Temporomandibular joint variation in anthropoid primates: functional, allometric, and phylogenetic influences

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Claire E. Terhune, Ph.D.

Introduction

The temporomandibular joint (TMJ) is a morphologically and functionally complex component of the skull. Temporomandibular joint shape varies considerably across mammals and within primates, and some aspects of the TMJ have been linked to differences in feeding behavior. Additionally, characters on and around the TMJ are frequently used in phylogenetic analyses of fossil hominins (e.g., Kimbel, 1986; Strait et al., 1997; Martinez and Arsuaga, 1997; Kimbel et al., 2004; Lockwood et al., 2004); as such, this region has proven to be useful for understanding evolutionary relationships. Although there is an extensive body of literature describing TMJ morphology in fossil and modern humans (e.g., Angel, 1948; DuBrul, 1974, 1977; Hinton and Carlson, 1979; Kimbel et al., 2004), few data are currently available regarding how the TMJ varies in non-human primates. As a result, a broad comparative context describing TMJ variation across primates is lacking. This dissertation therefore evaluated TMJ shape variation in the context of 1) biomechanical hypotheses regarding TMJ function, and in light of 2) phylogenetic and 3) body size variation across anthropoid primates.

Materials and Methods

Three-dimensional geometric morphometrics were used to quantify TMJ shape across a broad sample of anthropoid primates, and more narrowly among small groups of closely related taxa with documented differences in feeding behavior. A total of 81 homologous landmarks reflecting aspects of variation in the masticatory apparatus and cranium were digitized on approximately 1023 of specimens from 48 anthropoid primate taxa. Data were collected from specimens in five separate museums: the National Museum of Natural History at the Smithsonian Institution (Washington, DC), the American Museum of Natural History (New York, NY), the Field Museum (Chicago, IL), the Royal Museum for Central Africa (Tervuren, Belgium), and the Department of Primatology at the State Collection of Anthropology and Palaeoanatomy (Munich, Germany). The research predictions were then tested using geometric morphometric methods designed to examine shape variation within and among species, as well as a series of univariate analyses using measurements extracted from the landmark data.

Results and Conclusions

<u>Research Question1: Feeding Behavior and the TMJ</u>

The first research question addressed by this research is perhaps the most critical given the integral role the TMJ plays in the masticatory apparatus. Previous research has shown that this joint is indeed load bearing (Hylander, 1979; Smith, 1978; Brehnan and Boyd, 1979; Brehnan et al., 1981; Boyd et al., 1982, 1990), and the masticatory apparatus in general is best classified as a class three lever system (Hylander, 1975, 1979, 1991, 2006; Hylander and Crompton, 1980; Hylander and Johnson, 1985; Hylander et al., 1992; Hylander et al., 2005). In such a system, the joint reaction force and bite force must cancel out the muscle resultant force to maintain static equilibrium. However, there is likely to be considerable variation in the magnitude of the joint reaction force vs. the bite force depending upon multiple variables, such as muscle firing patterns, position of the bite point, height of the TMJ above the occlusal plane, and the overall configuration of the masticatory apparatus. The goal of a major portion of this dissertation was therefore to evaluate shape variation in the TMJ, and to link this variation to differences in feeding behavior among anthropoid primates. Three main research predictions were generated in this regard. These predictions had to do with three primary ways in which the TMJ is likely to vary as a function of masticatory demands: food material properties, bite point location, and jaw gape.

In regard to variation in food material properties, it was predicted that taxa who tend to consume more resistant food objects (whether this utilization is continuous or only as a fallback food) should exhibit adaptations in their TMJs associated with increased joint reaction force and range of motion, such as increased joint surface area and larger joint processes (entoglenoid process and articular tubercle). Similarly, the second prediction posited that the TMJs of taxa that intensively use their anterior teeth should show adaptations to resist larger centrally or medially located joint reaction forces. Taxa that repetitively load their posterior teeth should show adaptations within their TMJs related to increased joint reaction forces on the lateral surface of the TMJ. These adaptations would be represented by changes in the relative mediolateral and anteroposterior dimensions of the joint and the size of the entoglenoid process and articular tubercle. Finally, I predicted that taxa with relatively large gapes (whether for behavioral or dietary reasons) should have adaptations in their TMJ related to increased range of motion (e.g., sagittal sliding), such as an anteroposteriorly longer TMJ, large preglenoid plane, and anteroposteriorly flat mandibular condyle.

