# Functional Patterns of Molar Occlusion in Platyrrhine Primates[1]

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*ABSTRACT* Mechanico-functional features of molar form were studied in *Callithrix, Alouatta, Pithecia* and *Cebus*. Molars of *Callithrix* and *Alouatta* are adapted to loading foods under relatively high occlusal pressure; those of *Pithecia* and *Cebus*, under relatively low occlusal pressure. General functional considerations suggest that these taxa are adapted to insectivorous, folivorous, frugivorous and omnivorous diets, respectively. The physical properties of foods, principally mechanical strength and deformability, determine the selective pressures involved in the evolutionary adaptation of molar form. A dietary classification based upon percentages of foods eaten does not always reflect morphological adaptations. Homologous parts of teeth and homologous parts of the masticatory cycle do not always subserve equivalent functions. The relevance of functional occlusal analysis for deciphering phylogeny and explaining evolutionary grades is stressed.

The platyrrhine primates portray a wide diversity of morphological and behavioral adaptations. The diversity of their locomotor systems, relative to those of the catarrhine primates, has received considerable attention (*e.g.*, Erikson, '63; Schultz, '70; Stern, '71). At least as great a morphological (and presumably behavioral) diversity is present in the masticatory systems of the Platyrrhini. For example, molars vary from sharp-pointed (Callitrichidae) to bunodont (*Cebus*); premolars, from simple uni- or bi-cuspid teeth (*Cebuella*) to broad and highly molariform (*Alouatta*); canines, from ellipsoidal in cross-section, small and sexually nondimorphic in *Callicebus* (Kinzey, '72), to triangular, large and highly dimorphic in *Cacajao*; incisors, from broad and spatulate (*Cebus*) to narrow and stylate (*Cacajao*); condylar height above the occlusal plane from very low (*Cebuella*) to very high (*Alouatta*); and the dental arch from V-shaped to U-shaped. The number of teeth varies from a minimum of 32 in Callitrichidae to a maximum of 36 in Cebidae. These morphological features are related to differences in diet and reflect the adaptive diversity of the platyrrhine masticatory apparatus.

Long ago William K. Gregory recognized the adaptive significance of platyrrhine dental diversity and, with an eye to the future, aptly projected the direction of later research: "In general the Cebidae feed upon a mixed diet of fruit and insects; except *Alouatta*, which is said to limit its diet to leaves. Probably if we had fuller information we should find a closer correlation between the particular kinds of insects fed upon by the different genera and the detailed characters of the dentition." (Gregory, '20: p. 414). Due to recent field studies we now know that dietary habits of the Cebidae are considerably more eclectic, but the correlation between dental morphology and diet sought by Gregory has yet to be elaborated.

Except for the recent data collected on Barro Colorado Island (Hladik and Hladik, '69; Hladik et al., '71) the information in

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[1] A preliminary version of this paper was presented at the 43rd annual meeting of the American Association of Physical Anthropologists (Kinzey and Rosenberger, '74).

the literature concerning foods eaten by New World primates under natural conditions is very incomplete. Only recently have field workers begun to record food habits in detail, including proportions of food resources exploited, and seasonal variations. Of the South American primates for which the best data exist, Hladik and Hladik ('69) have shown that *Aotus*, *Saguinus*, *Cebus*, *Alouatta*, and *Ateles* all have diets containing between 60% and 80% fruits. It is hardly a useful classification to refer to all these animals as "frugivores." Not only does this oversimplify the mixed nature of their diets, but the differences in kinds of fruit eaten, given in great detail by the Hladiks, are not taken into account. More careful study of the data reveals that what makes their diets different, and by corollary, what is of primary selective value in determining dental morphology, is not necessarily their major dietary component. Thus *Saguinus* consumes the highest proportion of insects of any of the above five primates, *Alouatta* the highest proportion of leaves (twice as much as *Ateles*), *Ateles* the highest proportion of fruits, and *Cebus* the most nearly equal proportion of each of these food categories. While each genus is thus "frugivorous" in the broad sense, other components of their diets are perhaps more important in long term selection for dental morphologies.

The purpose of this paper is to present some observations on the form-function complex (Bock and von Wahlert, '65) of molars in several living platyrrhines in an attempt toward developing an approach which will help clarify their evolutionary adaptions. The functional relationship between a specific diet and a particular molar morphology is only indirect. Because mastication is a mechanical process, the masticatory potential of teeth can be directly associated only with the physical properties of food items. Additional faculties such as body size (Kay, '73), organization of the musculature and the form-function complex of other teeth contribute to the direction and manner of molar adaptation. Rather than attempting to develop a predictive model of dietary adaptation, our purpose here is to describe how these architecturally complex teeth function with respect to certain food properties. Several features of jaw shape are also briefly described, more to point out important differences between taxa than to explain their functional significance. Because of the range of adaptations in living Platyrrhini, understanding gained from the study of platyrrhine diversity should be of value in understanding evolution of the masticatory system not only in the Ceboidea, but in the Anthropoidea as a whole.

## METHODS

We have chosen four taxa of South and Central American primates whose molar morphologies are distinctly different from one another. We have studied one species of each genus in detail: (1) *Callithrix argentata*, (2) *Alouatta caraya*, (3) *Cebus capucinus*, and (4) *Pithecia pithecia*. To the limited extent that we have observed intrageneric differences, each of the four species studied appears to reflect the predominant morphological pattern of the genus. This is not the case with *Cebus*, however, with marked morphological differences between *C. capucinus* and *C. apella* (Hershkovitz, '49; Kinzey, '74) some of which are noted in the DISCUSSION. Except in the case of *Cebus*, we hereafter refer to the four taxa by their generic names.

We examined at least six specimens of each of the four species in detail. Observations of crown morphology were made with a stereomicroscope, fitted with a Wild wide-field goniometer eyepiece to measure the angles noted below. Angular measurements on molars were made on 12 specimens of each genus with comparable degrees of wear. All measurements were performed on females to reduce possible effects of sexual dimorphism.

