HYSTRICOMORPHY AS THE PRIMITIVE CONDITION OF THE RODENT MASTICATORY APPARATUS

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Received June 10, 1981; November 29, 1982

ABSTRACT: Hysticomorphy has been considered an important characteristic in the analysis of rodent relationships. Protrogomorphy has been considered as the primitive condition of the rodent masticatory apparatus. Detailed analysis of the only living "protrogomorph", Aplodontia rufa, reveals that it actually possesses an hystrichomorphous masseteric complex. Analysis of the fossil material permits the inference that all rodents originally possessed the hystricomorphous masticatory complex. Hystricomorphy, then, is a part of the primitive rodent masticatory form-function complex. Protrogomorphy is simply the primitive mammalian condition and is not part of the derived morphology that defines the earliest rodents. Niether hysticomorphy nor protrogomorphy, therefore, are of any significance in determining rodent inter-relationships.

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As part of an ongoing study of the anatomy and systematics of the Aplodontidae, three specimens of Aplodontia rufa have been dissected. Detailed analysis of their masticatory apparatus revealed information that may have a profound effect on concepts in rodent evolution. The masticatory mechanism of the mountain beaver, Aplodontia rufa, was previously described by Tullberg (1899), among others. In his description, however, he did not note that a portion of the medial masseter runs through the infraorbital foramen and originates on the rostrum.

Member of the order Rodentia have been traditionally divided into four sub-groups; the Protrogomorpha, the Sciuromorpha, the Hystricomorpha, and the Myomorpha (Wood, 1947). Originally, these groups were defined by the nature of the origin of their masseter muscles. These groups, when strictly defined by their masticatory mechanisms, are not usually considered monophyletic (Wood, 1958). Protrogomorphy and hystricomorphy appear to be the least indicative of phylogenetic affinities. Protrogomorphy refers to the primitive mammalian condition of having the origin of the masseter located strictly on the zygomatic arch. The mountain beaver is said to be the only living protrogomorph. Detailed study, however, reveals that a portion of the medial masseter passes through the infraorbital foramen and originates on the rostrum. Aplodontia rufa, therefore, is hystricomorphous. Many inferences may be drawn from this observation. Perhaps the most important is that there are no protrogomorphs and there may never have been any, depending upon how one diagnoses the rodents.

Constructing a diagnosis for the rodents might seem rather easy at first consideration. They have a number of derived features associated with their masticatory mechanism. The zygoma has been shifted forward so that it is anterior to the angle of the mandible. They all have two upper and lower ever-growing, gnawing incisors, a wide diastema and a premolar and molar tooth row of a relatively uniform sort. They often have replaced cusps with various cutting crests. Hypsodonty is fairly common. The molars often do not occlude at the same time as the incisors. None of these features are unique to rodents, however, since many other mammalian groups have evolved most if not all of these features independently.

There is one feature present in most living rodents that is unique to the group. The hystricomorphs and the myomorphs have at least a portion of the medial masseter running

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Evolutionary Theory 6: 163-165 (December, 1982)
The editors thank D. Klingener and another referee for help in evaluating this paper.

