ACTA PALAEONTOLOGICA POLONICA
Vol. 22 1977 Nr. 3

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EVOLUTIONARY RADIATION OF THE CHEEK TEETH OF CRETACEOUS PLACENTALS

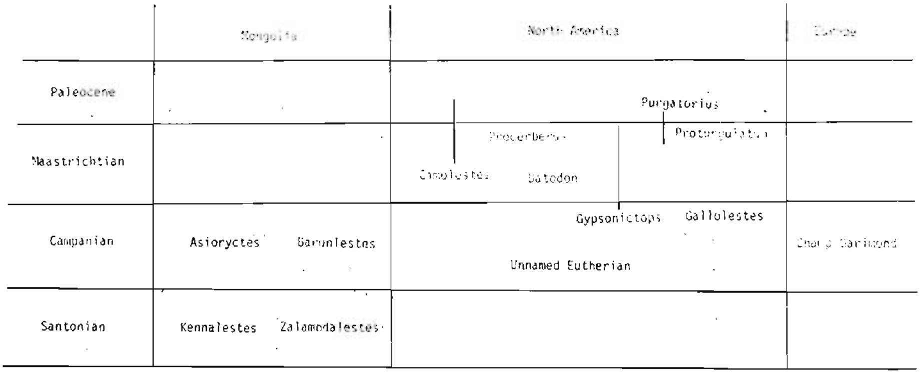
Abstract. — Included is a comparative study of the molars and posterior premolars of the Cretaceous placentals. Particular attention is paid to occlusal relations. An attempt is made to identify primitive characters, and the advance of each genus from the primitve condition is analysed. It is found that nearly all known genera are on different lines of evolution, indicating that a major radiation of placentals was taking place during the Cretaceous.

INTRODUCTION

The placental (= eutherian) mammals were formerly regarded as an essentially Cenozoic group that arose by an evolutionary "explosion" at the beginning of the Tertiary. This view was based mainly on their sudden increase in taxonomic diversity (appearance of some 20 genera) in the Early Paleocene of North America, the only continent from which a significant sample of fossil mammals of that age has been obtained (see, e.g. Sloan 1969). It is now, I believe, widely accepted that the diversity that we see in the Paleocene is the product of a long process of evolutionary radiation in the Cretaceous, masked by the incompleteness of the paleontological record.

It is largely because so little is known of their phyletic branching during the Cretaceous that the classification of the placentals is so difficult. The relationships of the small number of known Cretaceous placentals to each other and to their Tertiary successors are, with very few exceptions, problematic and controversial. Most genera are known only by teeth and jaws, and phyletic hypotheses must inevitably be based at present mainly on the dentition. No doubt the picture will become clearer as more information on cranial and postcranial anatomy is obtained. Nevertheless, the teeth still have a story to tell, if only because they can be compared in all the genera. This paper is an attempt at a comparative review of the molars and posterior premolars of Cretaceous placentals. The anterior part of the dentition, which is less frequently preserved and therefore less useful for comparative purposes, will not be discussed.

The first North American placental to be recognised as such, *Gypsonictops* Simpson (1927), appeared in the Campanian (Judith River Formation) (Sahni 1972) and survived till the end of the Cretaceous (Hell Creek Formation) with only minor change (fig. 1). It is not particularly primitive, and is generally believed to be an immigrant, probably from Asia. Older than *Gypsonictops* (Early Campanian) is an unnamed upper molar described by Fox (1970, 1975), who compared it with primitive "erinaceoids" such as *Leptacodon*. It shows no significant resemblance to *Gypsonictops*; neither does the Late Campanian *Gallolestes* (Lillegraven 1972, 1976). In the succeeding Maastrichtian appear *Cimolestes* and *Batodon* (Lillegraven 1969, Clemens 1973), clearly not derivable from any of the three Campanian genera. *Cimolestes* continued into the Early Paleocene as "*Puercolestes*" (Clemens 1973). Three more genera appear in the Late Maastrichtian: *Procerberus, Protungulatum* and *Purgatorius* (Van Valen & Sloan 1965). Various opinions have been expressed on their relationships to other Cretaceous genera: thus *Procerberus* was considered to be a leptictid, like *Gypsonictops,* by Van Valen (1967), and a *Cimolestes* derivative by Lillegraven (1969); *Purgatorius* has been considered as a derivative of *Gypsonictops* (McKenna 1969), but a possible relationship to *Protungulatum* has been suggested (Szalay 1968).



	Mongolia	North America	Europe
Paleocene		Purgatorius	
Maastrichtian		Procerberus Protungulatum Cimolestes Batodon	
Campanian	Asioryctes Barunlestes	Gypsonictops Gallolestes Unnamed Eutherian	Champ Garimond
Santonian	Kennalestes Zalambdalestes		

Fig. 1. Distribution of the genera studied.

The material from Mongolia is much better preserved, though taxonomically less diverse than that from North America. In the Djadokhta Formation (? Santonian) occur two very different genera, *Kennalestes* and *Zalambdalestes.* The later (? Campanian) Barun Goyot Formation contains *Barunlestes,* probably derived from *Zalambdalestes,* and *Asioryctes,* with some resemblance to *Kennalestes* but probably not descended from it (Kielan-Jaworowska 1969, 1975*a*, 1975*b*). *Kennalestes* has been regarded as related to *Gypsonictops,* and *Asioryctes* to *Cimolestes,* among the American forms, but there are significant differences that seem to exclude direct ancestry. The great difference between *Kennalestes* and *Zalambdalestes* implies that it would probably be necessary to go much farther back than the Santonian to find their common ancestor, and the reported presence of placentals, as yet undescribed but provisionally named *Prokennalestes* and *Prozalambdalestes* in the (?) Aptian Khovboor Formation (Beliajeva, Trofimow & Reshetov 1974) strengthens this probability. *Endotherium,* of possibly similar age from Manchuria, the specimens of which have unfortunately been lost, was compared with *Zalambdalestes* by Chow (1953).

Whether any placentals were present in the Albian Trinity fauna of Texas is uncertain. Partly molariform premolars and evidence of tooth replacement (Slaughter 1968, 1971), two characters lacking in later marsupials, might have been present in very early marsupials; Fox's (1975) argument that *Pappotherium* had only three molars is, I think, based on a misinterpretation of the evidence. The Trinity therians will not be regarded as placentals in this paper. The Deltatheridiidae are also excluded. As Fox (1975) believes, they may be a group independent of both marsupials and placentals, perhaps traceable through *Kielantherium* to *Aegialodon.* A radiation in the Early Cretaceous may well have produced several groups collateral with the marsupials and placentals (Lillegraven 1974), perhaps due to the fragmentation of the land surface that characterised that time. *Potamotelses* may represent another such group, if it is not a deltatheridian (Fox 1972, 1974, 1975) or an aberrant marsupial (Crompton & Kielan-Jaworowska 1977).

Apart from western North America and a small area of Asia, only two specimens of Cretaceous placentals are known from the whole world. One is an isolated molar from Champ-Garimond, France (Ledoux *et al.* 1966), of probable Campanian age (McKenna 1969). The other (*Perutherium*) is a fragment containing two molars from Peru (Grambast *et al.* 1967), dated as Late Cretaceous on the basis of the Charophyta, though McKenna (1969) and Simpson (1971) do not find this evidence completely convincing. *Perutherium* is very probably related to *Protungulatum.* It will not be discussed in this paper.

During visits to the United States, Poland and France, I have been able to examine at first hand a large proportion of the known specimens of Late Cretaceous placentals, including representatives of all the genera. The following abbreviations are used when referring to individual specimens: LACM, Los Angeles County Museum; ZPAL, Mongolian specimens in the Institute of Paleobiology, Polish Academy of Sciences; UCMP, Museum of Paleontology, University of California, Berkeley. Material was also seen from the American Museum of Natural History, the Carnegie Museum, the Museum of Comparative Zoology at Harvard University, the University of Kansas, the University of Minnesota, the U. S. National Museum, the Yale Peabody Museum, the University of Alberta, the Royal Ontario Museum, the British Museum (Natural History), and the Laboratoire de Paléontologie, University of Montpellier. I would like to take the opportunity to thank the many people, too numerous to mention individually, who so kindly made the specimens available and provided facilities for studying them.

The cusp nomenclature used follows as closely possible that of Osborn (1888, 1907), except that the term protoconule is replaced by paraconule (fig. 2). I have avoided the use of additional names for crests and cingula introduced by Van Valen (1966) and Szalay (1969) (see Butler 1977), but the term "stylocone" (Patterson 1956) is adopted for the cusp on the buccal margin of the upper molar, posterior to the parastyle. "Buccal" and "lingual" are preferred to "lateral" and "medial", but "anterior" and "posterior" are retained in preference to "mesial" and "distal".

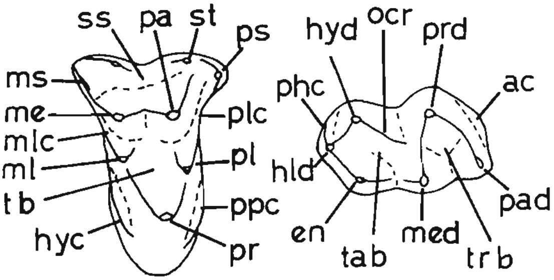


Fig. 2. Molar crown nomenclature used. The teeth are drawn in crown view, with anterior side to the right and buccal side above. Upper molar: *hyc*, hypocone cingulum; *me*, metacone; *ml*, metaconule; *mlc*, metaconule cingulum; *ms*, metastylar crest; *pa*, paracone; *pl*, paraconule; *plc*, paraconule cingulum; *ppr*, preprotocone cingulum; *pr*, protocone; *ps*, parastyle; *ss*, stylar shelf (= buccal cingulum); *st*, stylocone; *tb*, trigon basin. Lower molar: *ac*, anterobuccal cingulum; *en*, entoconid; *hld*, hypoconulid; *hyd*, hypoconid; *med*, metaconid; *ocr*, oblique crest; *pad*, paraconid; *phc*, posthypoconid cingulum; *prd*, protoconid; *tab*, talonid basin; *trb*, trigonid basin.