Terminology of molar crowns largely follows that of Szalay ('69) with the addition of several other standard terms. (Hershkovitz, '71). See figure 1. The indentation between protocone and hypocone as seen in occlusal view is referred to as an entoflexus (*e.g.*, *Alouatta*, fig. 5), and the indentation between protoconid and hypoconid is an ectoflexid (*e.g.*, *Callithrix*, fig. 4). In the case of *Cebus* the entoflexus forms a lingual fovea. The term postprotostyle is that of Kinzey ('73). Buccal notch (Delson, '74) refers to the angle between

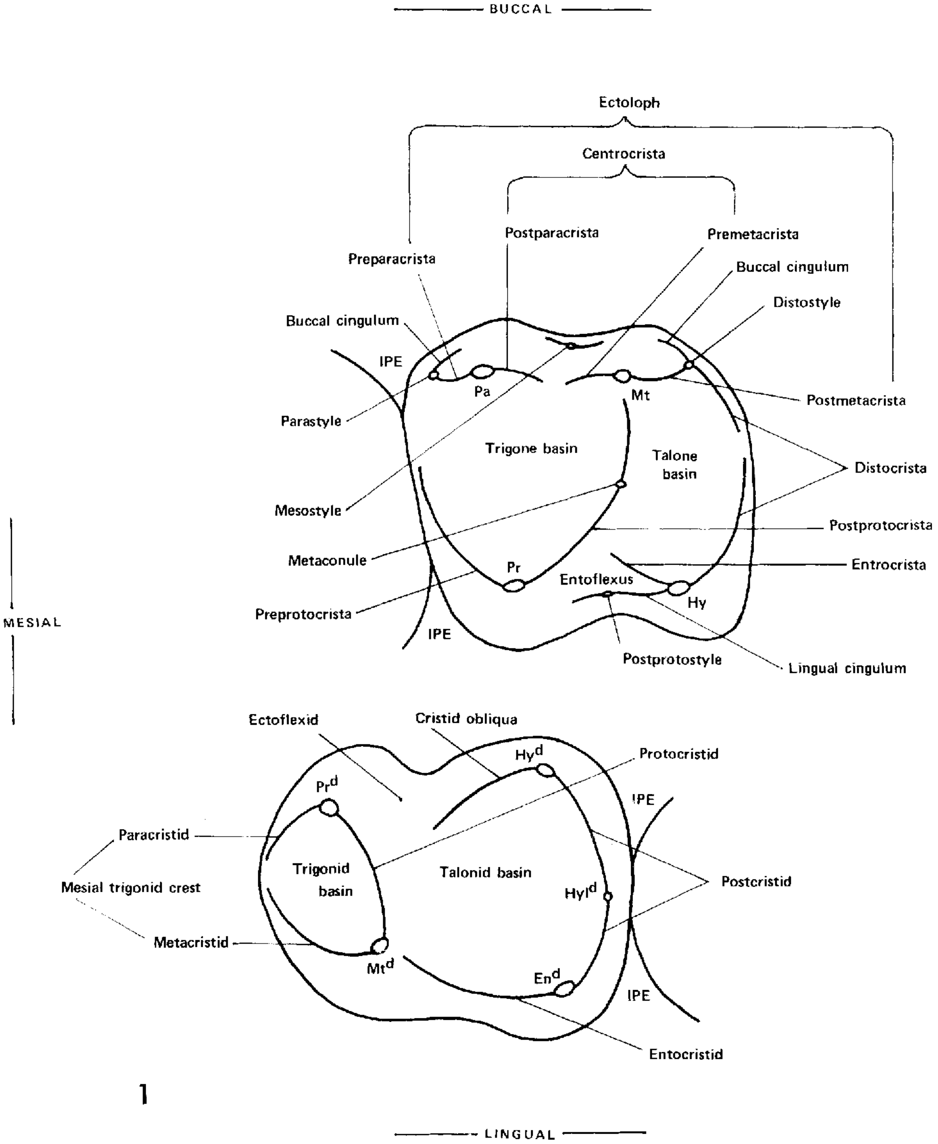

Fig. 1 Schematic diagrams of a cebid left upper molar (above) and a ceboid right lower molar (below). In *Callithrix* the talone basin and entoflexus are absent from the upper molar and a posterior cingulum, closely applied to the postprotocrista, is continuous with the lingual cingulum and generally lacking stylar cusps. The margins of adjacent molars are shown to indicate the interproximal embrasures. Abbreviations: Pr, protocone; Pa, paracone; Mt, metacone; Hy, hypocone; $Pr^d$, protoconid; $Mt^d$, metaconid; $En^d$, entoconid; $Hy^d$, Hypoconid; $Hyl^d$, Hypoconulid; IPE, interproximal embrasure.

paracone and metacone as seen in lateral view on upper molars. See figure 11.

Terminology of the masticatory cycles follows that of Hiiemae and Kay ('73) except, following the argument of Gingerich ('72), we prefer the terms "buccal phase" and "lingual phase" for "phase I" and "phase II" of the power stroke. The descriptive terms of food processing which we employ, cutting, crushing, shearing, and grinding, are modifications of Rensberger ('73) and Kay and Hiiemae ('74b). We de-

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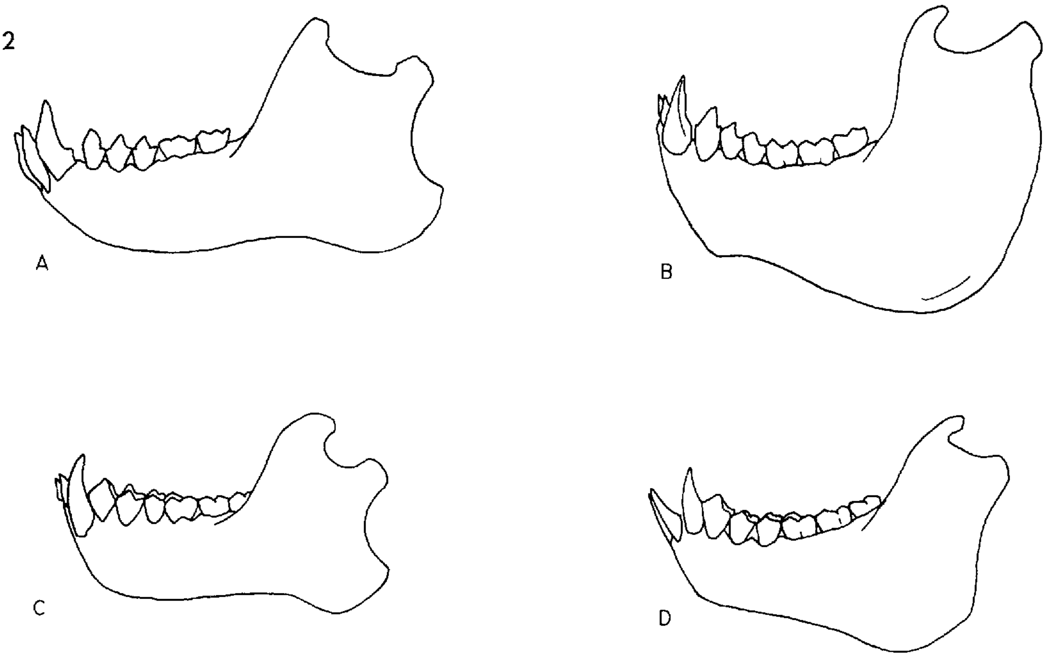

Fig. 2 Lateral views of mandibles of (A) *Callithrix argentata*, (B) *Alouatta caraya*, (C) *Cebus capucinus*, and (D) *Pithecia pithecia*, drawn to the same anterioposterior length of the tooth row.

fine the terms here, but consideration of which processes occur during the puncture-crushing cycle and which occur during the chewing cycle (Hiiemae and Kay, '72) is referred to the DISCUSSION.

