

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 1729

MAY 11, 1955

The Jaw Musculature in *Protoceratops* and in Other Ceratopsians

BY GEORG HAAS¹

INTRODUCTION

It is certainly almost impossible to get an unequivocal and precise idea of the muscular topography in an extinct vertebrate the systematic position of which precludes a close analogy with a recent relative. Nevertheless, many attempts to reconstruct parts or the whole of the muscular system of extinct vertebrates have been made. A complete skeleton tells only half of the possible function of the locomotor apparatus. I think that every worker on vertebrate muscles should try to get an idea of the possible location of the muscles in fossil animals, especially if the material is rich and complete enough, and if the animal in question has more or less related recent relatives which may be used for comparison.

After having seen the rich collection of ceratopsian skulls in the American Museum of Natural History, the author asked the help of Dr. E. H. Colbert, who kindly gave him every assistance in order to study the primitive ceratopsian *Protoceratops andrewsi*. Exceptionally well-preserved and ample material promised to lead to a closer understanding than had previously been possible of an early representative of a group that subsequently became very diversified. The attention of the author was especially attracted to this group because he is of the opinion that almost every reconstruction (of which there are a large number) of ceratopsids seemed to be conditioned by the notion that these reptiles must resemble in some way the rhinoceroses, especially because the animals of both groups are herbivorous, rather heavily built, and have horns. The same

¹ Department of Zoology, Hebrew University, Jerusalem, Israel.

tendency to "mammalize" the members of the ceratopsians also crept into the various papers dealing with the reconstruction of the head musculature.

Lull (1908) was the first author to approach the problem of the ceratopsian jaw musculature and of the origin of the frill by stressing its similarity to the helmet of the chamaeleons. Unfortunately he assumed a completely mammalian trigeminus musculature, even with an additional "cheek muscle," which is a purely mammalian structure, innervated by the facialis nerve and belonging to the group of the mammalian mimetic muscles. In fact, no sauropsid with cheeks is known. This musculature, according to Lull, composed of a temporalis, a masseter, and a pterygoideus internus and externus, appears strangely combined with the sauropsid depressor mandibulae muscle. Since the fundamental publications on the trigeminus musculature of the various lower vertebrate groups by A. Luther, this work has been continued in the field of the sauropsids by Lakjer (1926). It is therefore rather surprising to find in Russell's paper (1935) the same mammalian array of jaw muscles, together with a buccinatorius and a depressor mandibulae. Consequently we must attack the whole problem anew, keeping in mind the fact that we are dealing with a reptile, not with a mammal.

In the following discussion the nomenclature of the trigeminus muscles as used by Luther and Lakjer is employed. In the explanations of the figures, the adductor externus superficialis, medialis, and profundus are numbered 1, 2, and 3, respectively; the subdivisions of 1 are indicated as 1a and 1b; this system follows Lakjer's nomenclature. First, we must deal with the constrictor internus dorsalis (cid), muscles linking the brain case with elements of the palatoquadrate region and with the lower eyelid. The constrictor internus ventralis (mylohyoideus) has no masticatory function and is spread out between the mandibular rami. The adductor mandibulae represents a very complicated array of constant portions. All these portions are situated lateral to the epipterygoid, whereas the constrictor internus dorsalis occupies the region medial to this bone. The second and third branch of the trigeminus help to define three clear parts of the adductor mandibulae, which links parts of the lateral wall of the brain case, of the cranial roof, and of the palato-pterygoid series of bones with the mandible. The three portions of the adductor mandibulae externus (superficialis = 1; medialis = 2; and profundus = 3) are located lateral to both lower branches of the trigeminus; the internus (composed of the pterygoideus and of the pseudotemporalis) medially, and the posterior caudally. The pseudotemporalis group is very easy to define, because these muscles, bridged laterally by the trigeminus II, start at the latero-

cranial part of the brain case in front of the foramen for this nerve, which helps to delimit clearly the outermost posterior border of the group. According to Lakjer, the pterygoidei of the mammals are not at all homologous with the muscles bearing the same name in the sauropsids. The pterygoideus externus belongs to the externus-posterior group. The pterygoideus internus of the mammals should be homologized with the pseudotemporalis group of the sauropsids.

The whole configuration of the skull of *Protoceratops* lends itself easily to a discussion of the position possible for all the trigeminus muscles mentioned above and for the depressor mandibulae. In the following pages age differences, as well as the conjectural sex differences, are not stressed. The author used for his conclusions a rather limited number of medium-sized and large specimens (A.M.N.H. Nos. 6408, 6414, 6431), being guided by an intention to choose the most completely preserved specimens with their own mandibulae. Crests, muscular scars, and clearly defined depressions of the bones concerned give rather unequivocal hints as to the general topography of the different portions, but of course smaller subdivisions which may have existed cannot be determined and reconstructed, especially if all the portions involved converge to a rather restricted insertional area. The only recent archosaurs usable for this study are the crocodiles, with their akinetic, but strikingly different skulls. With even more caution we may use the muscular differentiations of the skull of birds, but here again we meet with many specializations not found in ceratopsians, such as the completely closed brain case, the suppression of the upper temporal arch, and especially the highly elaborated kineticism of the skull. In this connection the rather primitive arrangement of the temporal arches and the almost, but not completely, lost kineticism of *Sphaenodon* with its well-known muscular differentiations form a very useful type for comparison. Turtles and Squamata are so completely different in their skull architecture, with the exception of the frill-like structure of the helmet of the Chamaeleontidae and its muscular attachments, that they cannot teach us very much.

JAW MUSCLES IN THE CERATOPSIA

The discussion of the jaw muscles starts with the constrictor I dorsalis group. There is no doubt that the Ceratopsia have lost any kineticism in the skull. This fact is clearly shown by the morphological relation of the quadrate bone to the pterygoid, the squamosal, and the quadratojugal and by the complete absence of any areas on the skull roof adapted for a bending movement, such as Versluys' *Beugungslinien*. As in other akinetic skulls, such as those of crocodiles, turtles, or mammals, there is no

reason to assume that any muscle used for the movements of the palatopterygoid chain could have been developed. In other words, there was neither a protractor nor a levator pterygoidei, but we may expect, as in all other sauropsids (with the exception of the Chelonina), a well-developed levator bulbi, which may be a double muscle (*Sphaenodon* and most of the Sauria) or a single muscle (crocodiles and Aves), where the originally single levator bulbi dorsalis is subdivided into two portions.

