

ART. 13. A PROPOSED RECONSTRUCTION OF THE JAW
MUSCULATURE OF DIPLODOCUS

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An attempt to reconstruct the muscles of an extinct vertebrate is, of course, only guesswork, but, in spite of this fact, the preserved parts reduce the unlimited possibilities of such a reconstruction to a few alternatives only. In the case of a reconstruction of the cranial muscles of a fossil reptile belonging to the archosaur group, we may get some guidance from conditions found in recent representatives of this group, namely from crocodiles and birds. The only other type of recent reptile exhibiting two temporal arches, *Sphenodon* (*Hatteria*), is of rather doubtful value, but must be taken into consideration. On the other hand, a skull of such remarkable peculiarities and proportions as that of *Diplodocus* imposes in itself certain limitations of a reconstruction of muscles out of sheer phantasy. The relative positions of the orbit, the temporal arches, the endocranium, and the shape and inclination of the quadrate towards the lower jaw forces the investigator into a restricted area of several possibilities. One of those may offer the best approach to the real conditions enforced and caused by a very strange configuration of the skull. Many structures, like foramina for nerves or blood vessels, muscular scars, and the spatial compatibility of bulkier structures like muscles give, in many cases, a fairly accurate guide to reasonable guesses.

The skull of *Diplodocus* has a series of peculiarities which have a profound influence on the general arrangement of the jaw muscles, especially the adductors of the mandible.

The shifting of the fused nasal apertures to the top of the skull is accompanied by a strange elongation of the preorbital, and a very considerable shortening of the temporal, areas. The orbits have a very high position and are of spectacular size. The slanting position of an elongated quadrate brings the articulation of the lower jaw under the middle of the antero-posterior orbital diameter, whereas the small superior temporal opening remains in a fairly "normal" position, dorso-posteriorly of the orbit. The lower fenestra is brought into an oblique position. The antero-ventral end surpasses the anterior margin of the orbit by \pm the same distance by which the postero-dorsal end of the fossa projects behind the posterior border of the orbit. The fossa is of a very considerable depth, bordered posteriorly by the slanting external ridge of the quadrate, which projects rostro-medially into the temporal opening, mostly by the aid of the pterygoidal wing of this bone. The whole lower temporal window, together with the upper one, were, of course, the main places where the adductors could develop. As in birds, therefore, a good deal of the adductor mass had (according to the position of the lower temporal opening) a suborbital position. This similarity, however, should not be overemphasized. The quadrate in birds has a streptostylic dorsal joint and is a short and essentially vertically directed bone, and clearly delimited temporal fossae (in a normal reptile-like form) do not occur. As in birds, the post-temporal opening, usually totally absent in birds, is, here too, reduced.

The peculiar position of the articulation for the mandible precludes a mechanically feasible transfer of the pull of the adductor muscles to the lower

jaw. This may be inferred from the lack of significant muscular ridges on the external surface of the mandible, and from the shape and crowded disposition of the teeth on the cranial tips of both jaws, and the lack of any teeth on the palate. The whole, vertically deepened osseous lamina formed by the maxillary, jugal and quadratojugal, when the mouth is shut, closely overlaps the vertical wall of the mandible. Especially the medial surface of the lower temporal arch (much shortened by the elimination of the jugal) shows no indication of any muscular origins from the inside of this bar (as in birds). The peculiar dentition shows no traces of any wear in either specimen seen by the author. We shall, later, propose a new theory about the food and feeding of these animals which seems preferable to the prevalent idea of a floating vegetable food (algae).

The skull as a whole is of a very delicate structure; the contact of the neurocranium with the roof of the mouth (palatopterygoid series) maintained by very slender basiptyergoid processes seems to imply a streptostylic condition of some kind. This impression is even enhanced by an investigation of the skull kept in the collection of the American Museum of Natural History (969), where the upper end of the quadrate seems to form a bird-like articulation with the skull proper! The reconstruction of this skull has, however, been criticised by Holland (1906). The much better preserved and prepared specimen in the Carnegie Museum (C.M. 11161) shows a fixed attachment of the quadrate against the squamosal, the postfrontal, and postorbital, above; a long, ventrolateral smooth suture with the quadratojugal, and, still more important, a serrated, rigid, suture with the caudal end of the pterygoid (at the medial ventral surface of the "wing" of the quadrate).

A kineticism was, therefore, impossible in the sense of a mutual movement of cranial areas by aid of any articulations or flexible sutures. But as in the "akinetik" *Sphenodon*, a weak constrictor internus dorsalis musculature did exist, perhaps in order to stiffen elastic bony bars, in certain areas, perhaps simply as a remnant dating back from earlier kinetic stages.

Adductores externi.

We have had to exclude the possibility of the existence of a muscle rising from the lower temporal arch, owing to the lack of any scar of muscle origins at its flattened medial wall. The lower contour of this arch considerably overlaps the dorsal contour of the lower jaw when the mouth is closed. We are here, doubtless, in the region of the rictus oris, where the vertically elevated base of the lower arch fulfills the task of the external rictal plate in a recent saurian. The internal rictal plate was (as we shall see later), slightly more rostral in position, owing to cranially protruding muscles at the inside of the smooth coronoid prominence.

1. *Adductor mandibulae externus superficialis.* Fig. 1.

In a sharp contrast with the blade-like transverse section across the lower temporal arch, the suborbital bridge, formed by the jugal and postorbital, has a transversely broad base, which is deeply hollowed out by a longitudinal groove. This area certainly formed the elongated origin of the external adductor portion (*adductor medialis externus superficialis*: 1 in Luther-Lakjer's abbreviations). This muscle probably lost its thickness in ventral direction and dwindled down to a very thin muscular or only tendinous sheet at the level of the lower temporal arch. Certainly it inserted at the lateral surface

of the lower jaw, between the posterior slope of the coronoid prominence and the articular area. This muscle is probably the only one which inserted at the lateral surface of the mandible or at its dorsal margin. The very close fitting, almost shearing lower margin of the maxilla (ventrally of the pre-orbital aperture) leaves little room for an intervening muscular sheet, and a very shallow external insertional scar only is discernible at the external face of the mandible. A tendinous or a fleshy lateral insertion, very flattened along the dorsal ridge of the mandible are the only acceptable alternatives for the insertion (or a combination of both conditions could have taken place).

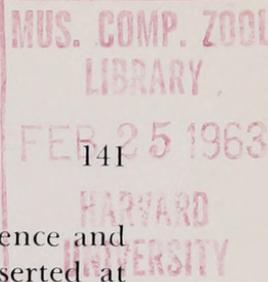
The muscle, whatever its insertion may have been, was a retracting adductor, filling the whole lower temporal fossa as an external layer, as in comparable cases in recent reptiles. Its posterior slope along the lateral ridge of the quadrate was probably connected with this bone by a tendinous layer. Externally, the thin muscle was probably covered by an insertional aponeurosis which reached the lateral surface of the mandible. Perhaps this lateral cover was partially backed at the medial surface by muscular fibers which reached up to the summit ridge of the mandible; this possibility would form a kind of reasonable compromise between the alternatives mentioned above.