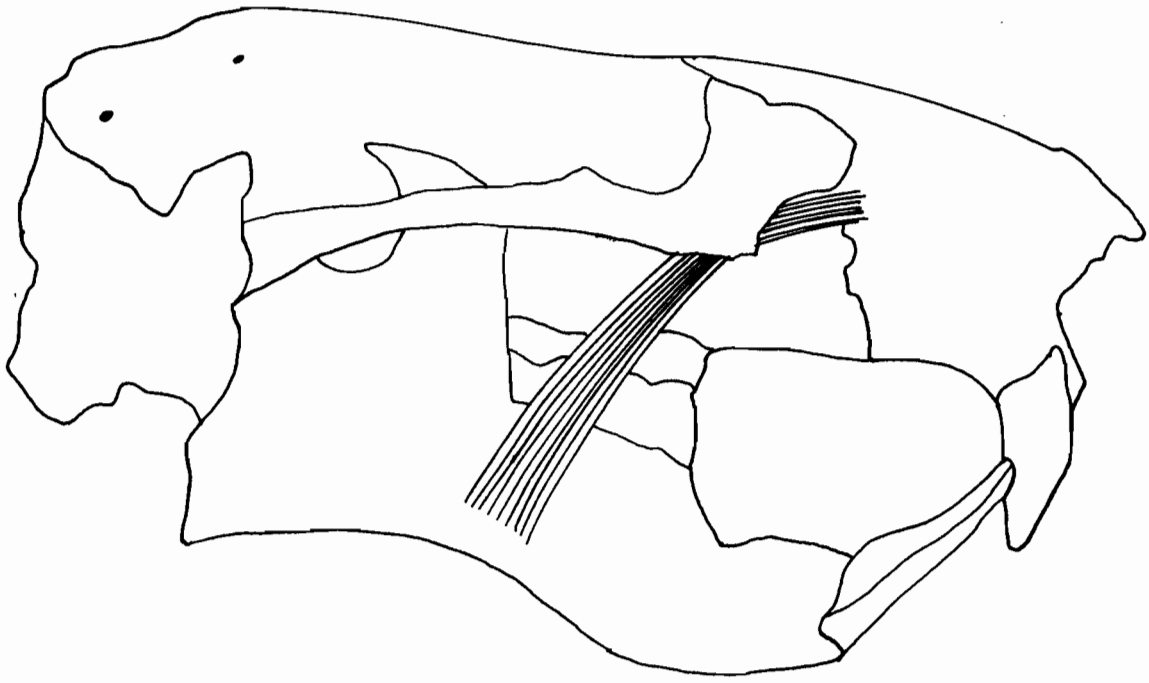
through the infra-orbital foramen and originating on the rostrum. In addition, the myomorphs have a lateral masseter that originates on the rostrum and runs along a groove on the outside anterior aspect of the zygoma, as do the sciuromorphs. It may be noted that the muscle which is here refered to as the medial masseter is sometimes described as the masseter lateralis profundus par anterior. The terminology of Hill (1937) is followed here. All these adaptations allow for a more horizontal action of the masseter and hence a more propalinal manner of mastication. All of the rodents have a propalinal action to occlude the incisors. Most rodents appear to have a propalinal occlusion for their molar tooth row also, although some (e.g. Rattus norvegicus) have a transverse molar occlusion (Hiiemae and Ardran 1968). While these functional interpretations are speculative, there is no other sort possible due to the lack of functional studies at this point.

Wood (1965) believed that hystricomorphy evolved several times independently. The Caviomorpha, the Hystricidae, the Phiomorpha, the Theridomyoidea, the Anomaluridae, the Ctenodactylidae, the Pedetidae, the Dipoidea, the Protoptychidae, the African glirids and possibly the paramyid Rapamys were all believed by Wood (1965) to have evolved the hystricomorphous condition independently. Landry (1957) argued that several of these groups had an hystricomorphous common ancestor.

The observation that Aplodontia rufa is hystricomorphous implies that hystricomorphy is primitive for the rodents, for a number of reasons. That hystricomorphy is the primitive condition for rodents is the most parsimonious conclusion considering the widespread distribution of the character within otherwise phylogenetically distinct groups. All of the living rodents excepting the sciuromorphs have at least a portion of the medial masseter that passes through the infraorbital foramen. In some, the amount of masseter passing through is rather small. The qualitative characteristic of having a branch of the medial masseter passing through the infraorbital foramen would be far more useful in determining phylogeny than the quantitative characteristic of percentage of muscle that passes through the foramen. The size of the infraorbital foramen is not a reliable estimator of the size of the masseter that passes through it. Anomalurus and Aplodontia have approximately equal amounts of masseter running through the foramen even though Anomalurus has a much larger opening (personal observation). In Anomalurus there is an even larger muscle, the nasolabialus profundus, which also runs through the infra-orbital foramen. The sciuromorphs, the only living exceptions, have so enlarged the lateral masseter, which originates on the rostrum and runs down a large groove anterior to the zygoma, that it nearly obliterates the opening of the infra-orbital foramen. Their ancestors, the Paramyidae, are not so specialized. Most of them have infraorbital foramina that are larger than those present in Aplodontia rufa or in mammals that do not have any masseter passing through theirs. This fossil evidence indicates that the ancestors of the sciuromorphs were indeed hystricomorphous.

One need not rely on parsimony to argue that hystricomorphy is the primitive condition of the rodent masseter musculature. The direct evidence also supports that hypothesis. All of the extant rodents and probably all the fossil rodents are either hystricomorphous or are descended from rodents that were. Hystricomorphy was not a derived condition evolved independently several times, but the primitive condition for rodents that has been retained in several distantly related groups. It is obvious, therefore, that hystricomorphy is of no consequence for classification within the Rodentia, other than the loss of the characteristic being a derived condition. Hystricomorphy is an integral part of the primitive rodent form-function complex. Other aspects of rodent anatomy should prove more useful in determining the relationships within the Rodentia. The tarsus may prove useful in further elucidating rodent systematics.

FIGURE Skull of Aplodontia rufa showing the intrusion of the masseter into the infra-orbital foramen



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