As two rather divergent groups of the archosaur stock, Crocodilia and birds, do not have a pars ventralis of the levator bulbi, we may safely assume a similar lack in ceratopsians. The single levator bulbi dorsalis is essential for the opening of the lower eyelid, but the upper eyelid was in ceratopsians, as in all the other sauropsids, an immovable, rather deep, fibrous structure, the lower boundary of which is clearly indicated in *Protoceratops* by the presence of a well-developed palpebral bone. The big orbita and the wide ring of scleral bones indicate the presence of a bulbus of very considerable size. As correlated with the rather horizontal and dorsal position of the palpebral bone, we may assume, following its ventral margin, a flattened, roof-like, immovable upper eyelid as in crocodiles or in varanids, and a very long, essentially horizontal slot between both eyelids, with a lower lid covering the whole lateral aspect of the orbita. All these facts are quite obvious, and the author cannot understand why almost all reconstructions of *Protoceratops* show a mammal-like, bulging upper eyelid, semi-detached from the palpebral bone and not flush with the bones of the upper border of the orbit as in any reptile, and a mammal-like lower eyelid of rather limited dimensions (see the reconstructions in Brown and Schlaikjer). These reconstructions give a rather mammal-like physiognomy to this animal which shows no bony structure postulating such an arrangement of the soft parts in the orbital region. This digression was necessary in order to explain the presence of a rather thin, fan-like expansion of the levator bulbi towards the whole upper border of the lower eyelid, almost from the anterior to the posterior border of the bony orbit. This expanded insertional area swung around the ventral part of the bulbus and at its medial surface upward again towards its origo. A bony ledge above the posterior foramen trigemini on the proötic could reasonably be interpreted as the origo crest for this muscle, but a more anterodorsally situated excavation at the anterior corner of the latero-sphenoid, at the same time the only possible origo area for the pseudotemporalis, as is shown below, is also a possibility. Perhaps two ventrally divergent portions of the levator bulbi dorsalis existed, as in *Crocodylus* (compare Lakjer, 1926, fig. 50, with Brown and Schlaikjer, 1940, fig. 15). Such a dorsal portion overlapped the pseudotemporalis

laterally, as in birds (Lakjer, 1926, figs. 44, 46), and would have been a very efficient depressor of the lid, following closely the rather hemispherical lower surface of the big bulbus oculi. The considerable expansion of the constricted area for the interorbital septum points as well to a very considerable size for the eye.

The adductor internus group of the Sauropsida is always divided into

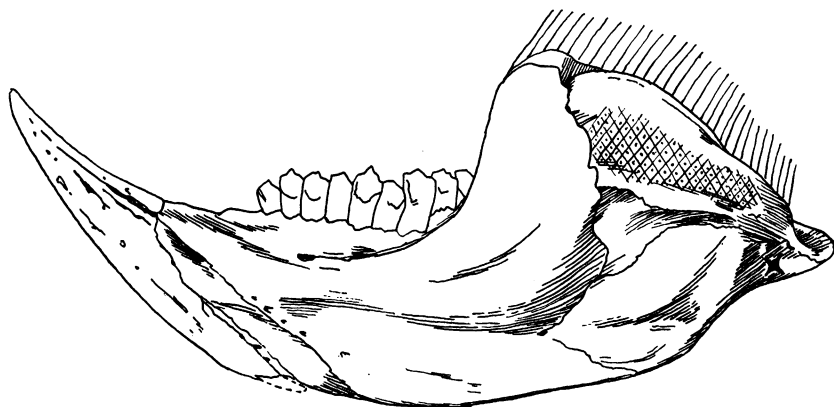


FIG. 1. Left mandibular ramus of *Protoceratops* (after Schlaikjer, redrawn), lateral view. Insertion of adductor externus superficialis lateralis, 1b of Lakjer, is indicated along dorsal margin of coronoid and surangular; insertional area of adductor externus superficialis, 1a of Lakjer, occupies lateral area of the surangular. Insertional facet of pterygoideus ventralis (the long portion) is marked by a star.

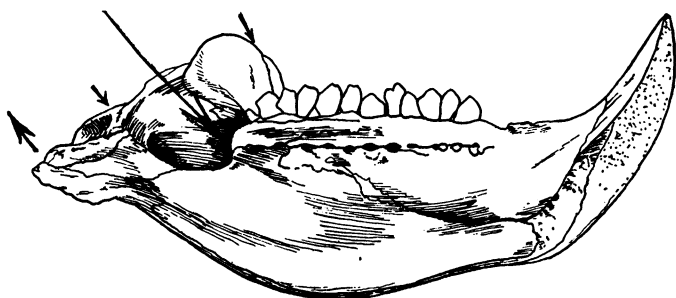


FIG. 2. Left mandibular ramus of *Protoceratops* (after Schlaikjer, redrawn), medial view. Two small arrows indicate approximate borders of adductor externus superficialis, 1b of Lakjer. Long arrow points into mandibular channel, the insertion of the adductor externus medialis and profundus. Arrow pointing upward shows direction of depressor mandibulae. Long ridge under muscle channel formed insertion of one portion of pterygoideus dorsalis medially and adductor posterior laterally.

the anterior pseudotemporalis and the posterior pterygoideus. Both muscles may be represented by single portions or by several distinct ones. The pterygoideus especially reached in certain cases a high degree of complication. The pseudotemporalis is a very constant differentiation; it may be single or represented by two distinct portions, the pseudosuperior and the pseudoprofundus of Lakjer, as in *Sphaenodon*, in birds, and in many Sauria. On the other hand, we stress the fact that this muscle is single in the akinetic Chelonia and in the akinetic Crocodilia, which belong to the archosaur stock. We see therefore that kineticism seems to

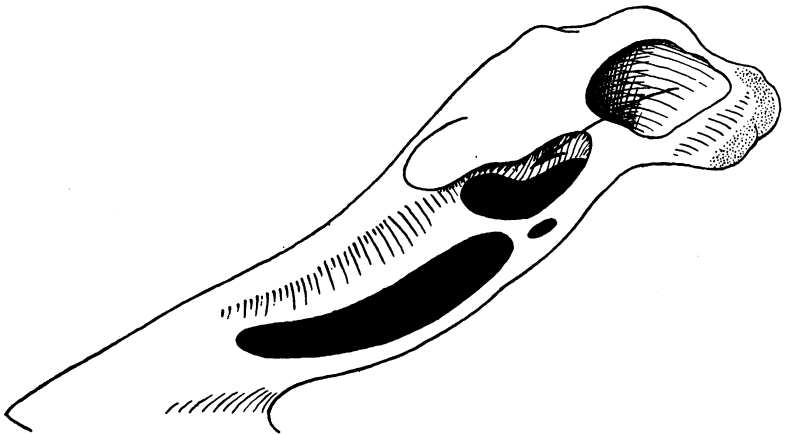


FIG. 3. Dorsal view of right ramus of mandible of *Protoceratops*. Arrow points into inframandibular channel; at its medial margin is the foramen trigeminum (foramen linguale). Dental area indicated by black shading. The depressor mandibulae inserted on the processus retro-articularis (dotted).