"Puncturing" is the pressing of a sharp point against a surface; "cutting" is the pressing of a sharp edge against a surface. In both cases there is a relatively small contact area so that occlusal pressure is high. "Crushing" is the apposition of two relatively blunt surfaces, resulting in large contact areas and low relative occlusal pressure. "Shearing" is the apposition of two leading edges which narrowly miss each other, resulting in a relatively small contact area so that occlusal pressure is high. In all four cases the largest component of force is directed normal to the occlusal surfaces and tangential motion is minimized. "Grinding" is the apposition of two relatively blunt surfaces, resulting in large contact areas thus relatively low occlusal pressure. Here the largest component of force is directed tangential to the occlusal surfaces effecting relative motion between them. These definitions are based upon a simple mechanical model of molar occlusion (Rensberger, '73; Kay and Hiiemae, '74b). Food is divided by the pressure exerted on its parts by the combined resultant of active and reactive forces set up during tooth-food-tooth occlusion. Analysis of the shape and manner of interdigitation of occluding surfaces yields information on the way in which food is loaded, while the amount of relative pressure applied to the food item is inversely proportional to the unit area of occlusal contact.

## RESULTS AND DISCUSSION

### *Description of genera*

*Callithrix.* The mandible is V-shaped in appearance in occlusal view. The mandibular angle projects posteriorly, and the coronoid process and mandibular condyle lie only slightly above the occlusal plane. See figure 2A.

Upper molars are tricuspid, lacking a hypocone, but differ significantly from the primitive tribosphenic condition in that the stylar shelf is much reduced, the ectoloph straightened, the paraconule and its cristae are absent, the metaconule markedly re-

TABLE 1

*Means and standard errors of the angle of the buccal notch in upper molars of four species of Ceboidea*

| Species | $M^1$ | | $M^2$ | |
|---|---|---|---|---|
| | Unworn | Worn | Unworn | Worn |
| *Callithrix* sp. | 90.3 ± 2.4 | 95.5 ± 1.9 | 100.8 ± 2.9 | 107.0 ± 2.3 |
| *Alouatta seniculus* | 109.0 ± 2.4 | 115.3 ± 4.2 | 105.3 ± 3.4 | 109.5 ± 3.3 |
| *Cebus capucinus* | 107.8 ± 3.0 | 135.3 ± 7.0 | 119.3 ± 2.9 | 139.0 ± 11.4 |
| *Pithecia pithecia* | 132.4 ± 1.0 | 135.8 ± 3.9 | 139.7 ± 2.7 | 140.3 ± 5.9 |

Sample size in each case is 6 unworn and 6 worn. Unworn specimens are defined as those with no dentine exposure; worn specimens are defined as those with dentine exposed on the lingual cusps of the first two upper molars but crown relief is still present.

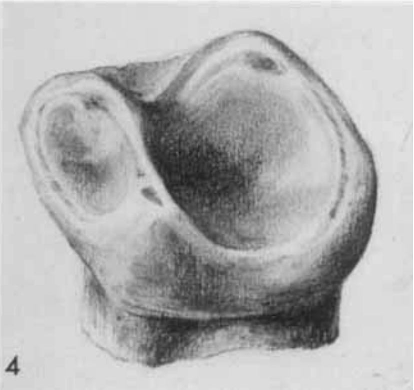

Fig. 3 *Callithrix argentata* upper left first molar, three-fourths occlusal view from the lingual side.
Fig. 4 *Callithrix argentata* lower right first molar, three-fourths occlusal view from the lingual side.

duced or absent, the protocone is situated opposite the buccal notch and the protocone is rimmed by a lingual cingulum (fig. 3). Several of these features are seen in the earliest primates (Szalay, '72), and are ultimately related to the primate trend of reducing shearing blades to accommodate enlarged basins especially active at the end of buccal and during lingual phases (Kay and Hiiemae, '74b). The ectoloph of *Callithrix* is high, the cusps and the buccal notch acute (table 1, fig. 11). This angle changes little with moderate wear. The distocrista is small and closely rims the border of the trigone.

In the lower molars of *Callithrix* the trigonid is small relative to the talonid, lies well above the latter and lacks a paraconid. The talonid lacks a hypoconulid and its basin is deep. A deep buccal embrasure, the ectoflexid, is formed by the angled cristid obliqua (fig. 4).

The absence of a paraconid increases the mesial or mesiolingual mobility of a lower molar once past centric occlusion. It is therefore associated with the evolution of lingual phase during which the lingual aspect of the protoconid moves across the hypocone of the preceding upper molar. Similarly, elimination of the paraconule opens the trigone basin, enabling the hypoconid to move mesiolingually across the mesiobuccal face of the protocone. Wear facets produced during the lingual phase are readily visible in the trigone and talonid of *Saimiri*, *Ateles* (Kay and Hiiemae, '74b), *Cebus*, *Alouatta* and *Pithecia* (see below), but not in *Callithrix*. In this genus a smooth contact facet is frequently seen at the base of the trigone. Its long axis is primarily mesial, the result of contact with the hypoconid apex and cristid obliqua at centric occlusion. But striations on the reciprocal faces of the hypoconid and protoconid, indicative of lingual phase occlusion, are consistently absent.

Molar morphology in *Callithrix* appears to be designed for shearing and compartmentalization (Kay and Hiiemae, '74b). Because occlusal pressure is inversely proportional to unit area of contact, acuteness of cusps and absence of large reciprocal planar contact surfaces assures that occlusal pressure will be high. The high ectoloph, preprotocrista and buccal portion of the distocrista function as shearing blades with their reciprocals, dividing food particles before they are compressed against the walls of the trigone basin. The triangular shape of upper molars, however, minimizes the absolute length of these circumferential shearing blades. Frequent apical cavitation of dentine (especially on the paracone, metacone, and metaconid, which do not participate in compressive occlusion during the chewing cycle) suggests that puncture-crushing plays a significant role in food processing.

Overall, this functional complex appears well suited to processing foods of high "impact strength." Impact strength refers to the amount of energy required to break a unit volume of material. Its calculation ($T^2/2E$) takes into consideration the material's tensile strength (T) and modulus of elasticity (E), a measure of stiffness or stress per unit strain (Alexander, '68). The chitinous exoskeleton of most insects is highly durable. Based on data supplied by Currey ('70), the impact strength of chitin is approximately 23.1 $kg/cm^2$. By contrast the impact strength of bone is only about 2.2 $kg/cm^2$. The most efficient way to reduce objects of such consistency, especially in absolutely small animals, is by concentrating stress. The acute cusps, shearing and compartmentalizing features of *Callithrix* appear well suited to perform this function. The apparent deemphasis on lingual phase processing, which disperses loads widely, is additional negative evidence in support of this hypothesis.