Results of the detailed analyses of the comparative groups examined suggest that these predictions are supported, although with some exceptions. In almost all of the comparative groups, taxa with more resistant diets tended to have significantly larger joint surface areas, relatively mediolaterally (ML) wider and anteroposteriorly (AP) shorter TMJs, and larger entoglenoid processes. In contrast, taxa that utilize resistant food objects, but process them on their anterior teeth (e.g., *Cebus apella* and *Pongo pygmaeus*) were found to have relatively small entoglenoid processes. This may suggest that the entoglenoid process is associated with increasing the range of motion of the condyle at larger gapes. These data therefore strongly suggest that TMJ shape varies as a function of food material property and relative use of the anterior or posterior dentition.

A very strong correlation between measures of gape (e.g., canine crown height and height of the TMJ above the occlusal plane) and aspects of the AP length of the glenoid (glenoid length and preglenoid plane length) was also found in this analysis. These data indicate that the amount of translation occurring at the TMJ during jaw opening and closing is important for maximizing linear gape, and those taxa with relatively wider gapes have more extensive anterior excursion of the mandibular condyle during wide jaw opening. These finding are consistent with recent analyses by Hylander and colleagues (Hylander and Vinyard, 2006; Hylander et al., 2008), who found a significant correlation between relative gape and canine crown height, and support the hypothesis that increased gape is partly manifested by alterations in joint surface area (Hylander, personal communication). Similarly, these data support the findings of Vinyard et al., (2003) who found that tree-gouging primates tended to have relatively AP longer glenoids than closely related taxa that do not practice tree-gouging.

<u>Research Question 2: Size and Scaling of the TMJ</u>

Any consideration of functional variation must also account for variation in size across the sample in question. Previous research on scaling in the masticatory apparatus has yielded mixed results. Multiple analyses have indicated that some features of the masticatory apparatus scale with positive allometry (Smith et al., 1983; Hylander, 1985; Ravosa, 1996; 2000; Vinyard, 1999; Anapol et al., 2008). Several authors have interpreted this scaling pattern to indicate a size-related increase in dietary toughness across primates. Other researchers have suggested that some of these features scale instead with isometry (Cachel, 1984; Bouvier, 1986a,b; Anton, 1999, 2000; Perry and Wall, 2008). It was predicted here that most features of the TMJ should scale with positive allometry, particularly if the hypothesis of a size-related increase in dietary toughness is correct. Scaling of food items relative to body size also suggests that, as taxa grow larger, food items should be relatively smaller, and therefore negative allometry in aspects of gape was predicted.

Results of the scaling analyses indicated that many features of the TMJ do tend to scale with positive allometry, but when these patterns are evaluated in platyrrhines, cercopithecoids, and hominoids separately, several distinct trends emerge. In both platyrrhines and cercopithecoids, the size of the processes in the joint (e.g., entoglenoid, postglenoid, and articular tubercle) scale with positive allometry, but these same relationships in hominoids are generally isometric. Similarly, glenoid length and preglenoid plane length tend to show a slightly negatively allometric scaling relationship in hominoids whereas in platyrrhines and cercopithecoids these variables scale with either isometry or positive allometry. These data may point to relative differences in gape in hominoids, since previous analyses by Vinyard et al. (2003) have demonstrated a correlation between relative gape and the anteroposterior length of the TMJ that is further supported by the strong correlation found here between aspects of glenoid shape and canine length and height of the TMJ above the occlusal plane.

The geometric morphometric analyses of scaling in the TMJ provide an interesting contrast to the univariate analyses conducted. The geometric morphometric scaling data indicated that TMJ shape is strongly correlated with variation in body size in platyrrhines and hominoids, but not in cercopithecoids, and that the pattern of TMJ shape change as related to size is reversed in platyrrhines and hominoids. These disparate patterns of shape change may again be associated with relative differences in gape, such that the larger bodied platyrrhines (e.g., *Alouatta*) and the smaller bodied hominoids (e.g., hylobatids) have similarly increased gape requirements that necessitate relatively anterioposteriorly long glenoids that would facilitate increased translation of the mandibular condyle during jaw opening and closing. However, mandibular and canine morphology differs considerably between these groups. *Alouatta* has a TMJ raised well above the occlusal plane and relatively smaller canines, while the hylobatids have TMJs that are considerably closer to the occlusal plane but very large canines. In *Alouatta*, increased AP translation of the condyle on the glenoid articular surface may somewhat compensate for the reduced linear gape associated with such high TMJs, regardless of the canine size in this taxon. In contrast, hylobatids may have wider gapes as a consequence of their enlarged canines.