play an important role in the differentiation of this adductor group. But the predominantly kinetic snakes always have an undivided pseudotemporalis. This fact may reflect an earlier phylogenetic stage of a burrowing, more or less akinetic forerunner for this group. By analogy with the Crocodilia, we may assume for the likewise akinetic *Protoceratops* the presence of an undivided pseudotemporalis muscle. This muscle is by definition bridged laterally by the second branch of the trigeminus. Therefore the foramen from which this nerve emerges in its craniad course indicates clearly the outermost possible posterior limit of this muscle, at least at the level of the emerging nerve. As in the crocodiles, there is a separate foramen for the first branch and a common foramen for the second and third branches (Brown and Schlaikjer, 1940, fig. 15, pl. 7). This latter, slightly lower and ventrally situated foramen shifts the bulk

of the pseudotemporalis towards the posterior orbital area, a rather surprising position in a reptile, where this muscle is generally found in the temporal region, covered laterally by the adductores externi. In birds, the muscle occupies as a rule a postorbital and suborbital position. For *Aprosictus cyanopygius*, however, Lakjer describes a completely orbital position, even an antorbital position for both pseudosuperior and pseudoprofundus. This analogy in structure between a parrot and a ceratopsian is rather remarkable. The origin of this muscle may be located precisely at the posterior part of the orbita (figs. 4-6, 8). The slightly developed descensus of the frontals and the anterior upper parts of the laterosphenoids form an arcade-like surface and thus an adequate origo surface for a rather moderately developed pseudotemporalis, a flattened muscular ribbon composed of vertically descending fibers which would reach the anterior slope of the coronoid prominence of the mandible. Such an insertion would allow for a slight fanwise anterior expansion of fibers along the border of the wide trough lateral to the lower dental battery. In this remarkable reptile the pseudotemporalis would have this strange cranial and rather laterocranially exposed insertion because of the exceptional orbital position of its dorsal part. It is impossible to decide if some of the most cranial of the insertion fibers could have enveloped the wide lateral fossa beneath the row of the teeth. This fossa almost certainly was provided with a big infralabial gland. In this case the muscle could have worked as a gland compressor and a certain part of the insertional fibers would have reached the ventral, ridge-like margin of the lateral trough of the dentary. It is important to mention again in this connection that this ventral ridge could not have been the insertion of a buccinator-like muscle linking the dentary ridge with a corresponding one on the maxillary. The lateral maxillary depression above the upper dental series was doubtlessly the site of a bulky supralabial gland, a very common differentiation in many recent reptiles. That such glands should be amply developed in a "chewing" reptile is a very probable assumption (compare the herbivorous *Uromastix*). The insertion of the pseudotemporalis was therefore probably expanded into a rather abnormal cranio-lateral direction.

There are many markings in the skull which give a clear indication of the topography of the complex pterygoideus, the second division of the adductor mandibulae internus. As a rule, this muscle links the posterior angle of the maxillary and the more or less expanded adjacent area (ectopterygoid, pterygoid, and basis cranii) with the posterior part of the mandible (mostly the ventromedial part), but a bulging caudal portion may invade a certain caudolateral area, as at the external side of the articular and angular. Very often this muscle is subdivided into more or

less individualized portions. Perhaps the highest degree of complication is found in the crocodiles, where no fewer than four different portions can be distinguished (Lakjer). His portion A, beginning at the posteroventral corner of the pterygoid, bends around the posterior angle of the mandible. Portion B links the posterior part of the pterygoid with a deep excavation at the inner side of the articular and the angular. Two other portions, C and D, which may be called the pterygoideus dorsalis, insert more dorsally and cranially at the inner side of the lower jaw. Both are clearly separated by a nerve from portions A and B, which may be called pterygoideus ventralis. Part C rises from the posterior dorsomedial portion of the pterygoid bone, lateral to the choanal aperture. Part D is a broadly expanded muscular sheet which fills the whole lateral palatal opening, rising from the inner side of the maxillary alveolar portion as well as from the palatal arcade of this bone, laterally and medially from the lateral border of the palatine and anterodorsal parts of the pterygoid. The proportions of the crocodile skull as a whole cause an extreme elongation of portion D in the sagittal direction, whereas portion C remains rather short, owing to its almost transverse direction (Lakjer, 1926, fig. 226).

A similarly high degree of complexity of the pterygoideus muscle is found in birds, which retain the same subdivision into a double dorsal and ventral portion. The pterygoideus ventralis surrounds the posterior end of the mandible, invading also a lateral area of insertion. The different parts of the dorsalis group insert at the inner side of the caudal end of the mandible. Both lateral parts of the dorsalis and ventralis start mostly from the lateral and posterior flanges of the palatine, both corresponding medial portions mostly from the pterygoid bone with some accessory origo areas from the medial flange of the palatine and from the basis cranii. The striking similarity of the muscular arrangement in birds and crocodiles shows the close relationship of both groups, in spite of the difference in the state of kineticism, of generally different proportions of both types of skulls, and of the divergent development of the bony roof of the mouth. This correspondence in the muscular arrangement is certainly due to divergent development from a common, generalized, archosaurian ancestor.

In *Sphaenodon* the pterygoideus muscle is of a simpler design, more in accordance with the saurian pattern. The muscle is not subdivided at all.

In trying to find muscular scars or other signs of the location of the pterygoideus muscle in *Protoceratops*, we may consider the mandible first. A clear sign of the insertion of the pterygoideus ventralis is indicated by a flattened lateral surface under the articular at the posteroventral outer surface of the angular. The plane of this area indicates a strongly bulging

muscle belly at the posterolateral end of the mandible (figs. 1, 5, 6). The upper border of this insertional area is clearly defined by an obliquely descending ridge at the external side of the angular. This ridge starts from the ventral slope of a similar crest across the external surface of the surangular. (See Brown and Schlaikjer, 1940, fig. 18.) The point of intersection of both ridges marks an abrupt angulation of the surangular crest, which runs up to this point in an almost exactly sagittal direction, in order to continue at an angle of 120 degrees. From this caudomedially converging ridge the insertional surface for the pterygoideus muscle slopes in a medioventral direction. This twist of the caudal angle of the mandible provides a mechanically excellent insertion for the muscle, which tapers gradually towards a deep excavation rostromedially of the pterygoid prominence. Fibers could have started from this spot and along the medial side of the prominence (fig. 7, the long arrow). Such a muscle would correspond to Lakjer's pterygoideus A of the crocodiles. Another portion like the pterygoideus B inserted at the osseous ridge under the infra-mandibular channel. As a rather flattened muscle it probably started from a deep excavation of the ventral surface of the pterygoid bone, where it sends a long flange towards the quadrate. It seems very probable that this depression with its medioventral, ridge-like border gave rise to a muscular sheet converging to the inner side of the mandible. The fibers of this muscle reach the mandible in a much steeper angle than those of the portion mentioned above. If members of the archosaur stock, as different in their skills as crocodiles and birds, adhere to the same muscular arrangement of the pterygoideus group, the same arrangement seems quite possible in this ceratopsian, particularly if we consider the double area of possible origins at the palate. A double pterygoideus ventralis may therefore be assumed for *Protoceratops*.

