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Skull Form and the Mechanics of Mandibular Elevation in Mammals

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ABSTRACT

A model of the mechanics of elevation in the mammalian mandible is described, in which rotation of the lower jaw, effected by a couple action between the anterior and posterior adductor muscle groups, takes place around the mandibular attachment of the sphenomandibular ligament. This system permits the generation of an occlusal force, variable in orientation according to the position of the bite-point along the tooth row, which is optimally absorbed by the facial skeleton. The requirements of the system are such that in long-faced forms the horizontal components of action of the masticatory muscles are emphasized, and the vertical components dominate in short-faced mammals.

INTRODUCTION

The past few years have witnessed a great deal of research on the operation of the masticatory apparatus in man and other mammals. Numerous theories are current, most of which represent variations on the concept of the mandible as a bent lever system rotating around the condyle. In the present paper we express a rather different view of the masticatory system and attempt to show the manner in which the components of the mammalian masticatory apparatus are related.

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Our analysis rests on two basic assumptions, neither of which appears greatly open to question. The first is that no significant force is expended at the temporomandibular joint during elevation of the jaw; the second is that there exists a direct relationship between the structure of the orofacial skeleton and the orientation of the resultant (bite) forces produced at the teeth during mastication.

The illustrations are the work of Mr. Nicholas Amorosi, Department of Anthropology, the American Museum of Natural History; the order of authors is alphabetical.

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TEMPOROMANDIBULAR JOINT

Figure 1 shows the human masticatory muscles represented as the applied forces in two bent-lever systems, one corresponding to temporalis (T), the other to the masseter-internal pterygoid complex (M). Both act under this scheme to rotate the jaw around the condyle (F). The efficiency of each of these systems depends on the ratio of the length of the power arm (T′, M′) to that of the load arm (L+L′). In the case of a human biting in the region of the first molar tooth, this ratio is approximately 1:2 in each instance. Quite evidently, then, the efficiency is low; only about 50 percent of the available muscular effort is expended at the dentition, and this proportion decreases as the bite-point is moved anteriorly.

More important, however, is that under this system the remaining effort is expended in producing reaction forces (not shown in the figure) at the temporomandibular joint, in which the condyle would necessarily have to rotate in the back of the articular fossa. Both of these propositions are untenable in the light of what is known about the structure and function of the joint. In contrast to those joints of the skeleton, which habitually transmit large compressive forces, the temporomandibular joint possesses, in addition to a fibrous meniscus, a lining of fibrous connective tissue ("fibrocartilage"), a substance best suited to provide a sliding surface and to accommodate shearing stresses. The meniscus, composed of parallel collagen fibers running in the sagittal plane, is heavily vascularized in its anterior and posterior thirds, although there is no blood supply to its central portion. This indicates that loading of the joint occurs only at the central part of the meniscus, which would not be the case were the condyle rotating in the articular fossa. Moreover, the load borne by this portion of the meniscus is not the force exerted at the fulcrum in a lever system; it

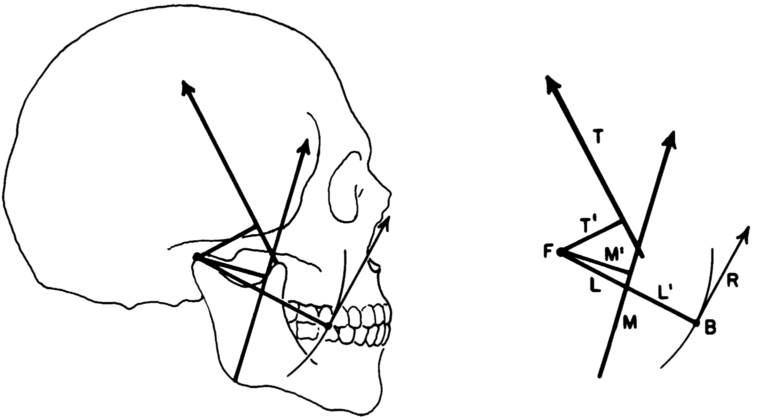

FIG. 1. *Homo sapiens*: temporalis and masseter/internal pterygoid viewed as independent lever systems. See text.

is merely that small force required to maintain the integrity of the joint which, after all, must operate as a normal synarthrosis.

As the biconcave morphology of the meniscus suggests, the functional surface of the cranial component of the temporomandibular joint is not the concave articular fossa, which merely serves as a receptacle for the condyle when the teeth are in occlusion; rather, it is the articular eminence, anterior to the fossa, that contributes to the joint during motion of the jaw. During depression of the mandible, the condyle rides forward and down the articular eminence; simultaneously, the mandibular angle moves upward and back. Obviously, the rotation thus produced is not around the transverse axis of the condyle, as it would have to be under a lever system. Instead, rotation occurs around a point intermediate between the centers of attachment of the two major adductor muscle groups, the temporalis and the masseter/internal pterygoid complex. This point coincides with the location of the lingula of the mandibular foramen, the site of attachment of the stabilizing sphenomandibular ligament. Thus the temporomandibular joint, although it is obviously the point of articulation of the mandible with the cranium, is not the point at which rotation occurs during mastication.

