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The Picrodontidae, a Family of Early Primates

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INTRODUCTION

The Picrodontidae are a Paleocene family of mammals known only from North America. The recognized range of the picrodontids is relatively brief; they occurred during the middle and late Paleocene. The genera included in the family are the Torrejonian and early Tiffanian *Picrodus* and the Tiffanian *Zanycteris*. By the time the picrodontids appeared on the record they were highly modified, peculiarly adapted, small mammals. The known genera are probably the most specialized of the Paleocene Theria. In spite of the much-modified morphology of the molar dentition, some relatively definite inferences can be drawn concerning the affinities of the family. A detailed study of important new material from the Torrejonian Swain Quarry and of the large collections made in the past from Silberling and Gidley quarries, and a careful re-examination of the only known crushed skull from the Mason Pocket, unequivocally point to derivation from paromomyine prosimians, at some time during the Puercan. Although still relatively poorly known, the Picrodontidae fully warrant superfamily recognition of equal rank to the plesiadapoids, tarsioids, and lemuroids of the early Tertiary.

The changes outlined under Evolutionary Trends, and Mastication

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and Occlusion, providing these treatments are correct, dramatically emphasize the stringent requirements that occlusion imposes on the manner of morphological and functional change in mammalian molars. Once the initial modification took place in the ancestral picrodontid, all subsequent alteration in response to the selective premium placed on flattened, squared-off teeth had to be in strict accord with the already ancient therian occlusion. The relatively simple adaptive response, once the slightly disproportionate alteration of the metacone area occurred, caused drastic modifications on the molar morphology in order to maintain the primitive occlusal contact between the teeth.

I thank Dr. Malcolm C. McKenna of the American Museum of Natural History and Dr. C. Lewis Gazin of the United States National Museum, Smithsonian Institution, for granting me permission to study the pertinent collections in their charge. Helpful comments by Dr. Malcolm C. McKenna and Dr. James S. Mellett are appreciated.

All illustrations in the paper, except figure 21, which was drawn by Miss Biruta Akerbergs, were prepared by me.

ABBREVIATIONS

The following abbreviations are used throughout the text:

A.M.N.H., Department of Vertebrate Paleontology, the American Museum of Natural History

C.M., Division of Vertebrate Fossils, Carnegie Museum, Pittsburgh

U.S.N.M., Division of Vertebrate Paleontology, United States National Museum, Smithsonian Institution

U.W., University of Wyoming, Laramie

N, number of specimens included in sample

OR, observed range

S^2 , variance

S, standard deviation

$\frac{V}{X}$, coefficient of variation

\bar{X} , mean

METHODOLOGY

The dental nomenclature used in this paper is the same as that in Szalay (in press), modified after Van Valen (1966). The homologies of many of the characters that are not immediately obvious in figure 2 are discussed under the section headed Function, below.

The descriptions of the species treated are intended as the raw data and are accompanied with as numerous supporting illustrations as was feasible. Purposely no comparative remarks are made under descriptions to similar aspects of related species. Descriptions skillfully interwoven

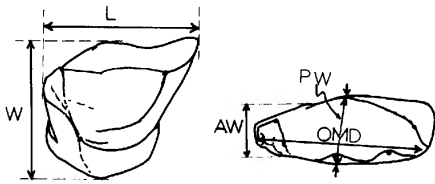
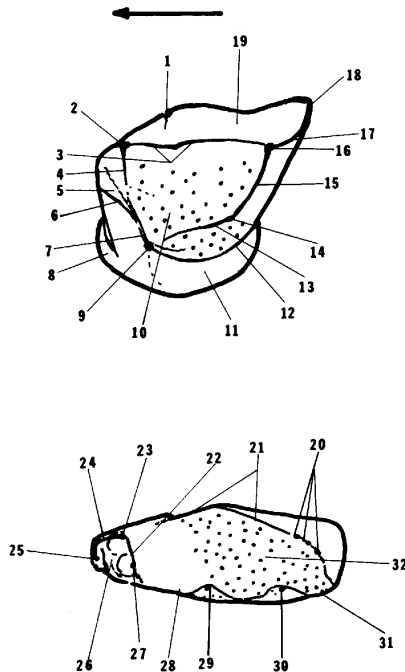


