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Dental function in the Palaeocene primate Plesiadapis

Introduction

The main function of mammalian teeth is to reduce food matter to a size and consistency that can be swallowed and digested. The wide range of dental types seen in living mammals is the result of successive evolutionary radiations of animals adapted to masticating specific diets. In each radiation the dental morphology and adaptation are modified from those of an ancestral species to produce descendant species with a range of dental adaptations. Thus within any radiation it is usually possible to identify a number of dental types, each derived from the ancestral morphology and retaining features of it. For example, the Palaeocene primates *Plesiadapis, Phenacolemur, Carpolestes,* and *Palaechthon* exhibit four rather different adaptive modifications of the ancestral primate molar morphology. They also share many features which presumably were inherited from a common ancestor. The adaptive significance of the morphological differences seen in the teeth of these early primates can only be determined by a detailed consideration of how the teeth function.

Functional occlusion produces matching striated wear facets on upper and lower teeth. Much of the chewing behaviour of an animal can be reconstructed by studying these striated wear facets. Butler and Mills were the first systematically to map wear facets and classify them according to the direction of their striations.[1,2] Mills distinguished two sets of wear facets on primate molars. One set is the result of an upward, medial, and slightly forward movement of the lower jaw into centric occlusion on the active side. This phase of occlusion Mills referred to as the 'buccal' phase. From centric occlusion the mandible moves forward, medially, and slightly downward on the active side, producing the second set of wear facets. This phase of occlusion Mills termed the 'lingual' phase.

Recent important cineradiographic studies of mastication in the opossum by Crompton and Hiiemae,[3] and in *Galago crassicaudatus* by Kay and Hiiemae,[4] have clarified several aspects of mandibular movement during molar occlusion. Fortunately, striated wear facets are as well preserved on the teeth of fossil mammals as on those of living animals. Thus it has been possible to identify both buccal and lingual phase facets on molars of the Eocene primate *Adapis*, as well as a third 'orthal retraction' set of facets indicating an upward and backward movement of the mandible during one stage of chewing.[5]

In this paper the wear facets on the molars and incisors of specimens of *Plesiadapis rex* (Gidley)[6] from the early Late Palaeocene Cedar Point quarry in northwestern Wyoming are described. This description will form the basis for a later comprehensive study of the evolution of dental function in the Plesiadapidae.

Molar morphology and function

Upper and lower molars of species of *Plesiadapis* have been illustrated and described in detail by Matthew,[7] Jepsen,[8] Simpson,[9] and Russell,[10] among others. The terminology used here in describing *Plesiadapis* molars is illustrated in Fig. 1. The lower molars are roughly rectangular; the protoconid and metaconid are joined by a strongly developed protocristid; the metaconid and paraconid are connate (as Matthew suggested, possibly what is here called the paraconid is really the metaconid, and what is here called the metaconid should really be considered a metastyle);[7] the paracristid runs forward to join the postcristid of the preceding molar; the cristid obliqua forms a strong shearing crest connected with the postcristid at the hypoconid; lingually the postcristid is supported by a well developed entoconid; a buccal cingulum is well developed on all molars, and a very weak lingual cingulum is suggested on some.

The upper molars are roughly triangular; the metacone and paracone support a continuous series of shearing crests: the paracrista, centrocrista, and metacrista; the paraconule and metaconule are joined to the protocone by the preprotocrista and postprotocrista respectively; the 'Nannopithex fold'[11] is invariably a well developed crest running posteriorly from the protocone and turning abruptly buccally at the posterior margin of the tooth to form a post-cingulum; a cingulum borders the molars buccally, and a lingual cingulum is developed along the anteromedial border of the molars. Both upper and lower molars are low in profile and bear bulbous cusps.