ARCHITECTURE OF THE FACIAL SKELETON

The bony structure of the splanchnocranium in man and other mammals appears to correlate strongly with the varying necessities of resolution of the masticatory forces generated at the dentition. There is of course a great deal of variation in the architecture of the facial skeleton within Mammalia, but if one ignores highly specialized forms such as some edentates, in which masticatory activity is reduced virtually to zero, a general *Bauplan* emerges. Thus among the primates, and particularly among those whose masticatory apparatus is adapted to heavy grinding, the facial skeleton is constructed as a bilateral tripodal structure, with a central member consisting of the median septa of the nasal cavity and frontal sinus. In man, for instance, the primary stress-bearing members of this tripodal structure are as follows: anteriorly, bite forces are conducted through the canine root and the nasal process of the maxilla to the frontal bone. From the region of the anterior molar, stresses pass through the anteroinferior root of the zygomatic arch and up the postorbital bar to the frontal. The inferior part of the posterior buttress of the tripod is formed of the anterior portion of the pterygoid laminae; stresses pass thence through the floor of the anterior cranial fossa to the frontal. These three major (although, of course, not exclusive) paths of stress transmission thus converge on an anterior point on the frontal bone (fig. 2). This bone in modern man is a dome-shaped structure ideally designed for the dissipation of forces thus arriving on it. It is noteworthy that this point of convergence, the apex of the pyramid, coincides roughly with the location of the bulk of the supraorbital torus in archaic hominids in which the frontal lobes did not invade the supraorbital area to produce a steep forehead of the modern type.

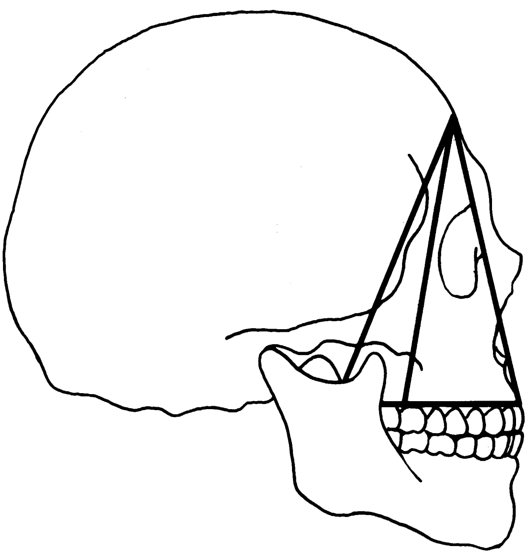

FIG. 2. Schematic representation of tripodal facial structure in *Homo sapiens*.

In order for a stress structure of this kind to be optimally functional, the resultant forces of mastication must be directed toward its apex. Obviously, then, it is necessary that the occlusal forces be variably oriented according to the position along the tooth row at which they are generated. How is this achieved?

FUNCTION OF THE MUSCLES OF MASTICATION

In a simple analysis of the mechanics of mandibular elevation, only three muscles require consideration: mm masseter, pterygoideus internus, and temporalis. Pterygoideus lateralis plays a significant role in masticatory activity, but need not enter this preliminary analysis because it is primarily a positioning muscle.

We have already noted that in both depression and elevation of the jaw rotation occurs around the mandibular attachment of the sphenomandibular ligament. This motion is produced by a couple action between the two primary groups of jaw-closing muscles: temporalis and the masseter/internal pterygoid complex (fig. 3). Under this system, the more anterior the point at which biting takes place, the more effort is required from the

