except for a rather large excavation in the anterior portion. This represents the posterior boundary of the narial passage as it turns sharply downward and forward to the internal naris. The flat, inner wall meets that of the opposite nasal and near its centre it is pierced by a large semi-reniform fenestra which allows communication between the large cavities within the nasals.

Narial Passage and Air Reservoir. The external naris appears to have been situated near the front of the premaxilla, and the narial passage throughout most of its length was within this much modified bone. In its anterior portion it is enclosed supero-externally by the upturned external edge of the bone. In this region the passage is fairly large, but just behind where the premaxilla divides into upper and lower limbs it narrows somewhat and then enters an enlarged cavity in the lower limb. From this cavity the passage turns sharply forward and enters a large chamber in the upper limb, runs backward in the upper limb to where it meets the nasal and then takes a sharp turn downward and forward to the internal naris. In their downward course the narial passages unite and are surrounded by the forwardly developed processes of the nasals. (In *Lambeosaurus* the greater development of the upper limbs of the premaxillæ seem to make the division of the narial passages complete.) What Parks referred to as the deep vault, on the under side of the crest of *C. intermedius* (14, page 15, Figure 1), represents the united narial passages. In the disarticulated hood (Plate I, figure 1, Nar. P.) this downward extension of the narial passage appears to lie in a deep trough in the nasal, but when the nasals are articulated it is subcylindrical in form and enclosed by these bones. The prevomers divide the narial passages at the internal nares. The internal naris is separated from the narial passage in the lower limb of the premaxilla by only a thin wall, yet the air must have come through a passage more than 500 mm. long, including S- and U-shaped traps, to reach this point.

The internal naris is bounded anteriorly and externally by the premaxilla and maxilla, posteriorly by the palatine and upturned edge of the pterygoid, and internally by the prevomer.

Within the swollen nasal bone is a large pocket which extends to the postero-inferior angle of the bone. This pocket is carried forward into the side of the hood and is flanked by the lower limb of the premaxilla, thus forming a large subsidiary air reservoir. There was free communication between this reservoir and the narial passage above where the nasals completely surround the united narial passages. There was communication between the right and left air reservoirs through large, semi-reniform fenestræ through the inner walls of the nasals and between the narial passages, by fairly large fenestræ through the inner walls of the upper limbs of the premaxillæ, just in advance of their contact with the nasals. In advance of this fenestra the right and left narial passages are completely separated by bone. Of course it is possible that these fenestræ were closed, in life, but their similar size, shape, and position suggest that they do not represent incompletely calcified areas. Aside from these there is no fenestra through the premaxilla or nasal.

This more detailed study of the narial passages and large air reservoirs does not seem to bear out the theory that the elongated air passage was for trumpeting and was possessed by the males only. It seems more likely that they assisted the animal in feeding under water. The double-trapping of the air would prevent water from getting into the lungs when feeding in the swamps and the extra supply of air might also permit longer submergence.

The cranium resembles that of *C. intermedius,* but the sutural surface on the frontal, for articulation with the nasals, is longer and less steeply inclined. The occipital region is low and lacks the conspicuous overhang seen in *Edmontosaurus* and other flat-headed hadrosaurs.

The supraoccipital is well defined and shown, beyond question, to be well removed from the foramen magnum. It is roughly triangular with the broad base on the coalesced exoccipitals and the rounded apex extending under the united posterior borders of the squamosals. Its stage of development is intermediate between that shown by Gilmore for *Bactrosaurus johnsoni* (6, Figure 22) and that prevailing in *Thespesius saskatchewanensis* Sternberg (16).

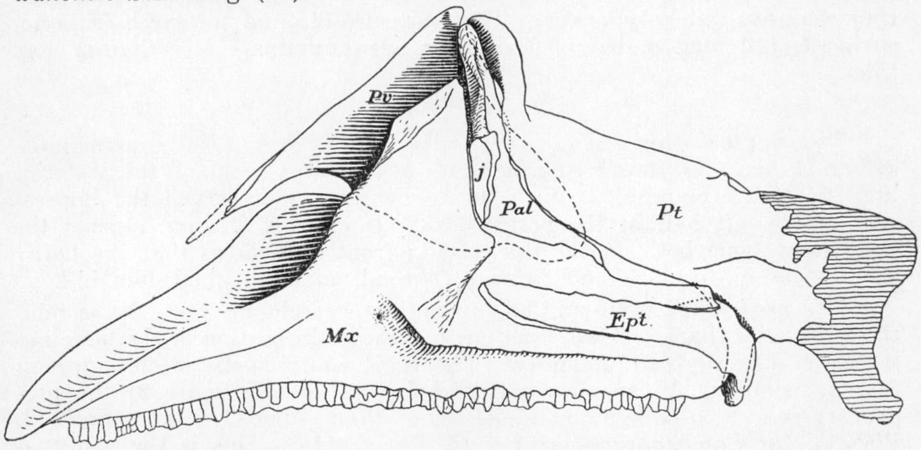

Figure 2. *Corythosaurus excavatus* Gilmore, Geol. Surv., Canada, No. 8676; external view of left maxilla and associated elements, with premaxilla and jugal removed; approximately X ⅓.

The maxilla (Plate I, figure 2, Mx; Figure 2) resembles that of *C. intermedius,* but the vascular groove on the internal surface of the bone, above the alveolar border, turns up and is deeper posteriorly and there are only 39 vertical rows of teeth as compared with 43 in Parks' specimens and the maxilla of *C. intermedius* No. 8704, Geol. Surv., Canada. In more than half of the tooth rows there are two functional teeth in the triturating surface. The total length of the maxilla is 280 mm. and the alveolar length is 240 mm.

The prevomers are represented by two very thin bones, which were found with the disarticulated skull (Figure 2, Pv.). They are unlike any other prevomers known to the writer, but the internal narial vacuity is also very different from that usually seen in reptiles. When viewed from the side the prevomer is triangular, with the supero-posterior angle about 90 degrees and the anterior point extending well forward. This point becomes much broader than the main part of the bone, is flat below, and rises gently in a low median ridge superiorly. The bone stood upright in the posterior nares and the forward prolongation apparently united with the premaxilla and maxilla, but this forward articulation cannot be determined with certainty. Posteriorly the sides of the bone flare out into vertically placed flanges which extend down the posterior edge for more than half its length. A moderately sharp ridge runs down the posterior edge and, with the flanging sides, makes a double articulating surface for union with the thin, upturned edges of the palatine and pterygoid, the central ridge fitting between the two bones and the thin out-turned edges covering them. Below mid-height the flanges and ridge disappear and the bone continues downward to a blunt point. This postero-inferior tip of the right prevomer is shorter than that of the left. Except for the expanded anterior tip and the flanged posterior edge, the bone is very thin throughout.

When the bones are properly placed in the skull, they form a high, thin division of the posterior nares. There is no indication of sutural contact between the prevomers on the mid-line, but it would appear that they were not widely separated. They measure 145 mm. in length (superior surface), 110 mm. in height (posterior edge), and are less than 2 mm. thick.

MANDIBLE

The dentaries and predentary were preserved naturally articulated (Plate II, figure 1), thus giving the shape of the lower beak and the posterior breadth of the mandible. With the predentary is preserved the impression of the left half of the horny beak. It extends 36 mm. beyond the predentary bone both on the side and in front and shows that the horny sheath was quite thick and formed a broad, squarish, duck-like bill.

The predentary is broad, flat, and fairly straight in front. It is relatively broader than in *C. intermedius*, but the main portion of the bone has a greater fore and aft diameter. The three sharp keels on the superior face are similar. When viewed from below (Plate II, figure 2) the predentary is seen to be less horseshoe shaped than either *C. intermedius* (14, Plate V) or *Lambeosaurus lambei* (5, Figure 11). This is the result of greater breadth of the bases of the postero-lateral processes. The thin bifurcated flange, which extends backward and slightly downward to embrace the lower antero-internal tips of the dentaries, is set farther back than in *C. intermedius* and the wings are relatively much shorter and broader. On either side of the base of this flange is a large foramen, which pierces the bone, and external to each tip is a smaller, but well-defined, foramen entering the dentary.

The dentary is moderately massive and the coronoid process is short and set well out from the main body of the bone. It is only slightly decurved anteriorly and the edentulous portion is relatively short and low.

The dentary teeth are well shown in Plate II, figure 3, and very little need be said about them here. The dental magazine is moderately shallow and usually there are but two teeth, in the vertical series, below the functional ones. The greatest depth of magazine from the foramina, at the base of the tooth row, to the cutting edge, is 77 mm. and it is much deeper anteriorly than posteriorly. There are 36 rows of teeth in the magazine, which measures 240 mm. The enamel face of the teeth is slightly broader, relatively, than in most members of the Lambeosaurinae. Papillæ are present on all the teeth but are more pronounced on the anterior ones. The anterior teeth are somewhat sigmoid in shape. This irregular shape may not be constant within the species, but it is shown in both dentaries. The triturating surface is composed of one enamel crown and two fangs except at the extremities.

SKELETON

The greater part of the skeleton in front of the sacrum was preserved, except the left fore limb and the phalanges of the hind feet. These bones have been only partly prepared, but certain information pertaining to the limbs and the integument is available. Measurements of the fore and hind limbs will be found in the comparative measurements of different species. The articulated series of 28 presacral vertebræ gives a length of 6 feet 2 inches. This does not include the first two cervicals, so there were at least 30 presacrals in the complete column. There were ossified tendons in the rock near the skull, which would suggest that they may have extended farther forward than is usually supposed.

The scapula is relatively very short and of light construction. The upper edge is straight, but below it flares out as it proceeds backward, thus making a fairly wide blade; postero-inferiorly it cuts off so as to give a broadly rounded corner. This is quite unlike the square termination usually seen in the hadrosaurian scapulæ.

The humerus is of moderate size, but the radial crest is very strongly developed and extends well below the mid-length of the bone.

The radius and ulna are moderately slender and much longer than the humerus.

The manus is of moderate size.

EPIDERMIS

A section of splendidly preserved skin impression from the upper side of the forearm is shown in Plate V, figure 2. The tubercles were of the usual polygonal non-imbricating type, but there is a greater variation in size than has been previously shown. It would appear that the large pavement scales covered the forearm much as Osborn shows in *Thespesius (Trachodon) annectens* (12, Figure 10), but the tubercles are much larger. The largest scales have a diameter of 18 mm., whereas the smallest ones measure less than 4 mm. in greatest extent.

Smaller pieces of well-defined skin impression from near the hind limbs show rather large scales without differentiated pattern. These tubercles were moderately high and show radial crinkling. Other bits of the impression from the neck show proportionately high but very small tubercles.

Corythosaurus intermedius Parks

University of Toronto Studies No. 15, pages 1-57, 1923

Among the specimens being studied is a well-preserved skull (Plate III, figure 2) and partial skeleton (Cat. No. 8704) which, except for size, compare closely with the types of *C. intermedius* Parks (14). The specimen was collected by the writer, in 1919, from the Pale Beds, Belly River series, about 3 miles south of the mouth of little Sandhill creek, 210 feet above Red Deer river, in Alberta. This locality is very near, and about 15 feet lower than, that from which the specimen of *C. excavatus* was collected. Only the head, right scapula, forearm, and manus have been prepared.