MOLAR OCCLUSION

In a phylogenetic study it is desirable whenever possible to keep function strongly in mind. Fortunately in the case of teeth the relation of structure to function is simple and direct: evidence of function is preserved in fossils by wear of the tooth surface. Teeth show two forms of wear, abrasion and attrition. Abrasion is a general wear of the surface, especially the more upstanding parts such as the tips of cusps, due to contact of the teeth with food. Attrition takes place when the teeth are in close contact with their opponents; it results in the formation of shiny, often striated wear facets. Abrasion is mainly produced during the "crushing-puncturing" stroke, attrition during the "power stroke" (Crompton & Hiiemae 1970). Crompton & Kielan-Jaworowska (1977) give a detailed description of the attrition facets. The relative movements of opposing teeth which produce the facets are illustrated in figure 3.

The power stroke has a lingual component, transverse and slightly anterior in relation to the tooth row. Among modern placentals, it is more steeply inclined in carnivores, where the scissor-like cutting action of crests is important, than in herbivores, which perform horizontal grinding movements; in insectivores the inclination is intermediate (Crompton & Hiiemae 1969). Though less extreme than in modern mammals, differences in the direction of the power stroke were present in the Cretaceous (Butler 1972), indicating that a dietary radiation was already taking place. Attempts were made to measure the angle of the stroke. As it was usually necessary to use isolated teeth for this purpose, the measurements could not be related to the sagittal plane, and they were therefore referred to a plane passing along the lower jaw through the axes of the molar roots. In relation to this, movement of the lower molar was estimated to be

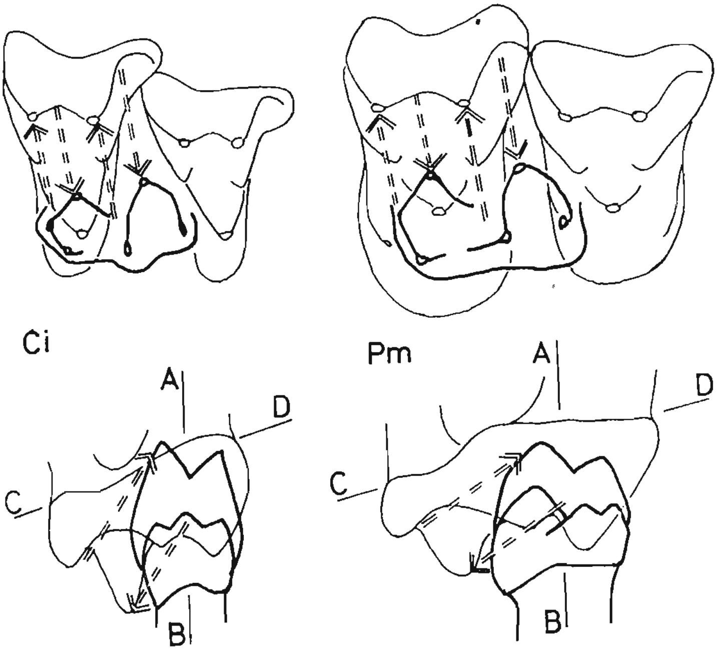


Fig. 3. Molar occlusion in *Cimolestes* (*Ci*) and *Protungulatum* (*Pm*). Drawings of upper and lower molars have been superimposed as if transparent; lower molars at the end of the power stroke. Above, crown view (anterior to the right); below, longitudinal view (lingual to the right). Arrows indicate paths of relative movement of selected cusps. *AB* is taken as vertical; *CD* is the basal plane of the upper molar.

inclined lingually at an angle of about 35° in *Cimolestes incisus* and about 55° in *Protungulatum donnae*. The angle made by the power stroke to the base of the upper molar (a line joining the buccal and lingual enamel margins) was about 40° in *Cimolestes* and about 20° in *Protungulatum*. The range of error is probably about 5°. The inclination of the upper molar base probably differs from one tooth to another within the series, being less in M^3 than in M^1.

Cimolestes and *Protungulatum* represent the extremes among Late Cretaceous North American forms, and might be regarded as diverging in a carnivorous and a herbivorous direction respectively. *Procerberus, Gypsonictops* and *Purgatorius* (this last based on Early Paleocene material) were intermediate, perhaps insectivorous. Among the Mongolian forms, *Kennalestes* seems to have had an angle of stroke similar to that of *Cimolestes*, i.e. about 40° to the base of the upper molar and about 35° to the lower molar root axis. In *Asioryctes* the power stroke might be steeper (about 45° and 30° respectively). In *Zalambdalestes* and *Barunlestes* the stroke seems to have been rather less steep than in *Kennalestes*, comparable with that of *Gypsonictops* (30—35° and about 45°). There are no Mongolian Cretaceous mammals in which the stroke is as transverse as in *Protungulatum*.

A steeply inclined power stroke is probably plesiomorphic for therian mammals: it is found in *Perămus*, in *Holoclemensia* and in *Deltatheridium*. Kielan-Jaworowska's diagram (1975*b*: fig. 6) of the occlusion of *Deltatheridium* shows a stroke at about 30° to the lower molar axis. This is steeper than in *Kennalestes* and quite possibly it has been secondarily steepened as a carnivorous adaptation. The equally steep stroke of *Asioryctes* cannot be explained in this way, however, for this genus does not otherwise show carnivorous characteristics.

Upper and lower molar patterns evolve together so that the interrelationships of the cusps are retained (Butler 1961). Despite the difference between *Cimolestes* and *Protungulatum* in the direction of the power stroke, occlusal diagrams of the two genera, when drawn in crown view (fig. 3: top) are remarkably similar: the principal difference lies in the development of a hypocone in *Protungulatum*, occluding against the paraconid. However, when the teeth are viewed horizontally (fig 3: bottom) the effect of the direction of stroke is more obvious. The grooves on the upper molar for the passage of the protoconid and hypoconid of the lower molar are less steeply inclined in *Protungulatum*, as are those on the lower molar for the passage of the paracone and metacone. It follows that in *Protungulatum* the buccal cusps of the upper molar and the trigonid of the lower molar are less elevated and blunter, less adapted for piercing than in *Cimolestes*, but more for crushing and grinding. Cutting edges, e.g. the metastylar crest, that operate like the blades of scissors, no longer constitute a major element of the occlusion, but the crushing functions of the protocone and hypoconid are more important. The buccal cusps occupy a smaller proportion of the crown width, and the lingual part of the upper molar is broadened anteroposteriorly, with correlative enlargement of its root. The interdental embrasures between upper teeth are reduced. On the lower molar the talonid is widened in comparison with the trigonid and the hypoconid has become the largest of the talonid cusps.

THE PRIMITIVE MOLAR PATTERN

There can be little doubt that these features of *Protungulatum* are secondary (apomorphic) and that *Cimolestes* stands nearer to the primitive (plesiomorphic) placental condition. This is confirmed by the numerous resemblances between *Cimolestes* (especially *C. incisus*) and *Kennalestes*, a much older (? Santonian) form which from its small size was almost certainly insectivorous (fig 4: *K*, *Ci*). The resemblances may be tabulated as follows:

1) The paracone is a high, acute cusp, with an unworn height (measured from the buccal enamel margin) at least equal to half the width of the molar.

2) The metacone is lower than the paracone, but still comparatively high, its height being equal to about 60% of the buccal length of the tooth. The notch between the paracone and metacone, through which the hypoconid passes, is at a level far above that of the buccal cingulum.

3) There is a well developed metastylar shearing crest, divided from the metacone by a notch. It functions against the anterior crest of the protoconid of the lower molar.

4) There is a prominent parastylar lobe, bearing the parastyle and the stylocone. It is more stoutly constructed in *Kennalestes* than in *Cimolestes*. The parastyle wears on its lingual surface against the tip of the protoconid as that cusp passes dorsomedially into the deep interdental embrasure. Between the stylocone and the metastyle the stylar shelf bears only indistinct cusps or none.

5) The protocone shelf occupies rather more than half the width of the tooth (about 55%). The protocone is a V-shaped cusp, with a height equal to about half the tooth width. The anteroposterior diameter of the lingual part of the tooth (measured lingually to the conules) is rather greater in *Kennalestes*, in comparison with the buccal length, than in *C. incisus*, owing to the presence in *Kennalestes* of cingula anterior and posterior to the protocone.

6) Para- and metaconules are present but not strongly developed. The paraconule is farther removed from the paracone (and nearer the

protocone) than the metaconule is from the metacone. The ridges of the conules supplement the action of the crests of the paracone and metacone, and therefore they have to lie in the same planes as these; hence when the teeth are seen in the direction of relative motion ("occlusal view" of Crompton & Kielan-Jaworowska 1977) the conules are hidden by the tips of the buccal cusps. The paracone, being higher than the metacone, casts a longer "shadow".