There remains the question as to whether there are indications of a single or a divided pterygoideus dorsalis. At the dorsal surface of the pterygoid-ectopterygoid prominence both bones form together a smooth ditch which could have lodged the emerging fibers of a rather large, undivided pterygoideus dorsalis. This muscle certainly ended at the inner side of the short processus retroarticularis (figs. 7 and 8). The whole configuration of the palate and the increased distance between the articular facet of the quadrate and the basis cranii preclude the existence of a second pterygoideus dorsalis muscle, which should rise from the basis cranii. The pterygoideus was therefore probably tripartite, being composed of a double ventralis (Lakjer's portion A from the base of the ectopterygoid prominence to the lateral insertional facet at the angle of the mandible; portion B from the ventral muscular groove and adjacent ridge of the

pterygoid wing to the lower margin of the bony ridge under the muscular channel of the mandible, overlapped by the belly of the first). The pterygoideus dorsalis developed from the laterodorsal surface of the pterygoid bone, and by by-passing portion A laterally, inserted on the medial side of the postarticular and subarticular region of the articular (fig. 7).

The adductor posterior in the crocodiles is a bipartite muscle linking the quadrate with the posterior part of the inframandibular fossa. The division of this muscle is accomplished by the intercalation of the slanting pseudotemporalis muscle into its insertional area, which separates a lateral portion from a medial one. In birds this muscles may attain a high degree of complication in connection with the development of the orbital process of the quadrate. Some portions may link this process with the mandible; others develop from the main body of the quadrate in rather diversified patterns. It is very improbable that the streptostylic and highly differentiated quadrate bone of this group can give us any clue for an understanding of the form of the adductor posterior in the akinetic skull of the Ceratopsia. The muscle is undivided in *Sphaenodon*, linking the anterior side of the quadrate with the posteromedial part of the lower jaw. As in many Sauria there is a partial fusion with the pseudotemporalis muscle near the lower end of the muscle. The highly kinetic snakes show,

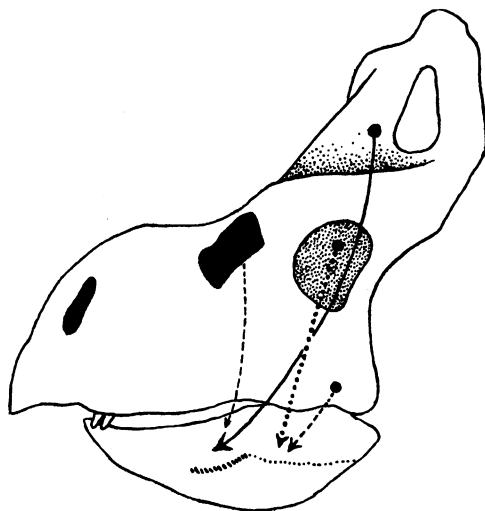


FIG. 4. Sketch of profile of *Protoceratops* (after Granger and Gregory, 1923). Arrow drawn as solid line shows pulling direction of combined adductor externus medialis and profundus. Broken line starting from orbit gives direction of pseudo-temporalis; arrow indicated by dots, that of adductor externus superficialis b. Short broken line shows the direction of adductor externus superficialis a.

as do the birds, an analogous tendency towards the subdividing of this muscle. We may therefore assume that some connection exists between the degree of kineticism and the fission of the muscle into several portions. Nevertheless, the akinetic crocodiles have a bipartite adductor posterior.

The quadrate of *Protoceratops* is, as is that of the other ceratopsians, solidly united with the adjacent elements of the skull, namely, with the palatine, the quadratojugal, and the squamosal. It is quite impossible to decide if the muscle was single or has been split up. It certainly developed from the transversely directed anterior slope of the quadrate and above it, in triangular form, as seen from the profile, and inserted at the medial surface and lower margin of the splenial, lateral to the trigeminal foramen, and somewhat overlapping the entrance of the mandibular muscular cavity. The insertional area ended caudally at the anterior border of the articular surface, rostrally probably somewhat in front of the foramen trigemini. The ramus mandibularis trigemini in its course towards the foramen separated the adductor posterior from the adductores externi (fig. 2). The whole muscle at its insertion was covered medially by the pterygoideus (ventralis) B of Lakjer.

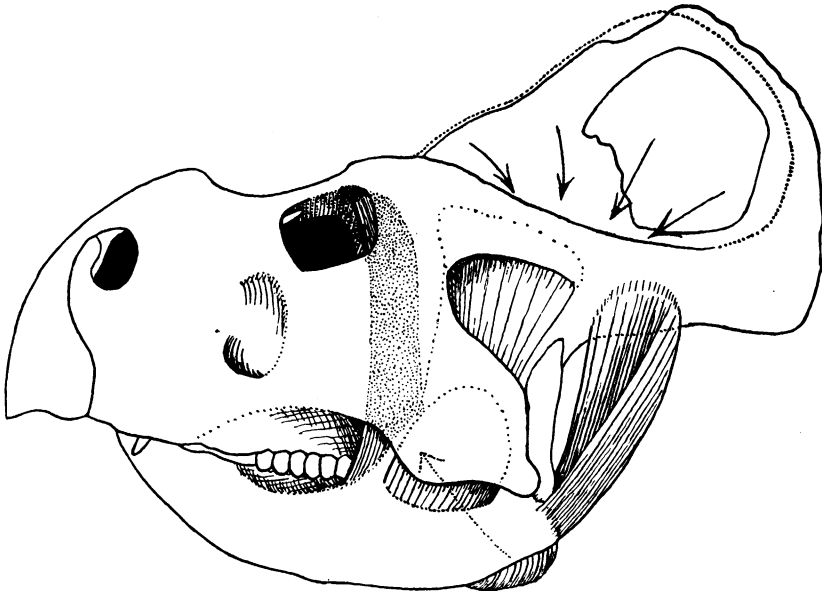


FIG. 5. Profile view of *Protoceratops* (drawn from A.M.N.H. No. 6413). Pseudotemporalis, both adductores externi superficiales, depressor mandibulae, and visible portion of pterygoideus added. Four arrows indicate main direction of frill musculature adductores externi (medialis and profundus). Arrow in dotted line shows direction of long portion of pterygoideus ventralis.

The arrangement of the adductores externi is extremely variable in the different groups of reptiles and birds. If we limit our discussion to the differentiation of these muscles in sauropsids possessing two temporal arches or, as in the birds, the lower one only, we find a surprising degree of variation even between the smaller systematic units. We are dealing, in fact, with the most inconstant element of the whole group of trigeminus muscles. This fact applies especially to the externus superficialis, which may split up into several portions with diverging fiber

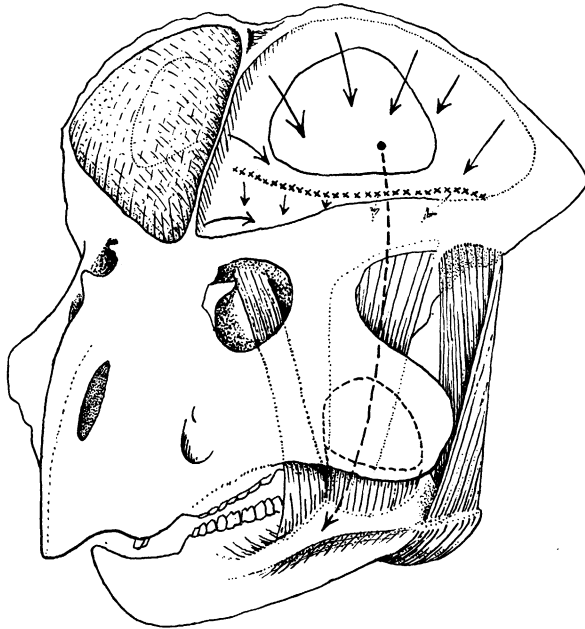


FIG. 6. Anterior three-quarter view of *Protoceratops* (drawn from photograph). Line of x's indicates origo of deeper frill muscle. Broken line circumscribes origo of la at inner side of jugal protuberance. Right upper temporal fossa shown as it probably looked, filled by a muscle mass covered by a thick aponeurosis.