The presence of a third specimen, which so closely resembles the types of *C. intermedius* and shows the same variation when compared with other species of the genus, seems to verify the establishment of this species. The main differences between this specimen (Cat. No. 8704) and the one of *C. excavatus,* previously discussed, are: steeper facial slope, posterior closing of the slit above the narial passage, union of posterior tip of lower limb of premaxilla and nasals, much higher hood and higher nasal, greater number of teeth, more decurved dentary, and longer forearm.

The posterior closing of the narial slit is the result of expansion of the superior edge of the premaxilla. In this respect it more closely resembles *C. casuarius* (1, Plate XLI) than *C. excavatus.* The broadening of the premaxilla is slightly more advanced than in *C. excavatus.* This would suggest that the narial passage enters the upper limb of the premaxilla slightly farther ahead in this species, but this cannot be definitely stated since it is not possible to work out the narial passage in detail. The diagonal groove is strongly developed. The foramina, shown by Parks, through the upper and lower limbs of the premaxilla, are not present in this specimen and there is no spike on the postero-inferior edge of the nasals, but these features are not here regarded as of specific importance. The lower limb of the premaxilla is strongly swollen, thus forming a buttress in front of the eye which must have obstructed the anterior view. The nasal is short, very high, and broadly swollen infero-posteriorly. The broadly expanded lower part of the nasal along with the swollen lower limb of the premaxilla suggest a large subsidiary air chamber.

The maxilla and dentary are similar to those of the types. There are 44 vertical rows of teeth in the maxilla and 39 in the dentary.

The forearm is very long and slender. When compared with the fore limb of *Lambeosaurus* (Cat. No. 8703) this slenderness is very noticeable, for whereas the bones are of subequal length, in *Lambeosaurus* they are very much more massive (*See* table of comparative measurements).

TETRAGONOSAURUS Parks

University of Toronto Studies No. 31, pages 1-11, 1931

Tetragonosaurus seems to resemble *Corythosaurus* more closely than *Lambeosaurus,* but the smaller size, long slender nasal, low forwardly placed dome or hood, development of the upper limb of the premaxilla backward to overlap nasal, and less steeply placed cranium seem to justify its assignment to the different genus. Members of this genus seem to have been more primitive than other described hooded hadrosaurs from the Pale Beds. In many respects *Tetragonosaurus* resembles *Cheneosaurus* of the Edmonton formation (8), but the open narial slit, less advanced nasal, steeper facial slope, and differently shaped jugal, as well as the great difference in geological age, seem sufficient grounds for their separation.

Tetragonosaurus cranibrevis sp. nov.

Plate IV, figure 1

Type. No. 8633, Geol. Surv., Canada, consists of complete skull and jaws except predentary, left lachrymal, jugal, quadrate, quadratojugal, and the small bones of the left ramus. Collected by the writer, 1928.

Horizon. Pale Beds, Belly River series, Upper Cretaceous.

Locality. 2¼ miles south of mouth of Berry creek, 140 feet above Red Deer river, Alberta.

Generic Characters. Skull short, high, and blocky; brain-case not strongly deflected; hood low in advance of orbit, not overhanging cranium; lower limb of premaxillæ extending backward, not separating upper limb and nasal; upper limb of premaxilla overlapping nasal posteriorly; nasal narrow and extending far forward; open slit above narial passage; narial passage enters upper limb of premaxilla through S-shaped tube; frontal long; lachrymal well developed; teeth more numerous in maxilla than dentary; jugal long and slender.

Specific Characters. Skull relatively large; cranium short; hood relatively high; facial slope gentle anteriorly, then sharply up-turned above maxilla; lower edge of premaxilla folded to cover narial passage except for narrow slit; posterior extremity of lower limb of premaxilla above centre of orbit, superior edge uniting with upper limb just in advance of tip of nasal; frontal and prefontal up-turned to unite with nasal; anterior prolongation of nasal flanking but not overlapping upper limb of premaxilla; dentary heavy and strongly decurved anteriorly; 40 teeth in maxilla and 33 in dentary; dental magazine in dentary deep, usually 4 teeth in vertical series.

The skull is larger and that portion behind the hood is relatively much shorter than in the types and only known representatives of the two species, described as *Tetragonosaurus praeceps* and *T. erectofrons* by Prof. Parks. The dome or hood is in a much more advanced stage of development, yet the open sutures suggest that it represents a less mature individual than either of the other specimens. Parks shows the narial passage as being open superiorly to above the orbits. In the present species this region is very similar to that seen in *C. excavatus* above described. Parks states (15) that "the exterior nares are of extraordinary length". It is hardly conceivable that the external nares occurred as long, narrow slits. It is the opinion of the writer that the external nares were located near the front of the premaxilla in all of the hooded hadrosaurs and probably in the other forms as well. When viewed from the side the skull resembles that of *T. praeceps,* but the hood is higher and longer. It has not, however, reached the stage of development found in the corythosaurs and the nasals do not appear to have been hollow.

The narial passage is partly covered by the upturned lower or external edge of the premaxilla back to where the bone divides into upper and lower limbs. From here it takes a sharp turn forward and enters the cavity within the upper limb, much as in *C. excavatus.* It has not been possible to trace the posterior part of the passage in detail, but it appears to have been bounded by the nasals postero-laterally, from where it was deflected downward and forward to the internal naris much as in *C. excavatus,* but the nasals do not seem to have extended forward and downward to surround the passage.

The premaxilla is square in front as in *T. erectofrons,* but its anterior portion is longer than in that species. The upper limb is broadly rounded to enclose the narial passage as in *C. excavatus,* and there is a thin inner wall where it unites with its fellow, thus separating the right and left narial passages. From about mid-length of the crest the upper limb narrows and extends backward, as a pointed finger of bone, overlapping the nasal, to the extremity of that bone. These tips do not divide the nasals posteriorly as they do in *Lambeosaurus.* The lower limb is very similar to that in *C. excavatus.* Its lower edge is grooved for strong sutural contact with the lachrymal and prefrontal. The groove that runs diagonally across the bone externally is moderately well developed. This groove is not shown in either of the other species. If this groove carried a special blood supply into the hood one would not expect it to be well pronounced in forms in which the hood was not well developed.

The nasal rests on the frontal with a strong sutural contact and its base extends slightly forward to unite with the prefrontal. The upper part of the bone unites with its fellow and extends forward as a broad, thin bone roofing the posterior portion of the narial passage or air cavity within the hood. From near the centre of the hood it narrows and continues forward as a broad tongue of bone flanking the premaxilla and covering the side of the air chamber. On the side of the hood, between this tongue of bone and the lower limb of the premaxilla, there is a considerable space that is not covered by bone. Similar uncovered spaces are seen in other hooded hadrosaurs where the nasals have not reached their full development.

Compared with *Corythosaurus* or *Lambeosaurus* the brain-case is not so strongly deflected and the frontal is very long. The frontal is somewhat comparable with that of *Bactrosaurus johnsoni* Gilmore (20, Figure 21), but unlike that species it is excluded from the orbital rim by the broad union of the prefrontal and postorbital. The anterior edge is thickened and upturned to meet the overlying nasal and elevated posterior edge of the prefrontal. The anterior edge is slightly overhung by the posterior tip of the nasal. The united frontals do not form a pronounced dome as in the two other species of the genus.

The prefrontal seems to be much higher posteriorly than in either of Parks' specimens. It more nearly resembles the prefrontal of *Lambeosaurus lambei* Parks in this backward elevation, but in its forward development it is more like that of the *Corythosaurus* and like that shown in *T. erectofrons.* It extends down to near the middle of the orbit as a well-developed process and it and the large lachrymal force the lower limb of the premaxilla well away from the orbital rim.

The jugal is long and relatively slender as in *T. erectofrons* and the postorbital bar extends up to the top of the lateral temporal fossa and almost reaches the anterior tip of the squamosal.

The sclerotic ring is fairly well preserved and suggests a very small eye located well up and back in the orbit.

The maxilla is more slender than in *T. erectofrons.* It contains 40 vertical rows of teeth and in most cases there are two teeth in the triturating surface. The enamel faces of the teeth are long and narrow, with the median carina very high at the base but low at the tip. The edges are almost flat and the borders are smooth.

The dentary is massive, strongly decurved anteriorly, and the edentulous portion is short and deep. The dental magazine contains 33 vertical rows of teeth. It is deep and there are usually three enamel crowns developing below the functional tooth. This is one more than in *C. excavatus.* Except at the extremities there are one enamel crown and two fangs in the triturating surface. The dentary teeth do not differ greatly from those of *C. excavatus* except that the edges show less papillation.

LAMBEOSAURUS Parks

Lambeosaurus clavinitialis sp. nov.

Plate IV, figure 2; Plate V, figure 1; Plate VI

Type. No. 8703, Geol. Surv., Canada, consists of complete skeleton except predentary, left quadrate, postorbital, and squamosal, dorsal vertebræ, left dorsal ribs, left ilium, and some distal caudal vertebræ. Skeleton only partly prepared. Collected by the writer in 1928.

Horizon. Pale Beds, Belly River series, Upper Cretaceous.

Locality. Two and a half miles south of the mouth of Berry creek, 140 feet (aneroid) above Red Deer river, Alberta.

Generic Characters. Hood high, variable in fore and aft length, thrown strongly forward, highest point in front of orbit; lower limb of premaxilla upturned and separating upper limb from nasal anteriorly, narial passage enters hood through swollen upturned lower limb of premaxilla; lower limb of premaxilla just barely cut off from orbital rim by slender process from lachrymal; upper limbs of premaxillæ separating nasals to their posterior extremity; cranium narrow; brain-case strongly deflected; maxilla in front of jugal, short, heavy, and convex; teeth more numerous in dentary than in maxilla; ilium not strongly decurved anteriorly; integument made up of small scales not differentiated into patterns and without limpet-like bosses.

Specific Characters. Skull and skeleton massive; hood of medium length (fore and aft); lower limb of premaxilla well developed, strongly swollen, and thrown forward; nasals forming side of hood posteriorly but separated by upper limbs of premaxillæ; posterior spike inceptive; orbit and lateral temporal fossa large; slit above narial passage open well back; maxilla massive; fore limb massive; anterior blade of ilium thick, posterior blade broad; pubis broad anteriorly, postpubis large; ischium massive, foot-like expansion only moderately developed; femur short; ossified tendons extending down in front of femur and over knee.

SKULL

When compared with the type of *L. lambei* this skull is very massive and the spike which is such a prominent feature in the genotype is only in the initial stage of development. A second skull in our collections (Cat. No. 8631), which is comparable in every way with the specimen chosen as the type of the new species, possesses a slightly longer, but still inceptive spike. The possession of a fully developed spike in the type, which is small, and in a large skull in the collections of the Royal Ontario Museum, seems to show that this cannot be regarded as an age or individual variation.

The crest is relatively lower than in *L. lambei* and the lower limb of the premaxilla is more strongly swollen and the superior edge bent forward. It has not been possible to work out the narial passage in detail, but it enters the hood through the lower limb of the premaxilla, but farther forward than in *L. lambei.* In this species the upper limb of the premaxilla is not so strongly developed posteriorly as in *L. lambei,* but the united bones divide the nasals to their posterior extremity. The posterior end of the lower limb of the premaxilla extends back to beyond the centre of the orbit. The diagonal groove that crosses the lower limb enters the air chamber near its base.

The nasal is broader and occupies a more prominent position on the side of the hood than in *L. lambei* and appears to have flanked the air chamber. There is a moderate-sized opening between the antero-superior edge of the nasal and the upturned lower limb of the premaxilla, but this is partly covered by fingering of bone from the premaxilla. This seems to show conclusively that the openings in the hood represent undeveloped or unossified portions of the bones.

