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OF THE MAMMALIAN ORDER DERMOPTERA**

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# DENTAL FUNCTION IN THE PLAGIOMENIDAE: ORIGIN AND RELATIONSHIPS OF THE MAMMALIAN ORDER DERMOPTERA

By

Kenneth D. Rose and Elwyn L. Simons

*Abstract.*— The obscure Paleocene and Eocene family Plagiomenidae is the only group of fossil forms referred to the Dermoptera. The family includes the North American genera *Elpidophorus*, *Planetetherium*, *Plagiomene*, *Thylacaelurus*, and possibly the European *Placentidens*. Although allocation of the Plagiomenidae to the Dermoptera is based on limited dental evidence, it remains the most reasonable interpretation. We present a study of molar wear patterns of plagiomenids that further supports their affinity with the extant dermopteran *Cynocephalus*. Plagiomenids share certain functional features of the molars with members of the Paleocene family Mixodectidae, indicating that these two families are closely allied. The features include development of *en echelon* shear, emphasis on shear facets 3 and 4 (Phase I), crenulated enamel, and grinding facets (Phase II). Both the Mixodectidae and the Plagiomenidae share somewhat more remote dental functional adaptations with archaic plesiadapiform primates, suggesting that all may be related through a common ancestor.

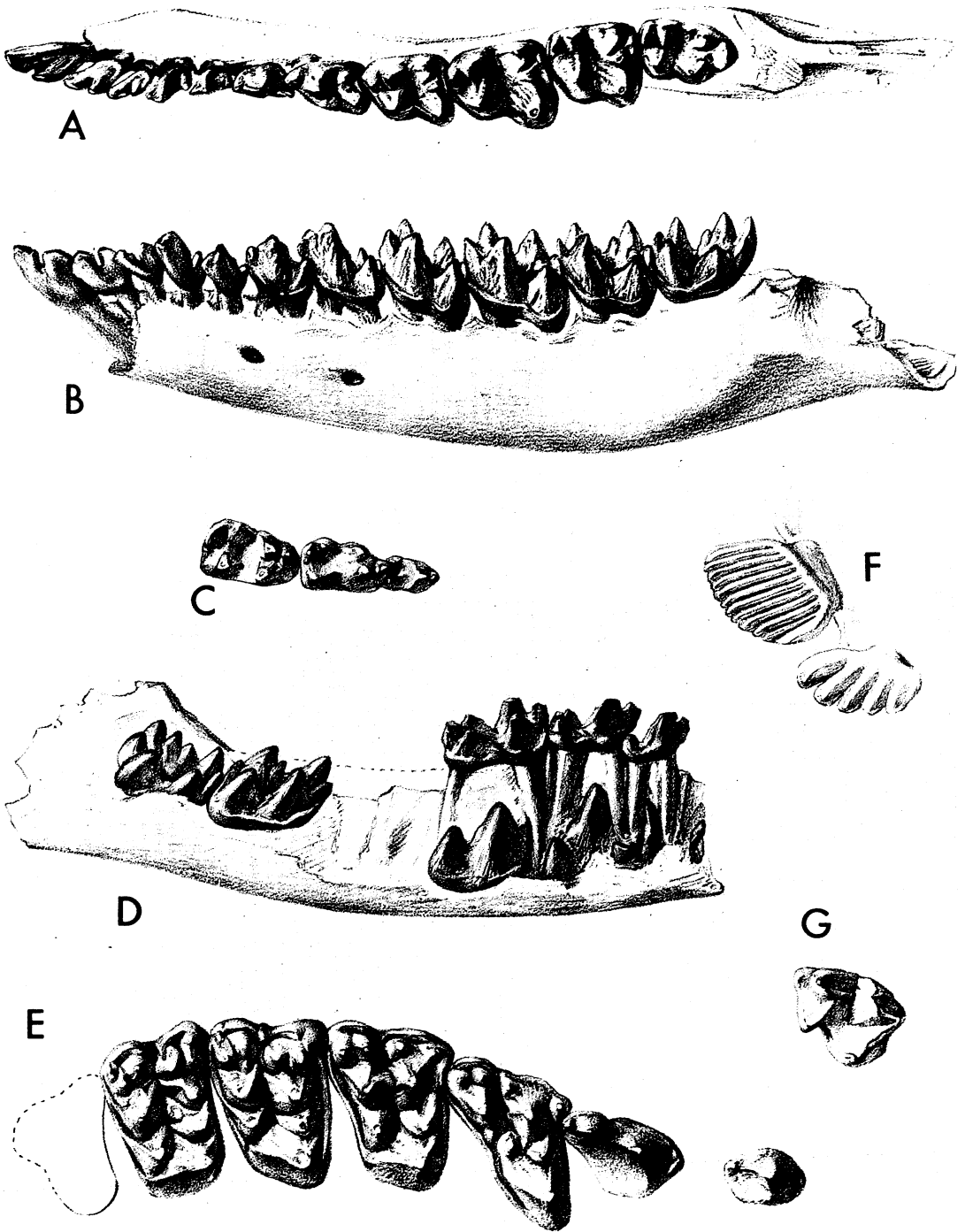
New plagiomenid fossils are reported, including a multilobate incisor, probably pertaining to a plagiomenid, from the early Eocene of Wyoming, and the first Clarkforkian specimens of *Plagiomene*, previously known only from the Wasatchian.

## INTRODUCTION

The Dermoptera — the colugos or flying lemurs — are among the most poorly known mammals. Two extant species of the genus *Cynocephalus* (= *Galeopithecus*)<sup>1</sup> are recognized by most authors (e.g., Findley, 1967; Medway, 1965, 1969; Walker *et al.*, 1975), but as many as 18 species pertaining to two genera have been considered valid (Cabrera, 1925). Living dermopterans are restricted to the mainland and islands of southeast Asia. They are difficult to study, because of their nocturnal and arboreal habits and their particularly poor acclimation to captivity (Lim, 1967); hence only sketchy information on the diet, behavior, and physiology exists, and this often in obscure journals.