*Alouatta.* The dental arcades of *Alouatta* diverge posteriorly but are very nearly parallel in some individuals. Cheek teeth rows are aligned in a superiorly concave arch, the curve of Spee. (See lateral view in fig. 2B.) There is very little change in the bucco-lingual plane of occlusion from mesial to distal end of the arch, however, in contrast to *Cebus* and *Pithecia* (see below). The articular condyle is unusually high and the coronoid process barely rises above it, if at all. The mandibular body deepens markedly posteriorly, inflating into a huge mandibular angle. Gonial enlargement and airorrhynchy of the skull have been related to enlargement of the hyoid apparatus (Biegert, '63), but we believe that this configuration can only be understood when its relationship of the masticatory system is thoroughly understood.

Upper molars are essentially rectangular in outline, but the talone region is smaller than the trigone. The preprotocrista runs obliquely mesiobuccally and the distocrista distobuccally, thereby forming a relatively large lingual embrasure between adjacent molars. The crown is dominated, even in worn specimens, by a tall ectoloph. The angle of the buccal notch averages slightly greater than that of *Callithrix* (table 1, fig. 11). A large buccal cingulum, frequently in two parts, lies external to the paracone and the metacone. Between them a cuspule lies on an outfolding of the ectoloph, frequently forming a distinct mesoloph. The latter, together with the outfolded posparacrista and premetacrista, add additional length to the ectoloph (fig. 5). The postprotocrista is strongly developed and there may be a metaconule at the base of the metacone. The hypocone is low and closely applied to the low protocone, forming a small vertical indentation, the entoflexus (fig. 5).

Lower molars are somewhat reminiscent of those in callitrichids. The talonid is much larger than the trigonid in length, less so in breadth (fig. 6), and the deep talonid basin lies below the level of the trigonid, exposing a tall, transversely broad protocristid. The metaconid, which occludes in the lingual embrasure between upper cheek teeth, is especially tall and acute. The cristid obliqua runs sharply lingually, delineating, together with the buccal aspect of the postcristid, a deep ectoflexid. The enlarged postcristid, which often bears a hypoconulid, forms interproximal embra-

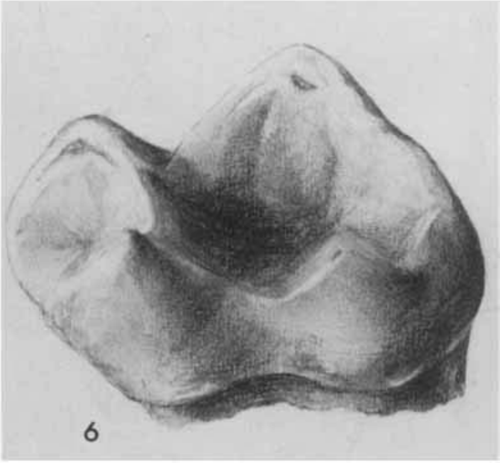

Fig. 5 *Alouatta caraya* upper left first molar, three-fourths occlusal view from the lingual side.
Fig. 6 *Alouatta caraya* lower right first molar, three-fourths occlusal view from the lingual side.

sures, both buccally and lingually, between it and the small mesially rounded trigonid basin of the succeeding molar.

Molar design in *Alouatta* is based upon a general framework of leading edges rimming the crown margin. The angular arrangement of the ectoloph maximizes the length of buccal crests within the mesiodistal limits of crown length. This pattern is mirrored lingually in the zig-zag configuration of the interproximal embrasure and entoflexus. The sharp cusps occlude in tight-fitting indentations during buccal phase. Their apical cavitation suggests the occurrence of puncture-crushing actions. The entire buccal side of the upper molar is modified in several ways to maximize shearing surfaces. The transformation of the mesostyle into a mesoloph increases the length of the centrocrista for shear against the hypoconid. In addition, the mesial edge of the parastyle together with the distal edge of the adjacent metastyle form a V-shaped interproximal shearing blade (as seen from occlusal view) for occlusion with the protoconid. After passing this composite shearing blade the protoconid sequentially shears against the preparacrista and the postmetacrista.

At the end of buccal phase, after the protoconid and hypoconid shear past the maxillary leading edges of the ectoloph, food particles are compressed in centric occlusion into the trigone and talone basins of maxillary molars and trigonid and talonid basins of lower molars. The apices of these roughly triangular basins point in opposite directions. During lingual phase food particles are compressed by the encroaching crests as the distance between opposing apices is reduced (Crompton and Sita-Lumsden, '70). Due to the opposing orientation of the reversed triangles, contact areas are small throughout the excursion (Rensberger, '73; Kay and Hiiemae, '74b). Although the direction of applied force during lingual phase is more tangential to the occlusal plane than perpendicular to it, the height of the operative crests, their orientation and the deep contours of the basins yield high applied occlusal pressures.

Like *Callithrix*, molar morphology in *Alouatta* appears to be suited to processing foods of high impact strength. *Alouatta*'s diet contains 40% leaves, the highest proportion of any ceboid studied (Hladik and Hladik, '69). A folivorous diet, especially one containing mature leaves, requires efficient oral preparation due to its high cellulose content. The impact strength of cellulose, as calculated from Currey's data


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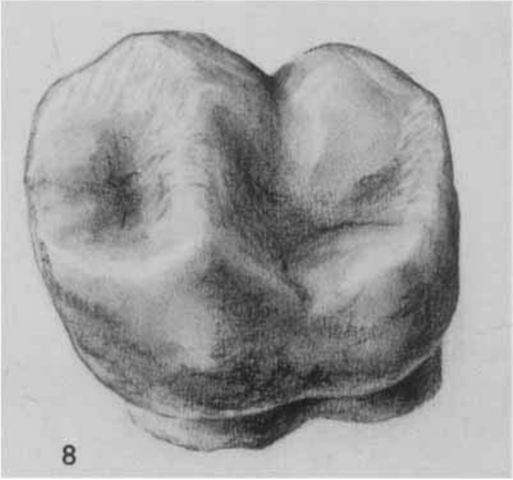
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Fig. 7 *Cebus capucinus* upper left first molar, three-fourths occlusal view from the lingual side.
Fig. 8 *Cebus capucinus* lower right first molar, three-fourths occlusal view from the lingual side.

('70), is approximately 76.8 kg/cm$^2$, even higher than that of insect chitin. The especially well developed puncturing and shearing features of *Alouatta* provide the high occlusal pressure required to break structural cellulose while the crests' zigzag arrangement maximizes their length. Grinding during lingual phase, while perhaps of greater importance than in *Callithrix*, is not especially emphasized.