The prefrontal is small and bounds only half of the superior border of the orbit.

The lachrymal is weak and situated well down on the anterior rim of the orbit, but it sends a long, slender tongue of bone up to meet the tip of the prefrontal and just cuts off the premaxilla from taking part in the formation of the orbital rim. Thus the lachrymal, in spite of its slenderness, forms the greater part of the anterior border of the orbit.

The orbit and postorbital vacuity are very large. The postorbital bar is slender.

The maxilla is massive and convex antero-posteriorly on the superior face of its forward half. It is rather broad superiorly to accommodate the swollen lower limb of the premaxilla. There are 39 or 40 vertical rows of teeth.

The dentary does not seem to differ greatly from that of *L. lambei,* but the teeth are slightly broader near the centre, thus giving them a more pointed appearance, and they are slightly notched below. This notching is not well pronounced as in the Hadrosaurinae, but the point of the succeeding tooth fits directly below the enamel crown rather than overlapping it as in the former species.

SKELETON

The fore limb and the pelvic arch with the femur, tibia, and fibula have been prepared, and a section containing the base of the tail has been opened. These with field notes give a fair idea of the more characteristic parts of the skeleton. It is slightly smaller than the type of *Corythosaurus casuarius,* but somewhat larger than the type of *Lambeosaurus lambei.* Field measurements give a total length of 3,000 mm. for the presacral vertebræ and 950 mm. for the scapula and coracoid. The greatest breadth of the scapula is 203 mm.

The humerus is relatively shorter than in *Corythosaurus,* as seen by the table of comparative measurements, but is of massive proportions.

The radial crest is of about the same relative length as in *Corythosaurus,* but is heavier. The width of the bone through the lower end of the radial crest is one-third its total length. It is difficult to give measurements of the fore limbs that indicate their relative proportions since most specimens are more or less crushed. Reference to Plate V, figure 1, which is a photograph of the left limb and the right manus and part of the forearm, gives a good concept of the bones.

The radius and ulna are much longer than the humerus, as is usual in the subfamily. They are of much heavier construction than in *Corythosaurus,* especially so when compared with *C. intermedius.* The olecranon process of the ulna is injured so there is some question as to the exact length of this bone, but otherwise the bones are splendidly preserved.

The manus is proportionately heavier than in *Corythosaurus* and the digits when compared with the metacarpals are longer, especially II and V. Metacarpal II is shorter than III or IV, but digit II is the longest of the series. Metacarpal III does not reach the same height, proximally, as II and IV, but it extends well beyond them distally. The foot is very similar to that of *Parasaurolophus walkeri* Parks (13, Plate VIII) but the phalanges are slightly longer. The proximal end of Metacarpal V is fully as large as that of any of the other metacarpals and this digit is much longer than in *Corythosaurus.* The phalangeal formula is the same as in *Parasaurolophus* and only digits II and III bore hoofs. The triangular form of phalanx 2 of these digits would suggest that these two toes would be turned in toward the body when in use.

Plate VI is a drawing of the pelvic arch and hind limb of the right side. Breaks and crushing of the bones are shown as such and portions of the arch that are hidden by the femur are indicated by the dotted line. The edge of the left ischium shows below the other, but otherwise only the bones from the right side are shown.

The ilium is very different from that of any previously described member of the *Lambeosaurinae.* The postacetabular portion is broader than in *Corythosaurus* (2, Plate XIV) and the preacetabular portion is less pointed, thicker, and less strongly decurved. In its posterior portion it resembles *Hypacrosaurus altispinus* Brown (1, Figure 4), but its anterior process is more like *Edmontosaurus regalis* Lambe, though not triangular in cross-section as in that species. The internal face of the preacetabular process is moderately flat, so far as seen, and at a point near its mid-length it is 40 mm. thick. The process that overhangs the ischiac peduncle is farther forward than in *Corythosaurus,* massive and well buttressed from below. In its posterior portion it extends only slightly beyond the buttress, but the anterior edge overhangs and blends in with the slightly rolled superior margin of the bone.

The pubis is broadly rounded in front and less constricted in its narrower part than in *Corythosaurus.* The peduncle for union with the ischium is of moderate length and narrow and there is a narrow notch between this peduncle and the postpubis. The postpubis is long and well developed. It is 55 mm. wide at the base, from which point it gradually decreases in breadth.

The ischium is slightly sigmoid in outline and more massive than in *Corythosaurus.* The proximal end is broad and the pubic articulation is much broader than the pubic peduncle. The antero-inferior edge is straight for a distance of 260 mm. and near the centre of this is a well-developed ischiatic notch which is partly closed by the forward development of the edge of the bone behind the notch. The antero-inferior edge of the bone behind the notch unites with that of the opposite ischium. This union appears to be natural, though it may be partly due to crushing. In its proximal portion the postero-superior edge of the ischium is moderately thin, but about one-third distant from the proximal end this edge expands into a broad, flat surface and from here distally unites with its fellow. The greatest thickness of the postero-superior edge of the ischium is about one-third distant from the proximal end, where it measures 64 mm. The antero-inferior portion of the bone at this point is 35 mm. in thickness. The antero-superior edge is quite thick just behind the ischic notch, but the rest of this edge of the bone is gently rounded and it does not unite with the opposite ischium except in its distal one-third. The narrowest point is beyond mid-length of the bone. The foot-like expansion is moderately developed and the end is thickened, especially anteriorly.

The femur is relatively short. This shortness is not clearly shown in the drawing because crushing of the greater trochanter has exaggerated the length. It is believed that in life this bone was little longer than the tibia. The proximal end of the bone is broad and the greater trochanter as preserved stands about 60 mm. above the head of the femur. The fourth trochanter is strongly developed and located well down on the bone. The distal condyles are developed well backward, giving a very long articulating surface. The fore and aft width of this distal end (over condyles) measures 270 mm.

The tibia is massive throughout and is almost as long as the femur. The cnemial crest is strongly developed and extends much farther down the anterior face of the bone than in *Corythosaurus.* In this respect it closely resembles the tibia of *Hypacrosaurus altispinus.* In fact the whole limb resembles *Hypacrosaurus* more than *Corythosaurus.* The proximal end of the tibia is 300 mm. in fore and aft diameter, and at a point 300 mm.

from this end it measures 190 mm. It is 100 mm. broad at its narrowest point near the centre of the shaft.

The *fibula* is more massive than in *Corythosaurus* but resembles that of *Hypacrosaurus*.

OSSIFIED TENDONS

Ossified tendons lie along the neural spines of practically all articulated skeletons of hadrosaurs that have been reported, but the writer is not aware of such ossifications having been reported from other parts of the skeleton. In the present specimen there is a well-developed series of ossified tendons running down the front of the femur, from the overhanging process of the ilium to the distal end of the femur and others at right angles to the distal end of the bone. An attempt has been made to show these in the drawing (Plate VI), but it is difficult to show them all as some lie beneath others. Some rock fell during the collection of the specimen and dislodged certain of the tendons so that some are left incomplete. The drawing shows only those that are actually connected.

One tendon reaches the apex of the overhanging process of the ilium and three end somewhat short of this point. Others, which are covered by the rock and skin impression, may have reached equally high. One reaches to above the ilium just ahead of the process and one runs at right angles to these from near the great trochanter to above the ilium. Three rather large tendons lie close to the femur and ahead of these is a bundle of six slightly smaller ones. Only those on the surface are shown in the drawing. In cross-section they vary from flat to oval and the terminal ends are bluntly pointed. Three tendons lie beyond the distal end of the femur at about right angles to the others.

Several ossified tendons are seen in the rock containing the base of the tail and others may be enclosed beneath the skin impression. These do not seem to follow a definite course, though all run diagonally back and down across the vertebræ and one extends to the base of the tail near the first chevron. Nothing can be stated regarding the tendons along the neural spine, for these are covered by rock and skin impression or, as in the dorsal region, were destroyed by erosion before the specimen was discovered.

SKIN IMPRESSION

In those sections that have been prepared the skin impression has been left undisturbed where it was preserved over the skeleton. In the pelvic region blocks of the sandstone, with skin impression, were removed and in other places tunnels were made beneath the impression to show the arch bones. The posterior ribs and that portion in front of the right femur up to the top of the ilium are covered by skin impression. This shows the usual type of small tubercles without differentiation of size or pattern and no limpet-like bosses are seen in any of the integument preserved. The integument seems to have covered the tendons and the femur, without sign of folding, to near its distal end. This would suggest that the femoral part of the limb was not free, but rather that it was largely enclosed within the flank.

The first 4 feet of the base of the tail has been partly prepared. It is covered by skin impression which has not been disturbed. There is some folding of the integument in this region. The tubercles are somewhat larger than those on the flank, but they are not differentiated into patterns and no limpet-like bosses are discernible.

It would seem most likely that if limpet-like bosses or differentiation into patterns were present in *Lambeosaurus* there would be some sign of them in the parts of the integument preserved in this specimen.

Lambeosaurus magnicristatum sp. nov.

Plate VII

Type. No. 8705, Geol. Surv., Canada, consists of skull and greater part of skeleton except left manus and part of forearm, right fore limb, ribs from right side, and some distal caudals. Skull and right ilium only have been prepared. Collected by the writer in 1919.

Horizon. Pale Beds, Belly River series.

Locality. About 3 miles southwest of mouth of Little Sandhill creek, near top of beds.

Specific Characters. Skull moderately massive; hood very long, high and thin superiorly; facial slope gentle anteriorly, then very sharply upturned and thrown strongly forward; upper part of premaxilla expanded to cover narial slit far forward; upper limb of premaxilla developed into very high, thin crest above narial passage; up-turned lower limb of premaxilla very large, strongly swollen and thrown sharply forward; diagonal groove across lower limb not well defined; nasal extending backward as narrow process to flank premaxilla posteriorly; orbit broadly rounded superiorly; prefrontal well developed and flanking lower limb of premaxilla and tip of nasal; ilium of light construction, moderately down-curved and thin interno-externally.

At first sight the skull reminds one of a glorified *Corythosaurus casuarius,* but on closer examination it is seen that the greater part of the long, high crest is made up of the upper limbs of the premaxillæ and that they separate the nasals to their posterior extremity. Also the narial passage enters the hood through the large, swollen, forwardly bent lower limb of the premaxilla. As these characters are typical of *Lambeosaurus* it is referred to that genus even though the crest or hood is so different from that expected. The hood is thick through the up-turned lower limbs of the premaxillæ and the nasals, but above this it is very thin.

The premaxilla is strongly developed and the upper limb bends so far forward as to overhang the beak. It is high, very long, and very thin throughout. This upper limb does not enclose the narial passage, though it comes in contact with it superiorly and may divide the two as it does in *L. lambei.* The upper edge of the anterior portion of the premaxilla is much broader than in *L. clavinitialis* and covers the narial passage far forward. The suture between the upper limb of the premaxilla and the anterior tip of the nasal is not positively determinable because much of the crest was preserved in a thin layer of carbonaceous shale and the bone was not well preserved. This suture is tentatively placed near the anterior tip of the lower limb of the premaxilla. The division between these bones farther back is well defined. Some of the centre of the thin crest had to be restored because the bone, though present, was too rotten to save. The restoration was made over the impression on the hard rock which enclosed the specimen, so there is no doubt as to its accuracy. This high, thin crest is thickened at intervals to give strength, but between these the united bones are very thin.