Fig. 2 illustrates upper and lower second molars of *Plesiadapis rex* and indicates the wear facets formed during function. Each of the major crests connecting the cusps on the lower molars supports a buccal phase wear facet on its buccal surface. For descriptive
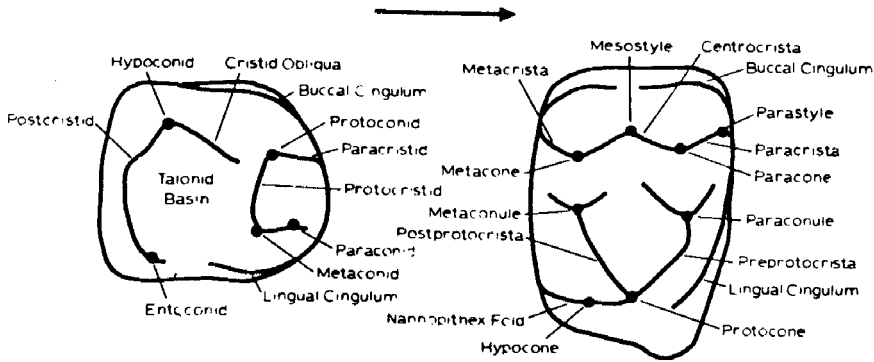
Figure 1. Terms used to describe molars of *Plesiadapis.* Lower molar is on the left, upper molar on the right. Heavy arrow is buccal to both molars and points anteriorly.
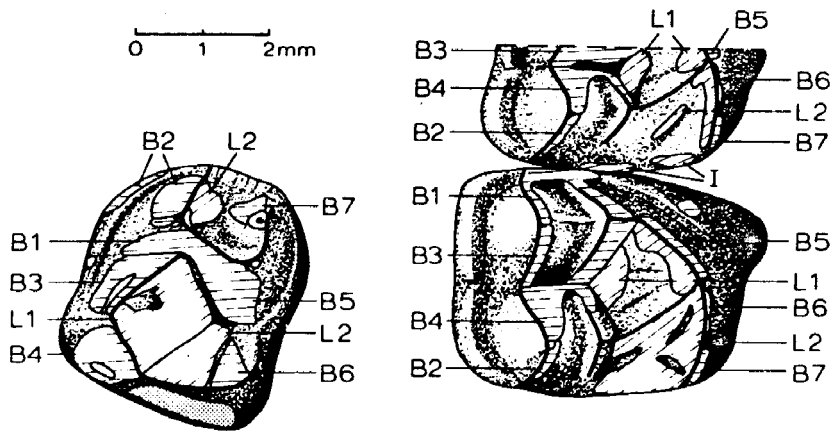

Figure 2. Wear facets on upper and lower molars of *Plesiadapis rex,* seen in occlusal view. On the left is a lower left second molar, on the right is part of an upper right first molar and an upper right second molar. Matching buccal (B) and lingual (L) phase facets are correspondingly numbered. Dotted area is an interstitial facet. Lines on the wear facets indicate the actual direction of striations and movement.

purposes, these are numbered B1-B6, following the numbering scheme recently introduced by Crompton.[12] An additional facet, B7, is present on the buccal side of the paraconid. Each buccal phase facet on the lower molars is matched by a buccal phase facet on the lingual side of the crests on the upper molars, correspondingly numbered B1-B7. The striations on all buccal phase facets are parallel, indicating that they were formed by a single jaw movement.

A second set of striated wear facets on the lower molars is formed mainly in the talonid basins. These are numbered L1 and L2 in

Fig. 2. The facet L2 generally continues posteriorly from the talonid of one molar onto the trigonid of the following molar. Thus the lower molar illustrated in Fig. 2 has a second L2 facet lingual to the protoconid, which is the posterior extension of the L2 facet on the preceeding molar. As the teeth become more heavily worn, this L2 facet on the trigonid may obliterate the neighbouring B7 facet. The L1 and L2 facets on the lower molars match facets developed on the upper molars, correspondingly numbered L1 and L2. Again, the striations on the lingual phase facets are parallel, indicating that they were formed during a single jaw movement. The two facets marked I on the upper first molar, and the corresponding area of L2 on the following molar have striation directions intermediate between those of the buccal and lingual phase facets. Matching intermediate facets are developed on the trigonid of the lower molars in some specimens. This confluency of buccal and lingual phase facets indicates that the buccal and lingual phases in *Plesiadapis* were consecutive components of a single transverse ectental jaw movement.

The buccal phase performs primarily a cutting function, with crests on the lower molars shearing past those on the upper molars. To better serve this function, the number of cutting edges on the molars was increased by two means. Cutting edges were added by developing new crests parallel to the previously existing ones. Thus the B1 protocristid cutting edge on the lower molars sheared past first the paracrista, then the preparaconule crista, and finally past the lingual cingulum on the corresponding upper molar. As the postmeta-conule crista on the upper molars was limited in development by the L2 facet, a second B2 cutting edge was developed from the buccal cingulum of the lower molars. The second means of adding cutting edges is illustrated by both the B3 and B4 facets on the lower molars. As is shown in Fig. 2, here the enamel has been worn through relatively early, resulting in two resistant enamel cutting edges on a single crest. On heavily worn teeth almost all the crests bear two cutting edges as a result of wear having penetrated the enamel.