*Cebus.* The maxillary dental arch in *Cebus* is roughly horseshoe-shaped in outline, diverging posteriorly to P$^4$ or M$^1$ and then converging to the distal end of the tooth row. The mandibular arch corresponds to this shape but begins to converge more distally than M$_1$. The occlusal plane in both upper and lower jaws traces a gentle change in angle, or torsion, from facing slightly buccally (at P$^2$) to facing slightly lingually (at M$^3$). See figure 2C. The gonial region projects posterio-inferiorly. The condyle is relatively low and the coronoid process rises above it.

Maxillary molars, by virtue of a fully developed hypocone, are roughly rectangular in outline (except for M$^3$). Cusps are low and bulbous and a prominent metaconule is generally present, as in figure 7. The interproximal embrasures between adjacent cheek teeth, unlike those of callitrichids and *Alouatta*, are not lined by cutting or shearing edges. The trigone basin is shallow and constricted by the bulbousness of the protocone. Wear of the protocone considerably increases both the shallowness and the area of the basin. The paracone and metacone are closely appressed to one another producing a short low ectoloph. The angle of the buccal notch may be similar to that of *Alouatta* in unworn specimens. Unlike the latter, however, the angle increases markedly with wear to average 135° or more in moderately worn specimens (table 1, fig. 11).

Although the protocone and paracone are situated transversely opposite one another, the hypocone lies more distal than the metacone, opening a deep entoflexus. The entoflexus in *Cebus* extends from the lingual perimeter of the crown, or from the postprotostyle on the lingual cingulum, to terminate at the metaconule. A postprotostyle is variously expressed among species in this genus (Kinzey, '73). The proximal and distal slopes of the entoflexus are worn flat by the entoconid during buccal phase, transforming the entoflexus into a shallow fovea or trough. The postprotostyle may also be worn flat by excursion of the entoconid. This is an important point, for the postprotostyle is a cingular derivative which, when enlarged in *Cebus*, functions as an additional occlusal surface during lingual phase.

Mandibular molars are relatively broad in *Cebus* and the cusps, as in the maxillary molars, are bulbous. The trigonid and talonid are at nearly equal elevations, of approximately equal breadth, and the basins are quite shallow. The cristid obliqua is virtually parallel to the entocristid, and both are relatively short. The postcristid is pronounced and transverse, squaring off the distal margin of the talonid basin and decreasing the interproximal embrasures buccally and lingually. See figure 8. These features maximize occlusal surface area within the trigonid and talonid rather than about their periphery.

Due to the bulbousness of the cusps, there is a general lack of sharp shearing and cutting edges. Although enamel appears relatively thick, molars become rather heavily worn, indicating that absolute force exerted by the musculature is large and has powerful components normal and tangential to the occlusal plane. Since the contact areas are large, however, distributing force over large areas, relative occlusal pressure is much lower than in *Alouatta*, for example. Because of the size and orientation of worn surfaces generalized molar function is best described as crushing and grinding.

As wear proceeds the metaconule together with the entocrista become incorporated functionally into a low crest between the metacone and hypocone. Thus, together with the large protocristid and postcristid of the lower molars, a triple series of transverse crests is formed. A weak morphologic analogy with cercopithecid bilophodonty may be drawn but certainly not a functional one. In cercopithecids, lophs are formed between buccal and lingual cusps of maxillary and mandibular molars, but in *Cebus*, the maxillary one is formed ontogenetically as a result of wear on a conule. Moreover, cercopithecid bilophodonty largely subserves a shearing function (Walker and Murray, '75) and is presumably operative during much of the transverse stroke. Lingual phase, according to Mills ('55), is simply a transverse extension of buccal phase without significant mesial excursion. In contrast, the masticatory cycle of *Cebus* includes two separate excursive modes, each with its own functional properties. Mesial excursion is especially well developed during lingual phase wherein food particles are ground, with the lophs functioning primarily to reduce food escapage and increase occlusal pressure.

Expansion of upper molars mesial to a line drawn from the tip of the protocone to the tip of the paracone increases the surface area for occlusion of the protoconid during its buccal and lingual excursion. The length of protoconid excursion is further extended during the lingual phase by movement across the distal side of the hypocone of the preceding molar. This condition differs from that in *Alouatta* in which the occlusal surface is not expanded mesial to the trigone, and in which lingual phase excursion of the protoconid is restricted to the hypocone.

Functionally, the molar configuration of *Cebus* appears well suited to a crushing-grinding mode of mastication. This suggests a diet containing foods of relatively low impact strength. Heavy enamel deposition and wear, on the other hand, suggest that food might be quite abrasive. Selection for processing a variety of foods is indicated. As such, *Cebus* may be termed an omnivore. *Cebus* eats a smaller proportion of leaves than any other ceboid studied, except *Saguinus* (Hladik and Hladik, '69). The dispersal of pressure over a large area and the lack of sharp leading edges on crests suggest that *Cebus* would indeed be inefficient at shredding plant materials high in cellulose. We would expect that the leaves which *Cebus* consumes to be primarily immature. Seeds, nuts and insects, even if hard, may be processed by crushing and grinding, provided that there is a large muscular force as compensation for pressure reduction at the bite points. Starck ('33) states that the masseter is powerful, and the medial pterygoid strong, especially in *C. apella*.

The emphasis on grinding, as opposed to crushing, is perhaps better developed in *C. capucinus* than in *C. apella* (Kinzey, '74). The previously noted difference in size of the third upper molar between these two species (Kinzey, '73) now takes on significance. In *C. capucinus* the development of the hypocone on the third molar and the higher incidence of the post-protostyle on

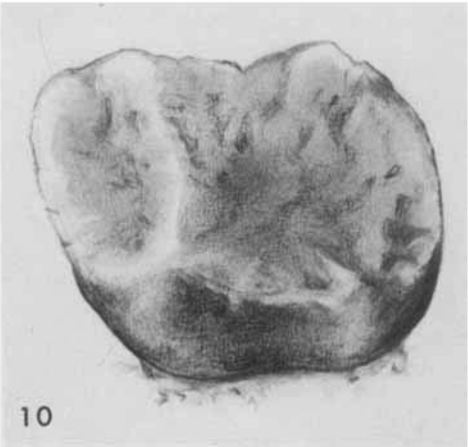

Fig. 9 *Pithecia pithecia* upper left first molar, three-fourths occlusal view from the lingual side.
Fig. 10 *Pithecia pithecia* lower right first molar, three-fourths occlusal view from the lingual side.

$M^1$ and $M^2$ are both related to the greater importance of lingual phase grinding in this species by increasing the surface area for occlusion (a) with the distal margin of the lower third molar, and (b) with the entoconid of $M_1$ and $M_2$. The temporomandibular joint of *C. apella* is higher than in *C. capucinus* and males of the former (but never the latter) frequently develop a sagittal crest which is maximally developed rather forward on the skull or at the vertex (Hofer, '73). This pattern further suggests that orthal forces are emphasized in *C. apella*, and that net occlusal pressure may be greater than in *C. capucinus*.