The nasal is a trifurcate bone. A short antero-inferior branch rests on the frontal, unites with the posterior tip of lower limb of the premaxilla, and is flanked by the up-turned prefrontal. This portion undoubtedly surrounds the downward course of the narial passage. The supero-anterior branch extends far forward as a moderately broad but thin plate of bone and covers the narial passage and air chamber. The posterior branch is a moderate-sized spike which tapers to a blunt point and extends backward to overhang the occiput slightly and flank the thin upper limb of the premaxilla.

The narial passage has not been worked out in detail in this species, but from a study of the contour of the bones and the analogy of other species, it appears to follow a course in the forwardly turned lower limb of the premaxilla to where it comes in contact with the upper limb of this bone, then being sharply deflected backward. From this point it continues backward in a horizontal plane, and is covered by the supero-anterior branch of the nasal. At the bifurcation of the anterior branches of the nasal the passage is again sharply deflected and continues forward and downward to the internal naris. Thus there are two U-shaped bends in the narial passage. Specimen No. 8631 shows that a somewhat similar course is followed in *L. clavinitialis,* though the fore and aft length is not nearly so great or not so nearly horizontal and thus the deflections are not so sharp.

The prefrontal forms the anterior half of the superior portion of the orbit and is strongly developed and upturned to flank the posterior portion of the lower limb of the premaxilla and antero-inferior branch of the nasal.

The lachrymal is similar to that of *L. clavinitialis* and the long, slender tongue of bone that extends upwards to meet the prefrontal just barely cuts off the premaxilla from the orbital rim.

The jugal does not differ greatly from that of *L. clavinitialis,* but the postorbital bar extends up to meet an anterior process from the squamosal.

The *maxilla* is moderatly massive and convex in front of the jugal overlap as in other species of the genus. It is not possible to give a detailed description of the teeth or the number or rows.

The skeleton has not yet been prepared except the right ilium, but it is known that the forearm is much longer than the humerus. Field measurements give the length of the femur as 1,090 mm. which is 70 mm. longer than that bone in *L. clavinitialis,* though the skull of the latter species is only slightly shorter.

The ilium is of much more slender construction and more down-curved than that of *L. clavinitialis* and both the anterior and posterior blades are thin. When compared with the former species, the great difference in the ilium and helmet-like crest suggests a distinct genus, but it is thought best to regard this new form as belonging to *Lambeosaurus* because of the analogy of the premaxillæ nasals and narial passages.

Comparative Measurements of Skulls

	Corythosaurus casuarius Type A.M. 5240	*Corythosaurus excavatus* G.S.C. 8676	*Corythosaurus intermedius* G.S.C. 8704	*Tetragonosaurus cranibrevis* Type G.S.C. 8633	*Lambeosaurus lambei* Type G.S.C. 2869	*Lambeosaurus clavinitialis* Type G.S.C. 8703	*Lambeosaurus magnicristatum* Type G.S.C. 8705
	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.
Length between vertical lines	812	632	?680	510	710	775	800
Tip of premaxilla to paraoccipital	....	660	?740	530	670	790	790
Tip of premaxilla to posterior tip of nasal	837	672	?680	470	822	775	850
Tip of premaxilla to tip of upper limb	....	662	720+	475	822	775	850
Tip of premaxilla to tip of lower limb	....	580	635	420	550	690	710
Length of cranium behind hood, midline	....	120	145	118	125	130	135
Front of hood to back of cranium, midline	....	380	385	300	340	410	690
Front of hood to back of paraoccipital	....	410	?425	345	....	448	730
Height of head to top of hood	708	550	665+	380	610	640	815
From maxillary teeth to top of hood	....	450	560+	275	370	530	660
Breadth of skull across orbits	....	150	176	138	150	145	160
Breadth of hood through lower limbs	....	115	127	90	117	137	180
Length of hood, fore and aft	....	320	275	200	185	290	745
Height of hood, above orbit	....	240	310+	105	302	275	395
Length of frontal on midline	....	32	58	43	....	45	....
Greatest breadth of united frontals	....	116	130	95	118	....	....
Length of nasal	....	250	220	175	340	260	490
Greatest height of nasal	....	195	240+	50	175	260	....
Length of quadrate	....	....	280	220	251	295	290
Length of jugal	....	....	250	215	240	260	260
Length of maxilla	....	280	303	240	284	310	....
Length of dental series of maxilla	....	240	285	215	253	290	....
Length of dentary	....	403	450	350	440	500	450
Length of edentulous portion	....	145	180	125	170	184	....

Measurements of Mandible

	Corythosaurus excavatus G.S.C. 8676	*Tetragonosaurus cranibrevis* G.S.C. 8633	*Lambeosaurus clavinitialis* G.S.C. 8703
	Mm.	Mm.	Mm.
Breadth of predentary, anteriorly	155	....	....
Breadth of predentary, posteriorly	150	....	....
Length of predentary, externally	110	....	....
Length of main portion at centre	51	....	....
Greatest thickness of main portion	16	....	....
Length of dentary	403	350	510
Length from tip to back of dental magazine	370	320	467
Length from tip to front of dental magazine	145	125	184
Length of symphysis	75	65	86
Inner face to outside of coronoid	87	77	97
Thickness of dentary near centre	48	40	52
Height of dentary near centre	100	93	120
Height just in front of teeth	64	72	85
Greatest depth of dental magazine	77	77	98
Length of dental magazine	250	220	305

Comparative Measurement of Skeletons

	Corythosaurus casuarius Brown A.M.N.H. specimens	*Corythosaurus casuarius* G.S.C. 8532	*Corythosaurus excavatus* G.S.C. 8676	*Corythosaurus intermedius* Roy. Ont. Mus. mounted skeleton	*Corythosaurus intermedius* G.S.C. 8704	*Lambeosaurus clavinitialis* G.S.C. 8703	*Parasaurolophus walkeri* Parks Type specimen
	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.
Length, scapula	890	810	660	930	820	?850	940
Width, blade of scapula	200	175	150	....	....	203	248
Length, humerus	585[1]	530	450	540	460	520	520
Length, radial crest	310	280	260	....	....	298	310
Length, ulna	660	650+	570	700	670	660	560
Length, radius	635	640	535	635	605	616	485
Length, Mc and digit III	410	375	320	390	330	415	....
Length, Mc II	216	215	185	220	....	220	173
Length, Mc III	260	255	215	260	....	265	208
Length, Mc IV	253	240	208	240	....	250	195
Length, Mc V	102	90	....	....	....	100	90
Illium, length	1,035	....	....	....	....	1,035	1,015
Illium, height, anterior peduncle	205	....	....	....	....	245	....
Pubis, complete length	1,000	....	....	....	....	890	?894
Pubis, length, anterior blade	490	....	....	....	....	450	516
Pubis, depth, anterior blade	270	....	....	....	....	230	260
Pubis, narrowest depth, blade	100	....	....	....	....	100	....
Ischium, greatest length	1,030	....	890	1,065	....	1,070	....
Length, terminal foot	220	....	....	....	....	180	....
Least vertical diameter	60	....	....	....	....	68	....
Length, femur	1,080	1,040	890	1,050	....	1,020	1,032
Length, tibia	1,000	980	813	990	....	1,000	....
Length, fibula	950	....	775	940	....	940	....
Length, Mt. II	310	....	270	....	....	....	....
Length, Mt. III	380	....	320	....	....	....	....
Length, Mt. IV	320	....	270	....	....	300	....

[1]Measurements of the fore limb of this species are taken from a second specimen which Mr. Brown states is the same size as the type.

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PLATE I

Corythosaurus excavatus Gilmore. Plesiotype No. 8676, Geol. Surv., Canada, $\frac{1}{7}$ natural size.

Figure 1. Disarticulated hood showing internal view of right premaxilla and nasal and external view of left premaxilla with part of narial passage exposed. L. N. left nasal (misplaced), N. nasal, Nar. P. narial passage, Pmx. premaxilla, $Pmx.^1$ tip of lower limb of premaxilla. (Negative No. 77068.)

Figure 2. Mounted skull and jaws. D. dentary, J. jugal, Mx. maxilla, Pal. palatine, Pd. predentary, Po. postorbital, Prf. prefrontal, Pt. pterygoid, P.V. prevomer, Q. quadrate, Sq. squamosal, Sur. surangular. (Negative No. 77939.)

PLATE I

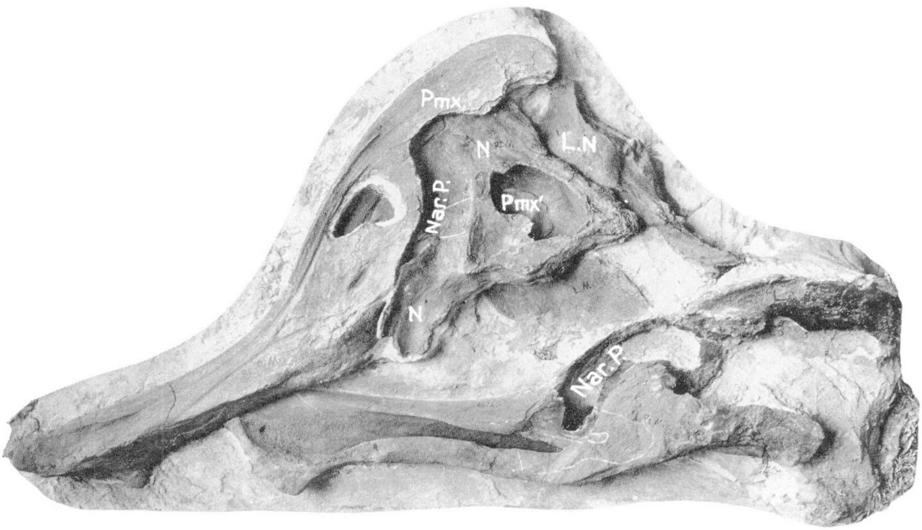


Fig. 1

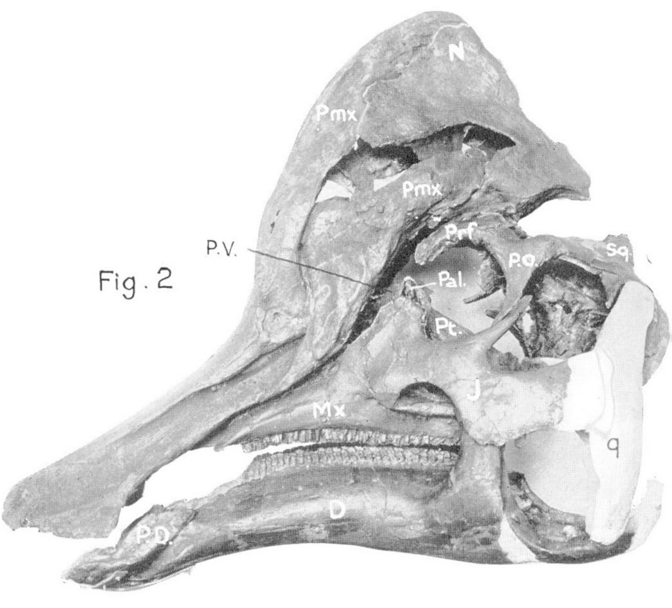


Fig. 2

PLATE II

Corythosaurus excavatus Gilmore. Plesiotype No. 8676, Geol. Surv., Canada.