FIG. 1. Outline drawings of the first upper and lower molars of *Picrodus*, to show the dimensions measured.

with comparative remarks can prejudice a reader (particularly when underdocumented because of a lack of adequate illustrations). They tend to impede an open evaluation of the writer's conclusions by preventing the unbiased study of the evidence. The discussions that follow the descriptive sections treat the comparative aspects of the morphology and

FIG. 2. Nomenclature and suggested homologies of the structures on picrodontid molars. 1. Small cusplule, probably equivalent to a small mesostyle. 2. Paracone. 3. Centrocrista (= postparacrista and premetacrista combined). 4. Crest on lingual slope of paracone probably homologous to similar, less-pronounced crest of paramomyids. Possibly (there is no evidence) the lingual part of the crest is homologous with part of the postparaconule crista. 5. Paracingulum(?), a shelf originally formed by the paraconule at the base of the paracone. 6. Preparaconule crista. 7. Preprotocrista. 8. Precingulum. 9. Protocone. 10. Trigon basin. 11. Hypocone. 12. Postcingulum. 13. Postprotocrista. 14. Metaconule (vestigial). 15. Lower part of this crest probably premetaconule crista. 16. Metacone. 17. Postmetacrista. 18. Metastyle. 19. Styler shelf. 20. Posterobuccal cusplules; one or more may be homologues of the hypoconid. 21. Cristid obliqua. 22. Protocristid. 23. Protoconid. 24. Paracristid. 25. Paraconid. 26. Area homologous to the obliterated trigonid basin. 27. Metaconid. 28. Talonid notch. 29. Entoconid. 30. Hypoconulid. 31. Area probably homologous to the notch between the hypoconid and hypoconulid of more primitive eutherians; in the text it is referred to as the spoutlike exit of the talonid. 32. Talonid basin.



deal with the evaluations of the data, as is the common practice in most other branches of the biological and geological sciences.

An attempt was made to keep the traditionally long descriptions as short as possible. Whenever previous workers have adequately described certain aspects of the morphology in question, a mere reference to the source suffices. It is hoped that the brevity of the descriptive sections is compensated for, in a more meaningful way, by the stereophotographs.

The scales used on the photographs have 0.5 mm. subdivisions.

The manner in which the measurements were taken is shown in figure 1.

SYSTEMATICS

ORDER PRIMATES LINNAEUS, 1758

SUPERFAMILY PICRODONTOIDEA (SIMPSON, 1937), NEW RANK

TYPE: *Picrodus* Douglass, 1908.

DISTRIBUTION AND DIAGNOSIS: Same as for the family.

REMARKS: Based on the degree of dental divergence from an alleged paromomyid ancestry (fully discussed under Relationships and Evolutionary Trends, below), the known picrodontid dentition is highly modified. The changes caused by disruptive enlargements of certain parts of the molars were profound and distinctive on the resultant structures and their occlusion. In order to express such unique morphology in proportionate taxonomic ranking in relation to other Eutheria, a superfamily designation is necessary. The modification of the morphology on the magnitude that the picrodontid molars display would fully warrant superfamily separation not only in the Paleocene but also during any other time during the Cenozoic.

FAMILY PICRODONTIDAE SIMPSON, 1937

Picrodontidae SIMPSON, 1937, p. 134.

TYPE: *Picrodus* Douglass, 1908.

DISTRIBUTION: Torrejonian and Tiffanian of North America.

DIAGNOSIS: Very small primates with at least one pair of enlarged incisors, reduced premolar row, molars with papillated enamel, squared off and flattened upper molars, relatively deep mandible, unreduced coronoid process, relatively slender articular condyle, and relatively wide palate. Differing from all other known primates and from any other known Paleocene and Eocene therian in having the first molars much enlarged relative to the more posterior ones. Differing from all other