2. *Adductor mandibulae externus medialis*. Fig. 2-3.

Two different interpretations will be found in the following paragraph; one based on a simple, the second (and preferred) based on a bipartite *pseudotemporalis*. The figures are based on the second interpretation.

The reconstruction of the adductor medialis was much more difficult, owing to probably incorrect restorations in the New York skull. The Pittsburgh specimen offered a much better chance to get appropriate results. There is no doubt that the upper temporal fossa was filled mostly by the wide upper ends of the sloping portions of the *adductor mandibulae externus medialis* (2), and the *adductor mandibulae externus profundus* (3) and the *pseudotemporalis superior* if this muscle was present. All these muscles could certainly not have reached the mandible in a course *medially* of the strongly developed anterior flange of the quadrate; therefore a rather narrow space between this flange and the *adductor mandibulae externus superficialis* must have contained these narrowed muscles on their way across the lower temporal fossa towards the lower jaw (at its medial face). But, an extensive transversely directed osseous shelf (between the upper temporal fossa and the posterodorsal part of the orbit) narrows considerably (Fig. 7) the straight access of muscles from the upper to the lower temporal fossa. Therefore, a simple, straight course of, at least a part of the adductors descending from the upper window was impossible. It was thinkable only for muscles rising from the posterior (and transversely directed) frame of the fossa, where the squamosal is deeply hollowed out for the scar of muscle origin of straight-fibered muscles, which could not have filled more than about the posterior third of the upper temporal fossa. It may be assumed that this muscle was an *adductor mandibulae externus profundus* (3). But how could adductors rising from the anterior and medial part of the periphery of this opening have reached the lower fossa and the mandible, by-passing the quadrate flange at their inner (medial) surface?

One possibility, which had to be envisaged, was deduced from the muscular arrangement found in many birds, where *adductores externi* invade suborbital



areas in connection with the preorbital position of the rictal area. I think that the funnel-shaped fossa (especially the caudally sloping, deeply excavated anterior and lateral margins of the fossa) inhibit a substantial penetration of adductors rising from the margins of the fossa into the orbital area. I would rather believe that a part of the *medialis* started, cranially of the *profundus*, from the medial periphery of the fossa, and a separate belly from the cranio-lateral anterior circumference. In the Pittsburgh specimen a vertically descending osseous ridge (Fig. 7, caudal view) clearly delimits both areas. We would have, therefore, a bipartite, "double-headed" *medialis*, a portion 2a, rising from the antero-lateral margin of the fossa up to the vertical ridge, and a portion 2b which was probably covered anteriorly by the cranio-lateral belly of 2a. In the description of the occiput (Gilmore, 1932) C.M. 662 this vertical ridge is not distinguishable but the complete skull (C.M. 11161) shows it very clearly. This structure probably corresponds with the dorsal wing of the so-called alisphenoid (Holland).

The general direction of the rostroventrally sloping fibers of 2 and 3 is determined posteriorly by the surface of the upper part of the quadrate "wing", and, anteriorly, by the position of the coronoid elevation.

3. *Adductor mandibulae externus profundus*. Fig. 2-3.

The scar of muscle origin of the *adductor profundus* (3) was, most probably, at the posterolateral part of the upper temporal fossa. Three muscles, therefore, filled this approximately circular window: 2a (cranio-lateral) the rostrolateral part; 2b the dorsomedial (probably largest) area, whereas 3a with straight and very slanting fibers, filled the latero-ventral part of the fossa (Fig. 3).

For alternative and preferable interpretations see below; the first one is based on a single, the second one on a bipartite *pseudotemporalis* muscle.

At least, one subdivision of the *adductor externus profundus* must be assumed; a deep belly, 3b,* which filled the small posttemporal fossa and crossed from caudodorsally into the deepest layers (the posteromedial ones) of 3a whose origin was limited to the posterolateral parts of the upper temporal fossa. Of course this part was very slender owing to the minuteness of the posttemporal window; its fibers started (as in saurians) from the lateral and dorsal margin of the opening, bending, in their way forwards, around the ventromedial periphery of this perforation (Fig. 7).

Medialis and *profundus* cross in their slanting descent to the mouth slightly towards the posteroventral corner of the large orbit in order to reach the insertional fields. An alternative interpretation of the same areas of origin, under the assumption of the existence of a bipartite *pseudotemporalis*, preferred to that given here, will be found below.

The inside of the mandible gives some information about the insertion of add. ext. 2 and 3, respectively, and other muscles. Four insertional areas may easily be distinguished at the inner surface; two caudal ones for the adductors rising from the quadrate and, near the posteroventral contour, the insertional groove for the *pterygoideus*. Two more rostrally situated muscle insertions consist in a deep groove inside the coronoidal elevation, and below this deeply hollowed longitudinal area. Another, very clearly marked, muscular scar is very obvious.

*Not shown on illustration

Discussion of both V_3 foramina at the medial side of the mandible.

The main branch of the trigeminal 3 seems to enter the mandible at the bottom of the deep muscular trough medially of the "coronoid elevation." The posterior foramen, situated in the groove in front of the articulation of the jaw is much narrower than the more cranial one, and is probably the entrance foramen for the posterior cutaneous branch of V_3 . The exit of this foramen at the lateral surface of the articular could not be found with certainty, but the whole interpretation given here agrees better with conditions found in recent sauropsids than the other alternative, seeing in the posterior foramen the entrance of the main mandibular branch, and in the anterior one a deepened muscular impression only; but, in any case, the posterior foramen would indicate the level separating the *adductor posterior* from the *adductor externus* group.

There can not be any doubt that the anterior ventral scar is the insertional area of the deepest of the anterior adductor muscles (the *pseudotemporalis* complex). The anterior dorsal groove accommodated the three muscles descending from the upper temporal fossa: 3a and the deep belly as the innermost, probably inserting more ventrally, perhaps even forming an intra-mandibular prolongation into the deeply enlarged Meckelian fossa as in crocodiles, where, however, the *medialis* penetrates into this field. In succession from medial to lateral 2b and 2a, the *adductor externus medialis*, respectively, occupied more dorsal areas of the lateral wall of this deep Meckelian groove. It is impossible to get a detailed idea of the shape of the insertions of the four parts of both adductors involved; whether some of them inserted in the form of aponeurotic layers which collected the more dorsally situated fleshy parts, or directly. Probably the first way of insertion was followed by one or both parts of the *medialis*.

We must try to get an idea about the muscles sloping down from the anterior wing and the stem of the quadrate.