The molar teeth of *Plesiadapis* occluded in such a way that they produced on the active side a series of three compression chambers for expressing juices. At the beginning of the buccal phase the B3, B4, and L1 facets on the upper molars, and the L1, L2, B5, and B6 facets on the lower molars completely enclosed a space, the volume of which was progressively reduced as the teeth approached centric occlusion. The pulp remaining after this compression was then ground during the lingual phase.

The lingual phase performs primarily a grinding function. Food is ground between opposing planar areas of the matching lingual phase facets. In *Plesiadapis rex* the relatively rough texture of the enamel in the areas where lingual phase facets developed, illustrated in Fig. 2, caused windows in the facets until they became heavily worn. These windows functioned as cutting edges, suggesting that in *Plesiadapis*

the lingual phase performed a cutting as well as a grinding function, at least in younger individuals.

Incisor morphology and function

The type species of *Plesiadapis*, *P. tricuspidens*, was so named because of its enlarged and distinctive tricuspid upper incisors.[13] The morphology of the lower incisors of *Plesiadapis* are also unique to the Plesiadapidae. These enlarged procumbent upper and lower incisors have been figured and described by Matthew and by Russell.[7,10] Both are illustrated in occlusal aspect in Fig. 3. The upper incisor (Fig. 3a) has a large anterior central cusp flanked by smaller medial and lateral cusps. Four ridges connect these three anterior cusps with a posterior cusp. These ridges became worn successively, beginning with the medial ridge, until the whole occlusal surface of the tooth anterior to the posterior cusp was excavated. A large interstitial facet developed where the right and left upper incisors contacted each other. With age, the large central anterior cusp and the medial and lateral cusps became heavily worn and blunted.

The lower incisor (Fig. 3b) has a slightly convex dorsal surface bordered laterally by a ridge of enamel running roughly parallel to the large interstitial facet on the medial side. The only cusp was small and developed at the posterior end of the lateral enamel ridge. With age, the tip of the incisor was gradually worn back. The tip was never sharply pointed. In some specimens the enamel is worn off on a large area of the central dorsal surface of the incisor crown; however, on other very heavily worn specimens this enamel covering is still complete.
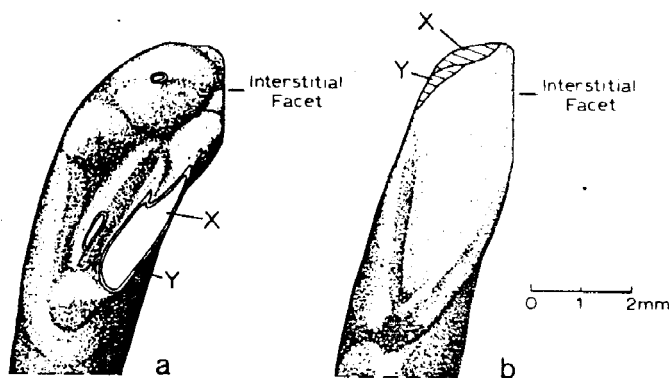

Figure 3. Wear facets on upper and lower incisors of *Plesiadapis rex*, seen in occlusal view. (a) right upper incisor; (b) left lower incisor. X and Y are matching facets on the upper and lower incisors.

The reconstructions of the skull of *Plesiadapis tricuspidens* by Simons,[14] Russell,[10] and Szalay[15,16] show that the function of these enlarged incisors was not fully understood. On the slightly worn specimens illustrated in Fig. 3 it is possible to distinguish two separate wear facets. The striated X facet on the lower incisors indicates an upwards, backwards, and slightly medial movement of the tip of the lower incisor across the ridges of the occlusal surface of the upper incisor. As the tip of the lower incisor approached the posterior cusp of the upper incisor it was forced more medially, and the leading edge of the Y facet on the lower incisor sheared past the enamel edge Y on the posteromedial side of the X facet on the upper incisor. The left and right lower incisors are just wide enough to have passed between the posterior cusps of the left and right upper incisors. From the wear on the incisors it is clear that the tips of the lower incisors functioned predominantly by shearing across the ridges (particularly the most medial ones) located just anterior to the posterior cusp on the upper incisors. The way the tip of the lower incisor closed the space in front of the posterior cusp on the upper incisor, shearing against the medial side of the posterior cusp, can best be seen in lateral view (Fig. 4). The result was a cutting device which would function most effectively in cutting stems of soft vegetation.