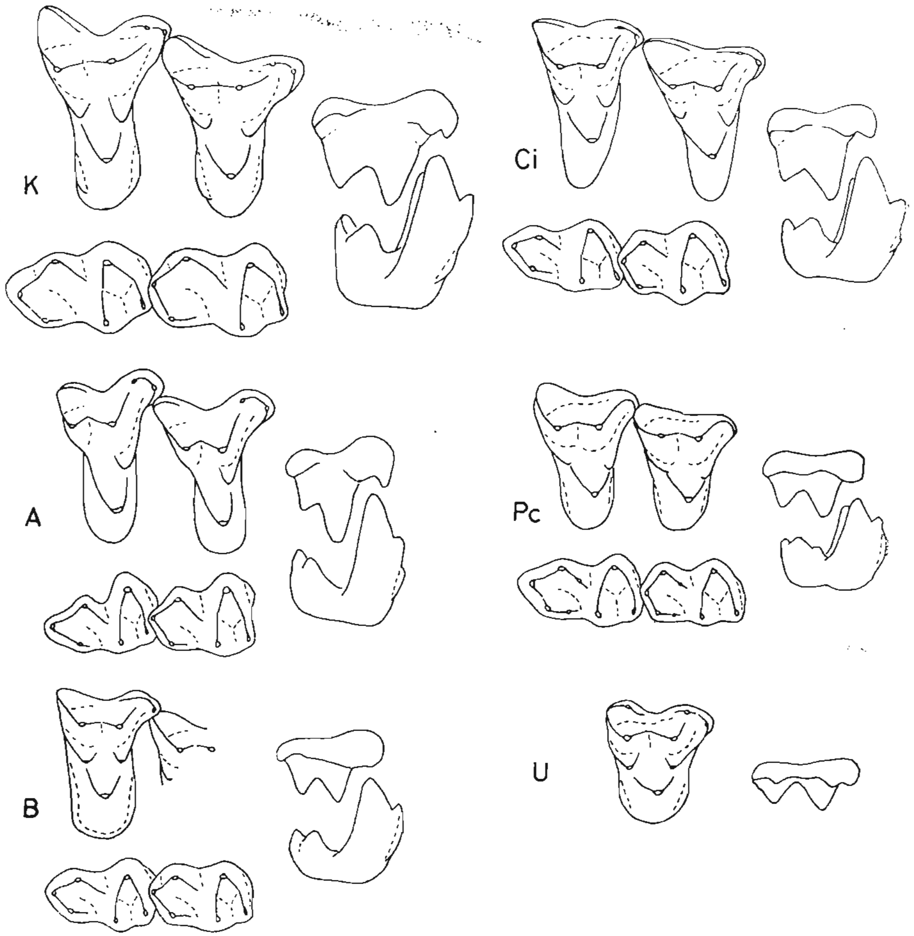


Fig. 4. Comparison of molars of Cretaceous placentals. Of each genus are drawn (where known) right M^2 and M^1 in crown view, left M_3 and M_2 in crown view, and right M^2 in buccal view. Not to scale. Key to lettering in this and succeeding figures: *A, Asioryctes nemegetensis*; *B, Batodon tenuis*; *Ci, Cimolesters incisus*; *Cm, Cimolestes magnus*; *CG*, Champ-Garimond molar; *G, Gypsonictops hypoconus*; *Ga, Gallolestes pachymandibularis*; *K, Kennalestes gobiensis*; *Pc, Procerberus formicarum*; *Pm, Protungulatum donnae*; *Pu, Purgatorius unio*; *U*, Unnamed eutherian (Fox); *Z, Zalambdalestes lechei.*

7) On the lower molar the protoconid is a tall, acute cusp, its height equal to or slightly greater than the length of the tooth. The metaconid

is also tall, though not quite as much as the protoconid. It stands directly lingually to the protoconid, and the posterior surface of the trigonid is nearly vertical and transverse. This surface shears against the anterior surface of the upper molar as the trigonid penetrates deeply into the embrasure.

8) The paraconid is lower than the metaconid, but it differs in the two genera. In *Cimolestes* it has the form of a ridge, directed anterolingually; it shears against the posterior surface of the metacone and metaconule. In *Kennalestes* it is also ridgelike, but higher and more nearly parallel to the protoconid-metaconid crest, so that the trigonid appears to be compressed anteroposteriorly; at the end of the stroke the paraconid meets the hypocone cingulum of the upper molar (Crompton & Kielan-Jaworowska 1977).

9) The talonid is narrower than the trigonid. It bears three cusps, of which the hypoconulid is as high as the hypoconid. The hypoconulid projects posteriorly, fitting into a groove in the anterior surface of the next tooth, between the paraconid and the anterobuccal cingulum. The hypoconid is much lower than the protoconid in accordance with the high level of the notch between the paracone and the metacone. The groove between the anterior hypoconid crest ("oblique crest") and the trigonid is steeply inclined. The oblique crest meets the trigonid midway between the protoconid and the metaconid. On M_3 the talonid is narrower and the hypoconulid relatively larger, but only moderately so: the talonid of M_3 is not appreciably longer than that of M_2.

The principal differences between *Cimolestes* and *Kennalestes* concern the existence of a paraconid-hypocone contact in the latter. It is to be noted however that in some species of *Cimolestes*, especially *C. magnus*, cingula are frequently present at the base of the protocone, though they appear to be functionless. They also frequently occur in *Procerberus*. In the only known specimen of the upper molars of *Batodon* (fig. 4,B) the cingula are well developed; they have united round the lingual side of the protocone, and show wear both anteriorly (against a metaconid?) and posteriorly (against a paraconid?). Both these genera have been placed with *Cimolestes* in the Palaeoryctidae. Could the posterior cingula of *Cimolestes* and *Procerberus* be relics of a formerly functional hypocone cingulum, lost with the development of carnivorous habits? Or did the cingulum primarily have a different function, such as preventing food from being forced between the tooth and the gingiva? In favour of the second alternative is the absence of a hypocone cingulum in *Zalambdalestes*, as well as in the Trinity therians, in the Deltatheridiidae, *Potamotelses* and most Cretaceous marsupials, and its occasional presence in other Cretaceous marsupials such as *Glasbius*, where it could not be interpreted as the relic of a formerly occluding structure. If the hypocone-paraconid contact of *Kennalestes* is an apomorph, as Crompton & Kielan-Jaworowska (1977) believe, it would exclude that genus from the ancestry of *Cimolestes*. In that case, the resemblances between *Kennalestes* and *Cimolestes* would be symplesiomorphs, i.e. characters inherited from a common ancestor.

COMPARISON OF MOLARS WITH THE PRIMITIVE PATTERN

A. *Palaeoryctidae* (fig. 4: *A, B, Ci, Pc*)

Symplesiomorphs provide an unsure ground on which to build phylogenetic hypotheses, for the same ancestral characters may be retained in two or more groups that in other respects have evolved in different directions. The Cretaceous genera placed in the Palaeoryctidae — *Asioryctes*, *Batodon*, *Cimolestes* and *Procerberus* — are conservative forms that retained plesiomorphic characters in their molars, but the differences between them indicate that they lie on more than one line of evolution. The greatest differences are in the antemolar teeth, but even the molars show some divergence.

Asioryctes (? Campanian) is characterised by anteroposteriorly shortened molars in which the metacone is proportionately reduced in height and the metaconule is rudimentary (Crompton & Kielan-Jaworowska 1977). Its shearing stroke appears to have been steeper than in *Kennalestes* or *Cimolestes*. Its parastylar lobe is more strongly constructed than in *Cimolestes*, probably a primitive character shared with *Kennalestes*. There is no hypocone cingulum, and the paraconid is small, close to the metaconid and quite probably secondarily reduced. On the talonid, which is much narrower than the trigonid, the hypoconulid is the highest cusp.

Batodon (Maastrichtian) is known only from fragments (Lillegraven 1969, Clemens 1973), some of which may not be correctly referred. The upper molars are known only from a single specimen which contains M^2 and part of M^1. The paracone and metacone are placed rather far buccally, giving a shorter metastylar crest and a wider lingual shelf than in *Cimolestes*; the notch between the paracone and metacone is at a lower level; the conules appear to have been more strongly developed; as mentioned above, the cingulum round the protocone is strong and apparently functional. On the lower molars, the talonids of M_1 and M_2 are as wide as the trigonids, though their disparity in height with the trigonids is as great as in *Cimolestes*.

A possibly significant difference between *Batodon* and *Cimolestes* is the existence of a groove in the buccal side of the talonid, marking off the hypoconid from the hypoconulid. This is not present in *Cimolestes*. The surface of the hypoconulid, posterior to the groove, slopes down buccally, forming a path for the tip of the metacone. In *Protungulatum* and some other genera a posthypoconid cingulum develops in this area, arising as a ridge at the tip of the hypoconulid. Together with the anterobuccal cingulum, anterior to the protoconid of the next tooth, it forms the floor of a buccally sloping valley down which the metacone travels during the power stroke.

Procerberus (Late Maastrichtian) has departed from the primitive condition much more than *Cimolestes incisus,* though some other species of *Cimolestes*, especially *C. cerberoides,* to some extent bridge the gap (Lillegraven 1969). Compared with *C. incisus*, the buccal cusps of the upper molars of *Procerberus* are less high, and the notch between them stands at only about twice the height of the buccal cingulum. The parastyle is less prominent, and the metastylar shear is shorter. The conules are weak. Cingula are usually present anterior and posterior to the protocone. On the lower molars the trigonid is less elevated and the talonid is as wide as the trigonid. The paraconid is higher in proportion to the other trigonid cusps than in *Cimolestes,* but it has the same shape. The anterobuccal cingulum, unlike that of *Cimolestes*, extends acress the anterior side of the tooth to the base of the paraconid. On M_3 the talonid is elongated owing to a considerable enlargement of the hypoconulid. The power stroke seems to be less steep than in *Cimolestes*, resembling that of *Gypsonictops.* The molars of *Procerberus* would be less effective for shearing than those of *Cimolestes:* Lillegraven (1969) noted that their cusps are blunted even when unworn and the edges of the crests wear off more rapidly than in *C. cerberoides.* At the same time the teeth do not seem to be well adapted for crushing. Perhaps the food was soft and nonfibrous, such as insect larvae, and the teeth were used more for holding and manipulating the food in the mouth than for its comminution. The frequent occurrence of additional cusps on the talonid, one on the oblique crest and another anterior to the entoconid, might be adaptive to such a function.

While it is highly probable that *Procerberus* has been derived from a form with plesiomorphic molars like *Cimolestes,* it does not follow that the ancestor was *Cimolestes* itself.

