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Mammalian Feeding and Primate Evolution: An Overview

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ABSTRACT Most of the papers included in this volume are derived from presentations in a symposium on Mammalian Feeding at the 65th Annual Meetings of the American Association of Physical Anthropologists in North Carolina in 1996. The aims of this symposium were to gather together the preeminent researchers on mammalian mastication and document the state of research in that field. The symposium emphasized *in vivo* studies of mammalian feeding because of a paucity of recent reviews of this field, but included morphometric and modeling papers as well. Subsequently the papers were revised, and were submitted in spring 1998 for publication, pending the outcome of peer review. *Am J Phys Anthropol* 112:449–453, 2000.

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The study of feeding behavior in nonprimate mammals is relevant to the study of primate mastication in two ways. First, comparison of primates and nonprimate mammals can reveal ways in which primates differ from other mammals, informing hypotheses of the origin and radiation of primates. Second, study of a broad range of mammals generates insights into the rules and principles governing the evolution of the feeding apparatus in general, of which the primate system is an example.

Many of the papers in this symposium dealt with issues surrounding anthropoid origins. The fossil record of the anthropoid stem group has greatly improved recently with the discovery of Early-Middle Eocene Asian taxa exhibiting a combination of prosimian-like primitive and crown anthropoid-like derived features of the jaws and teeth (Beard et al., 1996; Jaeger et al., 1999). Future work on these animals promises to greatly enhance our understanding of the origins of the anthropoid feeding apparatus. Extant anthropoids that have been studied differ from strepsirrhine primates in an array of features of the skull that are demonstrably or have been hypothesized to

be part of the feeding apparatus, e.g., ontogenetically early fusion of the mandibular symphysis, late activity in the balancing-side deep masseter muscle during the power of mastication (Hylander et al., 1987; Hylander and Johnson, 1994), relatively greater activity of balancing-side muscles (Hylander 1977), greater isognathly (widths of upper and lower dental arcades are roughly similar; Ravosa and Hylander, 1994), relatively larger phase II occlusal facets, a longer power stroke (Hiemäe and Kay, 1973), and a postorbital septum (Cachel, 1979). Ravosa et al. (2000a, this volume) observe that crown anthropoids have more isodontic molars (upper and lower molars roughly the same width) and more vertically oriented superficial masseters than do strepsirrhines.

Ross and Hylander (2000, this volume) evaluate hypotheses relating the function of the anterior temporalis muscles to the evolution of the postorbital septum (Ross,

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1996). The anterior temporalis is a good candidate for a catholically recruited muscle because its long lever arm and vertical orientation enable it to contribute vertical components of force to all biting and chewing behaviors. The vertical orientation of the anterior temporalis and the masseter (Ravosa et al., 2000a, this volume) may be due to repositioning and reorienting of the face, associated with increased basicranial flexion in anthropoids (Ross and Ravosa, 1993), as well as the increased orbital frontation characteristic of anthropoids. Ross and Hylander (2000) demonstrate that the anterior temporalis is active during all mastication, isometric biting, and incision power strokes, although it is not more consistent in its activity than other muscles. This is consistent with human data showing variability in anterior temporalis activity associated with differences in bite-force position and orientation (Spencer, 1998; Van Eijden, 1990; Blanksma and Van Eijden, 1990; Van Eijden et al., 1990). More data are needed on the relationship between muscle activity patterns, bite-force position, and bite-force orientation in primates. Unless a bite-force transducer can be developed for use during mastication, these data will necessarily have to be gathered during isometric biting. However, even isometric-biting data will be useful for evaluating important hypotheses regarding relationships between muscle activity and the geometry of the masticatory apparatus (e.g., Spencer, 1999).

Bone-strain data from the mandibular corpus suggest that anthropoids recruit more balancing-side muscle force than *Otolemur*, the only strepsirrhine genus studied to date (Hylander, 1977; Hylander et al. 1998). Hylander et al. (2000, this volume) demonstrate that anthropoids show a relatively greater activity of balancing-side masseter than *Otolemur*. The demonstration that low working/balancing ratios are characteristic of small (*Aotus*) and large (*Macaca*, *Papio*) anthropoids is important in demonstrating that the previously observed differences between *Otolemur* and *Macaca* were not due merely to differences in body size (see Hylander et al., 1998). Hylander et al. (1998) found the most pronounced differ-

ences in the deep masseter, with anthropoids showing relatively more balancing-side deep masseter activity than *Otolemur*. The transverse orientation of the deep masseter means that this higher balancing-side activity may well be responsible for the "wishboning" of the anthropoid mandible inferred from strain recordings (Hylander, 1984) and, possibly, more transverse movements of the anthropoid mandible during mastication (see below).