Figure 1. Articulated dentaries and predentary with impression of horny beak. H.B. $\frac{1}{4}$ natural size. (Negative No. 77488.)

Figure 2. Inferior view of predentary and tips of dentaries. $\frac{2}{5}$ natural size. (Negative No. 77524.)

Figure 3. Dental magazine, internal view. $\frac{2}{5}$ natural size. (Negative No. 77524.)

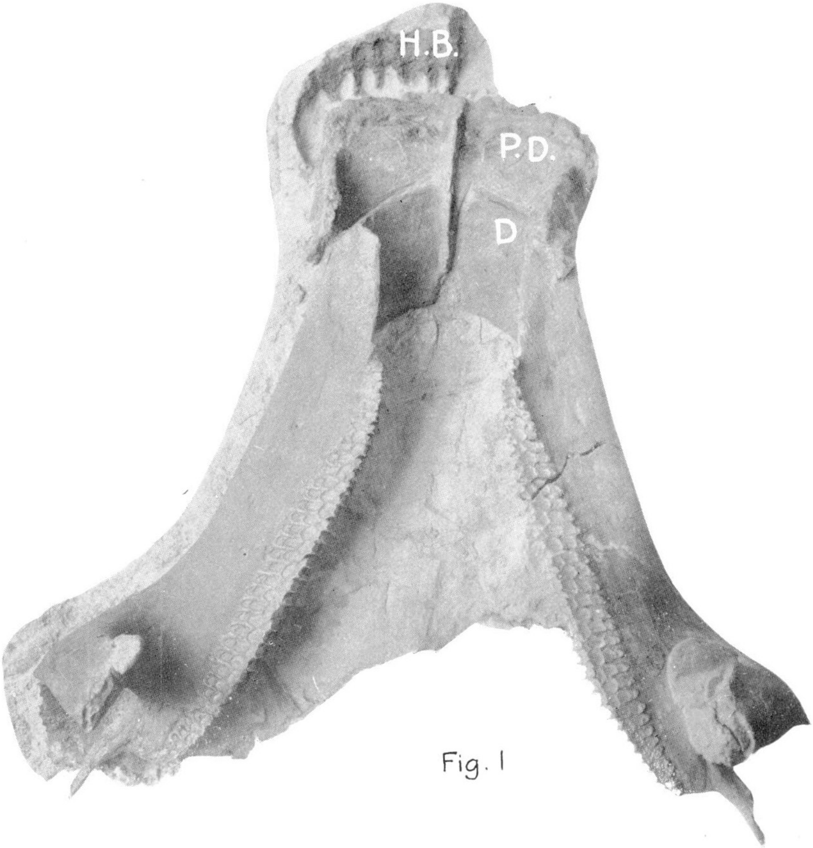


Fig. 1

Fig. 2

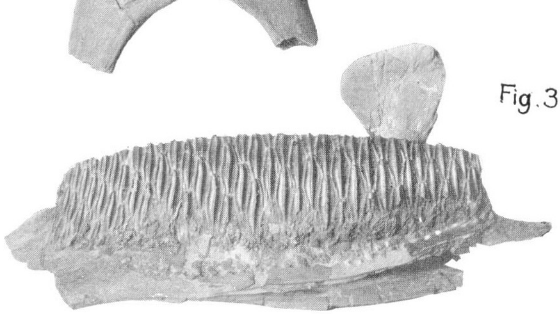


Fig. 3

PLATE III

Figure 1. *Corythosaurus excavatus* Gilmore. Plesiotype No. 8676. Disarticulated left nasal, $\frac{1}{3}$ natural size. (Negative No. 77486.)

Figure 2. *Corythosaurus intermedius* Parks. Plesiotype No. 8704, Geol. Surv., Canada. Skull and jaws. $\frac{1}{7}$ natural size.

Fig. 1

PLATE IV

Figure 1. *Tetragonosaurus cranibrevis*. Type No. 8633, Geol. Surv., Canada. Skull and jaw. $\frac{1}{7}$ natural size. (Negative No. 76987.)

Figure 2. *Lambeosaurus clavinitialis*. Type No. 8703, Geol. Surv., Canada. Skull and jaws. $\frac{1}{7}$ natural size. (Negative No. 77487.)

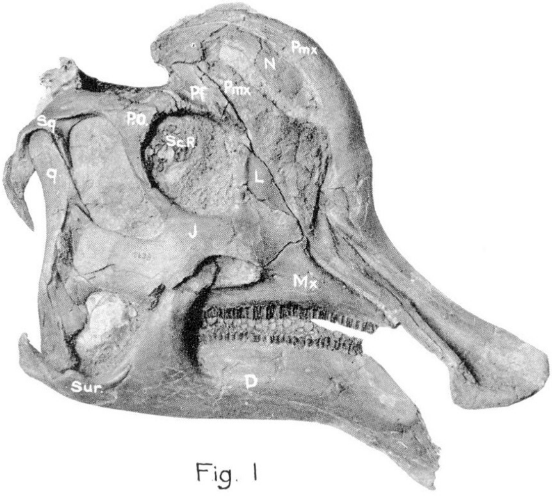


Fig. 1

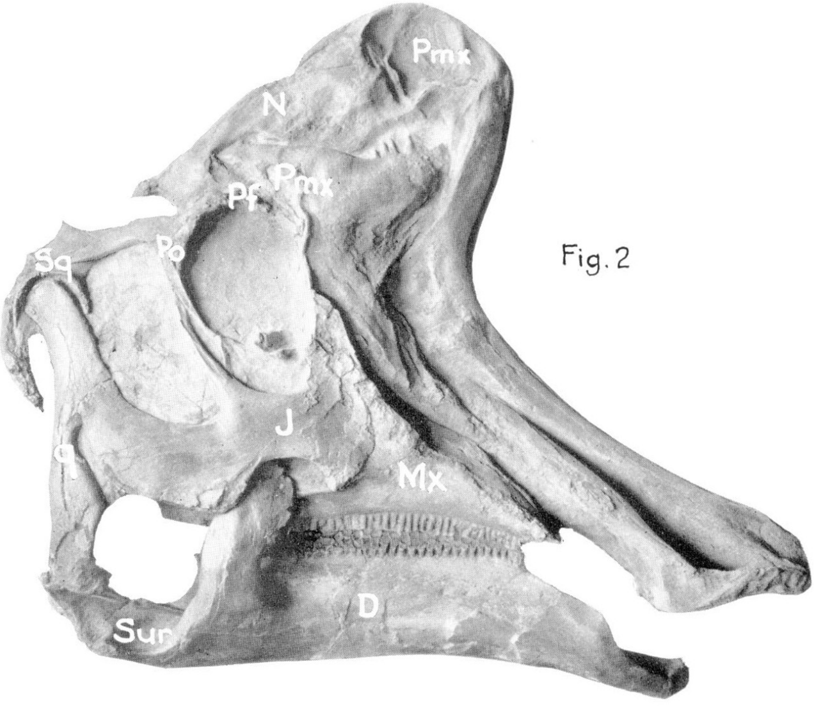


Fig. 2

PLATE V

Figure 1. *Lambeosaurus clavinitialis*. Type No. 8703, Geol. Surv., Canada. Left fore limb and right manus. $\frac{1}{9}$ natural size. (Negative No. 77937.)

Figure 2. *Corythosaurus excavatus* Gilmore. No. 8676. Geol. Surv., Canada. Impression of integument from upper side of forearm. $\frac{1}{4}$ natural size. (Negative No. 77065).

PLATE V

Fig. 1

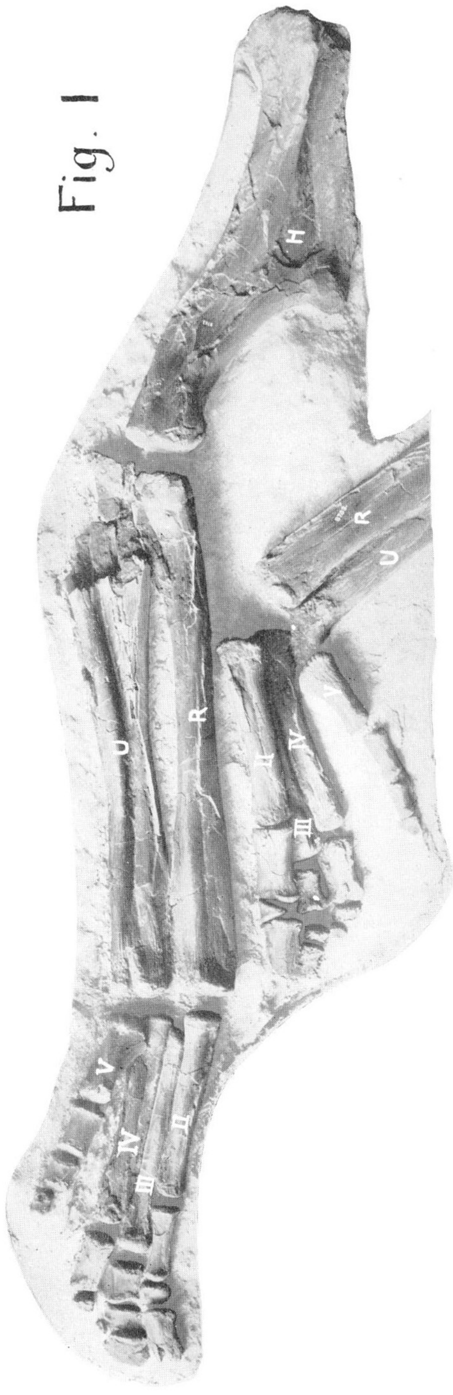


Fig. 2

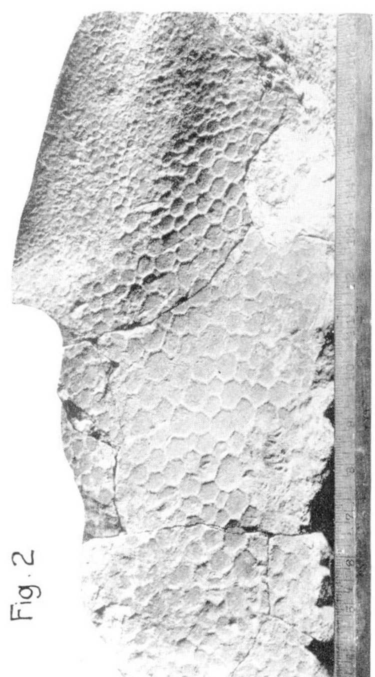


PLATE VI

Lambeosaurus clavinitialis. Type No. 8703, Geol. Surv., Canada. Pelvic arch, right femur, tibia and fibula, and ossified tendons. $\frac{1}{12}$ natural size.