*Pithecia*. The dental arcades of *Pithecia* consist of very nearly parallel rows of cheek teeth, and display a marked curve of Spee. The tooth rows show a moderate degree of torsion along their length as in *Cebus*. The mandibular profile is reminiscent of that in *Alouatta* but its posterior depth, gonial inflation and especially its condylar height are considerably less than in the latter (fig. 2). Also the coronoid process, unlike that in *Alouatta*, extends above the level of the articular condyle.

Upper and lower molars are rectangular, superficially similar in appearance, and highly modified. The trigone and trigonid are readily distinguishable by weakly developed postprotocrista and protocristid, respectively, but are fully integrated into the relatively flat crowns (figs. 9, 10). Otherwise, except for the perimeters of the molars, crests are absent. Cusps are located on the very perimeters of the crowns and are grossly inconspicuous, forming buccolingually thin crests on the buccal side above and on the lingual side below. The opposite margins are nearly flat. Consequently, molar occlusal surfaces are unusually large and are virtually flat, but with numerous shallow enamel crenulations. The angle of the buccal notch in the centrocrista of unworn specimens equals or even exceeds that found in worn specimens of *Cebus* (fig. 11). The angle changes little with wear, however (table 1).

The most important fact concerning molar occlusion in *Pithecia* is that there is no real interdigitation of cusps. It appears that the functional importance of buccal phase shearing is minimal, if it occurs at all. During buccal phase the marginal crests guide food into the large flat basins preparatory to being crushed. Some cutting may occur at the peripheral crests. Overall morphology and shape and size of wear facets indicate that the buccal phase is extremely short, followed by a long lingual phase. Orientation of wear striations indicates that mandibular motion is similar to that of the other taxa described above. The

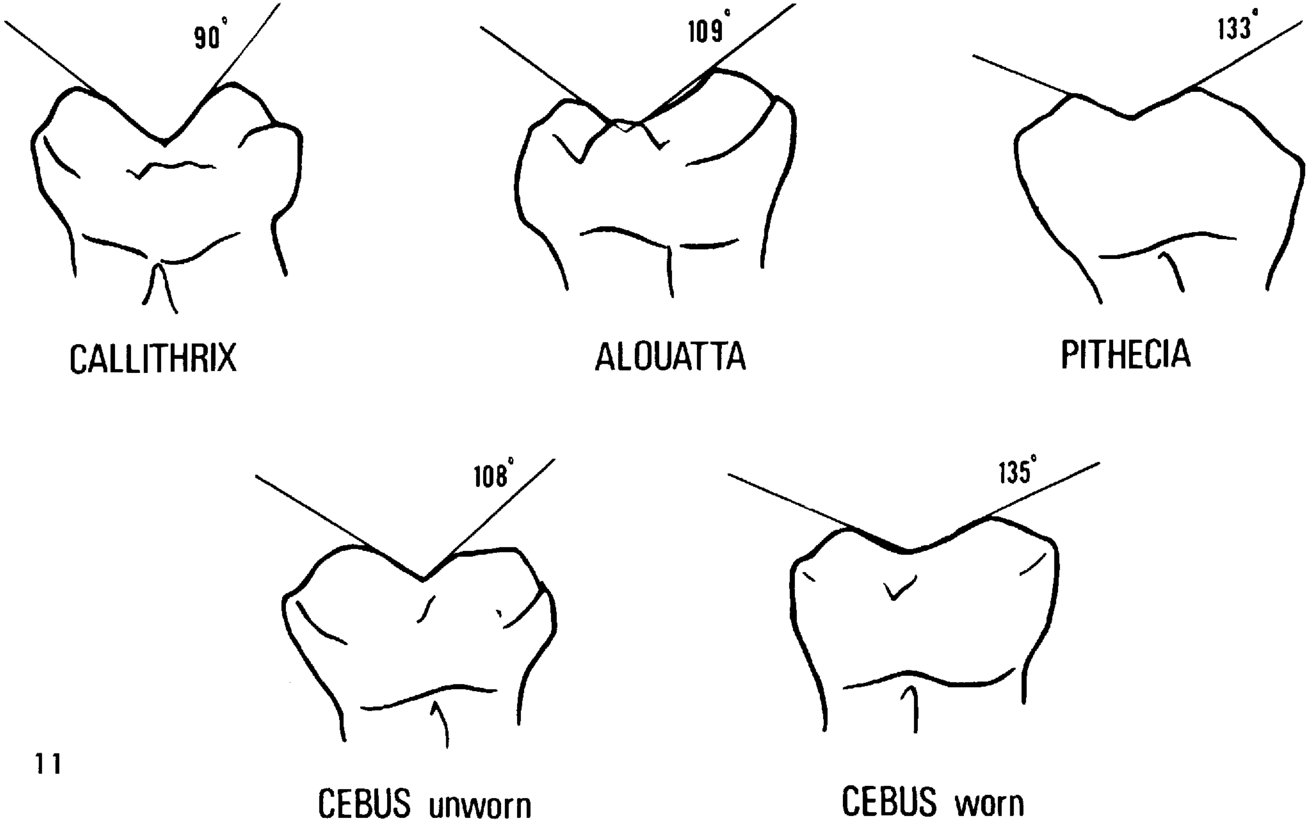

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Fig. 11 Buccal view of first upper molars illustrating the approximate mean angle of the buccal notch in unworn specimens (top row) and in unworn and moderately worn specimens of *Cebus* (bottom row). See also table 1.

lack of crown relief suggests that excursions could be very plastic; that they are probably not is additional evidence that the neuromuscular control of mastication in living primates is highly stable.

Functionally, it appears that *Pithecia* does not have the mechanical prerequisites for processing food items of high impact strength, nor the mechanical flexibility to process a diet having a large variety of physical properties. The natural diet of the pithecines is poorly known, although soft fruits and berries appear to be a major food item (Kay, '73). The pattern of molar features in *Pithecia* may be related to preparation of soft, succulent fruits. Clearly selection has not opted for a morphology geared to reducing objects such as leaves and insects. Specializations of the anterior teeth may compensate for the lack of flexibility in molar function.

The posterior premolars and molars, having large evenly distributed flat areas of contact and virtually no cutting and/or shearing edges, can reduce soft inner pulp of fruits and berries through crushing and grinding. This does not require high occlusal pressure. Crenulation of the occlusal surface may increase friction between the enamel and food matter. This may be a critical function, for the occlusal surface is otherwise virtually flat, and crenulation provides additional reaction force to masticatory forces tangential to the occlusal plane, especially significant during the long lingual phase.