In the crocodilians, where the quadrate has a sloping which is just in the contrary direction to that of *Diplodocus* (the lower end posteriorly of the upper one), the whole *adductor externus profundus* rises from this bone. Here, in *Diplodocus*, the same muscle developed mostly from the upper temporal fossa. There is no doubt that the following muscles could have risen from the anterior area of the quadrate:

1. The *adductor posterior* as a whole; this muscle has always such an origin in sauropsids and constitutes the innermost and most caudal adductor.
2. Parts of the *pseudotemporalis* group.
3. Possibly parts of the deepest layers of the *adductor mandibulae externus profundus*.

Because the course of the trigeminus 3 can be only approximately guessed, a delimitation of muscular portions in relation to the trigeminal branches can not be given precisely, but, some skeletal facts observable in the configuration of the quadrate give at least a clue. The wing represents a surface appropriate for the origin of a possibly composite *adductor posterior*. This muscle probably covered the more external parts of the sloping quadrate from its upper (posterior) end onto the lower border of the wing. Since the trigeminus 3 had to cross the ala quadrati in an oblique way forwards, covering a considerable

distance in order to reach the mandible (at a short distance in front of the articulation) we can not decide whether this slanting, external part of the *adductor posterior* was not duplicated by a deep portion of an *adductor externus profundus* (3c) at its lateral surface. In other words, we could admit the possibility of an *adductor mandibulae externus* 3c rising from the same area, but laterally of the descending V_3 ; otherwise, only an *adductor posterior* alone should be inferred. In birds, such an *adductor 3 caudalis* is well known (*Cepphus*, *Aprosictus*, *Crypturus*, *Oedemia* and *Gallus*). The topographic relation between the entrance of the trigeminal foramen into the mandible and the pre-articular muscular groove in front of the jaw-joint speaks more in favor of the presence of a well developed extra-trigeminal muscle rising from the quadrate; and this could be only a 3c "caudalis." The more or less parallel *adductor posterior* reaches the lower jaw somewhat in front of the *adductor profundus*. Fig. 3 represents such a 3c, a muscle which probably was connected with 3a and the insertional aponeurosis of the *pseudotemporalis* group. But the presence of a deeper, short-fibered, caudal *adductor posterior* with steeply descending fibers is certain; the lower end of the quadrate widens in the area of articulation transversely and a deep hollow faces cranially just above this hinge, clearly set off from the wing portion. From this deep niche the triangular, caudal part of the *adductor posterior* (B) could enter the furrow behind the trigeminal foramen. In other words, I think that this caudal *adductor posterior* (B) was inserted laterally and caudally of the long-fibered portion A, (Fig. 5, *adductor posterior* A, B).

The pseudotemporalis. (Fig. 3-4).

It can easily be seen that the cranial tip of the quadrate wing is the most medial part of the bone as in birds. This inward-bent part released a *pseudotemporalis profundus*, which inserted in the lower of both anterior muscular insertion scars at the medial face of the coronoid elevation of the mandible. This deep insertion is fitting for the innermost anterior adductor. But we wonder whether this muscle was laterally duplicated by a pseudosuperior, as in most lizards, birds, and *Sphenodon* (not in the crocodiles). This muscle is strictly postorbital in birds and *Sphenodon*. At the first glance there is no possibility of locating any temporal adductant muscle which would have to be almost the innermost at the inside of the mandible, and which should be situated medially of the V_2 and originate from a postorbital area. This same muscle should have a deep but rather cranial position compared with the *adductores externi* 2 and 3.

There is only one area, the laterally bulging ventroposterior wall of the orbital bar, which forms at the caudal end a clear muscular scar. Obviously a temporal muscle, rising from this area would slightly penetrate into the ventroposterior area of the orbit, swing medially of the suborbital wall forwards, and follow the deeper slanting temporal muscles, covered by the sub-orbitally rising *adductor externus* 1. If this possibility should be accepted, this muscle, owing to its position laterally of the muscles rising from the upper temporal fossa, could not possibly be a *pseudotemporalis superior*, but rather a separate portion of the *adductor medialis*; but, in this case, the muscle, sloping from the dorsomedial circumference of the upper temporal fossa, would be a *pseudosuperior*, squeezed in ventrally between the more dorsally inserting adductors 2 and 3 and protruding (as an aponeurosis) into

the anteroventral insertional field, joined medially by the *pseudotemporalis profundus* (Fig. 2-4).

Such an explanation would give the clue for the peculiar postorbital buttress (Fig. 7-8) and would place the *pseudosuperior* in a "normal" position inside the upper temporal fenestra (cf. *Sphenodon*). Such a caudomedial position would well correspond to the position of the trigeminal foramen; the nerve, in its course to maxilla and mandible, could without a detour swing around the posterior margin of this muscle.

It would, however, be very strange to see a *pseudoprofundus* much more lateral than the *pseudosuperior*, but the insertions would be possible and in proper sequence; e.g. the terminal tendinous sheet of the *pseudosuperior* could collect at its inner surface the *pseudoprofundus* or the latter only inserted directly at the mandible. I prefer this interpretation to the other given above and I named the muscles involved in accordance with this only feasible position of the *pseudosuperior*. Fig. 2 shows that a double-headed *adductor mandibulae externus medialis* could have been formed by the deep posteroventral bone partition between the orbit and the upper temporal fossa. A portion 2a rising suborbitally would join the deeper portion 2b from the anteroventral corner of the fossa: both would, fused, duplicate laterally the adductor 3a and the deep belly (36).

Summary of the adductor arrangement.

Origins from upper temporal fossa:	anterolaterally 2b posteriorly 3a medially <i>pseudosuperior</i>
from posttemporal fossa:	36 (deep belly)
from posterolateral corner of orbit:	2a
from suborbital bar:	1
from quadrate:	3c (laterally); post. A (ant.) and post. B (post.); <i>pseudoprofundus</i> (anterior wing)

The pterygoideus muscle.

The posterolateral surface of the mandible shows no traces of a lateral insertion of a *pterygoideus*. The "Kauballen" probably did not exist and the moderately swollen posterior end of the bipartite muscle inserted along a ridge close and almost parallel to the posteroventral contour of the lower jaw. This ridge extends also into the retro-articular process and is well separated by its lower position from the muscular scar for the *pseudotemporalis* group. In the lateral view this muscle probably did not extend beyond the ventral contour of the lower jaw.

One part of the *pterygoideus* started from the area, where ectopterygoid and pterygoid meet, i.e. from a point near the anchorage of the palatal skeleton with the maxillary. The whole dorsomedially flattened muscle had a caudal slope of about 15° (m. ptg. dorsalis) and was perhaps slightly covered by the ventrolateral "bridge" to the maxillary from above. A separate, medio-dorsal portion of the *pterygoideus* could have existed, rising from the (medial) inner slope of the pterygoid in front of the *processus basipterygoideus*. This portion followed a more transverse course and probably inserted ventrally under the long-fibered *pterygoideus dorsalis* (from the maxillary bridge).

These two parts would be roughly comparable with Lakjer's *pterygoideus* A-B and *pterygoideus* C., respectively, in *Crocodylus*.