arrangements. The most superficial layer of muscles is frequently connected with the rictal commissure (levator anguli oris of Lakjer). In all the recent groups of reptiles having a lower temporal arch no muscles are attached to this mechanically important structure. The loss of the lower arch has therefore no particular influence on the fundamental arrangement of the externus group, which can be clearly seen in a comparison of the diapsid groups with the different Sauria. On the other hand, all forms with the upper temporal arch reducing or wanting (snakes, amphis-

baenids, Gekkonidae, Pygopodidae, etc.) must shift the origin of the externus superficialis from this arch to the roof of the skull or to adjacent parts of the more or less complete postorbital bar. The upper temporal fossa of diapsid forms and birds is filled by bulging portions of the adductor medialis, and in several cases medially by parts of the pseudotemporalis muscle. The adductor externus profundus forms, as a rule, a lateral portion parallel to the adductor posterior, linking the anterior face of the quadrate with the lower jaw. Frequently, a second deep portion of the profundus bulges backward from the posterior margin of the caudal wings of the parietals and processus parotici (Lakjer's 3b). In the crocodiles particularly, the externi enter to a striking degree into the wide and deeply excavated muscular fossa at the inner side of the lower jaw. The Chamaeleontidae and the members of the genus *Phrynosoma* exhibit cranial peculiarities which give us some useful clues for an understanding of the "frill" of the ceratopsians, concerning the relation of such a structure with the external temporal muscles. This analogy has been stressed and usefully and ably discussed by Lull (1908) and later by Russell (1935). The adductores externi of numerous reptiles have the peculiar tendency to form vast aponeurotic sheets, which very often make a subdivision into portions more or less arbitrary, as they divide the muscles not completely but only at one end. Very often parts of the adductor externus medialis and profundus may be fused or may converge towards an only incompletely dividing aponeurosis.

From this general discussion of the external adductors four points emerge as of fundamental importance for an understanding of the muscles in a form such as *Protoceratops*.

1. The adductor externus superficialis rises normally from the inner surface of the upper temporal arch.

2. As a rule no muscular attachments are found on the lower temporal arch.

3. The whole structure of the "frill" is comprehensible only as an enormously enlarged frame for the origin of the externus medialis and profundus as in *Chamaeleon*.

4. The fossa muscularis of the inner side of the mandible of the crocodiles has its analogue in a very similar structure in *Protoceratops*, likewise forming an enlarged insertional area for several portions of the adductor externus.

The adductor externus superficialis arose from the medial side of the upper temporal arch which forms the anterolateral border of the frill depression, and probably from the postorbital bar as well. This muscle filled the lower temporal fossa, almost certainly covered by a thick fascia,

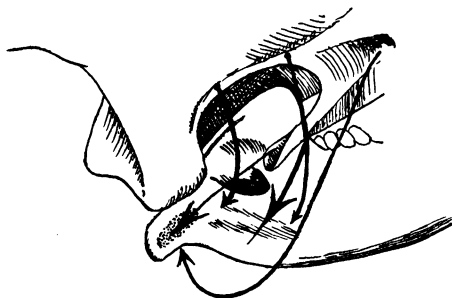


FIG. 7. Three-quarter posterior view of region of left mandibular joint of *Protoceratops*, showing topographic relation of ectopterygoid process to mandible. Long bent arrow indicates long portion of pterygoideus ventralis, together with long arrowhead. Pair of arrows pointing to bone crest at ventral border of inframandibular channel indicate direction of short pterygoideus ventralis. Pterygoideus dorsalis follows direction of straight arrow (insertion in dots).

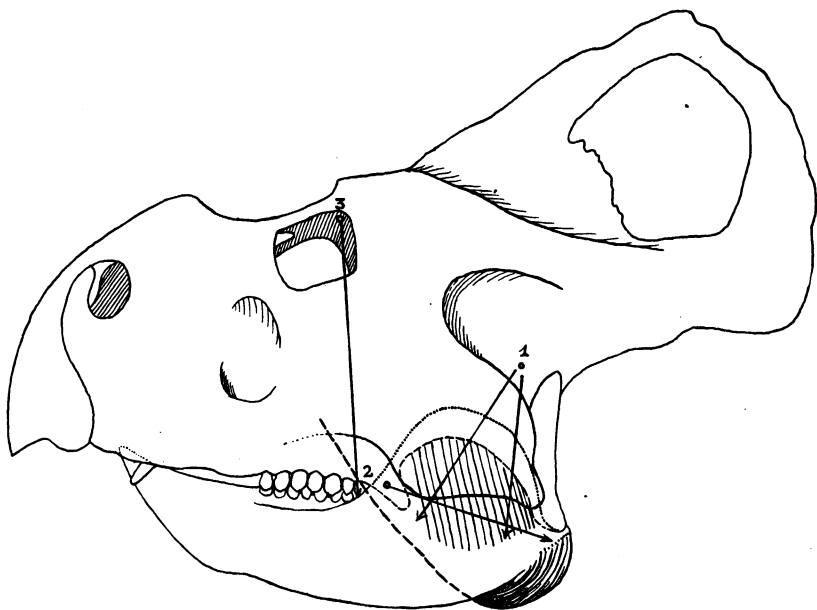


FIG. 8. Lateral view of skull of *Protoceratops*. Hidden contours of skull are added as hatched line, of mandible as dotted line. From 1 begins the adductor posterior; the two arrows indicate its approximate cranial and caudal borders. Arrow 2 marks direction of pterygoideus dorsalis. Arrow 3 indicates pseudo-temporalis. Short pterygoideus ventralis drawn as series of slanting, parallel lines. Anterior border of long pterygoideus ventralis indicated by broken line, and part of muscle bulges under mandible.