<sup>1</sup> Van Valen *et al.* (1967) petitioned for suppression of the genus *Cynocephalus* Boddaert 1768 (once used for a genus of baboon), in favor of *Galeopithecus* Pallas 1780, a name widespread in the literature. Subsequently Hershkovitz (1969) argued that *Cynocephalus* is well established as a dermopteran genus and its replacement now by the name *Galeopithecus* would promote confusion rather than stability. This opinion was unanimously upheld by the Commission on Nomenclature of the American Society of Mammalogists (Hershkovitz, 1969: 203).





TEXT-FIG. 2 — Dentitions of *Plagiomene multicuspis* and *Cynocephalus* drawn by Robert Bruce Horsfall. A and B: Crown view and lateral view of left dentary with complete dentition, PU 14552. C: Crown view of right  $dP_{2-4}$ , PU 13268. D: Lateral view of right dentary with  $dP_{2-4}$ ,  $M_{2-3}$ , jaw excavated to reveal unerupted permanent  $P_{2-4}$ , PU 13268. E: Crown view of right maxillary dentition,  $P^{1-4}$ ,  $M^{1-2}$ , composite based on fragments of both maxillae, PU 13272. F: Crown view of left  $I_{2-3}$  of the flying lemur *Cynocephalus*. G: Crown view of left  $M_3$  of *Cynocephalus*. Approximately  $\times 4$ .

*Placentidens* was recently described on the basis of a small number of isolated teeth from the early Eocene of France and referred to the Plagiomenidae (Russell, Louis & Savage, 1973). It lacks the crenulated enamel and polycuspidation typical of plagiomenids and its allocation to this family is equivocal. Indeed, Russell *et al.* (1973: 42) remarked that although its presence in the European Eocene is "not too unexpected . . . it is perhaps more surprising that the European form differs so markedly from its North American relatives."

As would be expected, in view of the 40-50 million years separating them, there is a considerable hiatus between the dental morphology of plagiomenids and that of *Cynocephalus*; therefore, any additional evidence bearing on plagiomenid relationships is of interest. In this report we present a study of molar wear patterns and other new data that bear on this problem. Specimens of *Elpidophorus* and *Plagiomene* are better preserved and more complete than for other plagiomenids, and their wear patterns can be confidently determined; therefore our study is based largely on these two genera.

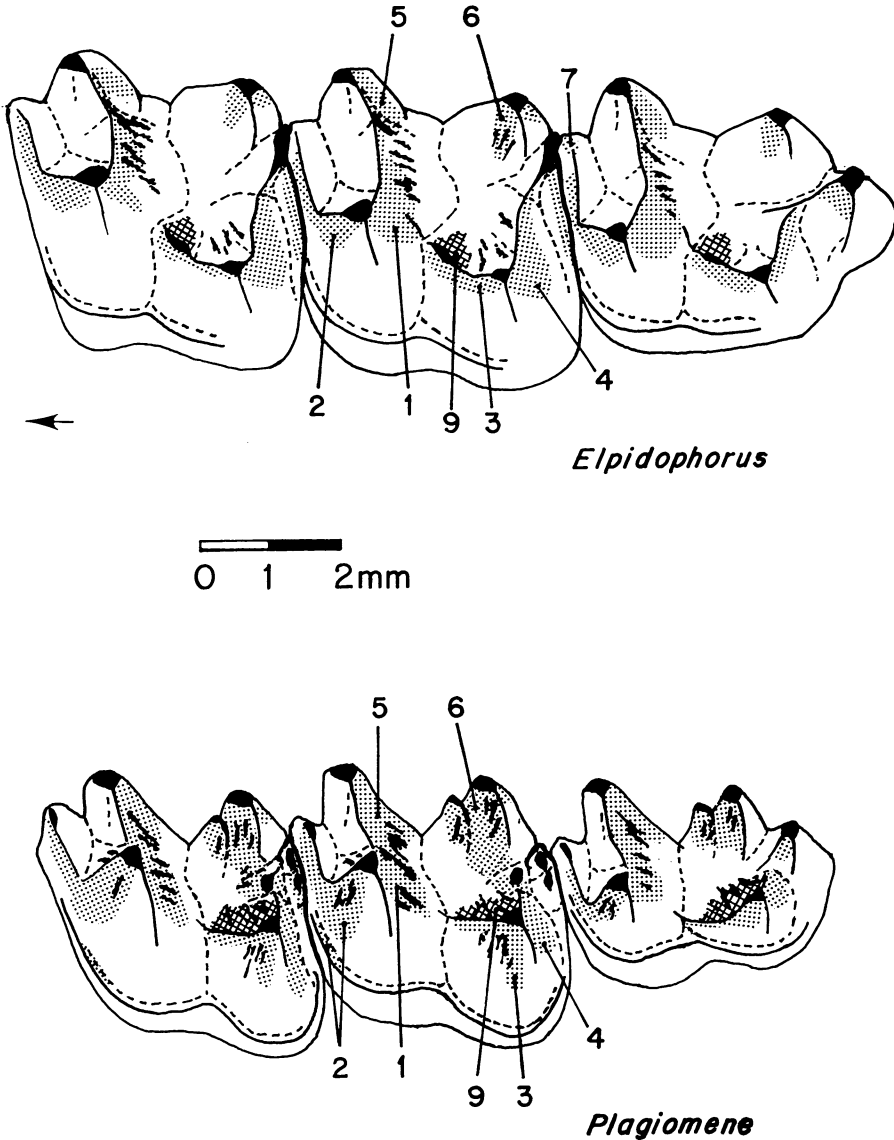
We have examined plagiomenids and comparative fossil specimens from the collections of the American Museum of Natural History (AMNH), Carnegie Museum of Natural History, Museum of Comparative Zoology at Harvard (MCZ), Princeton University Museum (PU), University of Kansas Museum of Natural History, University of Michigan Museum of Paleontology (UMMP), and Yale Peabody Museum (YPM). Recent dermopterans and other recent osteological material examined are from the mammalogy collections at the American Museum of Natural History, Museum of Comparative Zoology, and University of Michigan Museum of Zoology. All drawings were prepared using a camera lucida.