Ravosa et al. (2000a, this volume; see also Ravosa, 1999) make an important attempt to provide testable links between in vivo studies of extant animals and interpretation of the fossil record. They document increasing isodonty and isognathy in the anthropoid stem lineage and hypothesize a link between these features and both the transverse component to the power stroke and late activity in the balancing side deep masseter. In vivo cineradiography and dental morphology suggest that anthropoids are more dependent on transverse movements during the power stroke of mastication than are strepsirrhines (Hiimäe and Kay, 1973; Kay and Hiimäe, 1974). Ravosa et al. (2000a) argue that the comparatively vertical orientation of the superficial masseters compromises the ability of crown anthropoids to generate the transversely oriented forces used to move the mandible through the power stroke. Anthropoids may have evolved late activity in the balancing-side deep masseter to compensate, something that is only possible in animals with a stiff mandibular symphysis, like that resulting from symphyseal fusion. This is not to say that the anthropoid balancing-side deep masseter only functions to move the mandible through phase II of the power stroke and does not augment masticatory force production. Anthropoid balancing masseter activity overlaps extensively with working-side activity, although it does peak later and cease firing later than the working-side deep masseter (Hylander et al., 1987, Hylander and Johnson, 1994).

Lieberman and Crompton (2000, this volume) argue for a more general relationship between tooth cusp morphology and symphyseal morphology across mammals. Arguing that an unfused mandibular symphysis

can transfer vertically oriented forces from the balancing side almost as efficiently as a fused symphysis but is poor at transferring transversely oriented forces, Lieberman and Crompton (2000) hypothesize that symphyseal fusion is an adaptation for increasing efficiency of transfer of transversely oriented occlusal forces. Their data from opossums and goats (with unfused mandibular symphyses) reveal low working/balancing side adductor EMG ratios, similar to those seen in anthropoid primates with fused symphyses. Thus, *Otolemur* at least—and possibly strepsirrhines in general—may be unusual among mammals in having high ratios of working/balancing-side muscle activity during mastication. As they note, more EMG data are clearly needed on jaw adductors of strepsirrhines and other non-primate mammals to evaluate this hypothesis.

There is no substitute for direct observation of a biological phenomenon, and models are only as good as the data behind them. In vivo bone-strain data provide critical information forming the backbone of several current models of craniofacial form. However, in this issue, both Daegling and Hylander (2000) and Dechow and Hylander (2000) demonstrate how in vivo bone-strain data only give a partial picture of the stress environment of the whole bone. Daegling and Hylander (2000) discuss the relative merits of various approaches to understanding the stress patterns within bones during function: in vivo strain data, in vitro strain data, and data derived from finite element modeling. Using the robust jaws of *Paranthropus* as a case study, they conclude that it is possible to test many aspects of the stress patterns predicted by finite element models with in vitro bone strain data. Dechow and Hylander (2000) demonstrate how data on the elastic properties of the lingual and buccal cortices of the mandible can augment and potentially alter models based on in vivo bone strain data. Data on material properties of bone are needed to derive estimates of the magnitudes and orientations of in vivo stresses. Data on stresses in the mandible during mastication and isometric biting deemphasize the importance of torsion on the balancing side and emphasize

the range of loading regimes on the working side. Although their study largely corroborates prior hypotheses of mandibular loading based on strain data, it does demonstrate that knowledge of material properties is vital for precisely relating strains to stresses in primate biomechanics.

Herring and Teng (2000, this volume) use data gathered during both chewing and muscle stimulation to relate patterns of strain to external forces acting on the skull. They recorded in vivo EMGs from chewing muscles and bone strains from the frontal and parietal bones and from the interfrontal, interparietal, and coronal sutures during mastication and muscle stimulation. Their results indicate that asymmetrical activity in the chewing muscles is responsible for torsion of the braincase during chewing, a result that may well explain the patterns of strain reported for primates (Hylander et al., 1991; Hylander and Ravosa, 1992; Ross and Hylander, 1996). Notably, Herring and Teng (2000) find that suture strains during mastication are not a product of braincase torsion but instead are caused primarily by activity in nearby muscles, including the neck muscles. They conclude that skulls with patent sutures need to be analyzed as consisting of independent blocks of bone rather than a single structure. The extent to which this conclusion applies to primates with more tightly packed sutures remains to be determined.