and sloped downward at an angle of about 70 degrees in order to reach the dorsal margin of the mandible from the coronoid to the joint and to a slightly excavated area on the lateral surface of the surangular. This insertional field extends towards the coronoid bone and the ascending coronoid process of the dentary. A conspicuous horizontal crest through the surangular and adjacent posterior parts of the dentary indicates the outermost ventral border of the attachment of this muscle (figs. 1, 2, 4-6). A transverse section across the mandible passing through this surangular crest shows that the upper excavation faces the origo area of the superficialis, whereas the area beneath the ridge is abruptly bent into a slope from dorsolateral to ventromedial. This deflection of the lower part of the mandible precluded an extension of the superficialis beyond the crest. The most anterior fibers of the muscle reached the tip of the coronoid process, but the main insertion left a broad area of the posterior part of the mandible uncovered. The steep prominence of the surangular crest doubtlessly marks the inferior border of this muscle. With the lower jaw closed, the jugal-epijugal prominence comes into close proximity with the surangular crest, especially near the jaw joint. There is some indication of the presence of a second separate lateral portion of the externus superficialis, which would have had to rise from an area unknown in any recent diapsid relative, namely, from the lower face of the lower temporal arch. Comparing the more primitive skull of *Psittacosaurus* (fig. 9) with *Protoceratops*, we find a striking difference in the direction of this arch, which juts outward, forming a right angle halfway between the orbit and the mandibular joint in the former genus. Seen ventrally, both jugal and quadrato-jugal form a deep trough which is opposite an excavated lateral area of the caudal part of the mandible. Both concavities face each other in such a way that their connection by an accessory portion of the superficialis seems very probable. Such a muscle would explain the presence of the strange angulation of the lower temporal arch with the accessory epijugal at the top. The width of the ventral concavity of the arch points to the possibility of a very substantial muscular attachment. Such a muscle could have become differentiated from a normally situated superficialis by an extension of the orthodox origo at the upper arch onto the fascia covering the lower temporal fenestra, until the lowermost fibers reached the under side of the lower arch. Probably a stage of general enlargement of the origo area preceded the splitting into two separate bellies.

The same angulation of the region of the jugal and quadratojugal is overemphasized in *Protoceratops*. The jutting angle shifted backward to the level of the mandibular articulation; this shifting caused a reduction

of the protruding angle and a caudal rotation of the epijugal which, instead of being located in front of the lower end of the quadrate, bulges considerably beyond the level of the mandibular joint. A surprisingly deep niche is found on the lower surface of both jugal and quadratojugal at the corner of the backwardly rotated prominence. This excavation contained probably an accessory superficialis as in *Psittacosaurus*. From the same area there was easy access to the surangular crest. Such a muscle

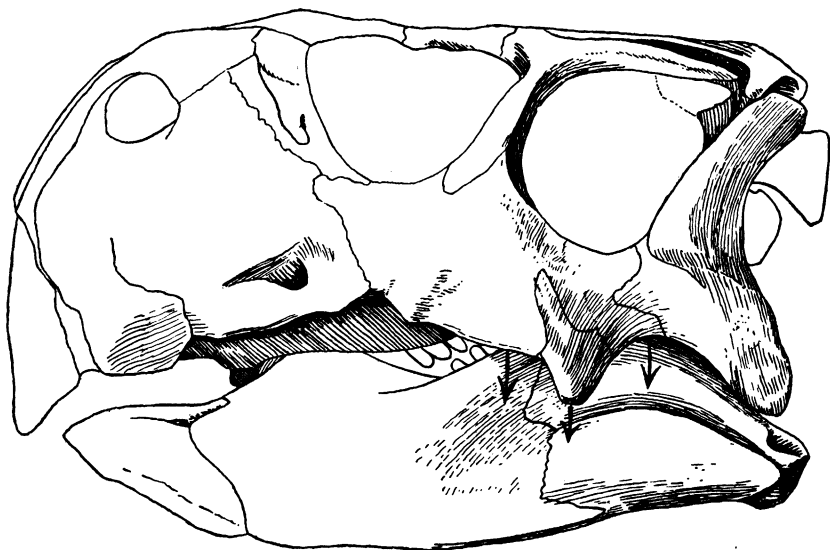


FIG. 9. *Psittacosaurus mongoliensis* (after Osborn, 1924). Notice extensive lower temporal fenestra. Arrows indicate direction of adductor externus superficialis (lateralis = 1a). Strong deeper portion 1b descended from upper temporal arch.

could have had excellent pulling power, with its fibers sloping downward from a caudolateral origin to a more ventromedian insertion. There was therefore a considerable divergence of the fibers of this muscle and the deeper, typical superficialis owing to its more medially situated origin. The lateral superficialis (1a of Lakjer) would logically reach the most lateral area of insertion, i.e., the above-mentioned surangular ridge. The deeper (1b of Lakjer) portion would end at the upper margin of the mandible, starting from the coronoid summit to the mandibular joint (figs. 1, 5, 6).

Certain Psittaci offer an interesting analogy to such an external derivative of the adductor externus (following Hofer's nomenclature) of the adductor externus medialis. This pseudomasseter muscle of the Cacatoes

links the suborbital process with the external surface of the lower jaw in a rostroventral direction, rising from the large suborbital process and remaining quite independent of the jugal arch in the more primitive types of differentiation. In the most elaborate forms, such as *Microglossus aterrimus* (Lubosch, 1933) or *Cacatoa ophthalmica* (Hofer, 1950), the enlarged suborbital bar may be linked by syndesmosis or even by synostosis with the processus zygomaticus squamosi. This again may be linked to the dorsal border of the jugal arch, and the posterior fibers of the pseudomasseter may use the connecting ligament as origo. In this way the lower jugal arch indirectly gives rise to a portion of the adductor externus group. This case occurred in a highly kinetic skull, but there is no doubt that a similar process of subdivision could have taken place in any sauropsid as well, in which the bony orbital frame was still in broad connection with the lower temporal arch, and under akinetic conditions as in *Psittacosaurus* and *Protoceratops*. Probably the double analogy in the adductor area, involving the pseudotemporalis and the pseudomasseter muscles between both groups, owes its origin to the anteroposterior shortening and the correlated transverse expansion of the temporal region, connected with the pincer-like function of the beak-shaped jaws.

The adductores externi medialis and profundus occupied, as in other reptiles with a wide upper temporal window, the large osseous frame of the frill, formed mainly by the unusual extension of the perforated parietal and by the squamosals that are abnormally extended beyond the upper end of the quadrate. The squamosals form together with the postorbitals the lateral frame of the frill. The depression at the posterior half of the frontals indicates the anterior border of what was probably a bulging muscle mass which filled the whole frame of the frill (figs. 5, 6). The slender sagittal crista of the parietal indicates that the two muscle masses were separated dorsally by this osseous lamina, which had perhaps a marginal continuation in the form of a vertical tendinous seam; from this margin developed covering fasciae for both muscle groups. Along the posterodorsal frame of the frill a distinct borderline marking the attachment of the fanwise diverging muscle mass is clearly distinguishable; this line parallels exactly the posterior margin of the frill. Both lines of attachment are confluent with the sagittal crest which posteriorly branches out for a short distance in a V-like fashion. The lateral frame of the frill, formed by the postorbital and the squamosal, has a rather sharp upper margin, which probably supported a tough aponeurosis extending across the whole enlarged upper temporal fossa. We may try to discuss the possible form of the externi medialis and profundus which filled the large cavity inside the frill. Unfortunately, these muscles are very much diversi-

fied in the different groups of sauropsids and may even exhibit a high degree of complete or incomplete subdivision caused by tendinous sheets penetrating from the insertional region into the fleshy portion, or, more rarely, in the opposite direction. If the mandible of *Protoceratops* is put in articulation, it is easy to see that a muscle mass with an enormously expanded area of attachment inside the frill depression had to constrict itself considerably in ventral direction in order to converge towards a rather limited possible insertional field at the medial side of the mandible. The over-all configuration of the skull clearly indicates that the whole muscle mass had to slope downward in a rostroventral direction in order to reach any area in front of the mandibular articulation.