In *Pithecia* (as in *Cebus*) the occlusal planes of the postcanine teeth exhibit a mild degree of torsion along their long axes. Torsion of the tooth row appears to have at least two functions: (1) to equalize occlusal pressure in compensation for the changing vector of muscle force along the tooth row, primarily during the long lingual phase, and (2) to provide additional reaction force against food during the power stroke. Due to the relatively flat occlusal surfaces, the latter function appears particularly important in *Pithecia*. The relationship of torsion of the tooth row to mandibular excursion is brought out by a comparison with the phyllostomatid bats. In those forms which, like *Pithecia*, have become adapted to fruit-eating with the development of large flat molar wear surfaces, there is no torsion of the tooth row since mandibular movement is purely translational with no "rotation" (Mills, '67). Again, to an even greater extent than in *Pithecia*, additional reaction force against food is provided by the high cusps on the margins of the molars.

### *Dietary adaptation and classification*

"The definition of an evolutionary adaptation must include two separate and different elements. An adaptation is (a) a feature of the organism that has a role in the life history of that organism (i.e., must perform some definite task, such as obtaining food or escaping from a predator), and (b) performs this role with a certain degree of efficiency" (Bock and von Wahlert, '65: p. 286). Since the biological role of an anatomical complex, its action or use, is only observable in the wild (Bock and von Wahlert, '65), the elucidation of evolutionary adaptation depends largely on analysis of the second criterion. That is, the variety of functions of an anatomical complex must be explored and the efficiency of each function weighed *vis a vis* the possible roles it may play in the organism's habitat. Thus we have attempted to generalize major functional properties of molar occlusion and hypothetically weigh their efficiency in processing different kinds of foods with differing physical properties.

The wide range of physical properties encountered by primates in their eclectic feeding habits complicates determination of dietary adaptation and dietary classification. Kay ('73) has suggested that the criterion for dietary classification be "primary specialization," when ". . . behavioral observations of wild primates indicate that a particular species consumes 45% by weight of a specific food on a yearly average" (Kay, '73: p. 124). A secondary specialization encompasses items providing 20% of a species' diet. According to these criteria, primates such as the undeniably folivorous *Alouatta* ought to be designated frugivorous, their "primary specialization"!

Based on this dichotomizing approach, Kay ('73) classifies primate diets as "animal," "fruits" and "folivorous materials," excluding the traditional "omnivore" category. It appears to us that there are at least four major functional themes within the adaptive array of platyrrhine molar morphology, and we have suggested that *Cebus* be classified as omnivore. We believe the field data are concordant with this determination. In addition, it is clear that the above categories ought to be refined if mechanical features of the masticatory apparatus are to be efficiently correlated with physical features of the environment. For example, frugivorous foods and insect foods are highly variable in composition and in the amount of stress which they can endure before rupture, putting a different evolutionary premium on taxa feeding at either end of the mechanical spectrum. Adaptation to a primary resource of soft fruits may preadapt a taxon to a soft insect source as a secondary supplement. Likewise, adaptation to hard fruits and insects may be preadaptive to omnivory. This we believe occurred in the evolution of the genus *Cebus*.

We believe that selection for a particular molar form can often be related to some "critical function" which must be performed during food processing, and that dietary classification should be based upon morphological inferences regarding these functions rather than upon behavioral observations alone. As suggested above these critical functions are most closely correlated with the physical properties of foodstuffs, their strength and deformability. An advantage to this approach is that it inherently incorporates evolutionary adaptation and does not merely reflect biological role. Thus if a diet includes a large bulk of cellulose, which must be effectively reduced orally but is indeed mechanically difficult to process, as well as more readily processed soft fruits, the focus of selection will be upon morphologies which are especially efficient in transferring relatively high stresses to any food object. *Alouatta* is an excellent example of this principle.

### *Tooth form and function*

Studies of the primate masticatory cycle have shown that the manner in which food is processed is dependent upon the nature of food triturated (Kay and Hiiemae, '74b). It is therefore important to distinguish among the various mechanical modes of food reduction as they relate to crown morphology. Accordingly, the terms used above are defined by the nature of the occluding surfaces and their relative movements. "Puncture-crushing," a mode of food reduction separate from the chewing cycle has been described in the literature. All three primates thus far studied with cinefluoroscopy (*Saimiri*, *Ateles*, and *Galago*) have both a puncture-crushing cycle and a chewing cycle (Hiiemae and Kay, '72, '73; Kay and Hiiemae, '74a,b). According to these authors, the puncture-crushing cycle results in a "distinctive type of wear [in which] the cusps are blunted, the enamel is worn away, and the exposed softer dentine cratered" (Hiiemae and Kay, '73: p. 51). We feel it important to distinguish between puncturing and crushing processes (see above) because their mechanical effects upon food are very different. Assessment of occlusal morphology suggests that during the puncture-crushing cycle in forms such as *Callithrix* and *Alouatta* puncture processing occurs at cusp tips. In forms such as *Cebus* and *Pithecia*, in which cusps are blunt, crushing, but no puncturing, occurs, and the distinctive wear pattern appears less significant. These distinctions are important evidence of dietary adaptation and can also be related to the physical properties of foods. Our interpretation of the adaptive significance of the puncture-crushing and chewing cycles appears concordant for the taxa studied herein.

The majority of studies on primate molar function pay little attention to the role of ontogenetic resculpturing of the surface of the tooth crown, i.e., to wear, whether by abrasion or by attrition (or thegosis: Every, '70; Every and Kühne, '71). We find it instructive to compare the effects of wear on an homologous structure across several taxa. In *Callithrix* and *Alouatta* the prominent ectoloph (figs. 3, 5) retains its basic morphological pattern until very advanced stages of wear. The angle of the buccal notch in these forms is not significantly different in worn and unworn specimens (table 1). This is important for the critical function here is preserving the ectoloph as a self-maintaining shearing blade and cusp apices as puncturing sites. The pattern seen in *Cebus* is quite different. While the angle of the unworn buccal notch of $M^1$ is similar to that of *Alouatta*, the mean angle enlarges significantly with wear. The ontogenetic angular increase averages 27.5° with moderate wear. Enlarging the angle of the buccal notch substantially increases the area of planar contact at the ectoloph, decreasing shearing and puncturing efficiency but perhaps increasing the crushing/grinding potential of the tooth surface. In all these instances wear itself, as in the case of canine-tooth-honing (Every, '70; Zingeser, '69), maintains or even increases the selective value of tooth crown topography. *Pithecia* presents a third pattern. The ectoloph is subject to little ontogenetic change even though it is not a self-maintaining shearing blade, for it plays only a small role in transferring loads to the food during buccal phase. The angle is already large in unworn specimens, consistent with the overall reduction in molar crown relief seen in *Pithecia*.