Plate VI

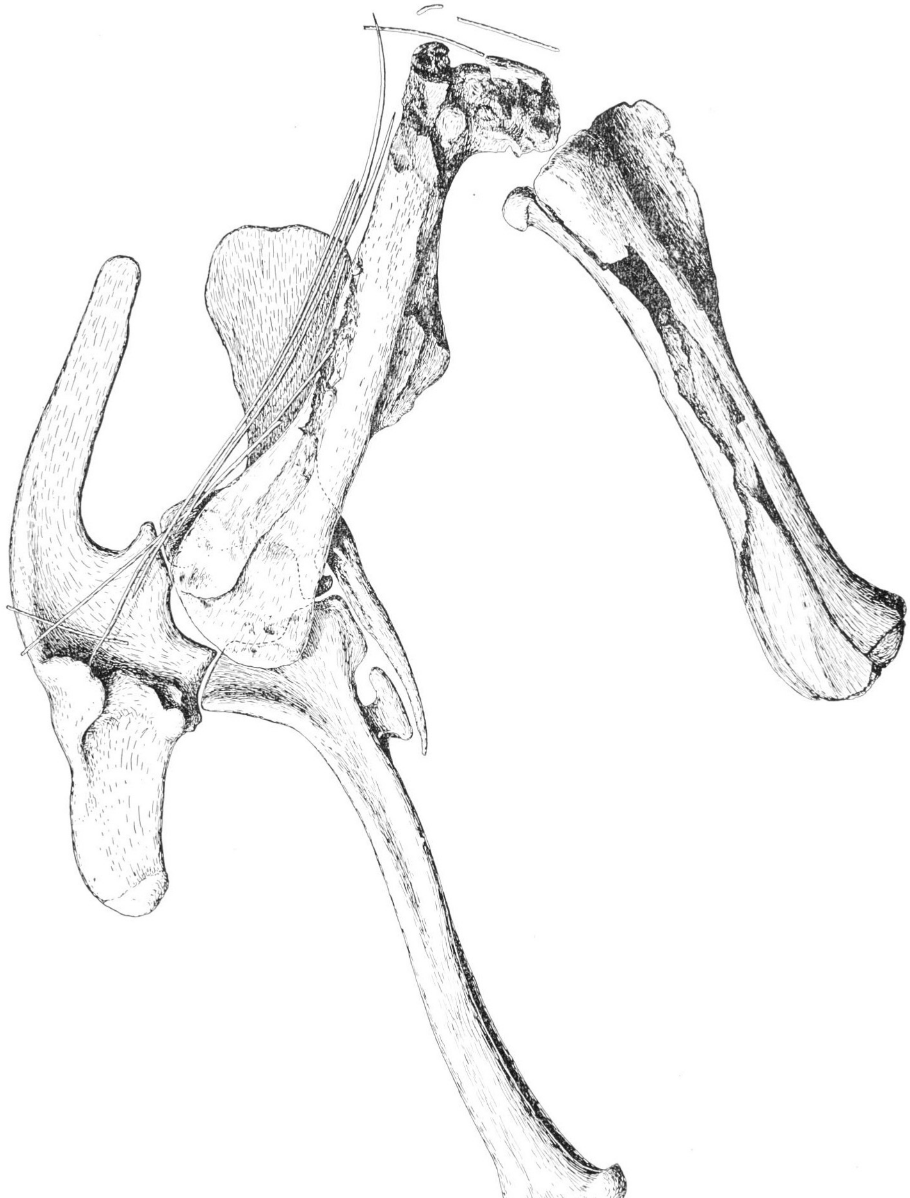
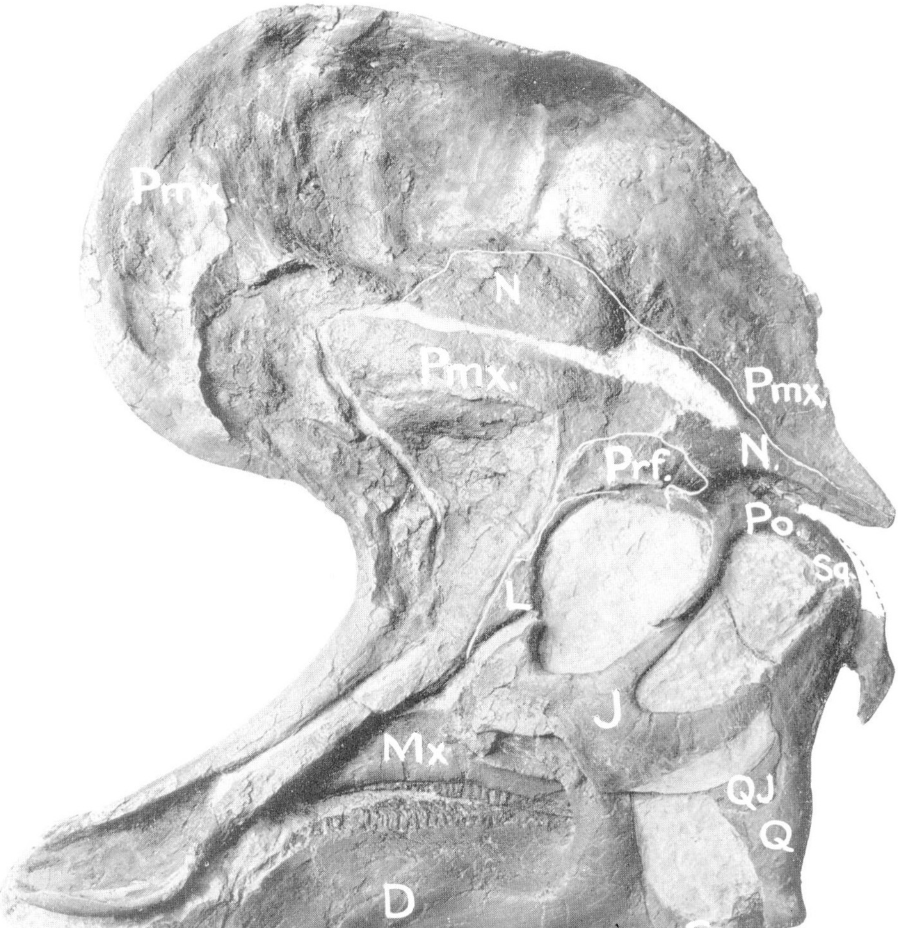


PLATE VII

Lambeosaurus magnicristatum. Type No. 8705, Geol. Surv., Canada. Skull and jaws from the left side. About $\frac{1}{7}$ natural size. (Negative No. 78468.)

PLATE VII



MUSCULATURE AND FUNCTION IN THE CERATOPSIA

By Loris S. Russell

Illustrations

The present paper is the outcome of an attempt to construct a life model of the horned dinosaur *Chasmosaurus belli* (Lambe). It was decided to prepare this model by a detailed reconstruction of the muscular system, a method that has been used in dinosaur restorations by Lull, Osborn, Gregory, and Romer. In addition to studying the methods and results of these workers, the writer made a complete muscular dissection of *Sphenodon,* using the monograph of Osawa (5). A partial dissection of the alligator was also made, to supplement the excellent account of the pelvic region given by Romer (6). The muscular anatomy of the bird was studied in Shufeldt's text (8) on the raven, which is very complete but lacks the comparative viewpoint. With this information obtained, a scale model of the *Chasmosaurus* skeleton was prepared, and upon this the principal muscles were reconstructed. The finished restoration, with its clothing of integument, was figured recently by Lull (3, Plate 17).

Some students think that such restoration methods are unnecessarily elaborate and probably no more accurate in results than the simpler process of modelling the animal directly from the skeleton. The writer admits that muscular reconstructions are more or less controlled hypotheses, having a debatable degree of accuracy, but it is contended that the restorations made by this method are at least plausible and life-like. More important, however, than the finished model are the ideas regarding movement and function that emerge during the reconstruction. It is the purpose of this paper to describe the probable form and function of the more important muscles in *Chasmosaurus* and other ceratopsians, and to deduce therefrom certain conclusions regarding the palæobiology of the horned dinosaurs.

The writer is indebted to Professor R. S. Lull for helpful criticisms.

THE HEAD

Lull (2) has given a very good account of the probable cranial musculature in *Triceratops.* This genus is the end member of the series, with certain specializations carried to the extreme. *Chasmosaurus* offers a sort of intermediate stage in the evolution of the ceratopsian skull.

Buccinator (Figures 8, 9, *b*). A sheet-like muscle, which extends vertically from maxilla to dentary, with a possible attachment to the angle of the mouth. In most genera the insertion ridge on the dentary extends almost from coronoid to predentary. Lull (1) interpreted this to mean that the oral opening was restricted to the premaxillary region. In his recent revision (3) he has modified this interpretation somewhat. The gape is extended back almost to the articulation of the jaw, thus eliminating the stiff integument from the cheek envelope, which is formed by the buccinator muscle. Nevertheless, the actual oral opening is still restricted to the premaxillary region. In the writer's restoration it was assumed, perhaps incorrectly, that the integument of this region was sufficiently flexible to form the outer layer of the cheek.

Parieto-mandibularis (depressor mandibuli of Lull) (Figure 8, *pm*). This corresponds, in function at least, to the digastricus of mammals. Lull postulated the origin from the posterior surface of the quadrate. In some ceratopsian skulls there is a ridge on the back of this bone, but usually it is quite smooth. It seems more probable that the origin was from a rather large, often vague area on squamosal and parietal, near the extremity of the paroccipital process (Figure 7, *pm*?). Lull assigned this area to the latissimus dorsi. If it was the origin of the parieto-mandibularis the fibres would converge downward to the rather restricted insertion area at the posterior end of the mandible, mostly on the articular. As noted below, the latissimus dorsi almost certainly did not reach the skull.

Pterygoidei. These are not clearly definable in *Chasmosaurus*. The internal pterygoid probably was large, as it had a well-developed insertion along the ventral margin of the posterior half of the mandible.

Massetericus (Figure 9, *m.*). This extended from the inner surface of the jugal to the outside of the coronoid process. It probably mingled fibres with the temporalis.

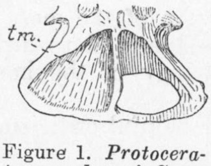


Figure 1. ***Protoceratops andrewsi*** Gregory and Granger, dorsal view of crest, drawn from a cast, with temporalis muscle (*tm.*) restored; X $\frac{1}{20}$.

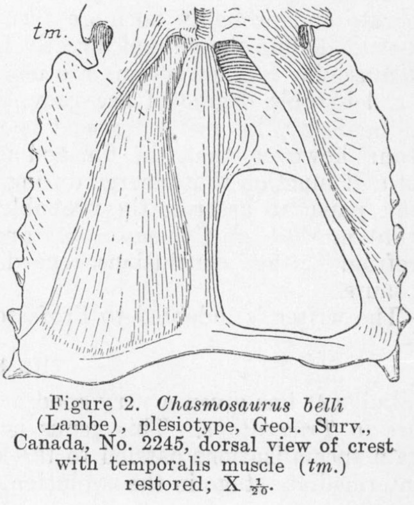


Figure 2. ***Chasmosaurus belli*** (Lambe), plesiotype, Geol. Surv., Canada, No. 2245, dorsal view of crest with temporalis muscle (*tm.*) restored; X $\frac{1}{20}$.