The long-fibered would be comparable with a *pterygoideus dorsalis*, the short-fibered (dorsal) would be comparable with a *pterygoideus ventralis* in birds.

Constrictores interni dorsales.

It has been remarked above that the skull of *Diplodocus* could hardly have been of a kinetic type but, as in *Sphenodon*, muscles which stiffened the link between the endocranium, the dermocranium and palatopterygoid complex, did exist. There are clear indications of the existence of a *protractor quadrati*, the specialised remnant of a *protractor pterygoidei*. Its traces consist in a concavity at the medial face of the ala quadrati which faces a muscular furrow at the posterior slope of the slender *processus basalis*.

The functional value of such an arrangement probably consists in establishing a stiffening pull of the quadrate towards the base of the endocranium. At the dorsomedial process of the pterygoid in front of the cavity for the basiptyergoideal articulation a muscular scar faces another, anterior, muscle groove along the dorsolateral surface of the *processus basalis*. This was, most probably, an appropriate area for a retrahent thin muscle, roughly corresponding to the retrahent and levator pterygoidei of different Sauropsida.

The lateral wall of the endocranium itself shows a number of muscular scars and ridges; but these structures are not traces of the jaw musculature. They form the origins of the muscles moving the eye and the eyelids (facing the orbit) or, posteriorly, of certain occipital muscles (facing caudally) and will not be analyzed here. It may be mentioned, however, that the anterodorsal flap of the quadrate wing dismissed perhaps, in a dorsal direction, a *pseudotemporalis bulbi*, a muscle found in birds, but missing in crocodiles and *Sphenodon*.

Depressor mandibulae.

In several details the *depressor mandibulae* left its traces; the postarticular portion of the articular bone exhibits two muscular scars of very different size. The whole lateral face caudal of the jaw articulation is deeply concave as seen from above; a muscular insertion covered, most probably, as a long sheet the whole outside of the postglenoidal region, reaching down to the ventral contour of the *processus*.

Another scar, a very sharp excavation, pointing in a posterodorsal direction, is situated at the very end of the lower jaw. We may, therefore, infer the presence of a double *depressor mandibulae* muscle:

1. A lateral, ventrally fan-shaped expanded portion, rising from the upper end of the quadrate (the most caudal area of this bone) and ending at the lateral insertional scar on the retro-articular process.
2. The second, and almost certainly spindle-shaped part of the *depressor mandibulae* starts at the end of the *processus paroticus* which overlaps caudally the upper end of the quadrate, and ends at the terminal muscular scar of the articular bone. Such a double *depressor mandibulae* is not rare in reptiles. The anterior and more lateral fan, because of the anteriorly directed curvature of the quadrate, would allow for sufficient room for the tympanic membrane under the posterodorsal part of the quadrate and along its ex-

ternal ridge; a vertically elliptical field would be left for it, sloping cranio-ventrally.

Stapedial traces. (Fig. 7).

Looking at the quadrate from a caudomedial direction (obliquely facing the internal and posterior surface of this bone), a vertically projecting facet forming a nearly straight, lateral border and a slight medial bay, being somewhat wider dorsally than ventrally, is very obvious. This slight prominence, 2 cm. under the inner, upper tip of the quadrate, is strictly symmetrically arranged on both sides, therefore not an accidental structure. There is no doubt that it had something to do with the stapedial apparatus. If it did not form the contact with the end of the stapes itself (a very improbable surmise) it certainly could have formed a contact with extrastapedial, cartilaginous structures or a ligament, linking extracolumellar parts with the quadrate. A *processus internus*, which is often linked with the posterior part of the quadrate, was most probably the structure adjacent to this little, but well elaborated, prominence. Perhaps, but less probably, conditions analogous to those in ophidians did exist in this dinosaur (implying a reduced tympanic cavity and membrane), where the stapes itself is linked with the quadrate by a cartilaginous intermediate nodule (the so-called stylohyal of the ophidians). Fig. 7 shows an artificial stapes inserted in situ, in order to show that this structure would not interfere with the position of the jaw muscles. Colbert and Ostrom describe several cases of preserved ear-ossicles in Dinosaurs, but in not a single one is an appositional facet at the upper posterior slope of the quadrate mentioned.

Discussion.

The whole differentiation of the jaw muscles in *Diplodocus* shows clearly, that the "awkward" angle of insertion and the peculiar forward thrust of the lower end of the quadrate, resulting in a disjunction of the lower temporal fossa from the upper one, by throwing the first directly under the orbit, precludes any substantial *biting power*.

Many authors have already described and discussed the very peculiar dentition of *Diplodocus*. But, besides the peculiar shape of the individual teeth and their exclusive disposition at the transversely truncated anterior ends of upper and lower jaws, respectively, the complete absence of any traces of wear is very remarkable. No doubt a scooping or combing out of the food from the water, a food which had to be swallowed without any mastication, was the only possible way of feeding. So far, floating water plants have always figured first as a possible source of food for *Diplodocus*. I feel quite unconvinced that such a source of nutrition could have been possible, especially if we take into account the certainly very low nutritional value of such a food and the very bulky mass of the body in contrast with a relatively extremely small "cropping apparatus." In the Jurassic period, especially in the Morrison beds, no substantial aquatic vegetable remains have been found together with the skeletal remains of the giant sauropods. Angiosperms must be excluded, and I do not know any "lower plants" frequent in fresh water and of a more substantial bulk which could be raked out from the water. Tough pteridophytes and *Characea* would not form an adequate food for such massive animals, and, especially, fronds of such plants, even if not

masticated (gastroliths!) would leave signs of use on the dentition owing to their rich mineral contents; but there is not a trace of any abrasion to be seen. This fact alone, together with the smallness of the head of *Diplodocus* and the poor nutritional value of any known fresh-water plants of this period induce me to put this problem again in the foreground. It should be stressed again that such a large animal could be dependent only on a floating food, occurring in great plenty and relatively rich in nutritional value. The scooping or raking of this submerged or floating food did not cause any abrasion; in other words, *Diplodocus* did not use its jaws for chewing but as a straining and raking device. The lateral posterior parts of the lower jaws, where teeth did not develop, were deeply overgrown and flanked by the sharp and vertically descending laminae of the maxillae; in fact, only the ends of the jaw apparatus were efficiently opened and closed again during this straining or raking operation. I see only one source of food which could fulfill the nutritional requirements of such a large animal; an invertebrate occurring in large numbers and large enough to be strained out by the very coarse device of the pencil-like fence of the dental series—relatively soft-shelled crustaceans of fairly large size and such enormous density that they could almost mechanically be scooped or raked out of the water, or as another alternative, relatively thin-shelled temporarily floating mollusks like lymnaeids, ampullariids or some other primitive pulmonates which have to surface in huge numbers in lagoon-like bodies of fresh water. Lamellibranchs could, in a similar way, have been sifted out of the soft mud of the bottom. Pulmonates very often form whole rafts at the surface of stagnant waters if the oxygen content in deeper water is getting low, especially under hot conditions. But even if such pulmonates did not really concentrate as whole carpets swimming at the surface (as I remember seeing in Anatolia in summer time), the raking in deeper layers could easily be done in soft mud or from algal or other (“higher”) submerged plant thickets. Gastroliths would, together with an acid gastric juice, quickly dispose of the relatively thin shells of fresh-water mollusks (gastropods or lamellibranchs). I would infer, therefore, that the big sauropods depended on animal food, and I think that mollusks (or perhaps some very large crustaceans, living in enormous numbers) could have been the basic food of these gigantic animals, which lived and fed wholly or partly submerged.