Research Question 3: TMJ Shape and Primate Phylogeny

Recent work with the temporal bone suggests that this region is particularly useful for uncovering the phylogenetic history of primate clades (Lockwood et al., 2002, 2004; Harvati and Weaver, 2006a,b; Smith et al., 2007; HF Smith, 2009; von Crammon-Taubadel, 2009). This has been demonstrated for great apes and humans, but it remains unclear whether this technique is broadly applicable across primates. Furthermore, whether different portions of the temporal bone are more or less useful for phylogenetic reconstruction is unknown. Yet researchers rely heavily on features of the temporal bone (including aspects of TMJ shape) to evaluate taxonomic and phylogenetic hypotheses, particularly in the fossil hominins. The third and final research question that was addressed in this project investigated the extent to which TMJ morphology is congruent with genetic data.

Analyses of the congruence between the genetic and morphological data for the TMJ indicated that these datasets are not generally congruent, although again, this relationship varied across taxonomic groups and levels. The highest degree of congruence was observed in platyrrhines; in all three of the platyrrhine family groups phylogenies created using the genetic data and TMJ morphology were highly congruent. In contrast, the least congruence between these datasets was found for cercopithecoids. The analyses of the hominid sample presented a particularly interesting result. Previous analyses by Lockwood et al. (2002, 2004), have indicated that temporal bone shape in this group can be used reliably to reflect phylogenetic relationships. This finding was not replicated when only landmarks on the glenoid fossa were used, suggesting that the bulk of the phylogenetic signal of the temporal bone lies in the petrous and tympanic portions. In general, the results of the phylogeny chapter indicate that the relationship between the molecular and morphological data is not consistent across anthropoid primates, and caution is therefore warranted in future analyses of TMJ and basicranial variation of fossil and extant primates.

Further analysis of the covariance between TMJ morphology and distance matrices describing size and dietary variation in the sample found strong correlations among these datasets in several clades. Shape variation in the platyrrhines and hominoids in particular was strongly correlated with body diet and size. Coupled with the relative congruence between the morphological and genetic datasets for the platyrrhines, these findings suggest that perhaps dietary differences, accompanied by changes in relative body size, were the main selective pressure driving the adaptive radiation of this clade that has previously been suggested by Rosenberger (1992). In contrast, data for the cercopithecoids do not suggest any particularly strong correlations among morphology, body size, or diet; although the observed patterns of variation in each of these datasets may suggest that the relative influence of these factors varies across taxa in this group.

Summary of Research

The analyses presented here indicate that the morphology of the TMJ covaries strongly with both masticatory function and body size, and to some extent TMJ morphology reflects phylogenetic history. To what extent are the findings of the dietary, scaling, and phylogenetic analyses related to one another? None of the three factors analyzed are likely to function in isolation, nor are they likely to be the only influences over TMJ shape variation. Dietary differentiation among closely related populations or species can easily drive changes in body size and ultimately lead to phylogenetic differentiation. For example, the data examined here seem to suggest that dietary divergence in platyrrhines is strongly correlated with both size and phylogenetic divergence, perhaps indicating that initial diversification of this clade was related to differences in feeding behavior (Rosenberger, 1980, 1992). Similarly, changes in body size as a result of other selective pressures (e.g., predation, climate, etc.) could necessitate a shift in nutritional requirements and therefore dietary intake. The goal of this study was to examine whether TMJ morphology accurately reflects differences in feeding behavior, body size, or phylogeny. The results presented here suggest that the extent to which these factors were acting on TMJ morphology varies across anthropoid primates, and, perhaps most critically, these data indicate that no single factor is responsible for the variation in TMJ morphology observed across primates. Functional differences in the masticatory apparatus appear to be particularly important in hominids and atelines, but both of these groups also tended to show a strong allometric signal, suggesting that, at least in these groups, diet and body size are interrelated. Results of the biomechanical scaling analysis also suggest this may be the case across the entire sample, as the overall size and most features of the TMJ scale with positive allometry against cranial size. This finding is consistent with previous analyses suggesting that dietary resistance also scales with positive allometry with body size (Kay, 1975; Hylander, 1985; Sailer et al., 1985; Ravosa, 1996, 2000).

In sum, although the TMJ is only a small portion of the skeleton, the morphology of this joint can provide valuable information with which to infer or reconstruct the biology of primate taxa. This project has allowed for the quantification of a poorly understood region of cranial anatomy that is frequently used in studies of fossil and extant primates. Significantly, this analysis linked TMJ shape variation to known dietary and shape differences among taxa, providing data regarding the functional and phylogenetic importance of this region. It is the ongoing goal of this research to further apply these data to a number of outstanding research questions in primate and human evolution. This research also has broader impacts for interpreting the evolutionary history and dietary adaptations of extinct primates, because it contributes to the growing set of three-dimensional data describing primate craniodental variation. Ultimately, these data will help to provide a framework for future analyses of primate, and particularly fossil hominin, TMJ variation, and more generally to contribute to the growing body of literature regarding form and function in the primate masticatory apparatus.

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