#### OCCCLUSION IN THE PLAGIOMENIDAE

Numerous recent studies have examined patterns of tooth wear as a tool for interpreting dental function and trends in tooth usage, with particular reference to primitive mammals and to the Primates (e.g., Crompton & Hiiemäe, 1970; Crompton, 1971; Butler, 1972, 1973; Kay & Hiiemäe, 1974).

Postcanine tooth wear can be designated as either abrasive or attritional. Abrasive wear, characterized by blunting and fenestration of the cusps, usually without clear wear striations, is produced during the initial stages of mastication when food is softened and "puncture-crushed" (Hiiemäe & Kay, 1973). Dental attrition results from the main stage of mastication when the molars come into precise occlusion and shearing and grinding of the food occurs, forming striated wear facets on the molars. The planar, mirror-like surfaces of the facets and the orientation of their striations indicate the precise relationships of the teeth and their direction of motion during occlusion.

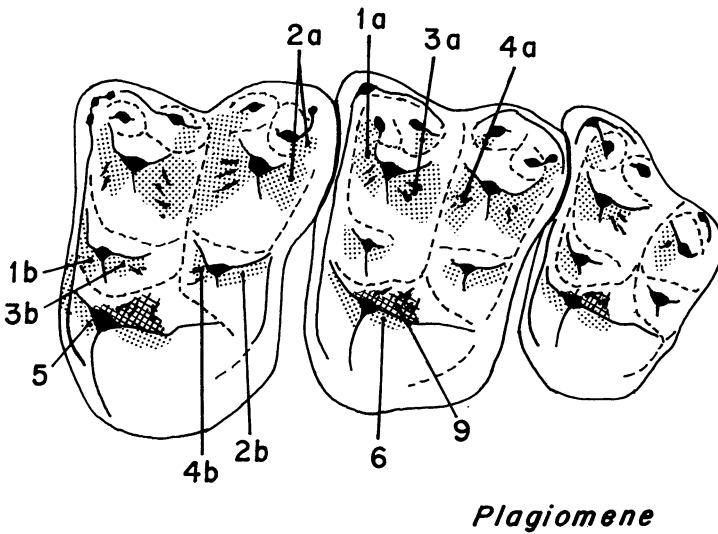
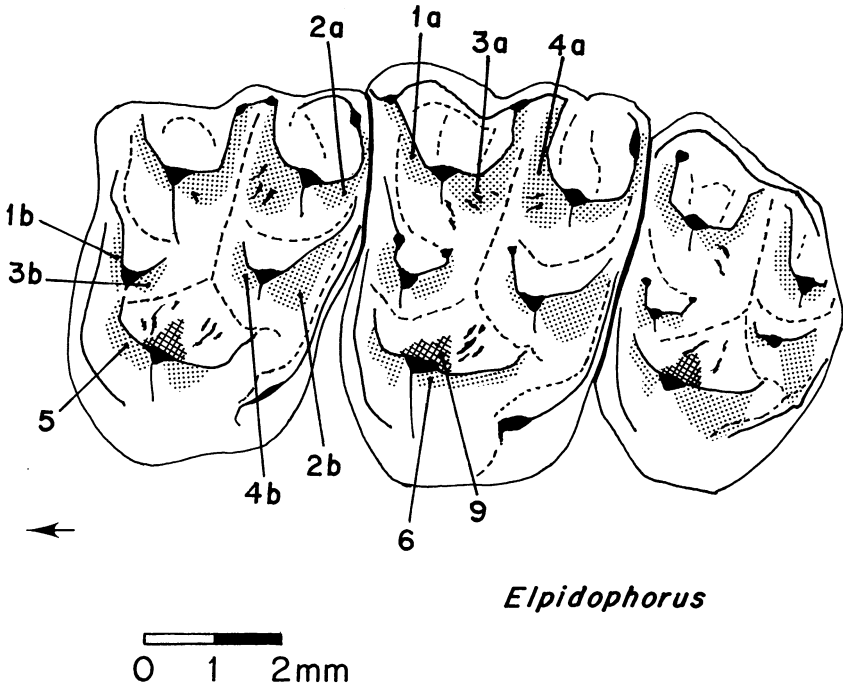
The stage of mastication causing attritional wear has been subdivided into two phases (Mills, 1955; Kay & Hiiemäe, 1974). Phase I involves shearing as the crests of the lower molars move past those of the uppers and the teeth enter centric occlusion. The direction of motion is often dominated by the vertical component but becomes increasingly horizontal in omnivorous and herbivorous species. The matching wear facets formed during Phase I face buccally on the lower teeth, lingually on the uppers. Phase II involves grinding as the lower teeth move down and anteromedially out of centric occlusion, and planar surfaces occlude with planar surfaces. The dominant motion is ectental (transverse). The matching facets formed in this phase face lingually on the lower teeth, buccally on the uppers. Thus Phase I and Phase II essentially correspond to the buccal and lingual phases, respectively, of Mills (1955), Butler (1973), and others. In general, carnivores and insectivores emphasize the vertical component and their teeth reveal predominantly or exclusively shearing (Phase I) facets. Herbivores, on the other hand, tend to emphasize transverse motion and their teeth usually show well-developed grinding (Phase II) facets.



TEXT-FIG. 3 — Lower molar wear facets in the plagiomenids *Elpidophorus* and *Plagiomene*. In this and later figures, the left series is shown, and the arrow points anteriorly. Matching wear facets on upper molars are designated by the same number. Phase I facets are stippled, Phase II facets cross-hatched. Irregular black patches indicate crenulations of the enamel.