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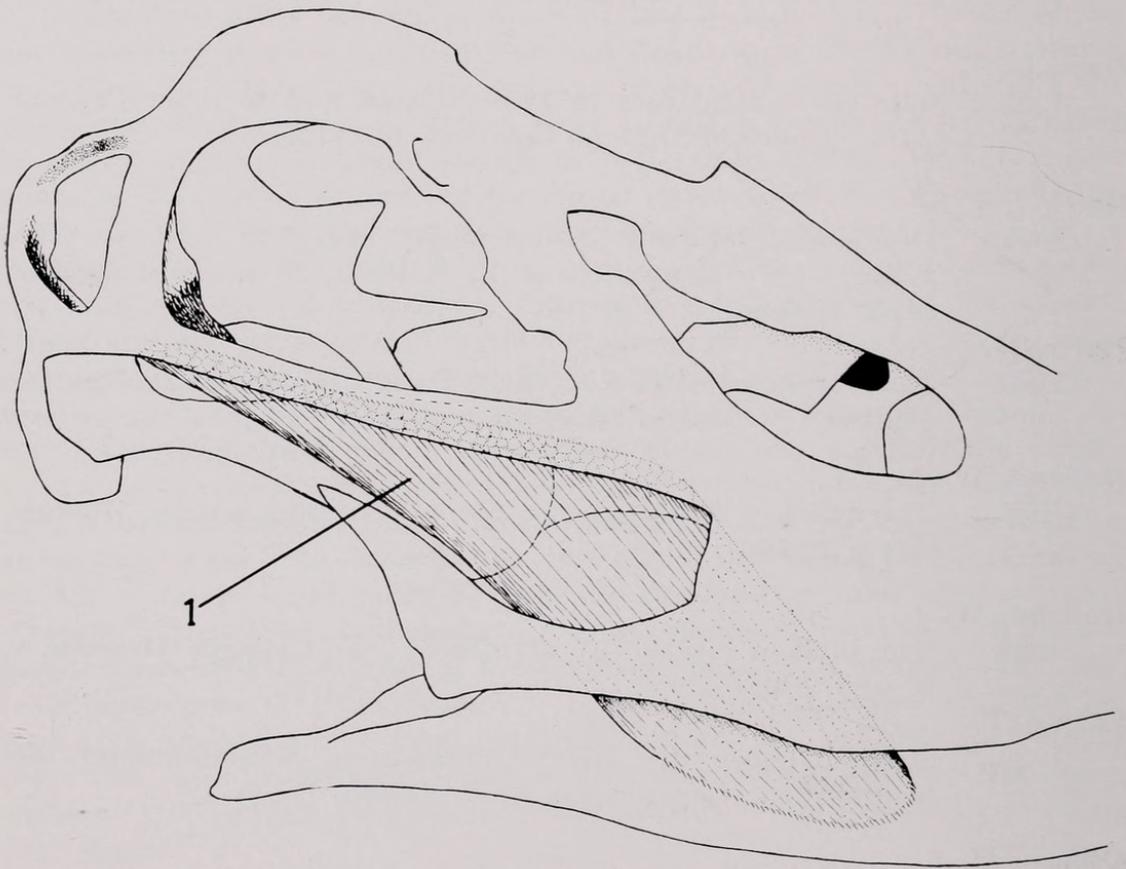


Fig. 1. Position of the *adductor mandibulae externus superficialis* (1)