The tips of the upper and lower incisors could be opposed in *Plesiadapis*, but the tips of both the upper and the lower incisors became blunted with use. They therefore cannot have functioned as do the incisors of living rodents and lagomorphs, and would not have been effective in taking bites from a larger mass of food. Possibly the most similar incisor mechanism among living mammals is that found in the marsupial macropodines.[17] From striations on the interstitial facets of some of the lower incisors it is apparent that the
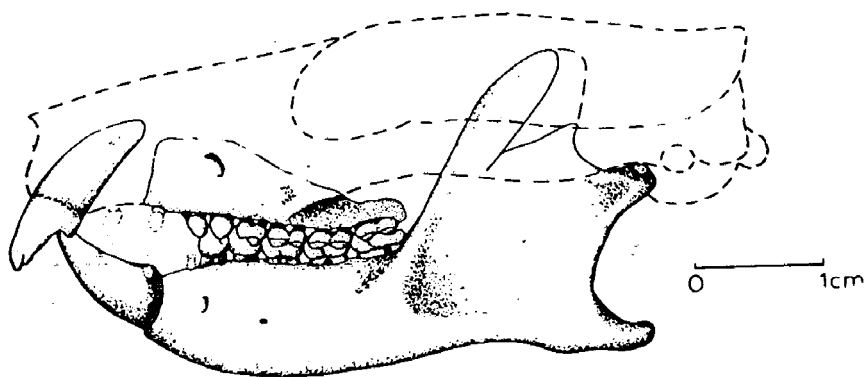

Figure 4. Reconstruction of centric occlusion in *Plesiadapis rex*, seen in lateral view. Stippled areas are actual specimens, dashed lines are hypothetical. Based on PU 21300, 21246, and an isolated upper incisor, all from the Cedar Point Quarry.

mandibular symphysis of *Plesiadapis* was highly mobile, as is true also of macropodines. The direction of movement of the lower incisors during function was upward and backward, the force for which was generated chiefly by the temporalis muscles.[18]

From this analysis of the function of the enlarged incisors of *Plesiadapis* it is apparent that when the molars were in occlusion, the incisors must have occupied approximately the position shown in Fig. 4. The lower incisors rested between and sufficiently far behind the upper incisors not to contact them during the buccal and lingual phases of molar occlusion. For the incisors to function it was necessary for the lower jaws to translate forward. With this forward translation, the mandibular condyle rode up on the articular tubercle and separated the upper and lower cheek teeth sufficiently for the incisors to function independently.

Discussion

Any attempt to determine the diet of an extinct mammal must consider the morphology of all the teeth: incisors, canines, premolars, and molars. The molars of *Plesiadapis* show relatively great development of buccal phase cutting edges, as do the molars of living grazing herbivores. The incisor mechanism of *Plesiadapis* indicates a cropping mode of food acquisition. The reduction and loss of canines and premolars in *Plesiadapis*, leaving a large diastema between the incisors and the remaining premolars and molars, is also consistent with a cropping incisor mechanism. The canine and premolar teeth of many mammals are used to shear and puncture large bites of food when they are first ingested. Reduction and loss of canines and premolars, with the resulting large diastema, is correlated with initial ingestion into the mouth of small pieces of food. Grazing mammals have a large diastema because they feed on food that is by its nature already in small pieces. Rodents have a large diastema because they gnaw a series of small pieces from a larger piece of food rather than ingesting the larger piece.[19] The great reduction of canines and premolars in *Plesiadapis*, compared for example with the large pointed premolars of *Phenacolemur*,[20] thus suggests that *Plesiadapis* also ingested food in small pieces. The shape of the cutting edges on the incisors of *Plesiadapis* further suggests that the original food mass was predominantly in the form of stems.

