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NOTES ON THE CRANIAL MUSCULATURE IN TWO SUBGENERA OF *REITHRODONTOMYS* (HARVEST MICE)

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THE principal object of the present study is to determine whether there are myological differences associated with differences in breadth of the zygomatic plate and of the mesopterygoid fossa in the subgenera *Reithrodontomys* and *Aporodon.* The diagnostic characters of these subgenera are mainly ones of the skull,[1] and the differences in breadth of the plate and fossa are two of the more striking and important of those characters. As examples of the subgenera we used *R.* (*Reithrodontomys*) *megalotis* and *R.* (*Aporodon*) *mexicanus.* In those species the cranial characteristics of the subgenera are well developed. Of those characteristics the following are important here: Compared with that of *megalotis* the brain case of *mexicanus* is broad (see sample, comparative measurements, below), the zygomatic plate is narrow, the mesopterygoid fossa is broad, and the molar pattern is complex, that is, mesolophs (ids) and mesostyles (ids) are present.

Four specimens were dissected. Two of them are examples

[1] A. H. Howell, "Revision of the American Harvest Mice (Genus *Reithrodontomys*)," *North Amer. Fauna,* 363 (1914).

of *R. megalotis longicaudus* from San Diego County, California. Two are examples of *R. mexicanus cherrii* from La Carpintera, Costa Rica. These were kindly provided by G. G. Goodwin from the collections of the American Museum of Natural History. Important myological differences were checked against other specimens. Magnifications of twelve and of twenty-four power in a dissecting microscope were employed. The drawings are by William L. Brudon, Artist of the Museum of Zoology.

Certain information regarding the shapes and sizes of the skulls and of relevant parts thereof, is presented here as groundwork for subsequent descriptions of the musculature. Approximate measurements, in millimeters, of the crania of the four specimens are as follows:

Species	Greatest Length of Skull	Breadth of Brain Case	Least Breadth of Zygomatic Plate	Breadth of Mesopterygoid Fossa
megalotis	20.2, 20.5	9.6, 9.6	1.8, 2.1	0.7, 0.9
mexicanus	21.5, 23.4	10.7, 11.2	1.4, 1.6	1.6, 1.8

The contrasts in dimensions and in structure as indicated above and below are typical of the two species, as will be shown by Hooper in a systematic review of the genus that is now in progress. Concomitant with variations in breadth of the zygomatic plate are changes in the relationships of some other parts at the anterior root of the zygomatic arch. In *mexicanus* the anterior border of the zygomatic plate is conterminous with the anterior border of the arch. Thus the anterosuperior border of the arch curves evenly away from the rostrum (Pl. I, Fig. 1). In *megalotis* the anterior border of the plate projects conspicuously beyond the arch, forming an anteriorly projecting keel that bounds a deep zygomatic notch—the superior lip of the infraorbital foramen (Pl. I, Fig. 2). Apparently associated with an increase in breadth of the mesopterygoid fossa is a decrease in size of the pterygoid fossae. In *megalotis* each pterygoid fossa is considerably broader than the mesopterygoid fossa, while in *mexicanus* there is less difference in size between the two (Pl. I, Figs. 1*c* and 2*c*).

One difference in the mandibles of the two species seems important. In our examples of *megalotis* the angular process of the mandible is inflected mediad and then dorsad, thus forming a broad, deep fossa (Pl. I, Figs. 2*a,* 2*b*). In *mexicanus* the angular process is inflected mediad but then scarcely, or not at all, dorsad; it forms a comparatively narrow shelf (Pl. I, Figs 1*a,* 1*b*). The cranial differences that are outlined above suggest that the masseter and pterygoid groups of muscles should be examined. They are described below. In the remarks that follow the specimens are compared as if they were identical in size. Any differences in size of the muscles, therefore, are not absolute but are relative to size of the skull.

DESCRIPTION OF MUSCLES

M. masseter superficialis

ORIGIN.—From the small tubercle located on the base of the zygomatic plate near its anterior border.

INSERTION.—On the ventral margin of the angular process of the mandible. A small slip passes around the ventral margin of the jaw, is reflected onto the medial surface of the mandible, and inserts on the posterior aspect of the bulge formed by the root of the incisor.

REMARKS.—The origins of this muscle are similar in the two species. In *megalotis,* however, the maxillary tubercle is more prominent. The fleshy part of the muscle is less massive and that portion which is reflected onto the medial surface of the mandible is smaller. Although in *megalotis* the muscle is smaller in total mass, it is wider, covering a greater part of the lateral surface of the masseter lateralis.

M. masseter lateralis pars anterior

ORIGIN.—From the lateral border of the cranial half of the zygomatic arch.