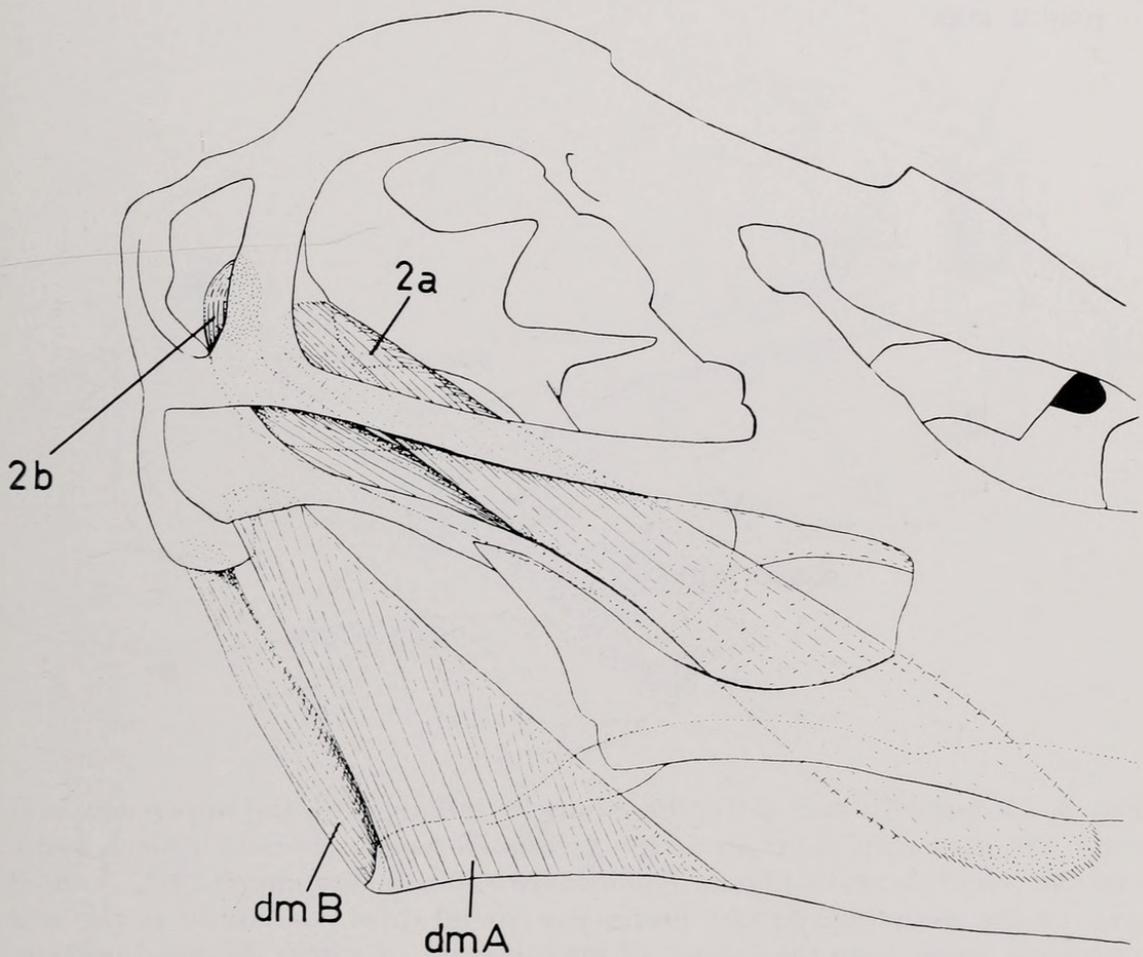


Fig. 2. The double *depressor mandibulae*. dmA inserts laterally at the retroarticular process, dmB at a strictly terminal insertional scar of the mandible. Both parts of the *adductor mandibulae externus medialis* are shown, rising from both surfaces of the postorbital bar and fusing anteroventrally according to the final interpretation given in the text. Portion 2a rises from the anterior, 2b from the posterior surface of the postorbital osseous frame

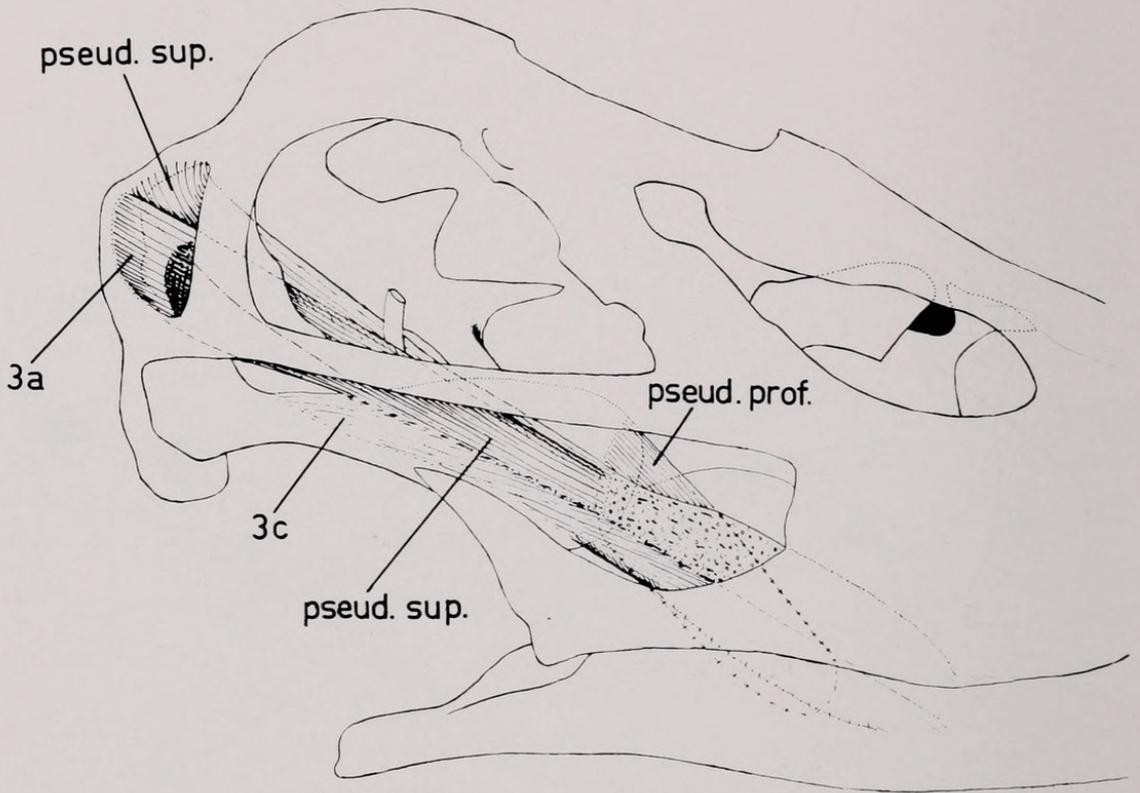


Fig. 3. Represents two of the three muscles bulging into the upper temporal fossa: the dorsomedial origin of the *pseudotemporalis superior* (pseud. sup.), and the posterolateral *adductor mandibulae externus profundus* (3a). A small part of the *pseudotemporalis profundus* (pseud. prof.) is visible at the scar of muscle origin from the "wing" of the quadratus. A rather doubtful portion, 3c, rising from the sloping anterior surface of the quadratus, has been added with some reluctance. Such a portion would have been partially fused with 3a and with the insertional aponeurosis of the pseudotemporalis group or both, but the trigeminal 3 had to pass downwards between 3a and 3c (laterally) and the pseudotemporalis group (medially). At the anteroventral corner of the upper temporal fossa the space of the scar of muscle origin of 2b is indicated as a concavity on the surface of 3a