Temporalis (Figures 1-6, 8, *tm.*). This was the principal agent in the closing of the ceratopsian jaws. In *Protoceratops* (Figure 1) it was a broad, fan-like sheet, covering almost the entire parietal portion of the crest, passing forward through the supratemporal opening, and attaching to the inner side of the coronoid process. The backward extension of the crest in *Chasmosaurus* (Figure 2) greatly lengthened this muscle, with corresponding increase in contractile power, but there was no essential change from the condition in *Protoceratops*. *Styracosaurus* (Figure 3) and *Centrosaurus* (Figure 4) have the origin area more restricted, owing to the smaller size of the crest and its fenestræ. The area of the muscle is clearly defined in *Styracosaurus*; on the medial side there is an unobstructed

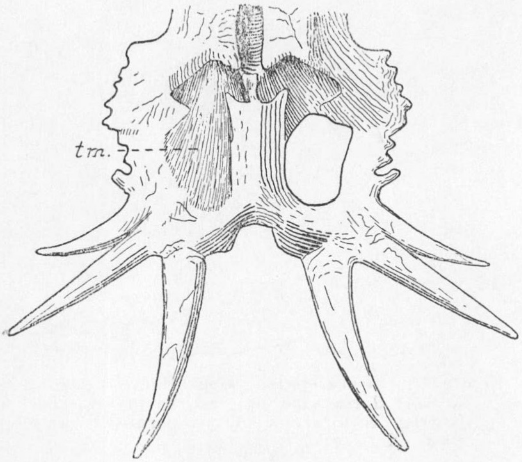


Figure 3. *Styracosaurus albertensis* Lambe, holotype, Geol. Surv., Canada, No. 344, dorsal view of crest with temporalis muscle (*tm.*) restored; X $\frac{1}{20}$.

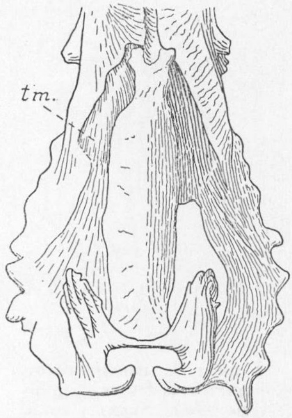


Figure 4. *Centrosaurus flexus* (Brown), Geol. Surv., Canada, No. 348, dorsal view of crest, with temporalis muscle (*tm.*) restored, also some correction for distortion; X $\frac{1}{20}$.

channel from fenestra to supratemporal opening, but more laterally the muscle is cut off abruptly along a transverse line. Similar conditions appear in *Centrosaurus* and the somewhat later *Anchiceratops* (Figue 5), but here the posterior portion of the muscle appears to have been thin and membranous. Finally, in *Triceratops* (Figure 6), the sharp line of origin first seen in *Styracosaurus* has become the posterior margin of the supratemporal opening, indicating that the temporalis muscle was restricted to that vacuity.

It is evident, therefore, that the crest or frill of the ceratopsians was primarily developed to extend the area of origin, and the size, of the temporalis muscle. This seems to have been the entire function of the crest in *Protoceratops*. In *Chasmosaurus* and *Torosaurus* this development reached its maxima, with the crest retaining large vacuities to permit expansion of the muscle mass. The blunt marginal serrations and spikes of the *Chasmosaurus* crest seem inadequate concessions to defense. Contemporaries of this genus, however, had already developed the defensive possibilities of the structure. In *Styracosaurus* the six great radiating spikes served this purpose, although the arrangement seems poor mechanically. The crest proper is shorter and heavier, and the fenestræ smaller, than in *Chasmosaurus*. Similar strengthening occurs in *Centrosaurus*. In this genus there are hook-like processes extending from the posterior margin of the crest forward over the fenestræ. Although these processes show considerable individual or specific variation, they seem to have formed a protection for the fenestræ, which were the weakest parts of the crest, closed as they were only by the temporalis muscle. The defensive function becomes completely dominant in the crest of *Triceratops,* but at the cost of reduction of the temporalis muscle.

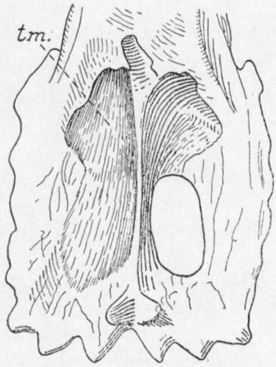


Figure 5. *Anchiceratops longirostris* Sternberg, holotype, Geol. Surv., Canada. No. 8535, dorsal view of crest with temporalis muscle (*tm.*) restored; X $\frac{1}{20}$.

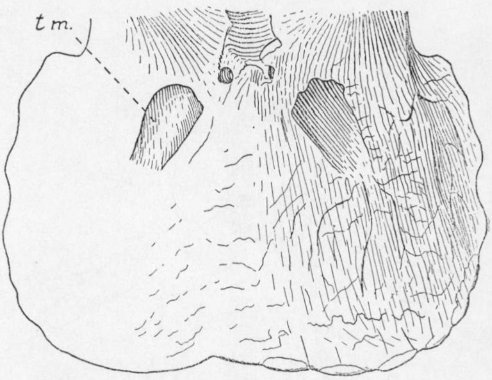


Figure 6. *Triceratops* sp., Geol. Surv., Canada, No. 8741, dorsal view of crest, party restored, showing restoration of temporalis muscle (*tm.*); X $\frac{1}{20}$.

With such development of the temporalis muscle the ceratopsian mandible must have been capable of closing with great force. Tait and Brown (10) have suggested that the beaked jaws were used to shear off small tree trunks. No doubt the necessary strength was there, if the head could have been brought into the required position. In a more normal posture the hooked beak, backed by the powerful jaw muscles, would have been a very efficient organ for tearing off branches or grubbing up roots.

THE NECK

The muscles of this region may be divided into two groups, those having attachment to the fore limb, and those that are anterior continuations of the trunk muscles. Only one of the former group will be discussed here. Lull (2) has described the muscle attachments visible on the posteroventral surface of the skull in *Triceratops.* The writer accepts the various attachment areas recognized by Lull, but differs considerably in the identification of the particular muscle concerned.

Capiti-dorsi-clavicularis (trapezius group of mammals) (Figure 9, *cdc.).* The long median groove on the ventral surface of the parietal in

Triceratops was identified by Lull as part of the origin area of the complexus or longissimus dorsi. This muscle, however, usually lies beneath, and lateral to, the cranial segment of the capiti-dorsi-clavicularis. An elongate attachment area like the one in *Triceratops* particularly suggests a sheet-like muscle, which is the usual form of the capiti-dorsi-clavicularis. In *Chasmosaurus* (Figure 7, *cdc.*), however, the corresponding area is sub-circular in shape, and is confined to the basal portion of the parietal. In *Styracosaurus, Centrosaurus,* and *Anchiceratops* the area is poorly defined, but seems to extend considerably back along the median line of the crest, as in *Triceratops*. The insertion of this muscle, in the absence of a clavicle, was probably on the anterodorsal angle of the scapula.

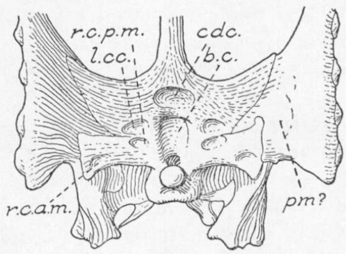


Figure 7. *Chasmosaurus belli* (Lambe), plesiotype, Geol. Surv., Canada, No. 2280, posterior view of occipital region, showing muscle attachments: *bc.*, biventor cervicus; *cdc.*, capiti-dorsi-clavicularis; *l.c.c.*, longissimus cervico-capitis; *pm?*, parieto-mandibularis?; *r.c.a.m.*, rectus capitis anticus minor; *r.c.p.m.*, rectus capitis posticus major; X $\frac{1}{20}$.

Biventor cervicis (spino-occipitalis). On the skull of *Chasmosaurus* there is an ovoid depression (Figure 7, *b.c.*) just above the foramen magnum, and below the attachment pit of the capiti-dorsi-clavicularis. The writer identifies this as the common insertion area of the biventor cerivicis muscles. The corresponding area is single in *Centrosaurus* and *Anchiceratops*, paired in *Styracosaurus* and *Triceratops*. Lull included these pits in the attachment area of the "complexus".

Longissimus cervico-capitis (complexus?). On the *Chasmosaurus* skull there are two ovoid areas situated on the parietal and exoccipital lateral to the biventor cervicis pit. The upper of these two depressions (Figure 7, *l.cc.*) may be assigned to the longissimus cervico-capitis muscle, one branch of the longissimus dorsi. In *Styracosaurus, Centrosaurus,* and *Anchiceratops* the two depressions are more or less subtrigonal in shape, and lie along the dorsal margin of the paroccipital process. *Triceratops* has a single, ovoid excavation in this region.

Rectus capitis posticus major. To this muscle the writer assigns the lower or inner one (Figure 7, *r.c.p.m.*) of the two depressions mentioned above. In *Triceratops* there appears to have been a common insertion with the longissimus cervico-capitis.

Rectus capitis anticus minor. A shallow depression (Figure 7, *r.c.a.m.*) in the lower distal angle of the exoccipital in *Chasmosaurus* probably represents the insertion area of this muscle. The area is not well defined in other forms examined.

Two other muscle attachments were noted by Lull in *Triceratops*. There is a small ovoid one well up on the parietal, near the squamosal suture. This was assigned with question to the levator scapulæ. It seems much more probable, however, that this muscle had its normal origin from the anterior cervicals. The writer is unable to suggest the identity of the attachment in question. Lull also noted the large area on the squamosal and exoccipital which he ascribed to the litissimus dorsi. Professor Lull[1] now agrees that this muscle did not extend to the head, but he still considers the attachment area as belonging to a neck muscle. The writer, as noted above, regards it as the probable origin of the parieto-mandibularis.

The pronounced attachment areas on the back of the ceratopsian skull indicate powerful neck muscles. Their function has been discussed by Lull (2) and by Tait and Brown (10). The latter authors conclude that the skull was capable of rotation on the longitudinal axis through angles up to 90 degrees from the vertical. Both Nopcsa (4, page 69) and Lull (3, page 22) reject this view, and to the present writer also it appears somewhat extreme. The ceratopsian neck is rather short to allow the necessary play of the cervico-cranial muscles. No doubt some rotation of the skull was possible, as well as up and down, and side to side, movement. Nevertheless, the functional adaptation of the jaws and crest can be explained without postulating marked rotation at the atlanto-occipital joint.

It should be noted that muscular attachments are not recognized on the posterior part of the ventral surface of the crest. Some restorations of ceratopsians show the lower side of the crest attached for its entire length to the neck. There is no direct evidence for this interpretation, and many skulls show subcutaneous vascular grooves in this region of the crest. Such an attachment would interfere seriously with the free movement of the head and crest.

THE TRUNK

There is not much direct evidence on the muscles of this region in ceratopsians. The *longissimus dorsi* (Figure 9, *lg. d.*) must have been large and powerful, reinforced by ossified tendons in the lumbar region. The *rectus abdominis* (Figure 9, *r.*) must have been rather attenuate posteriorly, as it had to stretch from the posterior ribs to the distal portion of the ischium.

FORE LIMB

It is not proposed here to attempt the description of all of the limb muscles, but only those having a direct bearing on the functional adaptations of the limbs.

Latissimus dorsi (Figures 8, 9, *l.d.*). This was a large, triangular sheet, originating from the spines of the anterior dorsal vertebræ about as far back as the twelfth. It converged downward and was inserted in the ulnar ridge and tuberosity of the humerus. Owing to the peculiar position of the humerus, this muscle served to rotate the limb, as well as to flex the shoulder joint.

"Levator scapulæ" (Figure 8, *l. s.*) (not the levator scapulæ or serratus cervicus of mammals). An elongate muscle that extended from the side of one or more cervical vertebræ to the coracoid border of the scapula. There may have been a ventral branch, corresponding to the levator claviculæ. Owing to the marked backward inclination of the scapula, the levator action of this muscle must have been rather ineffective.

[1] Personal communication.