Insertion.—On the lateral surface of the mandible, from the level of the anterior margin of M_1 to near the level of a vertical plane located just posterior to M_3.

Remarks.—There is little difference in the relative size of this muscle in the two species. There is, however, a difference in the position of the muscle. In *mexicanus* the anterior fibers arise slightly medial to the keel of the zygomatic plate and enfold its anterior margin. In *megalotis* the fibers arise entirely lateral to the zygomatic plate; none of them originate medial to the keel of the plate. In that species also the entire mass of the muscle occupies a position anterior to that in *mexicanus.* It inserts as far forward as the mental foramen. In *mexicanus* the insertion lies well posterior to the mental foramen.

The relatively greater area of the zygomatic plate in *megalotis* leads one to assume that this gives a greater area of origin for the anterior part of the masseter lateralis. The area of origin is not larger, however, because the muscle does not arise there. Rather it has its origin only on the superior border of the plate and the adjoining dorsolateral margin of the arch. Therefore, it is the length of the dorsal lip, rather than of the plate itself, that is important. Functionally, a wide plate would seem to be unnecessary. A long spine and a narrow plate would achieve the same end, as is seen in *Sigmodon,* for example.

M. masseter lateralis pars posterior

In many rodents this portion is a single mass of fibers. In the two species of *Reithrodontomys* it consists of two slips.

Anterior portion:

Origin.—From the lateral border of the zygomatic arch posterior to the masseter lateralis pars anterior.

Insertion.—On the lateral surface of the angular process.

Remarks.—This segment is smaller in *mexicanus.* The origin is similar. The insertion differs. The area of insertion in *mexicanus* involves only about two-thirds as much of the surface of the angular process as it does in *megalotis.*

Posterior portion:

ORIGIN.—From the "elbow" of the zygomatic arch, that is, the squamosal part of the arch.

INSERTION.—On the tip of the angular process.

REMARKS.—This segment seems to be more massive in *mexicanus.* In that species the origin extends farther anteriorly along the arch and the fibers pass deep to the posterior fibers of the anterior segment of pars posterior. Because of this the entire posterior border of the angular process is covered in *mexicanus,* while in *megalotis* a considerable part of the curve is exposed.

M. masseter medialis pars anterior

ORIGIN.—From the medial aspect of the cranial half of the zygomatic arch and from the preorbital fossa of the maxillary bone.

INSERTION.—On the lateral surface of the mandible, medial and dorsal to the insertion of M. masseter lateralis pars anterior.

REMARKS.—In *mexicanus,* a larger segment of the masseter medialis originates in the preorbital fossa and passes through the infraorbital foramen.

M. masseter medialis pars posterior

ORIGIN.—From the medial border of the posterior one-half of the zygomatic arch.

INSERTION.—In the groove between the cap of incisor and the articular process.

REMARKS.—No differences noted.

M. temporalis

There are two indiscrete segments described below as numbers 1 and 2.

Segment 1:

ORIGIN.—In the orbit from the posterior part of the frontal bone and by aponeurosis from the anterior half of the temporal line.

INSERTION.—On the medial surface of the coronoid process and in the groove between the alveolar and coronoid processes.

REMARKS.—The fibers of this segment lie superficial and anterior to the anterior fibers of Segment 2.

Segment 2:

ORIGIN.—From the entire temporal part of the cranium (the dorsolateral surface of the squamosal, the entire temporal line, and that part of the lambdoidal crest that lies ventral and lateral to the temporal line).

INSERTION.—On the tip and the immediately adjacent medial surface of the coronoid process.

REMARKS.—There are striking differences in mass and in area of origin of this muscle. It is much larger in *mexicanus.* In that species the ventral limits of the muscle extend below the level of the dorsal lip of the auditory meatus. In *megalotis* the ventral limits lie well above the meatus.

M. pterygoideus externus

ORIGIN.—From the anterior half of the external face of the pterygoid plate and from that adjacent part of the alisphenoid which lies anterior to the groove for the masticatory nerve.

INSERTION.—On the medial surface and the inferior border of the articular process of the mandible.

REMARKS.—No difference noted.

M. pterygoideus internus

ORIGIN.—From the pterygoid fossa.

INSERTION.—On the entire medial surface (the shelf and adjoining parts) of the angular process of the mandible.

REMARKS.—This muscle is absolutely, as well as relatively, larger in *megalotis*, and the bony surfaces for its origin and and insertion are correspondingly larger.