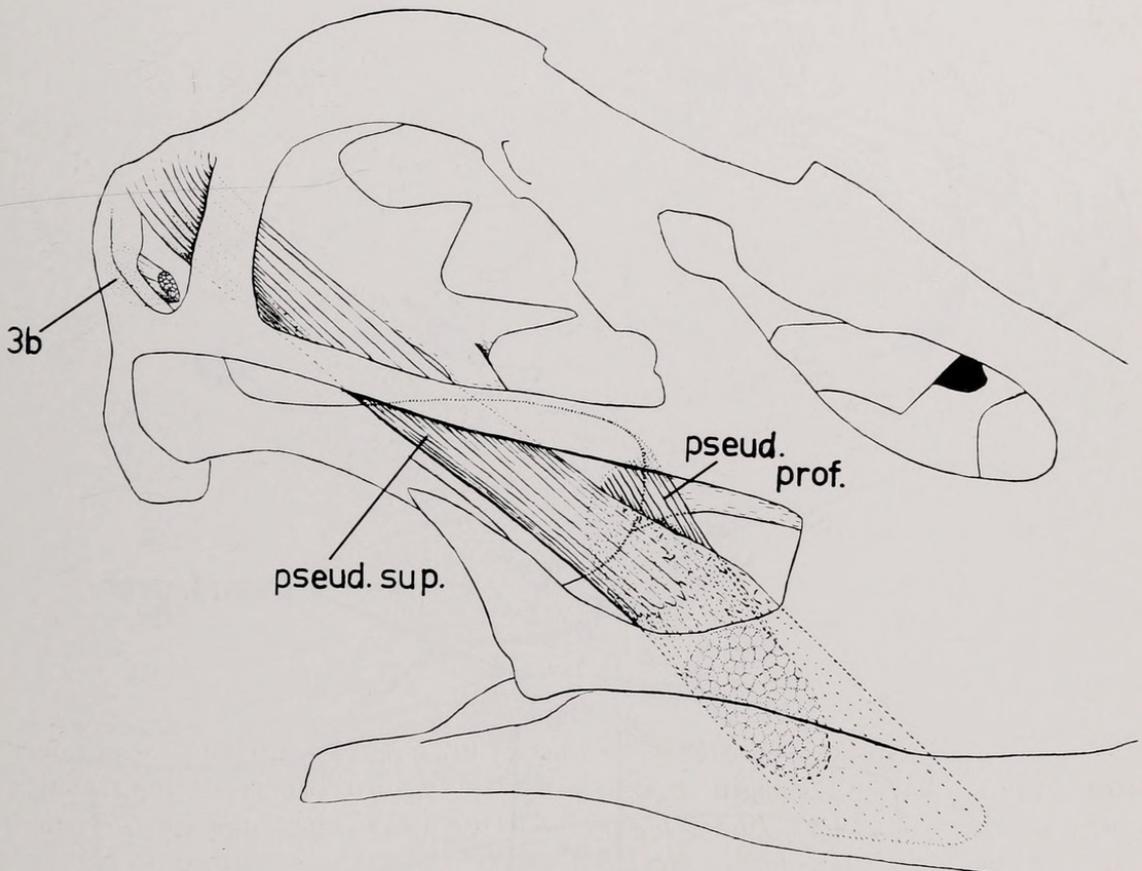


Fig. 4. Shows the emerging small portion 3b which joins 3a at its medial surface. Both parts of the *pseudotemporalis* (pseud. sup. and pseud. prof.) are drawn, but the insertions of the fused portions 3a and 3c at the surface of the *pseudotemporalis superficialis* and the common insertional aponeurosis have not been indicated specially. Compare with Fig. 3

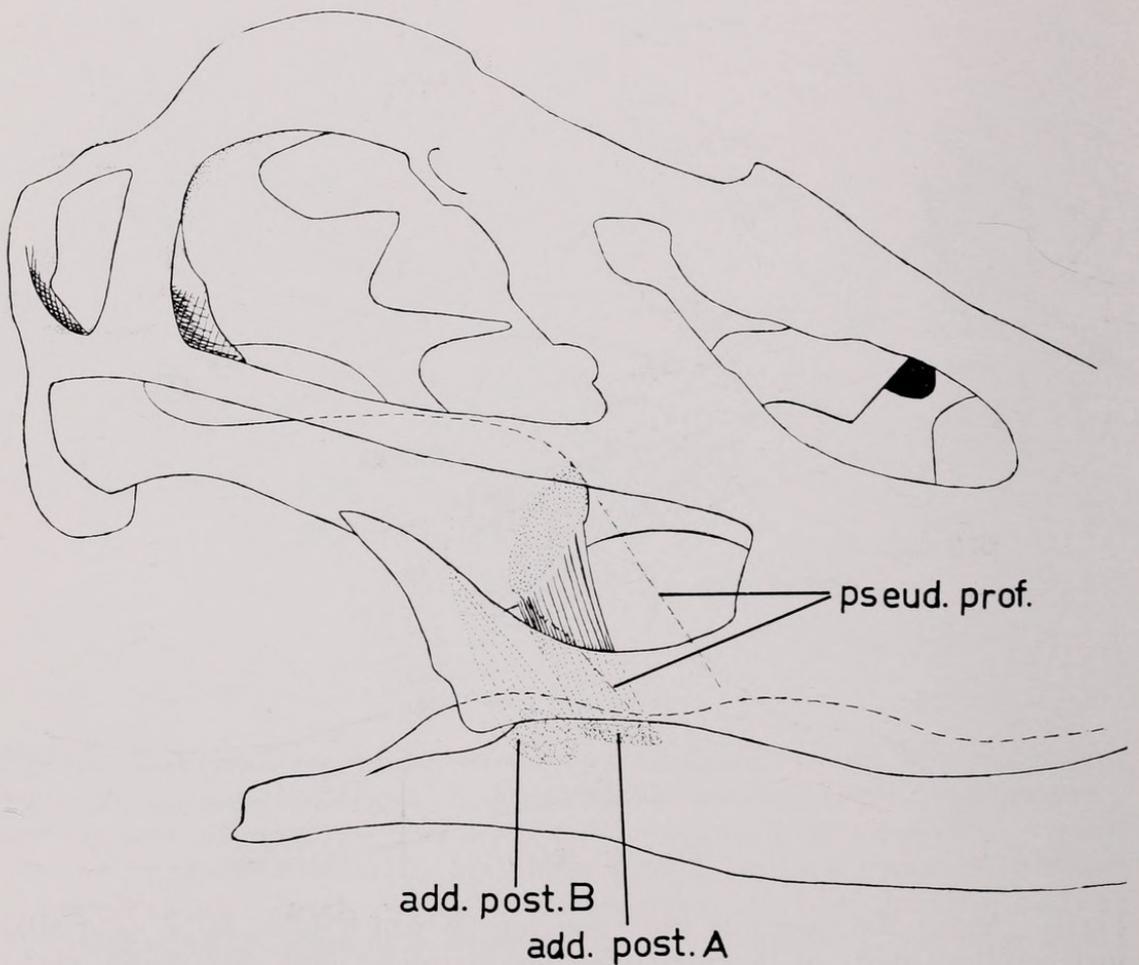


Fig. 5. The two distinct parts of the *adductor posterior* are shown. The anterior part is situated medially of the *pseudotemporalis profundus*, its contour indicated by the broken line