Pectoralis (Figure 8, *p.*). This was probably the most powerful muscle of the brachium. It originated from the coracoid, sternum, and perhaps the ventral portions of the anterior ribs, and converged to the radial tuberosity of the humerus. The strong development of radial crest and tuberosity indicates good mechanical advantage for this muscle. It served, as it were, to pull down the distal end of the humerus, thus actually elevating the trunk.

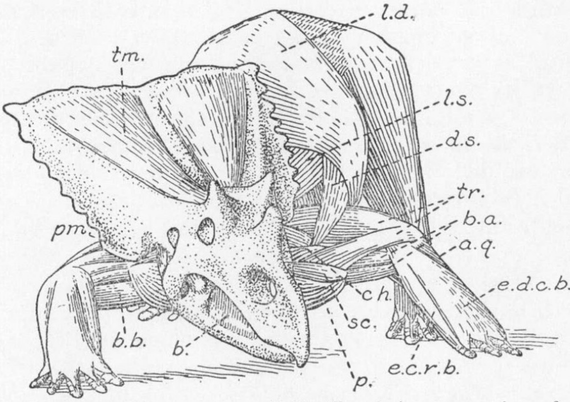


Figure 8. *Chasmosaurus belli* (Lambe), restoration of the musculature, anterior view; for names of muscles *See* under Figure 9; X

Dorsalis scapulæ (presumably equivalent to the scapular portion of the deltoid) (Figure 8, *d. s.*). This is believed to have originated from the external surface of the scapula dorsal to a low, oblique ridge, which runs from the posterodorsal to the anteroventral angle of the bone. The insertion apparently was on the dorsal (extensor) side of the humerus, near the base of the radial tuberosity. Probably not a very powerful muscle, it served to flex the shoulder joint and rotate the humerus.

Scapulo-humeralis posterior (teres major). It appears that this muscle originated from the external surface of the scapula ventral to the ridge described under dorsalis scapulæ, and was inserted in the ulnar tuberosity of the humerus. It served to adduct the humerus, and, with the dorsalis scapulæ, to flex the shoulder joint without rotation.

Brachialis anticus (humero-antibrachialis) (Figure 8, *b.a.*). There are two divisions of this muscle in *Sphenodon,* and probably there were two in the ceratopsians. The origin of one branch may be located in the depression on the flexor side of the humerus, at the base of the radial tuberosity. The other division probably originated from the ridge-like margin of the humerus distal to the radial tuberosity. The insertion would be on the preaxial side of the radius and ulna, near their proximal extremities. The function was essentially the same as that of the biceps.

Biceps brachii (coraco-antibrachialis) (Figure 8, *b.b.*). This muscle ran along the flexor side of the humerus from coracoid to proximal ends of radius and ulna. It is difficult to estimate the probable size, but as it was the main flexor of the limb, it must have been large.

Triceps (anconaeus) (Figure 8, *tr.*). This probably had four origins, one from the anterodorsal margin of the scapula, one from the postglenoid margin of the coracoid, and one from each side of the humerus. These all converged on the olecranon process of the ulna, forming a powerful extensor of the antibrachium.

All recent students of the Ceratopsia are agreed that the humerus was normally borne in a more or less horizontal position. In conjunction with this interpretation the radius and ulna are usually placed nearly vertical, making an angle of 90 degrees or less with the humerus. This, however, is the position of extreme flexion; that the limb was capable of marked extension is shown by the strong olecranon process of the ulna and the large olecranon fossa of the humerus. Probably the greatest flexion occurred as the limb reached the forward position. Then the thrust to the body would be given by rotation and adduction of the humerus, with extension of the elbow joint. In the forward stroke the limb would be lifted clear by flexion of the shoulder joint and extension of the limb.

HIND LIMB

The pelvic musculature in the ornithischian dinosaurs has been reconstructed by Romer (7), with special reference to the ornithopod *Thescelosaurus*. This form is very generalized compared with the ceratopsians, and the different structure of the pelvis no doubt was accompanied by differences in musculature.

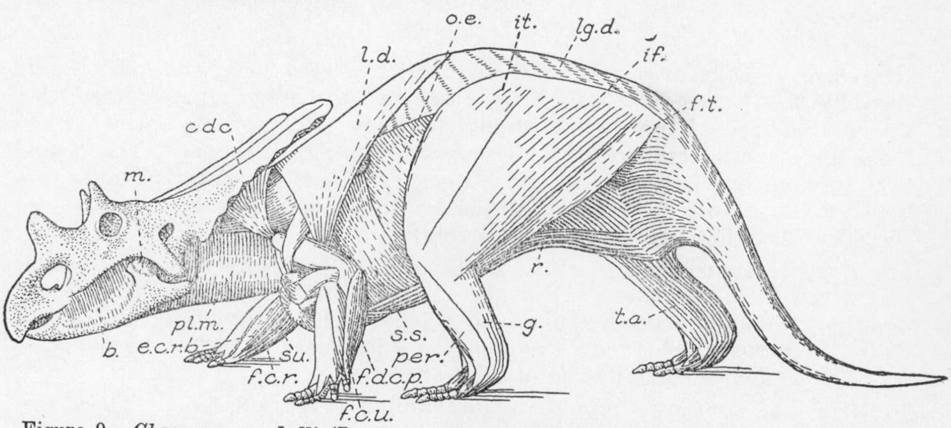


Figure 9. ***Chasmosaurus belli*** (Lambe), restoration of the musculature, left lateral view: *b.*, buccinator; *b.a.*, brachialis anticus; *b.b.*, biceps brachii; *cdc.*, capiti-dorsi-clavicularis; ***ch.***, cleidohumeralis; ***d.s.***, dorsalis scapulæ; ***e.c.r.b.***, extensor carpi radialis brevis; ***e.d.c.b.***, extensor digitorum communis brevis; *f.c.r.*, flexor carpi radialis; *f.c.u.*, flexor carpi ulnaris; *f.d.c.p.*, flexor digitorum communis profundus; *f.t.*, flexor tibialis; *g*, gastrocnemius; *if.*, ilio-fibularis; ***it.***, ilio-tibialis; *l.d.*, latissimus dorsi; *lg. d.*, longissimus dorsi; ***l.s.***, "levator scapulæ;" ***m.***, massetericus; ***o.e.***, obliquus externus; ***p.***, pectoralis; ***per.***, peroneus; ***pl.m.***, platysma myoides; ***pm.***, parieto-mandibularis; ***r.***, rectus; ***sc.***, supracoracoideus; ***ss.***, serratus superficialis; ***su.***, supinator; ***t.a.***, tibialis anticus; ***tm.***, temporalis; ***tr.***, triceps; X $\frac{1}{30}$.

Ilio-tibialis (rectus femoris of mammals) (Figure 9, *it.*). The probable origin of this muscle was from the dorsolateral margin of the ilium, from the anterior end to the so-called anti-trochanter. The muscle would traverse the knee joint and be inserted in the head of the tibia. This was the principal extensor of the knee joint and apparently a very powerful muscle. It was reinforced by the femoro-tibialis, corresponding to the mammalian vasti.

Ilio-fibularis (Figure 9, *if.*). This is the functional equivalent, at least, of the mammalian biceps femoris, although the origin is different. In ceratopsians the origin probably was from the dorsolateral border of the ilium, posterior to the antitrochanter. Such an origin implies a muscle almost as large as the ilio-tibialis. The insertion was on the external side of the fibula, near the proximal end. This was one of the principal flexors of the knee joint, but also served to rotate the lower part of the limb somewhat outward.

Flexor tibialis (ilio-flexorius, ischio-flexorius) (Figure 9, *f.t.*). This is a single muscle in *Sphenodon*, incompletely separate from the pubo-ischio-tibialis (gracilis). In the crocodiles (6) it is split into a confusing series of slips. Romer (7) recognizes two branches in the ornithopods, one arising from the posterior extremity of the ilium and one from the pubis. The insertion was on the inner side, proximal end, of the tibia. In the Ceratopsia these muscles would function as flexors and adductors; the limited areas of origin suggest only moderate power.

Adductor femoris. This probably originated from the pubo-ischiadic junction. As this area is restricted in ceratopsians, the adductor must have been relatively smaller than in ornithopods. The insertion would be on the posteromedial surface of the femur near midlength or below.

Coccygeo-femoralis. There are two muscles of this name in reptiles, both originating from the anterior caudal vertebræ. It is generally agreed that in dinosaurs they were inserted in the fourth trochanter of the femur, although it is possible that the anterior or *brevis* member of the group had a somewhat more dorsal attachment. As the fourth trochanter in most ceratopsians is relatively reduced, these muscles may be assumed to have been less powerful than in ornithopods. In bipedal dinosaurs the coccygeo-femoralis muscles would be very important, as they would serve to depress the tail, and thereby elevate the anterior part of the body. In the quadrupedal ceratopsians they naturally would be less important.

GENERAL BODILY FUNCTIONS

Locomotion. The most striking feature of the ceratopsian limbs is the marked difference in pose and mechanical arrangement between the anterior and posterior pair. This fits in well with the theory of bipedal ancestry for the ceratopsians. The fore limbs are typically reptilian, projecting out from the body, and suggesting that the thoracic region was supported free only by considerable muscular effort. The hind limbs, in contrast, have the mammalian posture, operating principally in the fore and aft plane. A certain amount of rotation was possible, but very little adduction, for the great trochanter is situated uncomfortably close to the overhanging margin of the ilium. Locomotion in the ceratopsians must have been very peculiar. We must visualize the fore limb, partly extended, being swung through an arc in the forward stroke. As it approached the forward position it would be flexed. The back stroke would be accomplished by extension of the limb, accompanied by adduction of the humerus. At the same time the hind limb would be going through a simple fore and aft step. It follows that the head and fore quarters would be swung from side to side during locomotion.

Feeding. There is no question that the ceratopsians were herbivorous. Tait and Brown (10) have described in detail their interpretation of the feeding habits, which pictures the ceratopsians shearing off the stems of small trees by the action of the beak. Lull (3, page 22) has expressed doubt as to the ability of these reptiles to rotate the head through a 90-degree arc, and similar objections are raised by the writer above. Lull considers it more likely that the heavy body was utilized to override vegetation, after which the edible parts could be cropped. To this interpretation the writer would add the possibility that the ceratopsians were also root grubbers, pulling up succulent roots with the hooked beak and powerful jaws. In this operation the hind legs would play an important part, owing to the great power that they could develop " in reverse."

Combat. There seems to be no doubt that the ceratopsian horns were primarily, if not entirely, used as weapons. Whether they were purely defensive weapons, or whether they were also used in duels between members of the same species is not yet established, although Lull (3, page 22) cites important evidence for the latter view. In the crest the ceratopsians had a more or less effective shield for the vulnerable neck region, although I have pointed out above that this was not the primary function of that structure. Lull (3, page 22) cites with apparent approval the views of Nopcsa (4, page 69), who pictured the ceratopsians constantly presenting the armed head to the enemy by rotating the body horizontally about the fore quarters. This, no doubt, is the most advantageous manner for a quadruped to change front rapidly. In ceratopsians, however, the evidence of the limbs indicates that the hind quarters were incapable of much lateral movement, whereas the fore quarters could be quickly displaced simply by flexion of one limb and extension of the other. Therefore, we must reverse Nopcsa's picture and imagine the embattled ceratopsian guarding itself by rapid shifts of the head and fore quarters to one side or the other, while the hind quarters remained relatively immobile. In a thrust, however, it was the powerful hind limbs that drove the body forward.

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