B. *Unnamed eutherian* (fig. 4: *U*)

A different direction of departure from the primitive molar pattern is shown by an isolated upper molar from the Early Campanian of Alberta, described by Fox (1970, 1975), who did not name it. A similar tooth from New Mexico will be described by Fox and Clemens.

A number of plesiomorphic characters are retained: the parastyle is very prominent, and the interdental embrasures must have been wide; there is a well developed metastylar crest, though it is shorter than in *Cimolestes*; the buccal shelf carries a stylocone and also a posterior style opposite the metacone, which occurs in some specimens of *Kennalestes.* However, the paracone is less elevated than in *Kennalestes* and the Palaeoryctidae, the paracone and metacone are equal, and the notch between them is only just above cingulum level. It follows that on the lower molar the trigonid must have been reduced in height. The protocone is quite a low cusp, its height only about a third of the width of the tooth. The conules are well developed, with well defined crests. Short lengths of cingulum are present anterior and posterior to the protocone, resembling some specimens of *Procerberus.* This tooth seems to have functioned by the cutting action of crests while the lower molar moved across it; the angle of the power stroke is estimated at 32° to the base of the tooth. The low cusps suggest that puncturing was unimportant, and crushing between the protocone and the talonid was probably also not very effective, as the reduced height of the protocone would not allow it to withstand much wear. A possible diet is one of soft leaves.

C. *Gypsonictops* (fig. 5: *G*)

The molars of *Gypsonictops* (Middle Campanian — Maastrichtian) on the other hand seem to be adapted for dealing with more resistant food, such as beetles and other thick-cuticled arthropods, or seeds. The power stroke was not quite as steep as in *Cimolestes* or *Kennalestes,* though the statement by Crompton & Kielan-Jaworowska (1977) that the movement was "far more horizontal than in *Kennalestes*" seems to me to be hardly justified. The difference in the direction of the arrows in their figures 11c and 13c has been exaggerated by the fact that the *Kennalestes* molar is drawn as it would appear in a skull, with the protocone shelf horizontal, while *Gypsonictops,* drawn from isolated teeth, is placed with the base of the tooth horizontal. The wear facets have been described by Kay & Hiiemae (1974), who compared *Gypsonictops* with the Paleocene primate *Palenochtha.*

Gypsonictops remains primitive in its high paracone, which is higher than the metacone and separated from it by a notch at a level far above the buccal cingulum; in the height of the protoconid, about equal to the length of the lower molar; in the approximate equality of the three talonid cusps, of which the hypoconulid is as high as the hypoconid and projects posteriorly; and in that the talonid of M_3 is similar in length to that of M_2, the hypoconulid being only moderately enlarged. In other respects however *Gypsonictops* has advanced. Its paracone and metacone are stout, conical cusps placed quite near the buccal margin, and the stylar shelf is represented only by a buccal cingulum. The metastylar shearing crest is shorter than in *Cimolestes* or *Kennalestes.* The protocone shelf occupies a larger part of the upper molar (about 70% of the width of the tooth) and carries more strongly developed conules; correlatively, the talonid is proportionately wider on the lower molar (subequal in width to the trigonid). The lingual part of the upper molar is broader anteroposteriorly: its diameter is about 70$^0/_0$ of the buccal length, compared with about 55$^0/_0$ in *Kennalestes*. The cingula anterior and posterior to the protocone are better developed, the posterior cingulum rising to form a small hypocone. The parastylar lobe is less prominent: this, together with the broader protocone region, results in a narrowing of the interdental embrasure between two upper molars. Consequently the trigonid of the lower molar no longer fits into the embrasure, but the paraconid makes contact with the hypocone. The paraconid is relatively high, in the form of a nearly transverse ridge. It would not be difficult to derive *Gypsonictops* from a form with molars like *Kennalestes*, which already possessed the paraconid-hypocone function.

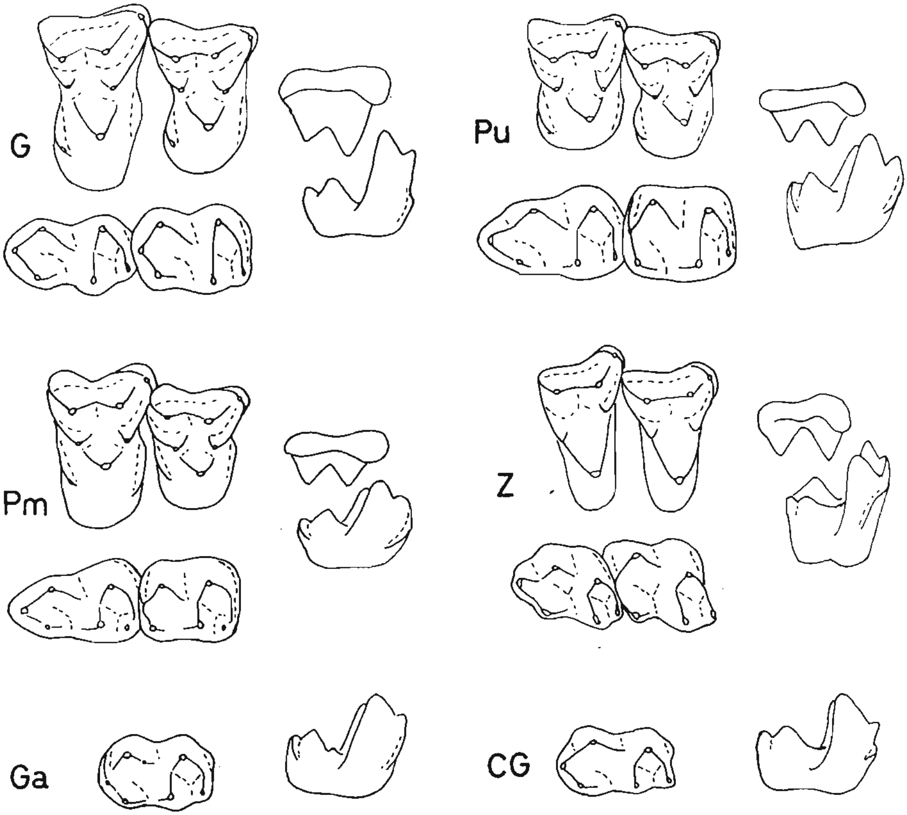


Fig. 5. Comparison of molars of Cretaceous placentals (continued). For key to lettering see fig. 4. In the case of *Gallolestes* only M_1 has been drawn.

Kay & Hiiemae (1974) have, in my view, misinterpreted the facets in the region of the hypocone. Their facet 10 on the upper molar is due to the entoconid (= 6 on the lower molar). Facet 6, on the edge of the posterior protocone crest, is probably due to abrasion. They show a facet 7 on the hypocone which they attribute to contact with the metaconid; this seems unlikely, as in *Palenochtha* facet 7 is shown as produced by the paraconid. They fail to show the wear that is commonly seen along the hypocone cingulum, more correctly interpreted by Crompton & Kielan-Jaworowska (1977).

I concur with Kay & Hiiemae (1974) however in their statement that there was a transitory phase II occlusal movement (= lingual phase, Butler 1973). The upward and medial movement of the lower teeth in the power stroke (constituting phase I) is continued as a more anterior and horizontal movement, during which the tip of the hypoconid passes through the notch between the paraconule and the protocone, and the lingual surface of the hypoconid slides across the buccal surface of the protocone. Some very lightly worn specimens show wear polish which could only be due to such a movement, though in more worn examples the surfaces concerned have been removed by abrasion. There is no evidence of phase II occlusion in *Kennalestes*. Phase II movement occurs in Tertiary primates and ungulates, and it was probably present at the end of the Cretaceous in *Protungulatum* and *Purgatorius*.

D. *Purgatorius and Protungulatum* (fig. 5: *Pu, Pm*)

Purgatorius is included in this survey on the strength of a lower molar from the Late Maastrichtian Hell Creek fauna, tentatively referred to the genus as *P. ceratops* by Van Valen & Sloan (1965). *P. unio,* from the Early Paleocene Purgatory Hill fauna, is much better known and it is discussed here as representative of the genus. The molars of *Protungulatum*, from the Hell Creek, are very similar, and the two genera will be considered together. Clemens (1974) figures a lower cheek dentition of *Purgatorius unio*, and briefly compares it with *Protungulatum*.

The power stroke of *Purgatorius* was not very different from that of *Gypsonictops*, but the movement in *Protungulatum* was more horizontal. The height of the paracone is reduced, less in *Purgatorius* than in *Protungulatum*. In both genera the notch for the hypoconid, between the paracone and the metacone, is less elevated above the buccal cingulum than in *Gypsonictops*. The metastylar shearing crest of *Purgatorius* is like that of *Gypsonictops*, but it is practically absent in *Protungulatum*. In both *Purgatorius* and *Protungulatum* the lingual part of the upper molar is broadened and the interdental embrasures are narrower than in *Gypsonictops*; the hypocone-paraconid contact is well developed. The trigonid is reduced in height, but less so in *Purgatorius* than in *Protungulatum*.

Unlike *Gypsonictops*, the metaconid in both genera is extended posteriorly as a ridge which projects beyond the posterior surface of the protoconid. The facet due to contact with the protocone forms on this ridge.

Whereas primitively the two facets on the posterior surface of the trigonid, due respectively to the protocone and the paracone, lie nearly in the same plane, in *Purgatorius* and *Protungulatum* the protocone has been displaced posteriorly in relation to the paracone, and its surface of contact with the trigonid has been displaced accordingly.

A further resemblance between the two genera lies in the structure of the talonid. On M_1 and M_2 the hypoconulid is reduced in height and does not project posteriorly. It is continuous buccally with a posthypoconid cingulum, absent in *Gypsonictops*. The hypoconid is the highest of the talonid cusps. On M_3 however the hypoconulid is greatly enlarged, especially in *Protungulatum,* where it is equal to or greater in height than the hypoconid. It functions against posterior side of the metacone of M^3.