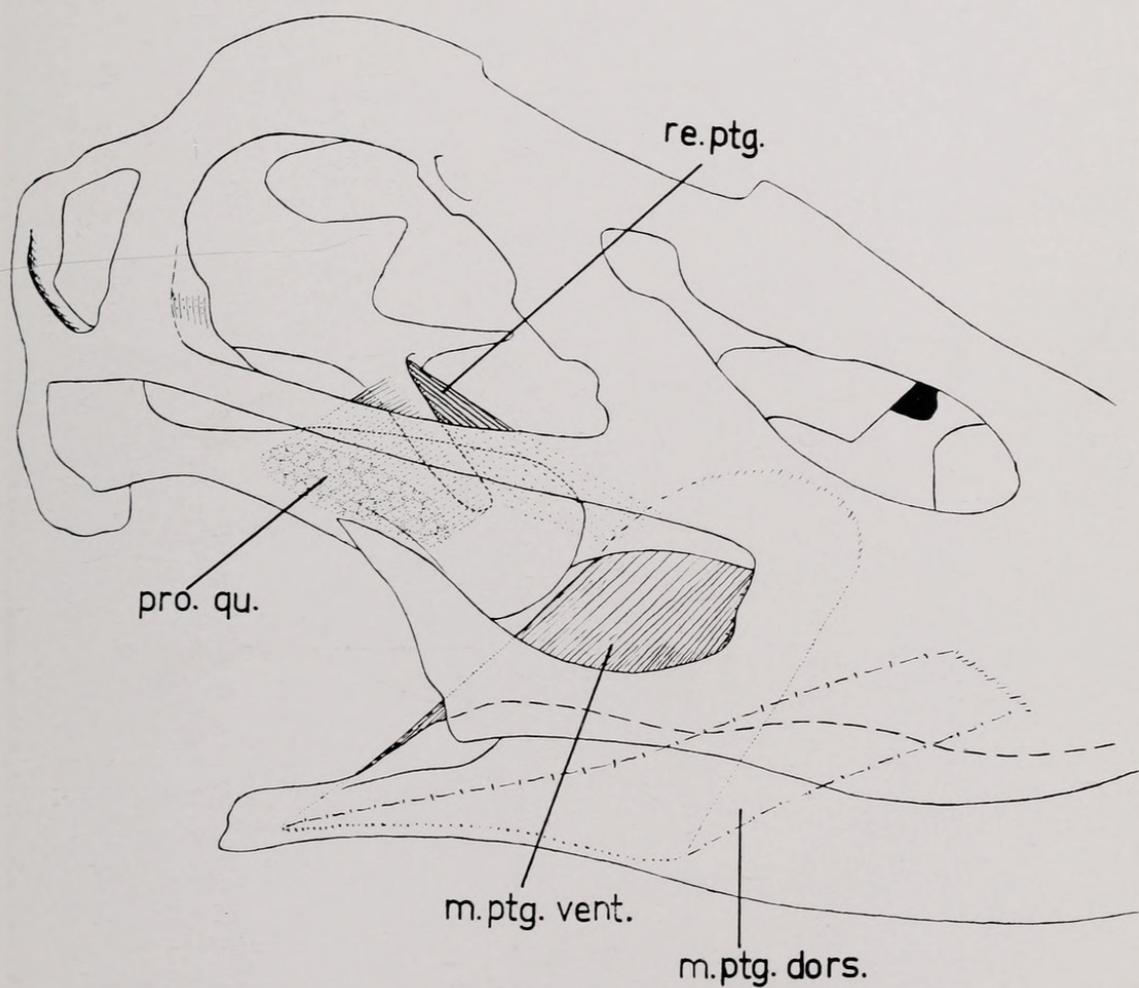


Fig. 6. Both parts of the *pterygoideus* are represented, partly in cross-hatching. The sloping *pterygoideus* "dorsalis" overlaps the insertion of the short-fibered *pterygoideus ventralis* near its insertion on the inner face of the mandible. The *protractor quadrati* (pro. qu.) and *retractor pterygoidei* (re. ptg.) are shown in their approximate positions

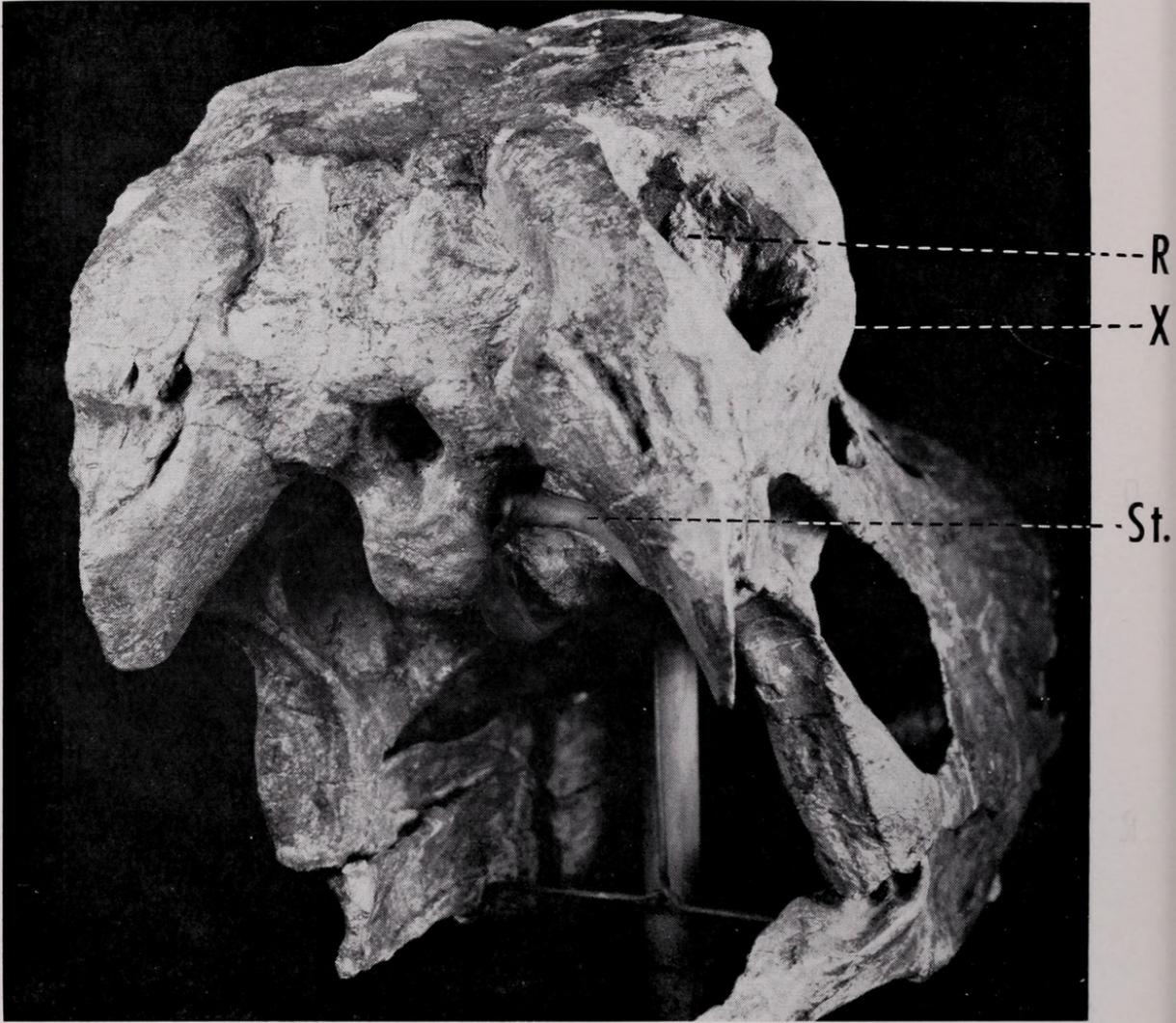


Fig. 7. Shows the position of an inserted artificial stapes (St.) and the ridge (R) at the posterior face of the postorbital shelf, facing the upper temporal fossa. Also shows the strongly projecting posteroventral rim of the orbit (X) and gives an idea of the shearing overlapping of the lower temporal arch across the mandible, with the shallow insertional scar on the latter for the *external adductor mandibulae* (1) muscle



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