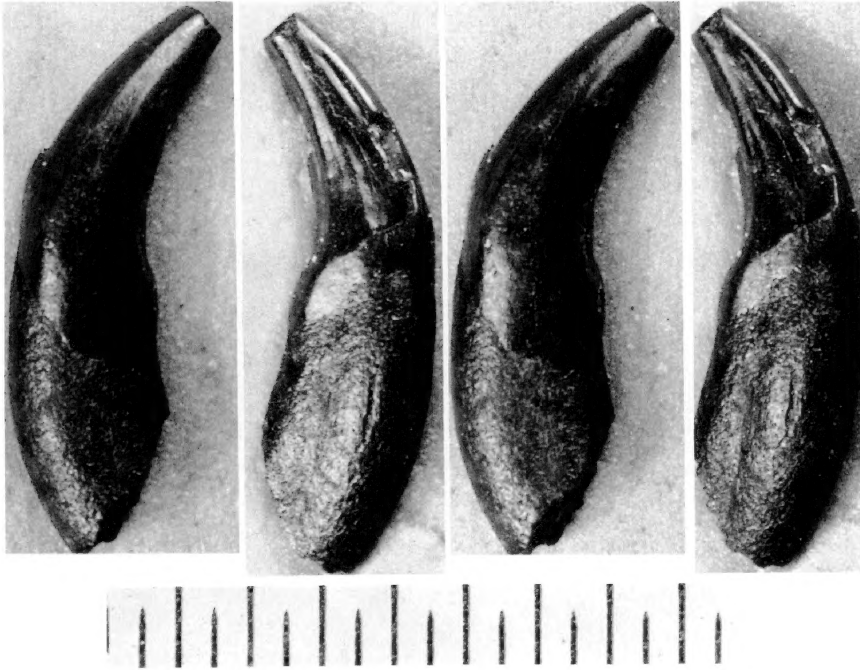


FIG. 3. Canine catalogued with U.S.N.M. No. 9866, Lebo Formation. This enlarged tooth was listed as being in probable association with a first lower molar of *Picrodus silberlingi*. I have no confidence in this alleged association. This tooth probably represents the lower canine of a small insectivore rather than the enlarged incisor of *Picrodus*.

known therians in manner of reduction and structuring of trigonid on M_1 , and in unique enlargement of the posterobuccal part of M^1 .

REMARKS: The discussion on the affinities of the family is dealt with following the taxonomy of the species and the genera.

PICRODUS DOUGLASS, 1908

Picrodus DOUGLASS, 1908, p. 17.

Megopterna DOUGLASS, 1908, p. 18.

TYPE: *Picrodus silberlingi* Douglass, 1908.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Torrejonian of Wyoming and Montana, and early Tiffanian of Wyoming.

DIAGNOSIS: Small picrodontids with enlarged lower (? and upper) incisors; both upper and lower first molars conspicuously larger and greatly modified compared with more posterior molars; trigon and talonid

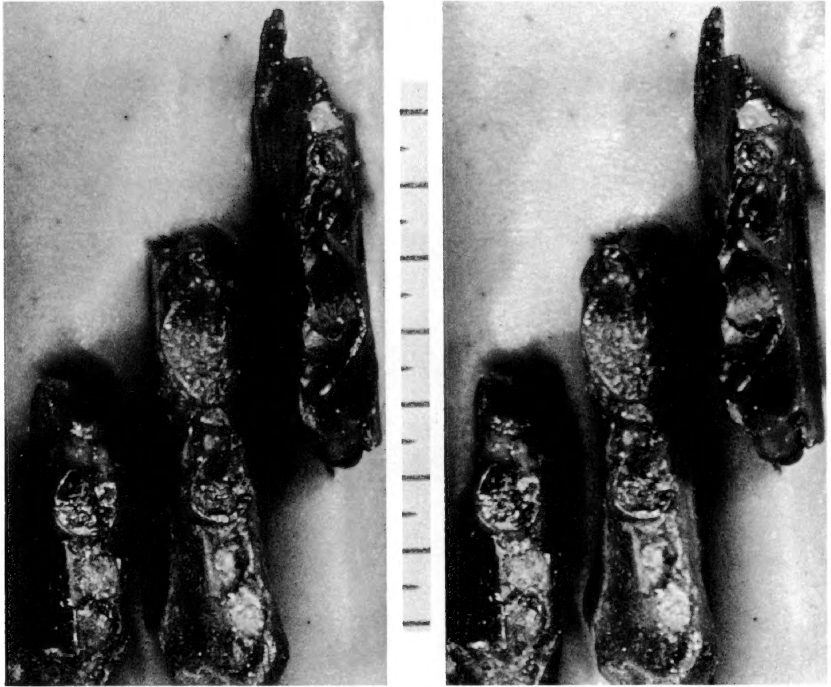


FIG. 4. *Picrodus silberlingi*. Left to right: A.M.N.H. No. 89503, M_2 ; A.M.N.H. No. 89504, M_{1-2} ; A.M.N.H. No. 89505, P_4-M_1 ; occlusal views; all from Swain Quarry.