The direction of the sloping surface of the parietals points to a rather limited region of insertion at the inner side of the mandible; thus the whole muscle or compound of muscles which filled the upper temporal fossa converged into the large inframandibular canal, as in the crocodiles (figs. 2, 3, 5, 6). There is no doubt that this big muscle mass was subdivided. There is a rather faint indication of such a division, probably into a *medialis* and *profundus*. From the middle of the length of the sagittal crista of the parietal a feebly sigmoid line of attachment crosses the upper temporal fenestra in front of the anterior border of the wide perforation of the parietal (fig. 6). This line, better felt by probing with the finger than really seen as a ridge, probably formed the base of an aponeurosis dividing two muscles. It ends where the posterior angle of the squamosal meets the parietal frill. If this interpretation of the slight ridge as a bearer of a connective tissue membrane is correct at least two main muscle portions filled the cavity of the frill. A posterior muscle covered the broad posterior part of the frill and was the dorsal one, overlapping the deeper muscle, the origo of which started more rostrally. We may assume therefore that the posterior and longer muscle was originally the lateral one, and that the other more rostral and shorter portion (rising from the prefenestral ridge) was originally the deeper part. In other words, the *externus medialis* covered and overlapped a rather small *externus profundus*, which had been pressed into a more cranial position. Both muscles probably developed as in the crocodiles, insertional tendons entering the *canalis muscularis* from behind. We may surmise that the tendon of the *profundus* occupied the posterior part of this channel.

Other more advanced ceratopsians with a fenestrated frill, particularly *Monoclonius* and *Styracosaurus* (figs. 10, 11), give rather useful clues in support of the above interpretation. Instead of a slight, ridge-like prominence dividing the two muscular areas in *Protoceratops*, a freely jutting

bony lamella is developed in *Monoclonius* and *Styracosaurus*, certainly the base for a tough fascia which ossified gradually as it approached the area of attachment at the parietal. In this particular case, however, both muscles took part in over-roofing and covering the perforation of the frill. This is shown quite convincingly by the posterior continuation of the accessory bone blade, which terminates at the posterodorsal end of the fenestration of the frill. Russell reconstructed his "temporalis" as a

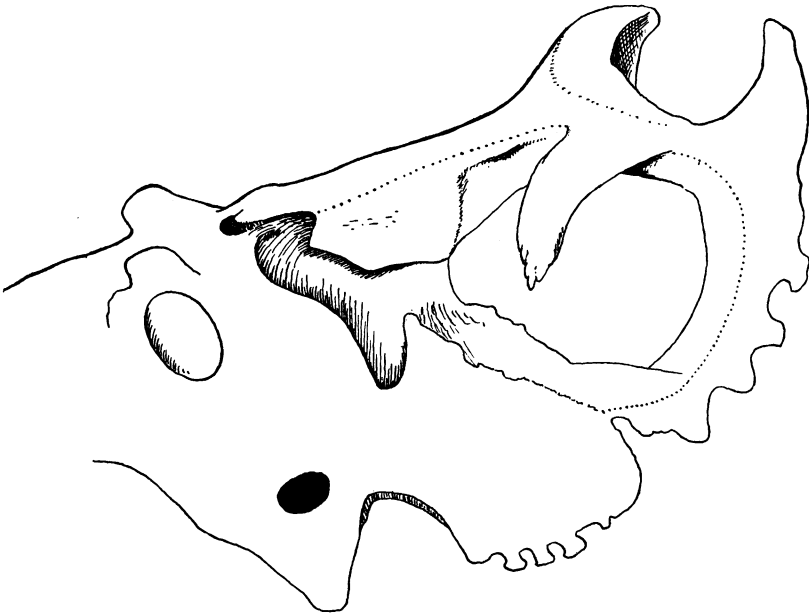


FIG. 10. *Monoclonius* (sketch from a skull in the American Museum of Natural History). Dotted line indicates markings of marginal attachment of external frill muscle. Jutting bony lamella in front of fenestration, continued as angular step above perforation of frill, marks origin of covering aponeurosis for deep frill muscle.

single muscle according to the different configurations of both frill and perforation in it in various genera of ceratopsians, but he did so by basing his conclusion on the very improbable assumption of the existence of a single temporalis. He gives no satisfactory explanation for the deep excavations found in many forms at the dorso-anterior corner of the upper temporal fossa and at the deepened area of the frontals and the neighboring parts of the parietals. I think that this excavation, forming the so-called false pineal foramen and the false roof of the skull in the most extreme forms, was filled by strong tendinous structures which predominated

in the gradually shrinking anterolateral muscle of the frill, situated laterally and in front of the protruding bony lamella of the parietals in forms like *Monoclonius*. Together with this reduction and transformation in a tendinous structure the perforation of the frill grew smaller and was lost in the genus *Triceratops*. The closing of the gap started from the antero-medial corner, but the whole structure wandered gradually away from the



FIG. 11. *Styracosaurus* (sketch from a skull in the American Museum of Natural History). The bony lamella is more extensive in this species, extending across the frill fenestration. Dotted line indicates probable border of superficial portion of frill muscle. The deeper muscle was, in correlation with wider expansion of long lamella, very much expanded, probably across whole fenestration.

posterior border of the frill towards the suture between parietal and squamosal. In forms with a very small upper temporal opening this latter appears to represent the last gap between the unaltered squamosal and the gradually advancing medial bony lamella covering the fenestra of the frill as a protruding, more laterally situated shelf of its margin. In this sense the rudiment of the temporal opening and the dislocated medial

border enable us to recognize in this gap as well the rudiment of the frill fenestration. This new sheet of the parietal was probably covered by a thick aponeurosis, which dispatched a rather inconspicuous muscle across the gap and to the inner side of the lower jaw. So far we have dealt with the lateral muscle at the surface of the new bony wall. The deeper, medial one, rising from the circumference of the frill perforation and the inner surface of the new bony extension in forms like *Monoclonius*, developed progressively as the outer muscle became reduced. A really enormous cavity at the medial side of the squamosal in *Triceratops* shows that this whole deeper muscle shifted its origo from the inner side of the parietal lamella to a new and more ventral area. However, this muscle had in its new position a very strong retracting, but at the same time a negligible adducting, effect. It is not easy to decide if this muscle represents the adductor externus profundus (the medio-anterior) or the medialis (the latero-posterior) of *Protoceratops*. The author feels rather inclined to suppose that the anterior muscle persisted in the higher Ceratopsia—in other words, the medialis had been reduced. In this case the line of attachment in front of the frill fenestra of *Protoceratops* did develop the new bony shelf of *Monoclonius* and similar forms. But it may be that more muscular portions had been involved in the process of the shift of the origo from the parietal to the inner side of the squamosal. During this transformation the lower temporal fossa diminished in size very considerably, and this indicates a reduction of the bulk of the adductor externus superficialis. It may be seen as well that in the later forms the subsquamosal muscle (adductor externus profundus?) inserted mostly from the posterior border of a very high coronoid process instead of from an elaborate muscular channel at the inner side of the mandible, as in *Protoceratops*. Russell neglected completely the shifting of the externus portions beneath the level of the gradually expanding roof across the frill perforation. Thus his higher ceratopsids had an extremely weak “temporalis.” This is a strange conclusion indeed in view of the enormous size and strength of the mandibles of these huge forms, especially because the progressively developing coronoid process finds no explanation. There is no doubt that it formed the insertion of an adductor of very great strength which descended in a relatively low angle towards the mandible (from the inner side of the squamosal, as described above). From the same area there developed in primitive ceratopsians only the adductor externus superficialis, here strengthened by the portion shifted from the frill.