Teilhard de Chardin was the first to suggest that *Plesiadapis* may well have been a terrestrial animal, based on the relative abundance of *Plesiadapis* remains at Cernay.[21] In the Princeton collection from the Cedar Point quarry approximately 140 out of 400 catalogued placental mammal specimens are *Plesiadapis*, further supporting Teilhard's observation of their abundance. Simons suggested that some species of *Plesiadapis* most probably were terrestrial to account

for the wide geographic distribution of the genus in North America and Europe.[22] The predominantly herbaceous diet and grazing feeding mode inferred above for *Plesiadapis* also suggest a terrestrial habitat. Among living gregarious terrestrial herbivores, the post-cranial remains of *Plesiadapis tricuspidens* compare closely in size and many morphological features with the skeleton of a marmot (genus *Marmota*). The habits and appearance of *Plesiadapis* may have been similar to those of living marmots, although this hypothesis must be tested by more detailed comparative work on the postcranial anatomy of *Plesiadapis.*

Recently Charles-Dominique and Martin suggested that allocation of *Plesiadapis* to the order Primates should be reviewed.[23] *Plesiadapis* is included in Primates by palaeontologists for two reasons. The first reason was most clearly stated by Gidley and by Simpson.[6,9] The structure of the upper and lower molars of *Plesiadapis* is virtually identical to the structure of the molars of the undoubted primate *Pelycodus* of the early Eocene. To quote Simpson:

> As regards molar pattern, *Plesiadapis* resembles the primitive Notharctinae more closely than any other group. . . . The resemblance to *Pelycodus*, most primitive known notharctine, is really amazing and extends to the apparently most insignificant details. The upper molars are of almost identical structure throughout, differing only in details of the cingula and proportions such as may characterise species of one genus. In the lower molars, *Pelycodus* has the paraconids slightly more distinct, but the resemblance is equally striking and includes even such features as the minute grooving of the trigonid face of the metaconid and the exact structure of the complex grooving of the talonid face of the hypoconid and of the whole heel of M_3.[9]

As will be discussed below, molar morphology similar to that of *Plesiadapis* is known in living mammals only within the order Primates.

The second reason for including *Plesiadapis* in Primates concerns the presence and construction of the ossified auditory bulla. The bulla of *Plesiadapis* is apparently composed of an ossification completely continuous with the petrosal,[24] a characteristic of all known adult primates.[25]

Martin employed the term *synapomorph* to designate characters acquired during the separation of a new stock, distinguishing them from *symplesiomorph* characters which are present in the ancestral stock as well as the new stock.[26] Thus it is the synapomorph characters which distinguish and define any new stock. In his list of synapomorph characters of Primates, Martin included features of the orbit, auditory region, limbs, nervous system, and reproductive tract. No mention was made of the dentition, on which the palaeontologist

must base much of his interpretation. In connection with the manner of elongation of M₃, the position and mode of disappearance of the paraconid, the structure of the paracristid, and the development of the '*Nannopithex* fold' to form a posterior basin on the upper molars (all of which are associated with increased propalinal mandibular movement and encroachment of the lingual phase facets from the talonid basin of one molar onto the trigonid of the following molar), Gidley stated:

> In fact, this peculiar development of the upper and lower cheek teeth apparently constitutes a distinctively primate characteristic, which while not found in all families of the order, seems to have been repeated over and over again, with slight variations, in several related or unrelated groups, and, so far as I am aware, is not found in any other order of mammals.[6]

As molar morphology similar to that of *Plesiadapis* and *Pelycodus* (in the manner of elongation of M₃, molar trigonid construction, and development of the '*Nannopithex* fold') is found only among living and fossil Primates, this morphology apparently constitutes an important synapomorph character of the order. Later radiations have modified this basic primate molar pattern, but it must, as it is present in all early members of the order, closely approximate the morphology developed by early primates during their separation from the ancestral mammalian stock. The fact that most Eocene tarsioid primates have enlarged central incisors similar to those of primitive plesiadapoids is additional evidence that the ancestry of Primates is to be sought in these archaic forms.

In conclusion, the Plesiadapidae are best considered an early, probably terrestrial, herbivorous radiation which shared little except common ancestry with the contemporary, presumably arboreal, primates that gave rise to Eocene and later radiations. The trends toward dental reduction and specialisation seen in plesiadapid lineages preclude their having had any close relationship with living prosimians, but the Plesiadapidae are nevertheless important in that further study should reveal much about the origin and evolution of the earliest primates.

Acknowledgments

NOTES

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