We have examined wear patterns on the cheek teeth of *Elpidophorus elegans* from the Tiffanian Scarritt and Cedar Point Quarries, and *Plagiomene multicuspis* from the Clarkforkian and early Wasatchian of the Bighorn Basin (see text-figs. 3 and 4).<sup>2</sup> Wear facets are most prominent in well-

<sup>2</sup> *Elpidophorus minor*, from the Torrejonian Silberling Quarry, is older than *E. elegans*. It is known only from a single specimen, a partial lower dentition which is relatively unworn, and its wear patterns cannot be accurately determined.



TEXT-FIG. 4 - Upper molar wear facets in the plagiomenids *Elpidophorus* and *Plagiomene*. Scheme as in text-figure 3.

preserved dentitions that are moderately to heavily worn. As in other fossil mammals examined, wear facets are not evident in all specimens, nor are all facets clearly developed on worn specimens. Hence the diagrams presented represent composites based on the entire sample studied. Facets are numbered according to the scheme introduced by Crompton (1971) and expanded by Kay & Hiemäe (1974), in which facets 1-8 are formed during Phase I and facets 9 and 10 form during Phase II.



The wear patterns of *Elpidophorus* and *Plagiomene* are very similar. In both genera, facets 1-6 are well developed, although facets 5 and 6 are usually less prominent on the upper teeth of both genera and on the lower molars of *Elpidophorus*. The paraconule and metaconule are large, and facets 1-4 are multiple on the upper molars, occurring on the conule cristae as well as on the paracone and metacone cristae (thus promoting "en echelon" shear); these facets extend to the styler shelf in both taxa. In *Plagiomene* the styler cusps are strongly developed and facets 1-4 extend onto them as well. Facet 2 extends onto the precingulid in heavily worn lower molars of *Plagiomene*. Facets 3 and 4, formed as the hypoconid travels through the median transverse valley of an upper molar, are always very well formed. In lower teeth of *Elpidophorus*, facet 1 is larger than facet 5 on  $M_1$ , but facet 5 enlarges at the expense of facet 1 progressively to  $M_3$ . In *Plagiomene*, while this probably still holds, the two facets are confluent and difficult to demarcate. Facets 2b and 6 extend onto the posterior cingulum of  $M^3$  in heavily worn specimens of *Elpidophorus*. A small facet 7 was observed on the paraconid of  $M_3$  in one individual of *Elpidophorus* (AMNH 33857). Both *Elpidophorus* and *Plagiomene* often possess a well-developed striated facet along the postcingulid of  $M_1$  and  $M_2$ , extending onto the hypoconulid and back of the entoconid. This is situated in the position of facet 8 in some primates, but appears to be formed by occlusion with the metacone or metaconule rather than the hypocone.

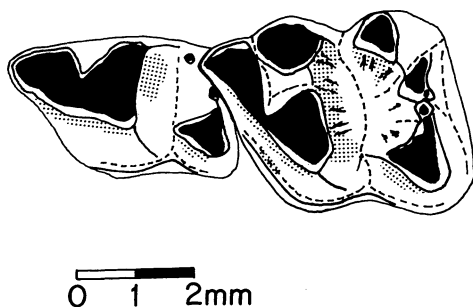
Phase II facets, as in many primitive eutherians, are less well defined than those of Phase I (perhaps due to their different mode of origin). Nevertheless, facet 9 can be detected on upper and lower molars of both *Plagiomene* and *Elpidophorus*, contrary to Butler's (1973: 24) finding that Phase II facets do not occur in Plagiomenidae. In lower molars of *Elpidophorus*, facet 9 is situated on the medial side of the mesoconid. In *Plagiomene*, which typically lacks a mesoconid, facet 9 covers the medial face of the cristid obliqua and of the hypoconid.

The masticatory efficiency of the molariform teeth in plagiomenids was enhanced by extensive crenulation of the enamel. Most wear facets are not continuous flat surfaces, but are perforated throughout as a result of the very wrinkled enamel. Hence wear results in multiplication of cutting edges on a single facet, in addition to the leading edge of each crest. This is in accord with Rensberger's (1973: 516) observation that "the cheek teeth in many groups of mammals probably approach optimum operational efficiency only after moderate wear." It should be noted that shearing facets are developed on the molariform premolars of plagiomenids as well as on their molars, i.e. on  $P_4^4$  of *Elpidophorus* and  $P_{3-4}^{3-4}$  of *Plagiomene*.

Abrasive wear on the apices of the cusps occurs in heavily worn premolars and molars of plagiomenids (text-fig. 5), exposing dentine through fenestrations in the enamel. Szalay (1969: 241-242) drew an analogy between plagiomenids and recent dermopterans, stating that both display "primarily apical wear on the cusps," which he attributed to an herbivorous diet. While such wear is common in heavily worn individuals, it is not the primary type of wear in plagiomenids, as shown above, although in recent dermopterans it is prevalent. In both groups, however, striated attritional facets are visible and well developed in specimens that show apical (abrasive) wear.

As far as can be determined, the wear patterns of *Planetetherium* and *Thylacaelurus* show no significant deviations from those observed in *Elpidophorus* and *Plagiomene*. Both forms are rare. Most specimens of *Planetetherium* are too poorly preserved to reveal clear wear facets, but a few that are better preserved show morphology and wear patterns very similar to *Plagiomene*.

Study of wear patterns relates tooth form to tooth function. Other mammals with dental wear patterns closely approaching those of plagiomenids are probably functionally similar and possibly phylogenetically related. Since plagiomenids are usually allied with *Cynocephalus*, the wear patterns in the latter are of interest. Fossil groups with particular functional resemblance are also of interest for determining functional analogues as well as possibly shedding light on the broader affinities of the Plagiomenidae. From fossil evidence, development of Phase II in the masticatory cycle appears to be an advanced feature. Butler (1973) has reported the presence of Phase II facets in Rodentia,



TEXT-FIG. 5 — Left  $P_{3-4}$  of *Plagiomene* (UMMP 63824) showing heavy abrasive wear. Extensive black areas represent dentine exposed through fenestrations in the enamel. Stippling denotes Phase I facets.