basins with papillated, wrinkled enamel; talonid of M_1 with spoutlike outlet between hypoconulid and entoconid.

Differing from *Zanycteris* in following characters: parastylar area more reduced, stylar shelf relatively more pronounced, premetacrista relatively longer than postparacrista, paracone more reduced, postprotocrista not joining apex of protocone. Dental formula: $I_{1(?)2(?)}$; C; $P_{3,4}$; $M_{1,2,3}^{1,2,3}$.

Picrodus silberlingi Douglass, 1908

Figures 4-18; table 1

Picrodus silberlingi DOUGLASS, 1908, p. 17.

Megopterna minuta DOUGLASS, 1908, p. 18.

TYPE: C.M. No. 1675, right dentary with P_4-M_1 ; type was collected from Silberling Quarry, upper Lebo Formation, Fort Union Group, Crazy Mountain Field, Sweetgrass County, Montana.

HYPODIGM: Type and C. M. No. 1675, U.S.N.M. Nos. 9626, 9866,

TABLE 1
 STATISTICAL DATA OF *Picrodus silberlingi* FROM SWAIN QUARRY,
 FORT UNION FORMATION, CARBON COUNTY, WYOMING
 (All measurements are in millimeters.)

	N	OR	\bar{X}	S ²	S	V
M ¹						
Length	10	2.13-2.48	2.26	0.009	0.097	4.32
Width	10	1.95-2.18	2.07	0.0036	0.06	2.90
Distance between paracone and metacone	11	1.47-1.90	1.58	0.02	0.144	9.11
Distance between paracone and protocone	11	0.85-1.03	0.95	0.002	0.053	5.58
Distance between metacone and protocone	11	1.50-1.75	1.62	0.008	0.093	5.74
M ₁						
Oblique maximum diameter	10	1.75-2.13	1.97	0.0147	0.122	6.19
Posterior width	10	0.87-1.00	0.95	0.0024	0.049	5.16
M ₂						
Length	2	1.50-1.60	1.55	—	—	—
Posterior width	2	0.87-0.90	0.88	—	—	—
Anterior width	2	0.85	0.85	—	—	—
M ₃ ^a						
Length	1	—	1.37	—	—	—
Posterior width	1	—	0.95	—	—	—
Anterior width	1	—	0.95	—	—	—

^a A.M.N.H. No. 25463, from Lebo Formation.

A.M.N.H. Nos. 35453, 35454, 35458, 35459. All previously listed specimens were collected from either Silberling Quarry or Gidley Quarry of the Lebo Formation. A.M.N.H. Nos. 89502, 89503, 89504, 89505, 89507, 89509, and 89510 were collected from Swain Quarry, lower part of the Fort Union Formation, Carbon County, Wyoming, SE. $\frac{1}{4}$, NE. $\frac{1}{4}$, sect. 3, T. 15 N., R. 92 W. The specimens of *Picrodus* sp. cf. *P. silberlingi* reported by McGrew and Patterson (1962) from the Bison Basin Saddle locality and from the Shotgun Member of the Fort Union Formation are also considered to belong to this species.

SPECIFIC DIAGNOSIS: Only known species of the genus.

DESCRIPTION AND INTERDEME AND INTRADEME VARIATION

MANDIBLE: Although no complete dentaries are known in the available collections, several relatively well-preserved mandible fragments allow a complete, accurate reconstruction of the lower jaw (fig. 18). A.M.N.H. Nos. 35453, 35459, 89502, 89504, and 89505 are the most



FIG. 5. *Picrodus silbertingi*, A.M.N.H. No. 89507, sample of first lower molars, occlusal views; Swain Quarry.