There can be no doubt about the place of insertion of the depressor mandibulae at the rather blunt processus retro-articularis. The possible areas of origo of this muscle, however, deserve some detailed discussion.

The whole configuration of the depressor has a fundamental bearing on the size and location of the tympanic region or, to be more exact, on the question as to whether *Protoceratops* had a tympanic membrane at all. Colbert has informed me that so far no stapes-like structures have been found in any ceratopsians or, to the best of his knowledge, in any higher dinosaur. The primitive prosauropod *Plateosaurus* had a stapes, according to von Huene (1926).

A clearly defined muscular groove for the insertion of the depressor can be seen if we look at the mandible from above. The oblong articular surface for the quadrate articulation has an oblique position, and both articular facets converge towards the rostral end of the mandible, enclosing an angle of about 90 degrees. The retro-articular process protrudes for the most part not so much caudally of the articular surface as medially, and forms a rather deep fossa parallel to the internal border of the mandibular joint. Insertional fibers filled this ditch and its lateral wall along the retro-articular process and along the inner side of the jaw articulation (figs. 3, 5, 6).

In chelonians, birds, and crocodiles, this muscle rises from the squamosal. In *Protoceratops* a rather prominent crista at the level of the upper border of the lower temporal fenestra separates a ventral, concave, and smoothed area from the dorsal part of the squamosal, which was covered directly by the skin. The ventral region offers an adequate field of origin for the depressor, which formed, in order to reach the somewhat U-shaped insertional area, a kind of double muscle, with two anteriorly sharpened edges or two completely distinct portions. The most cranial fibers descending from the squamosal reached an area at the inner side of the mandibular joint; the most caudal ones bent towards the lateral margin of the processus retro-articularis. It is impossible to decide if the muscle was completely or partially divided. The shape of the posterior end of the mandible rather points to the second alternative. But we cannot exclude another possibility, namely, that a muscle, innervated likewise by the facialis nerve, like the cervico-mandibularis in snakes, started from the external border of the retro-articular process and expanded fanwise towards the nuchal vertebrae. This possibility cannot be proved, because the main part of such a muscle would have a quite superficial expansion, leaving no traces in the skeletal system. An arrangement of the depressor as shown in the figures would leave room for a freely exposed tympanic membrane, the anterior border of which could have followed the slope of the quadrate, but such an arrangement is purely conjectural. The extraordinarily long distance between this region and the fenestra ovalis and the complete absence of any remains of a stapes rather point to an

obliteration of the tympanic membrane, perhaps even of the whole middle ear cavity.

SUMMARY

The strangest features in the arrangement of the head muscles in *Protoceratops* consist in the orbital location of the pseudotemporalis as in the Psittaci and in the slight muscular covering of the lateral surface of the mandible. In particular, the deep excavation at the ventrolateral face of the dentary and angular requires an explanation. Perhaps this area was filled with a bulky gland, something like an accessory infralabial gland, corresponding to the similar concavity along the upper dental series. Perhaps the peculiar type of dental occlusion caused a ventral shifting of the infralabial gland, whereas the supralabial remained near the upper dental series, as the lateral maxillary excavation seems to indicate.

Other peculiarities of the muscular arrangement consist in the differentiation of an accessory adductor externus superficialis, emerging from the jugal-epijugal prominence, and in the possibility of an encroachment of anterior pseudotemporalis fibers craniolaterally of the coronoid elevation.

BIBLIOGRAPHY

- BROWN, BARNUM, AND ERICH M. SCHLAICKER
 1940. The structure and relationships of *Protoceratops*. Ann. New York Acad. Sci., vol. 40, pp. 133-266, pls. 1-13.
- GRANGER, WALTER, AND WILLIAM K. GREGORY
 1923. *Protoceratops andrewsi*, a preceratopsian dinosaur from Mongolia. Amer. Mus. Novitates, no. 72, pp. 1-9.
- GREGORY, WILLIAM KING, AND CHARLES C. MOOK
 1925. On *Protoceratops*, a primitive ceratopsian dinosaur from the lower Cretaceous of Mongolia. Amer. Mus. Novitates, no. 156, pp. 1-9.
- HOFFER, HELMUT
 1950. Zur Morphologie der Kiefermuskulatur der Vögel. Zool. Jahrb. Anat. Ontog. Tier, vol. 70, pp. 427-556.
- HUENE, F. VON
 1926. Vollständige Osteologie eines Plateosauriden aus dem schwäbischen Keuper. Geol. u. Palaeont. Abhandl., new ser., vol. 15, fasc. 2, 43 pp., 4 figs., pls. 1-7.
- LAKJER, TAGE
 1926. Studien über die trigeminus-versorgte Kaumuskulatur der Sauropsiden. Copenhagen, C. A. Reitzel, 154 pp., 26 pls.
- LUBOSCH, W.
 1933. Untersuchungen über die Visceralmuskulatur der Sauropsiden. Morph. Jahrb., vol. 72, pp. 584-666.

LULL, RICHARD S.

1908. The cranial musculature and the origin of the frill in the ceratopsian dinosaurs. Amer. Jour. Sci., ser. 4, vol. 25, pp. 387-399, pls. 1-3.

1933. A revision of the Ceratopsia or horned dinosaurs. Mem. Peabody Mus. Nat. Hist., vol. 3, pt. 3, pp. i-xii, 1-135, pls. 1-17.

RUSSELL, LORIS S.

1935. Musculature and function in the Ceratopsia. Bull. Natl. Mus. Canada, vol. 77, geol. ser., no. 52, pp. 39-48.

OSBORN, HENRY FAIRFIELD

1924. *Psittacosaurus* and *Protiguanodon*; two lower Cretaceous iguanodonts from Mongolia. Amer. Mus. Novitates, no. 127, pp. 1-16.

STERNBERG, CHARLES M.

1951. Complete skeleton of *Leptoceratops gracilis* Brown from the upper Edmonton member on Red Deer River, Alberta. Bull. 123, Ann. Rept. Natl. Mus. Canada, pp. 225-255, pls. 47-57.