DISCUSSION

Some muscles, or parts thereof, are essentially identical in the two species. Others differ interspecifically in size and/or position. The differences are summarized below in terms of relative size of skull of *megalotis*. Thus the statement below that M. pterygoideus internus is larger means that relative to size of cranium M. pterygoidus internus is larger in *megalotis* than it is in *mexicanus*. The muscle may or may not be absolutely larger, although in this instance it is.

M. masseter	
superficialis	Slightly smaller; a thinner sheet.
lateralis pars anterior	Originates and inserts farther anteriorly; no fibers insert in zygomatic notch.
lateralis pars posterior	
anterior portion	Slightly larger.
posterior portion	Slightly smaller; arises farther posteriorly.
medialis pars anterior	A smaller segment arises in preorbital fossa, and passes through infraorbital foramen.
M. pterygoideus internus	Conspicuously larger, with larger area of origin and insertion.
M. temporalis	Much smaller, with smaller area of origin.

In the masseter complex there are few features that can be correlated with breadth of the zygomatic plate and of the mesopterygoid fossa, the two items that we have had in mind in this study. We did not expect the masseter complex to have any direct bearing on the mesopterygoid fossa, but we did suspect that it might be modified concomitant with increase or decrease in diameter of the zygomatic plate. Probably one reason that it is not modified is that none of the masseter muscles attach on the face of the plate; they attach only on its superior margin—the anterodorsal rim of the zygomatic arch. The total masseter muscle mass is approximately the same in the two species. In *megalotis,* which has the smaller skull yet absolutely and relatively the broader plate, there is relatively as much muscle bulk as in the larger and small-plated *mexicanus*. M. m. superficialis and the posterior portion of M. m. lateralis pars posterior are relatively smaller in *megalotis,* but that deficiency is roughly equalized; the anterior part of the M. m. lateralis pars posterior is relatively larger. M. lateralis pars anterior attaches farther anteriorly in *megalotis*. Its anterior fibers originate on the dorsal lip of the zygomatic plate, which projects farther anteriorly in *megalotis* than in *mexicanus;* they insert on the ramus as far forward as the mental foramen. Apparently the position of the anterior fibers is a function of the position of the dorsal lip of the zygomatic plate. As indicated above, this anterior position could be accomplished by a spine on the plate, as is seen in *Sigmodon,* for example. Hence, we see myological differences that relate directly to the two positions of the dorsal lip of the zygomatic plate, but we cannot see the functional necessity for the variation in width of the plate itself. Apparently it is merely one of several ways to achieve the same end.

The pterygoideus internus is larger in *megalotis*. Correlated with the larger muscle are the greater areas of origin and insertion. The greater area of the pterygoid fossa, where the muscle originates, apparently has been gained, in part, at the expense of the mesopterygoid fossa (Pl. I, Figs. 1*c,* 2*c*). One result is the narrow mesopterygoid fossa which is characteristic of *megalotis* and the subgenus *Reithrodontomys*. The relatively broad surface for insertion of the muscle is provided by the broad inflected part of the angular process (Pl. I, Figs. 1*b,* 2*b*).

The temporal muscles are absolutely much smaller in *megalotis* and although the brain case in that species is smaller, the muscles are relatively smaller. Their area of origin covers a conspicuously smaller segment of the temporal area of the brain case and, perhaps of particular importance, a smaller fraction of the origins and of the muscles themselves is situated ventrally, below the squamosal root of the zygomatic arch. Fewer of the fibers, therefore, approach or parallel the long axis of the skull.

The greatest myological differences between the species are in the size and origin of the M. pterygoideus internus and M. temporalis, and in the origin of the anterior fibers of M. masseter lateralis pars anterior. The differences in the other elements of the masseter complex are comparatively small and need not be given further consideration. The effects that the differential size and positions of those three sets of muscles will have on the motions in gnawing and mastication cannot be determined precisely. The interaction of the muscles in chewing is complex and the action of the individual muscles is not well understood. The inferences that follow are not necessarily conclusive, but they fit the facts, and they are in accord with those of Tullberg.[2]

From their positions, origins, and insertions, we judge that the primary actions of the three sets of muscles are as follows: the internal pterygoids acting together elevate and slightly protrude the jaw; acting alternately they draw the jaw from side to side. They should be important in crushing and grinding actions of the molar teeth and in gnawing actions of the incisors. The temporal muscles also should close the jaw, but perhaps their strongest action is in retracting the jaw. They should work on a depressed mandible in a manner somewhat as follows: In contracting they should draw the jaw dorsad and posteriad. Initially, their pull is primarily dorsad. But as the insertions of the muscles (the tips of the coronoid processes) approach the level of the origins of the horizontal fibers of those muscles, the horizontal component of their force becomes the principal one, and further contraction serves only to draw the jaw directly posteriad. The temporal muscles, then, should be important in an anteriad-posteriad grinding action of the molar teeth and perhaps in a shearing action of the incisors. The masseter medialis pars anterior also assists in closing the jaw. Its anterior fibers are in a position to oppose the temporals, or when contracting alternately with them, to contribute to the anteriad-posteriad motion of the lower jaw. And within the