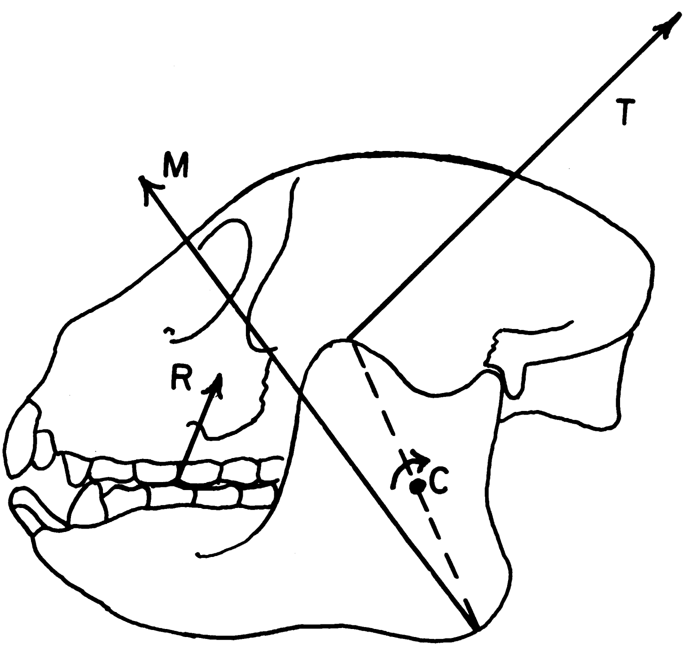

FIG. 3. Couple action of temporalis and masseter/internal pterygoid in producing mandibular elevation in *Archaeolemur edwardsi*. From Tattersall (In press).

posterior fibers of temporalis. This latter muscle is alone (with a limited exception to be mentioned later) among the jaw-closing muscles in being capable of varying significantly its line of action. The basic workings of the system are very simply explained by reference to figure 4.

In figure 4 an arbitrary magnitude and line of action (M) is established for the masseter/internal pterygoid complex; this remains constant. Three resultant forces are defined; these are constant in magnitude, but are of differing orientation according to the position of (B), the bite-point: anterior bite (R_3), middle bite (R_2), and posterior bite (R_1). In order for the system to be in equilibrium, i.e., that there should be no force exerted

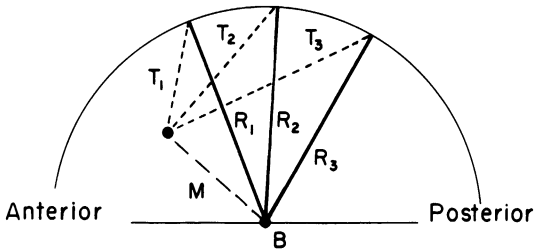

FIG. 4. Interactions of muscles and resultant forces (reciprocals) in producing mandibular equilibrium at different bite-points along tooth row. See text.

at the temporomandibular joint, the triangle of forces must be closed by the vector of temporalis. From the figure it is evident that, given a constant magnitude and direction of masseteric pull, and a resultant force at B which is of constant magnitude but variably directed to permit the most efficient force resolution, the pull of temporalis must not only be variable in direction, but also be of varying magnitude. Thus T_3 is greater in magnitude than T_2, which is in turn greater than T_1. Provided, then, that temporalis is able to exert the required force in the required direction (T_1 is less than M, but both T_2 and T_3 are considerably greater), the system will always be in equilibrium. Of course it may be claimed that this represents a static analysis of what is under most conditions a dynamic situation; but since, at least for the purposes of a simplified argument, and assuming for convenience the absence of acceleration, the jaw in elevation may be visualized as passing through an infinite series of static equilibria, it is permissible to generalize, within limits, from the static to the dynamic state.

Although the system does require a great deal of the posterior moiety of temporalis during posterior biting, the effort required of this muscle is considerably relieved by the division of the masseter into two functional components. Thus in man the deep masseter is composed of fibers that run more or less directly vertically, while the superficial masseter consists of fibers which are inclined obliquely forward. Figure 5a shows that, were

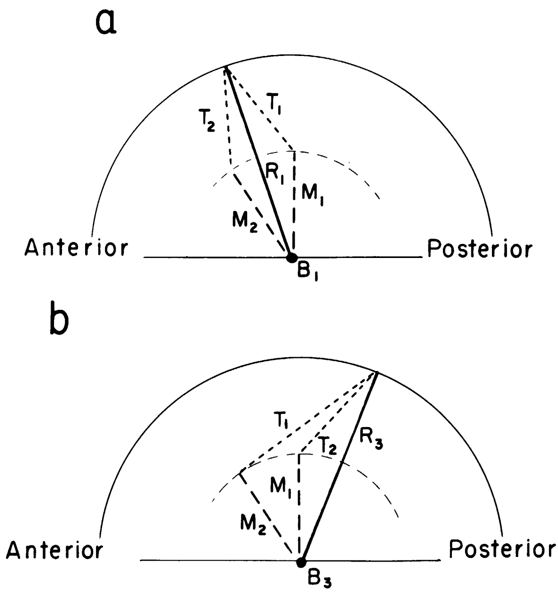

FIG. 5. Role of superficial and deep masseteric portions during biting (a) at posterior teeth and (b) at anterior teeth. See text.

only the deep masseter (M_1) present, provision of the appropriate resultant (R_1) at this point would require a more anterior pull of the temporalis (T_1) than even the most anterior fibers of the muscle are able to provide. In this situation the triangle of forces could not be closed, and disequilibrium would result. The orientation of the superficial masseter (M_2), on the other hand, enables the anterior temporalis (T_2) to maintain equilibrium. Conversely, as is evident from figure 5b, the opposite result occurs when biting takes place anteriorly. Here the resultant force (R_3) must be directed upward and back, and if only the superficial masseter (M_2) were involved, the posterior temporalis would have to exert a disproportionate effort (T_1) to maintain equilibrium. The presence of the deep portion of the masseter (M_1), on the other hand, permits the maintenance of equilibrium without placing so heavy a strain on the posterior temporalis (T_2). Thus the superficial masseter is of the greatest importance when dental activity is concentrated toward the back of the mouth, while the deep masseter is more concerned with biting anteriorly.