In neither genus does the protocone shelf occupy so great a proportion of the width of the upper molar as in *Gypsonictops,* but it was evidently effective for crushing against the talonid. The conules are well developed. In *Protungulatum* the tip of the protocone is displaced farther from the lingual edge of the tooth, bringing it closer to the paracone and metacone and reducing the area of the trigon basin; in *Purgatorius* however the protocone is more upright and the basin is larger. Correspondingly, the talonid basin is proportionately smaller in *Protungulatum* owing to the lingually inclined hypoconid.

Protungulatum also differs from *Purgatorius* in that the lingual part of its upper molar is more symmetrical. In *Purgatorius* the protocone appears to lean forwards, its anterior surface being the more vertical; moreover, the whole of the lingual part of the crown has the appearance of having been bent posteriorly: there is a distinct indentation of the posterior edge near the metaconule. These features are also present in *Gypsonictops,* but are very little developed in *Protungulatum.*

The numerous apomorphic resemblances between *Purgatorius* and *Protungulatum* indicate that they have evolved in much the same direction, but the differences between them show that they are on different lines. *Purgatorius* is less different from *Gypsonictops;* if *Protungulatum* is regarded as a primitive herbivore, *Purgatorius* might be considered as retaining some insectivorous adaptations. Both genera can be regarded as having passed through a stage when the molars were more like *Gypsonictops,* although it is unlikely that they were derived from *Gypsonictops* directly. Their more remote ancestors would, like the ancestor of *Gypsonictops,* possess molars resembling *Kennalestes.*

E. *Zalambdalestidae* (fig. 5: *Z*)

Despite its early (?Santonian) date, *Zalambdalestes* has departed rather far from the hypothetical primitive molar pattern. The paracone is less high; the notch between the paracone and the metacone is deeper; the metastylar crest is short on M^1 and absent an M^2; the parastylar lobe is smaller, only slightly prominent on M^1 and not at all on M^2; the stylocone is rudimentary; the protocone shelf occupies a greater proportion of the tooth width (about 60%). On the lower molars the trigonid is less elevated than in *Kennalestes;* the metaconid is higher relatively to the protoconid, exceeding that cusp on M_3; the paraconid is nearly as high as the metaconid and closely appressed to it, especially on M_2 and M_3; the talonid is subequal in width to the trigonid; the oblique crest of the hypoconid meets the trigonid at the base of the protoconid; the entoconid is higher than the hypoconid; the hypoconulid is the most weakly developed talonid cusp except in M_3, where it is enlarged; a posthypoconid cingulum is present. Many of these characters are shared with *Gypsonictops*, others with *Purgatorius* and *Protungulatum*, but *Zalambdalestes* differs from these significantly in the absence of a hypocone cingulum, presumably a primitive character, and in the weak development of the conules, perhaps also primitive. Its teeth wear most rapidly on the protocone shelf and on the talonid, indicating that they functioned largely for crushing between these structures. There would be some cutting function, involving mainly the trigonid and crests of the protocone, but vertical surfaces show less wear than horizontal surfaces. *Barunlestes* is very similar in molar pattern.

F. *Champ-Garimond molar* (fig. 5: *CG*)

The lower molar from the Campanian of Champ-Garimond, France (Ledoux *et al.* 1966), was considered as a possible palaeoryctid by McKenna (1969). It resembles *Cimolestes* in the paraconid, which is a low, forwardly projecting and apparently purely cutting cusp. However, the trigonid is less elevated: the hypoconid height is 60% of that of the protoconid, rather more than in *Gypsonictops* and similar to *Zalambdalestes* M_2. The talonid is as wide as the trigonid, and as in *Zalambdalestes* the oblique crest meets the base of the protoconid. The hypoconid is the largest talonid cusp, a resemblance to *Purgatorius*; a groove on the buccal surface divides the hypoconid from the hypoconulid. The latter cusp is situated rather far from the hypoconid, indicating that on the upper molar the metacone was well separated from the paracone. There is some resemblance to *Pediomys*, a Cretaceous didelphoid, but in this the hypoconulid is nearer the entoconid and the paraconid equals the metaconid in height. The tooth is rather narrow, and its open trigonid suggests that it may be a first molar.

G. *Gallolestes* (fig. 5: *Ga*)

Gallolestes, from the Late Campanian of Baja California (Lillegraven 1972, 1976) shows some resemblance to the Champ-Garimond tooth. The holotype is a mandible with five teeth, four of them molariform. The first molariform tooth is much narrower and lower than the second, and also more worn. Lillegraven (1976) rightly rejects it as molariform premolar, and considers the possibility that it is a first permanent molar, in which case *Gallolestes* would have four molars like a marsupial. Howewer, the molar pattern differs from those of Cretaceous marsupials. It seems to me that the first molariform tooth is probably dP_4, despite its well developed roots: the roots of all the teeth are exceptionally robust. The incompletely preserved premolariform tooth anterior to it would then be dP_3.

LACM 27600, in which M_1 — M_3 are present, is remarkable for a Cretaceous placental in the very heavy abrasive wear it shows: all the cusps have been removed. Even in the supposedly juvenile type specimen the tops of the cusps have worn off on M_1 and M_2. This type of wear occurs in *Onychodectes* among Paleocene mammals, a genus that shows some resemblance to *Gallolestes* in pattern, ond it is possible that *Gallolestes* was an early taeniodont. It would make a better candidate for the ancestry of taeniodonts than *Procerberus,* proposed by Lillegraven (1969), the teeth of which are adapted in a quite different direction.

LACM 27599 is an almost unworn M_1. The elevation of its trigonid is comparatively low, about the same as in *Purgatorius.* The paraconid, which is only a little lower than the metaconid, projects forward in M_1 but not so much on M_2 and M_3. There is a ridge on the posterior surface of the metaconid as in *Purgatorius* and *Protungulatum.* The talonid is equal in width to the trigonid on M_2 and wider on M_1. The oblique crest joins the trigonid at the base of the protoconid on M_1, as in *Zalambdalestes* and the Champ-Garimond tooth, but the junction becomes more lingual on passing to M_2 and M_3. The hypoconid when unworn is slightly the highest talonid cusp. The hypoconulid is well differentiated, but it does not project so far posteriorly as in the Champ-Garimond specimen, except in M_3 where it is enlarged, though the enlargement is less than in *Procerberus* and *Protungulatum.* The hypoconulid is slightly nearer the entoconid than the hypoconid, indicating a relatively large metacone on the upper molar. A posthypoconid cingulum arises from the hypoconulid.

M_1 of *Gallolestes* and the Champ-Garimond tooth agree with *Zalambdalestes* in that the oblique crest joins the base of the protoconid, instead of meeting the trigonid at a point midway between the protoconid and the metaconid. This character, associated with a large talonid basin, is certainly apomorphic, and it excludes these forms from the ancestry of the known Maastrichtian genera. *Gallolestes* shares some other apomorphic characters with *Zalambdalestes*, with *Purgatorius* or with both, but whether these are indications of relationship, or whether are due to parallel evolution, cannot be decided in the incomplete evidence available.

PREMOLARS

Premolars (figs. 6,7) may be regarded as undeveloped molars, reflecting to various degrees the evolution of the molar pattern. However, standing farther forward in the jaws, nearer to the mouth and in a region where the opposing teeth can be more widely separated and so more rapidly closed together, the premolars usually differ from the molars functionally. They are more effective than the molars for piercing, holding, manipulating and often also for cutting the food. In adaptation to these functions they may become diversified even while the molars remain little changed, and therefore they can provide additional data bearing on phylogeny.

In the more primitive of the Tertiary placentals the number of premolars in each quadrant was four, but it is possible that the original number was 5. Several specimens of *Gypsonictops* have 5 premolars in the lower jaw, of which the third is the smallest. A juvenile specimen of *Kennalestes* (ZPAL MgM — I/1) contains a small additional tooth anterior to the location of dP^3, presumably an additional deciduous premolar; the adult dentition contains only 4 premolars. In order to avoid the confusion that would result from re-numbering the premolars from 1 to 5, I suggest that the last two premolars should continue to be called P3 and P4, and the additional teeth P_x in *Gypsonictops* and dP^x in *Kennalestes*. McKenna (1975) has postulated a reduction in premolar number from 5 to 4 by loss of the posterior premolar, the milk tooth at that location persisting to become the first permanent molar. The considerable functional readjustement that this process would involve seems to me to make such a change unlikely; it is more probable that a premolar could be lost in the middle of the series, between P_2 and P_3 of the Tertiary sequence. Anterior to this position P_1 and P_2 would tend to be involved in the canine function as holding teeth; posteriorly, P_3 and P_4 would be more effective as piercing and cutting teeth, as owing to their greater proximity to the jaw muscles more force could be exerted through them.

Owing to the alternation of upper and lower teeth, each premolar has occlusal relations with two teeth in the opposite jaw; thus P^4 occludes with M_1 and P_4, P^3 with P_4 and P_3. These relationships must be kept in mind if the structure of the premolars is to be understood.

The relation of P^4 to M_1 has much in common with that of M^1 to M_2. In *Kennalestes, Asioryctes, Cimolestes* and *Batodon* there is a well developed metastylar shearing crest, comparable with that of the molars, which cuts against the anterior crest of the protoconid of M_1. It is probably to be regarded as a plesiomorphic feature. It occurs also in *Zalambdalestes*, where it is better developed than on M^1. It is reduced in *Procerberus, Gypsonictops* and *Purgatorius* and absent in *Protungulatum.* There is no metacone on P^4 in *Kennalestes* or *Asioryctes*, where the posterior crest of the paracone runs directly to the metastyle, from which it is separated by a notch. In *Zalambdalestes* a rudimentary metacone is present on the posterior paracone crest, and this occurs also in some specimens of *Cimolestes*. The statement by Kielan-Jaworowska (1969) that an incipient metacone is present on P^4 of *Kennalestes* is erroneous: the cusp identified as the metacone is the metastyle. The metacone of P^4 is more clearly differentiated in *Batodon, Procerberus, Gypsonictops* and *Purgatorius,* but not in *Protungulatum*. It seems that the development of a metacone on P^4 is to be regarded as apomorphic.