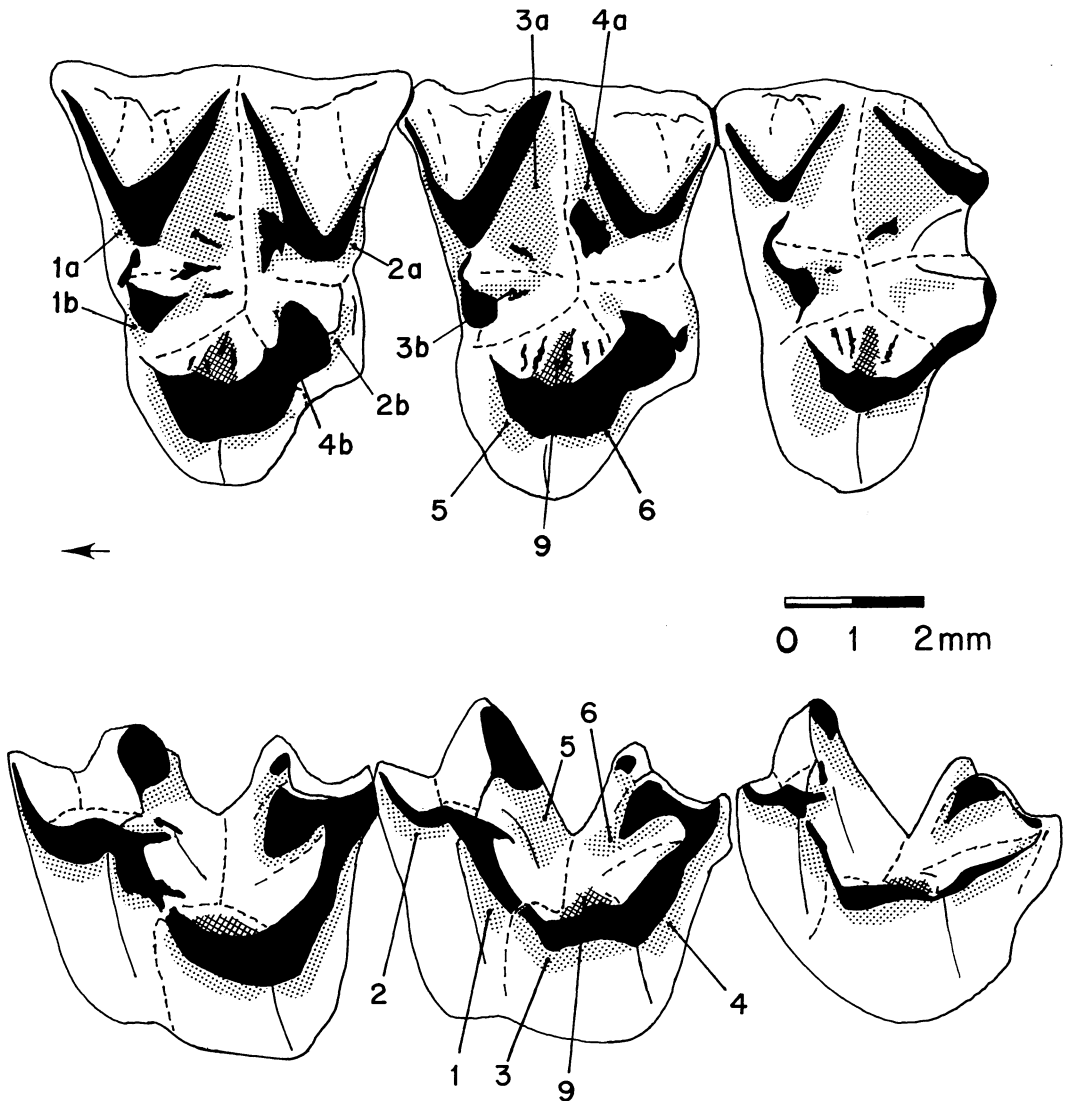
Condylarthra, various ungulate groups, Mixodectidae, and Primates (including Plesiadapiformes), but not in Palaeoryctidae, Leptictidae, Apatemyidae, Pantolestidae, or Lipotyphla. Among fossil forms, certain mixodectids and plesiadapiform primates most closely approach plagiomenids in tooth morphology and wear patterns.

Although highly specialized in certain respects, such as its comb-like incisors, *Cynocephalus* retains relatively primitive tritubercular molars and molarized posterior premolars. Matthew (1918) drew on the similarity in structure of the cheek teeth to ally *Plagiomene* with *Cynocephalus*. Although the resemblance is far from compelling, certain characters that may reasonably be considered derived occur in both groups: incisors with digitate crowns, highly molariform posterior premolars, lower teeth anterolingually procumbent (i.e., lingual cusps higher than buccal cusps and set more anteriorly than is typical in teeth of primitive mammals), upper molariform teeth with deep transverse median valley, hypocone of upper molars small or absent (the absence of the hypocone in most dermopterans appears to be a derived feature), enamel of molariform teeth extensively crenulated.

Wear patterns in *Cynocephalus* (text-fig. 6) also display a number of similarities to those in plagiomenids, although of course they are not identical. Among the resemblances is the particularly strong development of facets 3 and 4, 3a and 4a (in the upper teeth) extending fully to the buccal edge of the teeth. Facets 1, 2, 5, and 6 are also prominent, facet 6 developed closely to that in *Plagiomene*. Facets 1 and 5 are essentially confluent on the lower molars, but may be differentiated on  $P_4$  or  $M_1$  of some specimens. Facet 9 (Phase II) is developed on the molars of most individuals and on  $P_4^4$  in heavily worn specimens.

Especially characteristic of *Cynocephalus* teeth is heavy apical wear on cusps and crests, exposing broad areas of dentine. The attritional wear facets described above develop on the edges of these areas of abrasive wear (for example, along crests) and sometimes bridge them (the wear facet is thus interrupted by a dentine valley, as in facets 1a-4a on the upper molars). Wear facets are also perforated by crenulations of the enamel (as in *Plagiomene*, but to a lesser degree), resulting in the multiplication of cutting edges.