Another important point which may be inferred from the foregoing analysis is that homologous features, such as the ectoloph, do not necessarily serve the same function in molars of different primate species.

### *Implications for anthropoid evolution*

It is instructive to compare and contrast the feeding adaptations of New and Old World monkeys to a particular diet. *Alouatta* and the colobines are highly folivorous but, as noted above, the former employs a buccal and lingual phase power stroke whereas the latter reportedly does not. *Alouatta* retains a generalized primate molar pattern with superimposed specializations. Colobines, like all cercopithecids, have a bilophodont pattern without cingular derivatives, save perhaps buccal flare (Delson, '74). Details of molar form are similar only in that each has high pointed cusps and a deep buccal notch (Delson, '74; Swindler and Orlosky, '74). Both *Alouatta* and the colobines have adapted to a folivorous diet by increasing the length of shearing blades. In *Alouatta*, where molar morphology is easily derived from that of a generalized frugivore, the increase in blade length is through modification of the buccal side of the upper and lower molars. There is little sacrifice of basins where crushing and grinding actions occur: *Alouatta* eats both leaves and fruits. Colobines, especially with highly developed bilophodonty, have essentially created shearing blades at the expense of planar contact surfaces. Many colobines, such as *Nasalis* (Kern, '64) and *Colobus guereza* (Clutton-Brock, '74) eat virtually nothing but leaves, at least during part of the year.

The earliest ancestral cercopithecoids certainly did not have a fully-developed bilophodont pattern. Also, because all primates studied thus far manifest buccal and lingual phases in the power stroke, earliest cercopithecoids must also have had such a pattern; a more medial translation is certainly a derived condition in living cercopithecids and is inevitably related to increase in cusp height. Since behavioral changes generally precede anatomical adaptations, and certain aspects of feeding behavior are obviously detectible by studying tooth occlusion and wear, we might expect ancestral cercopithecids to have exhibited a behavioral tendency toward an increasingly transverse movement during the power stroke.

Simons ('72) and others consider *Parapithecus* and perhaps *Apidium*, both of the Fayum Oligocene, as possible ancestors of bilophodont Old World monkeys. Delson ('74) maintains that *Parapithecus* exhibits several derived characters which would necessarily have to be lost if it were so related phylogenetically. One such character is the "incorporation of large conules into possibly functional lophs" (Delson, '74). Delson (personal communication) has drawn our attention to the fact that the metaconule of *Parapithecus* is ontogenetically resculptured in a manner similar to that which we have described for *Cebus*. On the basis of our argument above, the presence of such a metaconule, later incorporated into a posterior loph, might be expected in a cercopithecoid ancestral morphotype. We do not imply that *Parapithecus* is therefore ancestral to living cercopithecoids. Rather, we wish to emphasize that studies of occlusion and function can contribute significantly to understanding primate phylogeny as well as adaptation.

Further study of the platyrrhine masticatory system, and dental form and function, can shed considerable light on the evolution of the anthropoid dental grade, a topic of current interest. One of the features of this grade is symphyseal fusion (Simons, '72) which has been related to absorption of incisal stress (Kay and Hiiamae, '74b), to horizontal stress (Crompton, in Simons, '72), and to "rotational" jaw movement (Mills, '73). Symphyseal fusion may be a postadaptation (Bock and von Wahlert, '65) to the evolution of a crushing-grinding mode of mastication, reducing torsional stresses at the symphysis and increasing the efficiency of transferring contralateral muscle force to the active side. Similarly, symphyseal fusion may be related to the development of torsion-producing canine honing (Zingeser, '69; Every, '70), possibly an important behavioral mechanism in Anthropoidea. Fusion of the dentaries has occurred convergently in several living and extinct primate lineages of varying body sizes, anterior dentitions, and molar occlusal patterns. Although several of the above independent explanations are applicable to the case of Anthropoidea, it is most likely that a combination of mechanical advantages was gained. Should one of these have been predominant, only the fossil record can tell.

## CONCLUSIONS

The diversity of molar form seen among platyrrhine primates reflects evolutionary adaptations of the masticatory apparatus to the physical nature of differing dietary resources. Strength and deformability of the intrinsic structure of edible materials are the principal combined factors governing the selection for molar form. Molars of *Callithrix* and *Alouatta*, by virtue of their shape, load foods under relatively high occlusal pressure, indicating that their diet is largely composed of tough materials such as chitin and cellulose. The lack of hypertrophied shearing blades and the deëmphasis of features important during lingual phase (Phase II) processing suggests that *Callithrix* cannot efficiently reduce large amounts of leafy material and is not particularly suited to processing softer foods, such as fruits, by grinding. In contrast, emphasis upon circumferential shearing blades and maintainance of relatively large, planar basins indicates that *Alouatta* can efficiently masticate quantities of leaves, and supplement this staple with fruits, which does not require application of high occlusal stresses. In each of these forms, the morphological integrity of the ectoloph is maintained even into well marked stages of ontogenetic wear, attesting to the functional importance of puncturing and shearing during the puncture-crushing and masticatory cycles, respectively. This too suggests adaptations to mechanically tough food items.

Molars of *Cebus* and *Pithecia* differ from the above conditions in transferring relatively low occlusal loads to food objects. They manifest markedly reduced shearing blades, rounded or entirely flattened cusps, and hypertrophy of planar surface features, indicating the predominance of crushing rather than puncturing actions during the puncture-crushing cycle and the importance of lingual phase grinding. This functional complex would be markedly inefficient at reducing leaves. Specific features of *Pithecia* suggest adaptation to soft fruits while features of *Cebus* molars, and analogy with those of other taxa, suggest a highly plastic, non-folivorous feeding pattern. We believe *Cebus* is adapted to an omnivorous diet and that an "omnivore" dietary category should be utilized where appropriate. The functional components and evolutionary pathways toward omnivory are yet to be elaborated and future work might be profitably directed toward this problem, an important one in the history of nonhuman and human primates alike.

The diversity of foods eaten by primates, and their concomitant broad physical makeup, raises important theoretical questions regarding the criteria used in classifying primate dietary adaptations. Mastication, a primary medium of consumption, is by now well recognized as a strictly mechanical process. Classification ought to reflect the mechanical nature of an evolutionary adaptation, taking time-tested functional aspects of molar form fully into account without undue weight given to the necessarily incomplete observations of feeding behavior in the wild. The primary focus of molar adaptation is probably coincident with critical functions which molars must perform in reducing food items of varying consistencies.

The mechanical potential of a given area of tooth surface may remain essentially constant or become modified as a byproduct of ontogenetic wear. Similarly, homologous parts of teeth of different taxa do not necessarily serve the same function, nor do homologous parts of the masticatory cycle.

Functional studies of the masticatory system can yield important information on the adaptive significance of evolutionary grades, and important clues concerning the cladistic relations among fossil and living taxa.

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