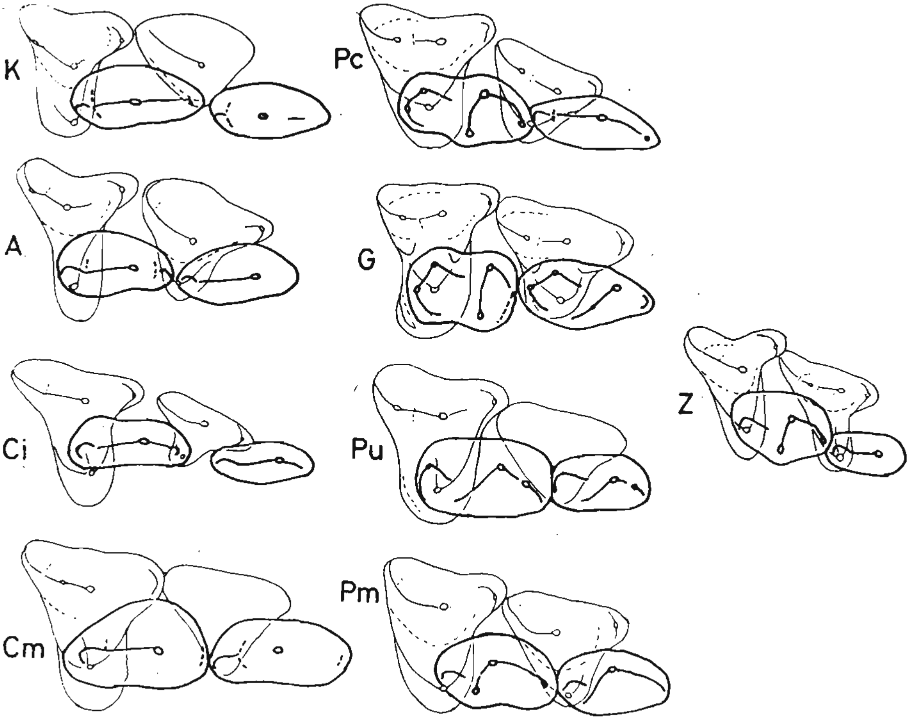


Fig. 6. Superposition of drawings of the last two right upper and left lower premolars to illustrate occlusal relations. Not to scale. For key to lettering see fig. 4.

The protocone of P^4 is always well developed. It is most molariform in *Gypsonictops*, where conules are present on its crests and there is a posterior hypocone cingulum which functions against the paraconid of M_1. In the other genera, except *Purgatorius*, the posterior (metaconular) ridge of the protocone is replaced by a posterior cingulum that continues up to the tip of the protocone at its lingual end; in *Purgatorius* the cingulum does not join the protocone but runs past its base. This cingulum functions like a hypocone cingulum, meeting the paraconid of M_1 at the end of the stroke, even in *Cimolestes*, *Asioryctes* and *Zalambdalestes* in which there is no hypocone function on the molars. Apart from this, the protocone of P^4 functions against P_4. In a number of genera (*Cimolestes, Batodon, Purgatorius, Zalambdalestes*) a transverse ridge connects the tip of the protocone with the base of the paracone; the area posterior to the ridge occludes with the paraconid of M_1, while the edge of the ridge and the area anterior to it occludes with the talonid of P_4.

The relation of P^4 to P_4 consists of the talonid function, together with a shearing action of the trigonid of P_4 against the anterior surface of P^4. The talonid of P_4 in *Kennalestes, Asioryctes, Zalambdalestes, Cimolestes, Batodon* and *Protungulatum* has a simple structure, consisting of a longitudinal crest which meets the protocone of P^4 at the end of the stroke. There is a lingual cingulum, representing the lingual margin of the talonid basin. This is presumably the plesiomorphic condition. In some specimens of *Cimolestes*, especially of *C. magnus*, a rudimentary hypoconid is developed on the crest. In *Purgatorius* the lingual cingulum is more elevated, producing a small talonid basin. In *Procerberus* the talonid of P_4 is molariform in structure, though smaller in proportion to the trigonid than on the molars. The highest level of molarisation is found in *Gypsonictops*, which also has the most molariform P^4: the talonid differs from that of M_1 only in the frequently smaller entoconid.

The trigonid of P_4 in *Kennalestes, Asioryctes* and *Cimolestes* consists only of the protoconid and a small anterior paraconid; the metaconid is absent. The protoconid meets the forwardly projecting parastyle of P^4 and passes up into the embrasure between P^4 and P^3. At the same time the paracone of P^4 passes down the buccal surface of the talonid crest of P_4. Although there is some contact between the posterior surface of the protoconid and the anterior surface of the paracone, this is probably not of much functional importance. However, a metaconid is developed on the lingual side of the protoconid in *Batodon, Procerberus, Zalambdalestes* and *Protungulatum*, and *Purgatorius* possesses a rigde in a corresponding position (Clemens 1974). In these, an extensive wear facet develops across the anterior surface of P^4, involving the protocone as well as the paracone, in a manner similar to the molars. It would appear, then, that the presence of a metaconid on P_4 is an advanced (apomorphic) character, although the existence of the metaconid on premolars from the Trinity fauna (Slaughter 1971) suggests the contrary.

The occlusal relations of P^3 in general repeat those of P^4 but on a reduced scale. Shear between the posterolingual side of the paracone of P^3 and the anterobuccal side of the protoconid of P_4 is almost certainly plesiomorphic. It is modified by the development of a metacone on P^3 in *Gypsonictops* (absent in the Campanian species; Sahni 1972) and *Procerberus*. In *Purgatorius* the paraconid of P_4, situated high on the anterior crest of the protoconid, is involved in the shearing function.

The protocone shelf of P^3 varies in size, and also in the relative importance of its contact with the paraconid of P_4 and the talonid of P_3. In *Cimolestes incisus* the protocone lobe of P^3 points posteriorly rather than anteriorly as in P^4 (Clemens 1973: fig. 15a, b), and it probably occludes only with the paraconid of P_4. P_3 is separated from P_4 by a space (Clemens 1973: fig. 13), and its small talonid probably functioned only against the tip of the paracone of P^3. *C. magnus* appears to have a different arrangement, though unfortunately P^3 is very imperfectly known. The paraconid of P_4 is rudimentary; it is closely applied to and partly overhung by the talonid of P_3, better developed than in *C. incisus*. Here it would seem that the protocone of P^3 occluded with the talonid of P_3. *C. propalaeoryctes* is different again (Lillegraven 1969). Here the paraconid of P_4 is absent, and P_3 is separated from P_4 by a space. It is likely that the (unknown) P^3 did not have a functional protocone; in the Paleocene *Palaeoryctes*, believed to be descended from this species, the protocone of P^3 has disappeared.

Batodon has a very small and low paraconid on P_4 and a space between P_4 and P_3, so presumably the protocone of the unknown P^3 was also functionless. In *Procerberus* P^3 seems to have functioned both against the rather large paraconid of P_4 and the small talonid of P_3, for its protocone shelf has a structure resembling P^4 of *Cimolestes* (seen in UCMP 102235), a transverse ridge joining the protocone to the base of the paracone. In *Asioryctes* the paraconid of P_4 is higher than the low talonid of P_3, but the protocone of P^3 does not seem high enough to make more than a transient contact with the lower teeth. In *Protungulatum* the lingual lobe of P^3 is directed forwards, and the protocone occluded mainly with the talonid of P_3, but there was contact also with the rather large paraconid of P_4. This is also true of *Zalambdalestes*. P^3 of *Purgatorius* is unknown to me, but it is unlikely that the elevated paraconid of P_4 was in a position to contact the lingual part of P^3; on the other hand the talonid of P_3 is better developed than in *Protungulatum* and probably functional. In *Gypsonictops* the paraconid of P_4 is much reduced and it could not have taken part in occlusion with P^3; the talonid of P_3 is more molariform than in other Cretaceous mammals, and it occluded with the relatively molariform P^3 in a molariform manner. In this respect *Gypsonictops* contrasts with the Tertiary Leptictidae, where the paraconid of P_4 is enlarged and has taken over almost completely the function of the P_3 talonid, which is greatly reduced.

P^3 of *Kennalestes* is very distinctive. The paracone is a very high, stout cusp, standing on a triangular base supported by three roots; the protocone shelf is represented only by a narrow cingulum. P_4 and P_3 are best preserved on the left side of ZPAL MgM-I/5: the teeth identified by Kielan-Jaworowska (1969) as dP_4 are damaged examples of P_4. P_4 has a low anterior paraconid and P_3 a simple talonid; both are worn on the buccal side by the tip of the paracone of P^3 as the jaw closes. P^3 seems to have functioned as a piercing structure, placed far enough back in the mouth to apply force, and it might have been used for penetrating insect cuticles and similar resistant materials. It is markedly different from P^4, in which the paracone has a similar height to the molars. The structure of P^3 is clearly derivative, having almost certainly undergone a secondary reduction of the protocone. *Asioryctes* seems to be specialising in the same direction, but it is still at an earlier stage: the paracone of P^3 is elevated,