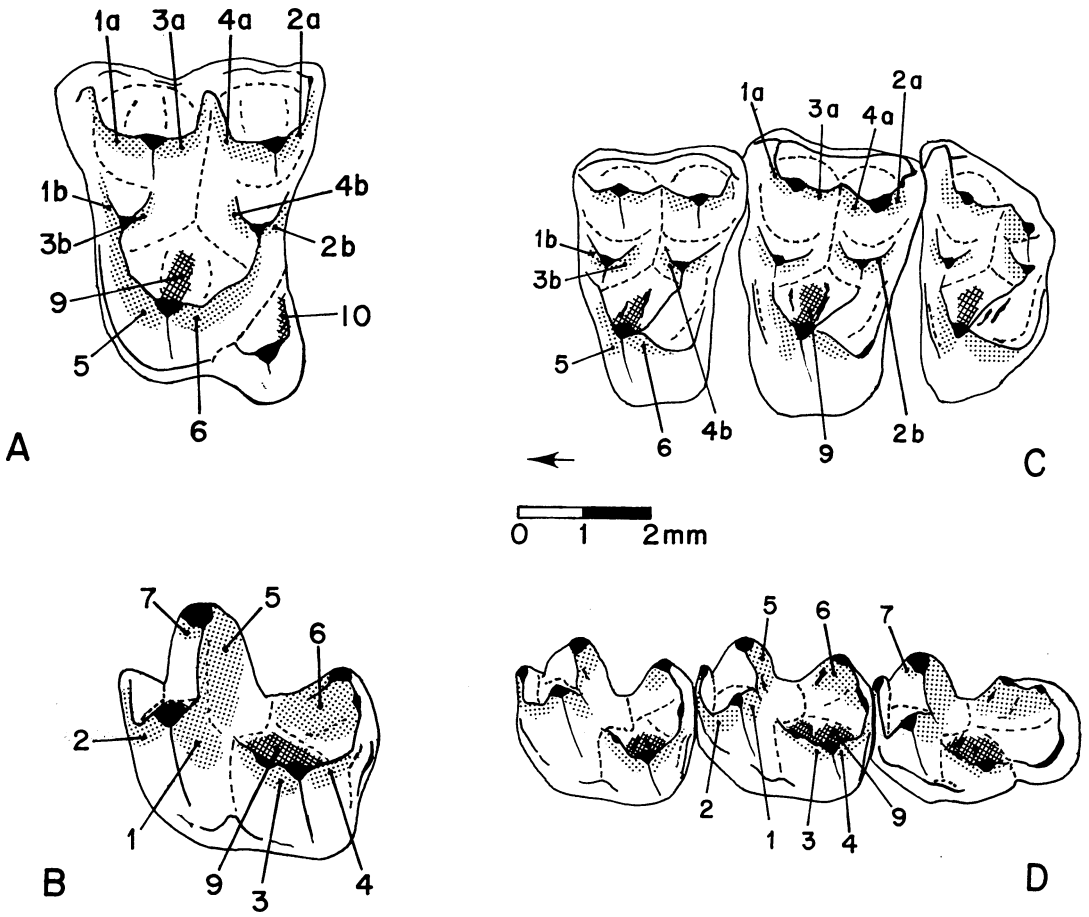
In both plagiomenids and *Cynocephalus*, Phase I has a large transverse component, as indicated by the angle of the wear striations. The inclination of shearing movement relative to the lower molar roots is about 45-50° in plagiomenids examined, comparable to that in most plesiadapiform primates (Butler, 1972), and about 55-60° in *Cynocephalus*. As demonstrated by Butler, such values are typical of herbivores. In *Cynocephalus*, the mandibular condyle is transversely elongated and in dried skulls there is considerably mediolateral freedom at the temporomandibular joint, probably facilitating transverse movement of the mandible during mastication. It may be noted, however, that the mandible of adult *Cynocephalus* is firmly synostosed at the symphysis, whereas in *Plagiomene* the symphysis is unfused.



TEXT-FIG. 6 - Molar wear facets in *Cynocephalus*, the flying lemur. Scheme as in text-figure 3.

Several authors have remarked directly or indirectly on resemblances between the Plagiomenidae and the Mixodectidae, comparisons with the latter usually centered on *Elpidophorus* (e.g., Simpson, 1936, 1937; Van Valen, 1965, 1967; Sloan, 1969; Szalay, 1969), reaching varying opinions as to the degree to which they are or are not related. I have proposed (Rose, 1975b) that *Elpidophorus* be regarded as a plagiomenid and that its similarities to mixodectids, particularly the Torrejonian *Eudaemonema*, indicate probable common ancestry.

Molars of mixodectids are structurally similar in most respects to those of plagiomenids and their wear patterns are correspondingly close (text-figs. 3, 4, 7a, 7b). Both Phase I and Phase II facets are strongly developed in specimens of the Torrejonian genera *Eudaemonema* and *Mixodectes* we examined. As in plagiomenids, facets 3 and 4 are particularly prominent, 3a and 4a extending to the



TEXT-FIG. 7 - A and B: Molar wear facets in the mixodectid *Eudaemonema*. Left  $M_2^1$  (A) and left  $M_2$  (B) are shown. C and D: Molar wear facets in the Torrejonian plesiadapiform primate *Palaechthon* (= *Plesiolestes*). Scheme as in text-figure 3.

mesostyle at the buccal margin, and 3b and 4b present although the conules are smaller than in plagiomenids. Facets 1 and 5 are distinct in lower teeth of *Eudaemonema*, with facet 1 larger than facet 5 on  $M_1$  but diminishing as facet 5 expands on  $M_2$  and  $M_3$  (as in *Elpidophorus*). In *Mixodectes* facets 1 and 5 are confluent, much as in *Plagiomene*. The median transverse valley characteristic of upper molariform teeth of plagiomenids is noticeably less well formed in mixodectids. Phase II facets are better developed than in plagiomenids, with an extensive facet 9 and small facet 10 visible in several specimens. The latter facet, not present in plagiomenids, is associated with the presence of a large, lingually situated hypocone that occludes with the medial side of the protoconid during Phase II. The enamel in mixodectid cheek teeth is usually smooth, or shows only very minor crenulation.