DISCUSSION

The foregoing theoretical considerations appear to be borne out by comparative examination of mammalian skulls and promise to be of considerable value in the functional interpretation of mammalian skull form. The size and morphology of the facial skeleton and dentition are determined largely, if not entirely, by the requirements of the feeding habits of the particular animal. These in most cases include the obtaining of food as well as its mastication. Facial development may thus be considered as "preceding" the system directly concerned with producing mandibular motion. Faced, then, with a splanchnocranial structure related to a given dietary habit, it is possible to "explain," or predict, the remaining features of the masticatory apparatus, i.e. the muscles and the bones supporting them, in terms of the model of mandibular operation which we propose.

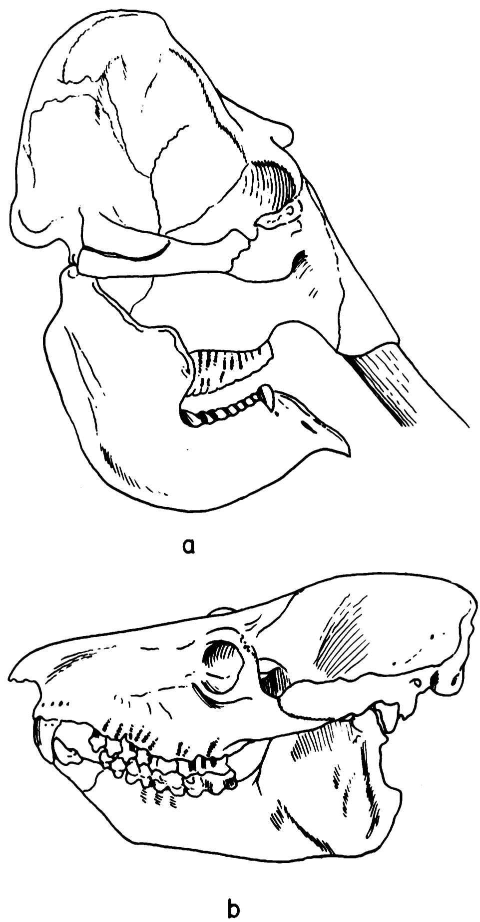

FIG. 6. Lateral views of skulls of (a) *Elephas indicus* and (b) *Megaladapis edwardsi*. Not to scale.

In particular, we should expect a short-faced form to emphasize the vertical components of the musculature (especially the anterior temporalis), and a long-faced form to emphasize the more horizontal ones.

This may best be illustrated by taking two extreme examples. The extinct Malagasy lemur *Megaladapis* (fig. 6b), for instance, is a large-bodied but small-brained form whose dietary habits (Tattersall, 1972) dictated extreme elongation of the facial skeleton. In consequence, the postfacial skeleton is likewise extremely elongated, despite the tiny size of the brain (the remaining portion of the neurocranium is taken up by the compensatory development of enormous frontal sinuses), reflecting the great hypertrophy of the posterior (horizontal) moiety of temporalis. The anterior (vertical) portion of the muscle is relatively reduced.

Precisely the opposite effect is found in the elephant (fig. 6a). In this form the necessity of development of the anterior dentition as a food-gathering mechanism is obviated by the animal's possession of a trunk. Hence, all elements of the anterior dentition (with the exception, of course, of the tusks) have disappeared, permitting the extreme shortening of the face and very strong specialization for efficient, powerful, posterior grinding. As a result the neurocranium has become extremely foreshortened, while its vertical dimension, related to the vertical fibers of temporalis, is emphasized to the point of exaggeration. At the same time the raising of the temporomandibular joint and zygoma considerably above the level of the tooth rows produces a similar emphasis on the vertical component in the masseter and internal pterygoid.

In most mammals, of course, the situation is less clear-cut. Thus, for instance, the muscular arrangements in the horse, which crops with its anterior teeth and grinds with its posterior ones, and in the lion, which stabs with its canine and slices with its carnassial, represent accommodations to two opposite sets of requirements. Nevertheless, they may equally satisfactorily be explained in terms of our simple (and admittedly mechanically simplistic) model. It is not our intention in this preliminary paper to enter into exhaustive analyses of individual cases, however; we wish merely to point out the potential of this model in functional anatomical studies of the mammalian skull.

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