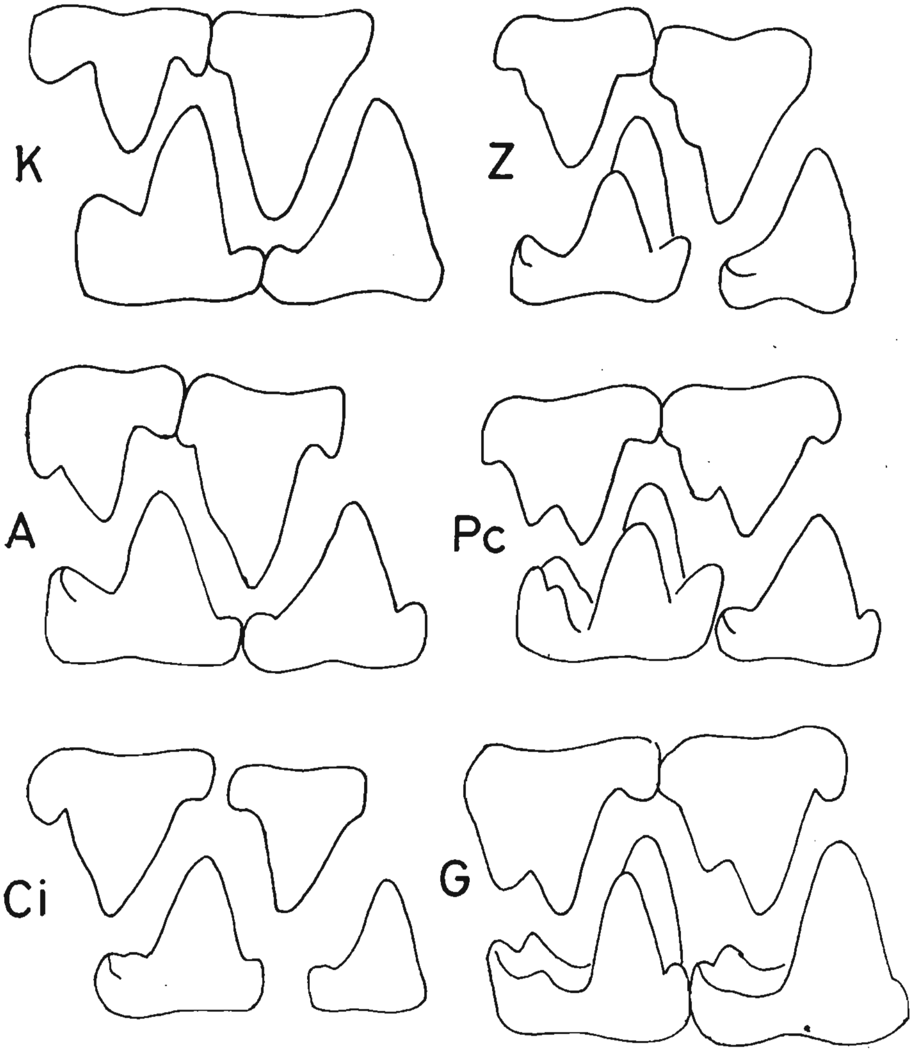


Fig. 7. Buccal outlines of the last two upper premolars and lingual view of the last two lower premolars. Not to scale. For key to lettering see fig. 4.

in contrast with that of P^4, but the protocone is retained though largely functionless. In most Cretaceous placentals both P^4 and P^3 have elevated paracones, and in *Cimolestes* P^4 is taller than P^3.

MILK MOLARS

The milk molars (fig. 8) of Cretaceous placentals are inadequately known. A juvenile specimen of *Kennalestes* (ZPAL MgM-I/1), which will shortly be described by Professor Kielan-Jaworowska, contains dP^4 and dP_4. Of *Asioryctes* there is a juvenile mandible (ZPAL MgM I/74) with dP_4 — dP_2, but the upper milk molars are unknown. dP_4 is shown in *Zalambdalestes* (Simpson 1928), and ZPAL MgM I/107 shows worn and damaged dP_4 and dP_3 of *Barunlestes*. Lillegraven (1969) and Clemens (1973) have identified some isolated milk molars of *Cimolestes*. Of these, dP^4 of *C. incisus* (Clemens 1973: fig. 18*h*, *h*), dP^4 and dP^3 of *C. magnus* (Lillegraven 1969: fig. 18-1), dP_4 of *C. incisus* (Clemens 1973: fig. 18a-c) and dP_4 of *C. stirtoni* (Clemens 1973: fig. 23*a*-*c*) are acceptable, but the teeth identified as dP_3 and dP^3 of *C. incisus* (Clemens 1973: fig. 18*d*-*f*, *i*, *j*) are too large in comparison with other teeth, and might belong to a larger species such as *C. stirtoni*. The milk teeth of *Procerberus* have not been described, but specimens of dP_4, dP_3 and dP^4 from Bug Creek exist in museum collections. In the case of *Gypsonictops*, Clemens (1973: fig. 11*e*, *f*) identified dP^4 of *G. hypoconus* and Lillegraven (1969 : fig 27-2) dP_4 of *G. illuminatus*, but the supposed examples of dP^3 (Lillegraven 1969: fig. 27-1; Clemens 1973: fig. 11d) seem to be indistinguishable from *Cimolestes*. Also the tooth regarded as dP_3 (Clemens 1973: fig. 11*a*, *b*) is much too large and dissimilar in pattern from P_3; it has some resemblance to P^2 of *Leptictis* and might be an upper premolar. Some undescribed teeth resembling M_1 of *Protungulatum*, but smaller and with a prominent low paraconid like P_4, are identified as dP_4. The only other milk molars known to me are dP_4 and part of dP_3 of *Gallolestes* if they have been correctly identified (see above, p. 257).

dP^4 (known in *Kennalestes*, *Cimolestes*, *Procerberus* and *Gypsonictops*) is similar in length to P^4, but it resembles M^1 in pattern, except that it is narrower transversely and has a more prominent parastyle. It is most like M^1 in *Kennalestes*.

dP_4 is known in nine genera (*Kennalestes*, *Asioryctes*, *Zalambdalestes*, *Barunlestes*, *Cimolestes*, *Procerberus*, *Gypsonictops*, *Protungulatum* and *Gallolestes*). In all cases it has a molariform talonid, which must have occluded with the protocone shelf of dP^4 in a completely molariform manner. The protoconid and metaconid are also molariform, except that they are lower than on the permanent molars, but there are differences in the paraconid. This cusp stands in an anterior position, separated from the other trigonid cusps to different degrees in the different genera. In *Kennalestes* and *Asioryctes* dP_4 is very much like M_1, but in the other genera the trigonid angle is more open, moderately so in *Zalambdalestes, Gallolestes* and *Protungulatum,* and more widely in *Cimolestes, Procerberus* and *Gypsonictops,* where the paraconid is most distant from the other trigonid cusps. In *Cimolestes* it is a fairly high cusp, joined to the protoconid by a strong crest which would shear against dP^3. dP^3 resembles P^3 except for the presence of a metacone, which takes part in the shear. Its protocone shelf points backwards, and it shows a backwardly facing wear facet that must be due to contact with the paraconid of dP_4. In *Gypsonictops* the paraconid of dP_4 is lower and more shelf-like; it probably occluded with the protocone shelf of dP^3, perhaps more extensively than in *Cimolestes.* In *Procerberus* the anterior end of dP_4 is still more specialised. It has developed into a talonid-like structure, bearing in addition to the paraconid a smaller lingual cusp. These are placed so far forward that they must have occluded with the lingual shelf of dP^3. A groove on the buccal surface of dP_4 between the protoconid and the paraconid would provide a path for the metacone of dP^3.

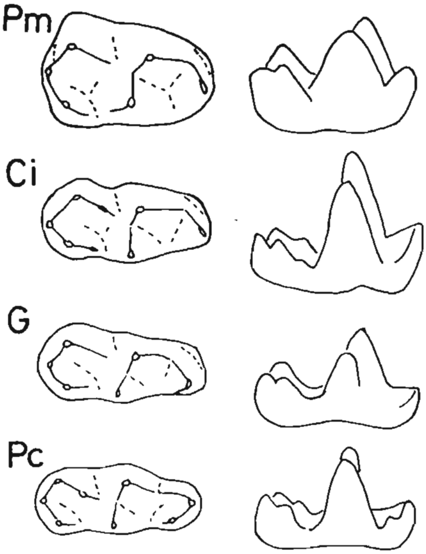


Fig. 8. Last lower milk molars (dP_4) in crown and lingual view. Not to scale. For. key to lettering see fig. 4.

Thus the evidence suggests that the trigonid of dP_4 was primitively molariform, and the more elongated trigonids with wide separation of the paraconid from the metaconid are apomorphic.

Unfortunately dP_3 is known only in *Asioryctes, Cimolestes, Procerberus* and (talonid only) *Gallolestes.* In all these the talonid is relatively small and not molariform; it is particularly reduced in *Procerberus* where it would not have functioned against the protocone of dP^3. Its buccal surface occluded with the paracone of dP^3. There is a small metaconid in *Cimolestes* and *Procerberus*, and probably also in *Asioryctes*, situated on a posterolingual crest of the protoconid; it would shear against the anterior side of the protocone of dP^3.

The milk dentition has to function in a shorter jaw than the permanent dentition, and hence the molariform teeth are situated farther forward in the dental sequence: the milk molars are usually more molariform than the premolars that replace them. Molarisation of the premolars in *Procerberus* and *Gypsonictops* might be regarded as a reduction of the difference between the two dentitions. In *Gypsonictops* however P_4 differs markedly from dP_4 in the paraconid, and it is possible that P_3 is more molariform than dP_3; the Tertiary Leptictidae do not show such differences. The development of a metaconid on the premolars might be regarded as an aspect of molarisation of the trigonid, even when the talonid remains simple, as in *Zalambdalestes.* Such a process might explain the presence of a metaconid on P_4 of some Tertiary Palaeoryctidae such as *Didelphodus*; if they have been derived from a *Cimolestes*-like ancestor their premolar metaconids would be a secondary development. The specialisation of the paracone of P^3 as a piercing tooth in *Asioryctes* is not reflected on the milk dentition, perhaps because the musculature of the young animal is not strong enough for such a tooth to be used.