In addition to mixodectids, various members of the Plesiadapiformes have molar morphology and wear patterns reminiscent of those in plagiomenids (text-figs. 7c, 7d), though to a lesser extent than the mixodectids. This is not surprising in view of the perennial confusion among genera of Mixodectidae and Microsyopidae, the latter family including some of the most primitive plesiadapiform

primates such as *Palaechthon* (= *Plesiolestes*) (Gingerich, 1975; Bown & Rose, 1976). Many plesiadapiforms emphasize *en echelon* shear involving facets 1-4 on the upper molars, facets 3a, 3b, 4a, and 4b being particularly pronounced. Phase II facets are also well formed in plesiadapiforms (Butler, 1973; Gingerich, 1974; Kay & Hiiemäe, 1974; Rose, 1975a). Separation of facets 1 and 5 on the lower molars is typical of most plesiadapiforms (as in *Eudaemonema* and *Elpidophorus*), with progressive reduction of facet 1 and expansion of facet 5 from  $M_1$  to  $M_3$  sometimes apparent (see Rose, 1975a: fig. 37). The extent of development of these features in plesiadapiform primates seems to be specialized and may be synapomorphic also in mixodectids and plagiomenids.

This is not to say that such features have not arisen in other primitive eutherians. Some leptictids and erinaceoids approach plesiadapiform primates in these respects, but are not so close to plagiomenids. In leptictids, facets 1-4 on the upper molars are typically developed *en echelon*, but there is less emphasis on facets 3 and 4 than in plesiadapiforms and much less than in plagiomenids. This situation, as well as development of Phase II facets, obtained in late Cretaceous *Gypsonictops* (Kay & Hiiemäe, 1974), widely but not universally considered an early leptictid. Some erinaceoids also possess these features. Both taxa have been regarded as possible antecedents of the Plesiadapiformes (e.g., McKenna, 1966; Clemens, 1974).

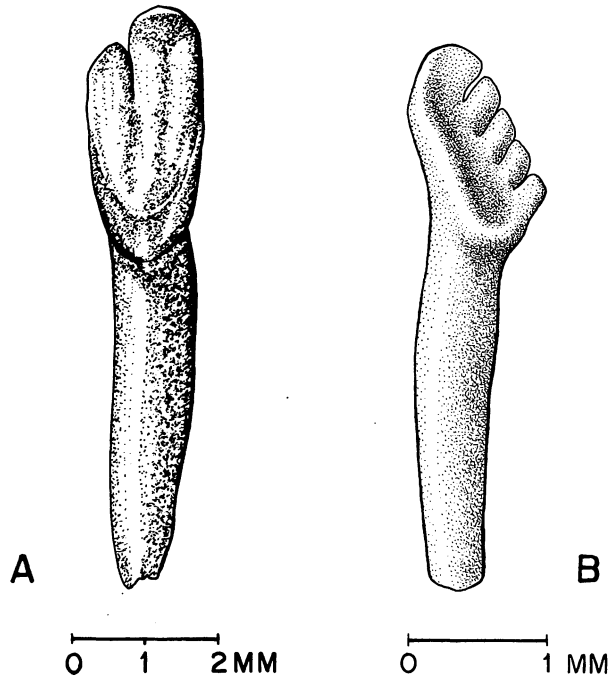
#### NEW MATERIAL

We take this opportunity to report some of the important recent discoveries of early Eocene plagiomenids. Yale Peabody Museum expeditions to the Bighorn Basin during the last decade have amassed the largest known samples of *Plagiomene multicuspis*, now numbering more than 50 specimens from about 20 Gray Bull localities concentrated between the 400-800 ft. interval as depicted by Gingerich (1976: fig. 2). These consist mainly of fragmentary mandibles and maxillae and provide the first samples sufficient for variational and statistical studies. It is primarily this collection that has provided the basis for the functional study presented here.

University of Michigan investigations in the Sand Coulee area, northwestern Bighorn Basin, during the summers of 1975 and 1976 recovered additional specimens of *Plagiomene* and extended its geologic range down into the upper Clarkforkian.<sup>3</sup> The two Clarkforkian specimens (UMMP V65472 and V65636) are noticeably smaller than most Graybullian specimens and may represent a new species. However, there is considerable variation in size among specimens of *Plagiomene* from the Bighorn Basin, all of which are currently referred to *P. multicuspis*; hence it is possible that more than one species is involved. The small sample of *Plagiomene* from the Graybullian of the Sand Coulee Basin comes from a few localities that span the entire thick Graybullian section in this area. Among the sample is the first known partial skull of a plagiomenid (currently being prepared at the University of Michigan), found by G. F. Gunnell in 1975. The posterior half of the skull, including the basicranium, is preserved and should reveal important data bearing on the affinities of the Plagiomenidae.

An isolated lower incisor (MCZ 19929, text-fig. 8b) was recently recovered by screen-washing matrix from Graybullian strata in Big Horn County, Wyoming. Although much smaller than incisors of *Plagiomene*, the lobation of its crown is so similar that plagiomenid affinities seem quite possible. The new incisor, however, has five distinct lobes rather than two as in *Plagiomene multicuspis*, and in this respect resembles very closely some of the multilobate incisors which Setoguchi (1973) referred to the late Eocene possible plagiomenid *Thylacaelurus*. It is also similar to the deciduous incisors of the macroselidid *Petrodromus* (an extant form in which the configuration of the incisors is particularly close to that in *Plagiomene*; Rose, 1973), where the milk incisors are multilobate but the permanent incisors are bilobate. Thus it is possible that the new specimen is a deciduous incisor

<sup>3</sup> For a discussion of the Clarkforkian fauna and its distinguishing elements, see Gingerich and Rose, 1977.