[2] *Ueber das System Der Nagethiere* (Upsala: E. Berling, 1899).

limits observed in our material, the effectiveness of the muscle should be partly a function of the size of the bundle of anterior fibers of that muscle. Stronger opposition to the temporals should be provided by a large mass of masseter fibers in the preorbital fossa than by a small mass in that fossa.

If these interpretations are correct, then the forces operating in movements of the lower jaw are unequal in the two species. In *megalotis* the internal pterygoids are large, the temporal muscles are small, and the slips of the masseter medialis pars anterior that originate in the preorbital fossa are small. In *mexicanus* the internal pterygoids are small, the temporal muscles are large, and a comparatively large segment of the masseter medialis attaches in the preorbital fossa. Thus, in *megalotis* the muscles that close the jaw are strong; those that might move it in an anteriad-posteriad direction are comparatively weak. In *mexicanus* muscles that appear to move the jaw forwards and backwards are more strongly developed, and those affecting direct occlusion are weaker.

Whether these myological differences pertain primarily to the process of gnawing or to that of mastication we do not know. We suspect the latter, and we infer that in *mexicanus* there is more of a forward-and-back motion added to the up-and-down movement in chewing than there is in *megalotis;* in each species, lateral movements also probably are involved, and the full motion in mastication is probably one of rotation. We see no differences in the incisors of the two species that might reflect either different gnawing motions or different gnawing strengths in the two species. There are differences in the molar teeth, however, which may indicate different chewing motions. Both species have bunodont teeth. In *megalotis* the cusps are alternate in position and the enamel pattern is simple; there are no complete mesolophs (ids). In *mexicanus* the cusps tend to oppose each other and the enamel pattern is complex; there are complete mesolophs (ids) in all molar teeth. The mesolophs figure prominently in occlusion of the molars and thus in mastication.

Is the development of accessory lophs between the primary cusps of the teeth a step toward a lophodont type of dentition? If it is, the musculature of *mexicanus* also appears to be progressing in that direction. In rodents with a lophodont pattern, for example in *Neotoma* and in the microtines, the temporal muscles are large and the internal pterygoids are small. Also in them, an important part of the total masticatory motion is in an anterior-posterior direction.[3]

SUMMARY

With reference to the primary purpose of this study, the following conclusions are warranted. Between the subgenera there are myological differences that correspond to differences in breadth of the zygomatic plate and mesopterygoid fossa. The differences correlated with the broad and narrow plate are slight. Those involving the fossa are greater.

The size of the mesopterygoid fossa is related to the size of the pterygoid fossae and of the internal pterygoid muscles that have their origin there. Functionally, therefore, emphasis should be on the pterygoid fossae, rather than on the mesopterygoid fossa as set forth by Howell.[4] Finally, the musculature, bony structures, and teeth of *R.* (*Reithrodontomys*) *megalotis* appear to be adapted for strong crushing motions, while in *R.* (*Aporodon*) *mexicanus* they suggest that anteriad-posteriad directed forces also are prominent in gnawing and mastication. Of the two species, *mexicanus*, structurally and functionally, appears to be the more specialized.

[3] Tullberg, *op. cit.*, pp. 230, 245.

[4] *Op. cit.*

PLATE I

Skull and some cranial muscles of *Reithrodontomys* (*Aporodon*) *mexicanus* (Figs. 1–*c*) and R. (*Reithrodontomys*) *megalotis* (Figs. 2–2*c*). Drawn to the same size from specimens of *mexicanus* from Costa Rica and of *megalotis* from California.

FIGS. 1–2. Lateral view of the skull, showing the size and position of the zygomatic plate (outlined by broken lines), zygomatic notch, and parts of the masseter and temporal muscles. Note particularly the area and position of origin of M. temporalis, of the anterior fibers of M. masseter medialis pars anterior and of M. masseter lateralis pars anterior.

FIGS. 1*b*–2*b*. Tranverse section of ramus showing size and shape of the shelf formed by inflection of the ventral border of the angular process. Drawn at planes indicated by broken line in Figures 1*a* and 1*b*.

FIGS. 1*c*–2*c*. Ventral view of pterygoid region of cranium, showing size and shape of the pterygoid and mesopterygoid fossae.

Drawings by William L. Brudon.

PLATE I