The milk teeth function for a time together with at least some of the permanent molars. In the juvenile specimen of *Kennalestes* (ZPAL MgM I/1) M_2 has just erupted and M^2 is erupting; in the juvenile *Asioryctes* jaw ZPAL MgM I/74) M_1 is in function but M_2 has not erupted; in *Barunlestes* (ZPAL MgM I/107) M_3 and M^3 are in process of eruption.

DISCUSSION

Despite the very small number of Cretaceous placentals known, the foregoing comparisons show that a considerable diversification had taken place in the group before the end of the Cretaceous. The sample is too small to provide a clear picture of the subgroupings that had become established, let alone their relationships to each other. Each of the known genera seems to have specialisations that would exclude it from the ancestry of later genera; in other words, all the genera are on different evolutionary lines. To which Tertiary groups these lines lead is not discussed here: suffice it to say that the derivation of numerous orders from *Cimolestes* and *Gypsonictops*, as postulated by Lillegraven (1969), seems rather improbable, and the reference of *Gypsonictops*, and still more of *Kennalestes*, to the Leptictidae is open to considerable doubt.

An attempt has been made to identify plesiomorphic dental characters, present in the ancestral placental stock and retained to various degrees in the different descendant lines. It is believed that *Kennalestes, Asioryctes* and *Cimolestes* have the largest number of such characters, many of which are present also in related supposed non-placentals like the Deltatheridiidae and the Trinity therians. Each of the three genera has departed in a different direction from the ancestral condition: *Kennalestes* developed the hypocone-paraconid function and adapted P^3 as a piercing tooth; *Asioryctes* had shortened, very transverse molars, and its P^3 was evolving in a direction parallel to *Kennalestes,* but less rapidly; *Cimolestes,* while avoiding the specialisation of the molars found in the other genera, differs from them greatly in its premolars and milk molars. The poorly known *Batodon,* if correctly interpreted, was more advanced than *Cimolestes* in the presence of a metacone on P^4, a metaconid on P_4 and a functional cingulum on the molars. It could have had a common ancestry with *Cimolestes,* or alternatively it could represent a fourth line derived from the basic placental stock.

Procerberus is an advanced derivative of a *Cimolestes*-like form (Lillegraven 1969). If it originated in North America it could be related to *Batodon,* with which it agrees in the metacone of P^4 and the metaconid of P_4, but a direct derivation would require the degeneration of the cingulum round the protocone. In molarisation of the premolars *Procerberus* parallels *Gypsonictops,* and its dP_4 is very specialised and leptictid-like. The molars, however, show little resemblance to *Gypsonictops,* and it is unlikely that the two genera were related.

The unnamed eutherian of Fox (1970), known only by the upper molar, is an isolated form not closely related to any other known Cretaceous placental. Its low cusps seem to have operated by a slicing action during transverse jaw movements.

Gypsonictops has molars which could be derived from those of *Kennalestes,* but the premolars and milk molars are adapted in a different direction, making a direct derivation impossible. Presumably it represents another branch of the primary placental radiation, with a piercing and crushing dentition capable of dealing with resistant food. Reduction of the P_4 paraconid, a character already present in the Campanian, excludes *Gypsonictops* from the ancestry of the Leptictidae.

Purgatorius resembles *Gypsonictops* in such characters as the development of the hypocone and the existence of phase II occlusion, but again the premolars prevent a direct derivation. *Protungulatum* is very much like *Purgatorius,* but it is more advanced in its transverse chewing action and low cusps, and its premolars are organised in a different way. It was the most herbivorous of the Cretaceous placentals. Perhaps *Protungulatum* and *Purgatorius* were both derived from a pre-Campanian common ancestor with *Gypsonictops*, but the widespread occurrence of parallel evolution in the mammalian dentition should be borne in mind.

Zalambdalestes and *Barunlestes* represent an early specialised sideline, characterised by crushing molars with wide talonid, high entoconid and no hypocone, in combination with high-cusped, piercing premolars.

Gallolestes has crushing molars in which the tops of the cusps wear off rapidly. It shares some advanced characters of the molars with *Zalambdalestes*, such as the wide talonid, but in the absence of upper teeth it is impossible to judge the significance of these resemblances. A possible distant relationship with *Protungulatum* cannot be excluded. The Champ-Garimond molar agrees with *Zalambdalestes* and with M_1 of *Gallolestes* in the relation of the oblique crest to the trigonid.

Although the number of known Cretaceous placentals is very limited, the wide range of dental structure that they show, together with the lack of close relationship between most of the genera, indicates that we have only a small sample of a much larger number of placentals that must have existed at the time. The radiation that resulted in the diversity of Tertiary mammals was evidently well under way before the end of the Cretaceous, and it may be expected that further light will be thrown on it by palaeontological discovery, especially in regions hitherto unexplored.

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RADIACJA EWOLUCYJNA ZĘBÓW POLICZKOWYCH U KREDOWYCH SSAKÓW ŁOŻYSKOWYCH

Streszczenie

W pracy przeprowadzono porównanie zębów policzkowych (trzonowe i ostatnie dwa przedtrzonowe), u następujących rodzajów późnokredowych ssaków Eutheria: *Kennalestes, Asioryctes, Cimolestes, Batodon, Procerberus, Gypsonictops, Purgato-*

rius (materiał paleoceński), *Protungulatum, Gallolestes, Zalambdalestes,* nienazwany ząb Eutheria opisany przez Foxa (1970) oraz trzonowy z Champ-Garimond.

Wyodrębniono cechy zębów trzonowych wspólne dla *Cimolestes* i *Kennalestes*, które uznano za prymitywne (plezjomorficzne).

Porównując trzonowe każdego z rodzajów z przypuszczalną formą prymitywną, wykazano że stopnie i kierunki rozwoju są bardzo różnorodne. *Asioryctes* i *Batodon* wykazują wiele cech prymitywnych i mogą nie być blisko związane z *Cimolestes. Protungulatum* i *Purgatorius* wykazują wiele wspólnych, progresywnych cech i mogą mieć (przypuszczalnie przed kampańskich) przodków z *Cimolestes*, i bardziej odlegle z *Kennalestes. Zalambdalestes* jest stosunkowo zaawansowany, lecz reprezentuje odrębną linię ewolucyjną. Wykazuje on pewne progresywne cechy wspólne z *Gallolestes* i zębem z Champ Garimond.

U różnych rodzajów stwierdzono specjalizację zębów przedtrzonowych: tak więc u *Kennalestes* P^3 jest dużym, przebijającym zębem, bez protokonu; u *Asioryctes* P^3 jest również powiększony, a jego protokon, chociaż występuje, wydaje się niefunkcjonalny; molaryzacja P^4 i P_4 miała miejsce u *Gypsonictops, Procerberus* i w mniejszym stopniu u *Purgatorius;* u *Gypsonictops* P^3 i P_3 są również częściowo zmolaryzowane. U *Gypsonictops* parakonid na P_4 jest zredukowany, gdy natomiast u trzeciorzędowych Leptictidae jest on powiększony; różnica ta wyklucza *Gypsonictops* z przodków Leptictidae.

Jeżeli Eutheria pierwotnie miały pięć zębów przedtrzonowych, wydaje się bardziej prawdopodobne że redukcja miała miejsce po środku serii, niż na jej końcu, tak jak to przypuszczał McKenna (1975).

Silne zróżnicowanie zębów trzonowych u Eutheria wykazuje, że grupa ta przeszła w kredzie znaczną radiację, która rozpoczęła się przypuszczalnie przed santonem i dała w wyniku bogactwo form znanych z paleocenu.

ПЕРСИ М. БАТЛЕР

ЭВОЛЮЦИОННАЯ РАДИАЦИЯ КОРЕННЫХ ЗУБОВ МЕЛОВЫХ ПЛАЦЕНТАЛИЙ

Резюме

В статье проведено сравнение щёчнух зубов (коренные и два последни предкоренные) следующих позднемеловых родов млекопитающих Eutheria: *Kennalestes, Asioryctes, Cimolestes, Batodon, Procerberus, Gipsonictops, Purgatorius* (палеоценский материал), *Protungulatum, Gallolestes, Zalambdalestes,* неназванный зуб Eutheria описанный Фоксем (1970), а также коренной зуб из Шамп-Гаримонд.

Выделены общие признаки коренных зубов для *Cimolestes* и *Kennalestes*, которые были отнесены к примитивным (плезиоморфичные).

Сравнивая коренные зубы кождого из родов с предполагаемой примитивной формой, было показано, что степени и направления развития являются очень разнообразными. *Asioryctes* и *Batodon* проявляют много примитивных признаков и могут быть близко связанными с *Cimolestes*. *Protungulatum* и *Purgatorius* проявляют много общих прогрессивных признаков и могут иметь предков из *Cimolestes* (предполагаемых докампанских), более далёких с *Kennalestes*. *Zalambdalestes* является относительно развитым, но представляет собой отдельное эволюционное направление. Он проявляет некоторые прогрессивные признаки, общие с *Gallolestes* и зубом из Шамп-Гаримонд.

У различных родов определена спеицализация предкоренных зубов, так у *Kennalestes* P^3 является большим колющим зубом без протокона; а у *Asioryctes* P^3 также является увеличенным и его протокон, хотя и существует, но, по-видимому, являеятся нефункциональным; моляризация P^4 и P_4 существует у *Gypsonictops*, *Procerberus* и в меньшей степени у *Purgatorius*; у *Gypsonictops* P^3 и P_3 также частично уже моляризованы. У *Gypsonictops* исчез параконид на P_4, в то время как у третичных Leptictidae он увеличен, это различие исключает *Gypsonictops* из предков Leptictidae.

Если Eutheria вначале имели пять предкоренных зубов, то, может быть очень правдоподобным, что редукция была в середине серии, а не в конце, как это предполагал Мак-Кэнна (1975). Сильное различие коренных зубов Eutheria показывает, что эта группа в меловой период прошла значительную радиацю, которая началась, по-видимому, до сантона и дала в результате богатство форм известных от палеоцена.