TEXT-FIG. 8 — A: Incisor (UMMP 67021) probably from a plagiomenid, possibly *Planetetherium*. B: Lower incisor (MCZ 19929) probably from a plagiomenid, possibly a deciduous incisor of *Plagiomene*.

of *Plagiomene* or a closely related form. However, it is also possible that this tooth is an incisor from a nyctitheriid insectivore: some European nyctitheriids possess incisors very much like MCZ 19929 (Sigé, 1976). Digitate incisors are not unique to the Dermoptera; indeed they occur in several other early Tertiary eutherians (see also Sulimski, 1968; Schwartz & Krishtalka, 1976). If this incisor is correctly allocated, it would seem to indicate that *Plagiomene* already possessed the genetic basis for formation of multilobate incisors. This suggestion is supported by the discovery of *Plagiomene*-like dermopterans from Eocene deposits on Ellesmere Island (Dawson, 1976), some individuals of which preserve multilobate incisors (Dawson and McKenna, pers. comm.).

Among the discoveries of the University of Michigan 1976 expedition was an edentulous mandible and two upper teeth of *Planetetherium mirabile* (UMMP V66542) found at an upper Clarkforkian site (UMMP Loc. SC-100). This is the only specimen of this rare species to be found in many years, and it is of interest primarily because all previously known specimens are from a single Clarkforkian locality, the Eagle Coal Mine at Bear Creek, Montana (Simpson, 1928, 1929). In addition, an isolated bilobed incisor (UMMP V67021, text-fig. 8a), probably from a plagiomenid (cf. *Planetetherium mirabile*), was recovered from a middle Clarkforkian locality (UMMP Loc. SC-120). It is virtually identical to an incisor from Bear Creek (AMNH 22152) described by Simpson (1928) and tentatively referred to *Planetetherium* (Rose, 1973).

In 1975 the University of Michigan expedition found a mandible of *Elpidophorus elegans* at the Tiffanian Cedar Point Quarry, Big Horn County, Wyoming, the first representative of this taxon from that productive site. This Tiffanian species has been previously reported only from the Paskapoo (Simpson, 1927) and Ravenscrag Formations (Krishtalka, 1973) of Alberta and the Melville Fm. Scarritt Quarry of Montana (Simpson, 1936).

## CONCLUSIONS

The molar wear patterns and dental structure of *Elpidophorus* are so similar to those of *Plagiomene* that its allocation to the Plagiomenidae can hardly be doubted. Sloan (1969: fig. 6) indicated *Elpidophorus* as a possible ancestor of *Plagiomene*. We find no evidence inconsistent with this view, inasmuch as the features in which *Plagiomene* differs from *Elpidophorus* appear to be specializations. Plagiomenids possess a peculiar suite of morphological and functional characters of the dentition not duplicated in any other known mammals, but recent *Cynocephalus* and Paleocene Mixodectidae and Plesiadapiformes share with them certain probably derived features, as outlined above.

The evidence linking the Plagiomenidae with *Cynocephalus* remains meager; nonetheless, if plagiomenids are related to any extant mammals, the Dermoptera are still the most likely candidates. Conversely, the Plagiomenidae remain the only known fossil group possibly related to *Cynocephalus*. Although the study of wear patterns presented here does not confirm the dermopteran status of the Plagiomenidae, it is consistent with it. The additional evidence on incisor morphology in plagiomenids further supports alliance with the Dermoptera.

Despite the relatively primitive insectivore-like aspect of its molars, *Cynocephalus* is, as far as known, exclusively herbivorous (Walker *et al.*, 1975; Lim, 1967). A closer examination reveals that the cheek teeth are broad and shearing involves a relatively large transverse component. Phase II, most prominent in herbivores, is moderately developed. Finally, highly crenulated enamel is also characteristic of herbivorous mammals. When crenulated enamel is worn, cutting edges are proliferated, enhancing masticatory efficiency. This complex of traits occurs also in plagiomenids, thus we may speculate that they, too, were largely herbivorous. In spite of the distinctive morphology of the incisors in both groups, practically nothing is known of their function.

Among fossil forms, certain members of the Mixodectidae and the Plesiadapiformes most closely approximate the morphology and wear patterns that occur in plagiomenids. It is possible that these resemblances are convergent, but the degree and nature of similarities suggest that the groups are probably phylogenetically related and that the functional adaptations they display were at least incipiently present in a common ancestor. The Mixodectidae are decidedly closer in structure to the Plagiomenidae and may lie near their ancestry, as indicated by Van Valen (1967) and Sloan (1969).

The possible relationship (through common ancestry) of plagiomenids and plesiadapiform primates, suggested by the dentition, is particularly interesting in light of recent independent data which have been similarly interpreted. Szalay (1975) indicated that he has identified early Eocene tarsal elements that resemble those of *Cynocephalus* as well as both plesiadapiform and adapid primates. Citing these as evidence, he concluded that the Dermoptera were derived from primitive primates. It should be emphasized, however, that whereas early primates are relatively common, plagiomenids are rare and no associated postcranial elements are known. There was no direct association between the tarsals Szalay studied and plagiomenid dentitions.

In a comparative immunological study of recent primate albumins and transferrins, Cronin & Sarich (1975) found that *Cynocephalus* falls within their clade Primates. In addition, Simons (1967) has noted that the claws of *Cynocephalus* closely resemble those of the Paleocene primate *Plesiadapis*. McKenna (1975) classifies the Dermoptera as one of four orders in the grandorder Archonta, which comprises in addition the orders Chiroptera, Scandentia (tree shrews), and Primates. Dene *et al.* (1976), and Goodman (1976) found support for this arrangement from their biochemical studies on recent mammals. Further evidence bearing on this possible relationship may soon be forthcoming. In addition to the new cranial evidence mentioned above, new material of the early Paleocene primate *Purgatorius* (now much better known, thanks to the collecting efforts of Clemens and his colleagues, see Clemens, 1974) is potentially significant to this problem. A careful functional study of its dentition should shed light on the degree of affinity between plagiomenids and early primates.

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