Anapol and Herring (2000, this volume) studied the ontogeny of fiber types in the masseter muscle of miniature pigs and correlated changes in electromyographic activity. The masseter muscle of neonatal pigs is composed primarily of fast-twitch, oxidative fibers. This changes gradually during growth so that the adult muscle contains significantly more slow-twitch fibers that predominate in the deep and anterior portions of the masseter muscle. They find that the amplitude of EMG activity in the superficial part of the muscle is much higher during feeding on resistant foods as compared to soft foods, whereas the amplitude of EMG activity in the deep part is consistently high whether feeding on soft or resistant foods. They conclude that the ontogeny of the masseter muscle involves a functional compart-

mentalizations that is importantly related to the morphological and histochemical compartmentalizations that occur. Similar work on primate chewing muscles would be of interest, given the evidence for significant functional and histochemical compartmentalization in the temporalis muscle of baboons (Wall et al., 1999), the relevance of masseter functional compartmentalization for symphyseal fusion, and the hypothesis that early fusing symphyses are related to deep masseter-mediated wishboning and that late fusing symphyses are related to increased dorsoventral shear (Ravosa, 1999).

The papers in this volume emphasize the power of experimental approaches to the study of primate skull form and function, but also demonstrate the value of morphometric analyses. Clearly there is fertile ground for interaction between experimental and morphometric approaches, and this interaction is necessary for significant progress. Two examples suffice.

The first example demonstrates how morphometrics can generate large comparative data sets at a scale that experimentalists can only dream about, whereas experimental approaches are invaluable for determining how animals actually function. In vivo studies on several primates reveal low strains in the circumorbital region (Hylander et al., 1991; Ross and Hylander, 1996; Ravosa et al., 2000b), suggesting that circumorbital structure may not be adapted for resisting masticatory stresses. However, morphometric analyses demonstrate important functional constraints on the geometry of the masticatory apparatus in anthropoids (Spencer, 1999). This suggests that although the circumorbital skeleton may not need to be strong to resist masticatory stresses, it may need to be appropriately positioned to satisfy constraints on the positions and orientations of the masticatory muscles. Comparative morphometric and experimental approaches to this question can easily be imagined.

The second way that morphometrics and experimental approaches must interact is in the interpretation of function in fossils (Ross et al., 2000). Fossils are primarily studied through morphometrics, yet the

meaning of measurements is heavily reliant on experimental studies of extant animals. A good example is the function of "phase II" facets on anthropoid molars. Extant anthropoids have larger "phase II facets" than *Otolemur* and *Tupaia*, a pattern confirmed for the fossil catarrhine *Aegyptopithecus*, the parapithecids *Parapithecus* and *Apidium*, and the oligopithecid *Oligopithecus* (Kay, 1977). Cineradiographic and morphometric studies demonstrate that primates (*Otolemur crassicaudatus*, *Saimiri sciureus*, and *Ateles* sp.) and primate relatives (*Tupaia glis*) have very similar patterns of jaw movements, but that anthropoids have a slightly longer power stroke, suggesting that the enlarged phase II facets might reflect enhanced use of grinding during phase II in anthropoids (Hiemäe and Kay, 1973). However, peak strains in the mandibular corpus are often highest near the end of phase I, prior to centric occlusion, and much lower during phase II (Hylander et al., 1987), suggesting that the importance of "phase II" facets might not inhere in the grinding of food during phase II, but in the crushing of food at the end of phase I (Teaford, 1985). Thus, the experimental data suggest that enlarged "phase II" facets in fossil anthropoids enabled a greater amount of food to be crushed or higher crushing forces to be exerted against the tooth during phase I.

Finally, as many of the papers here demonstrate, experimental data are needed for a greater range of primates, particularly strepsirrhines. Hypotheses regarding the function of many features of the primate skull are based on a small number of readily available primate taxa. Among strepsirrhines this is almost exclusively restricted to *Otolemur*. We can only hope to fully understand the full array of primate craniofacial adaptations when a wider array of species is examined experimentally.

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