FIG. 6. *Picrodus silberlingi*. Left to right: A.M.N.H. No. 25453, M_{1-3} ; A.M.-N.H. No. 35348, M_{1-2} ; occlusal views; Lebo Formation.

important specimens that served as bases for the reconstruction of the dentary. Each of these specimens is figured.

The posterior limit of the symphysis extends under the anterior root of P_4 . It is difficult to estimate the extent of the genial pit, although it is undoubtedly a large part of the relatively concave middle section of the symphyseal surface. The deep mandible is relatively short. The masseteric fossa is large and relatively well excavated; it is well demarcated anteriorly by a distinct crista coronoidea. The coronoid process is relatively very large, and the articular condyle (see A.M.N.H. No. 35459, figs. 12 and 13) is above the level of the lower dentition. The articular surface of the condyle is not very extensive; the condyle itself is very small compared with the size of the mandible. A detailed description of the chipped and worn articular surface is not possible. Although the angle is thickly coated to hold the fragmented bone together on A.M.-N.H. No. 35459, it can be clearly seen that it is wide at its base and tapers into a slightly hooked, dorsally turned point. On the medial sur-

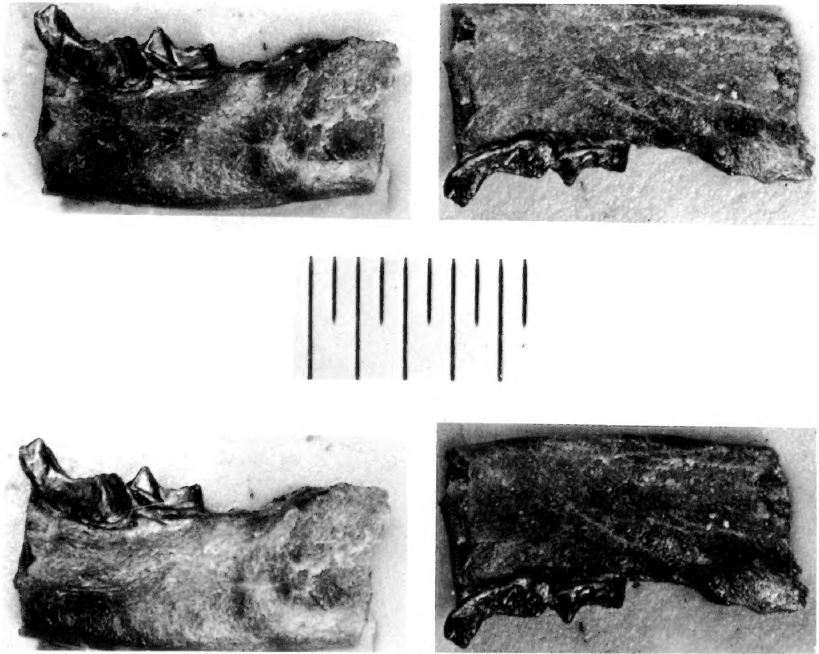


FIG. 7. *Picrodus silberlingi*, A.M.N.H. No. 89504, lateral and medial views of posterior half of horizontal ramus of left dentary with M_{1-2} ; Swain Quarry.

face of the angle there is a pronounced crest from the base to the tip for the insertion of the internal pterygoid muscle.

The number of mental foramina appears to be variable, although the largest foramen appears to be quite consistently under P_3 or slightly anterior to it. The number of dentary fragments that show the area in question, however, is not more than five. On A.M.N.H. No. 89502 (fig. 8), immediately behind the large mental foramen, which is partly under P_3 and partly under the tooth anterior to P_3 , there is a somewhat smaller foramen under the anterior root of P_4 . Both of these foramina are approximately equidistant from the dorsal and ventral limits of the dentary above and below them. On this specimen there is a tiny third foramen above the posterior mental foramen. On A.M.N.H. No. 89505 (fig. 9) the large anterior foramen is completely under P_3 , and the foramen posterior to it is under the anterior root of M_1 . There is no indication of a third foramen as on A.M.N.H. No. 89502, also from Swain Quarry. The two principal foramina are more separated on A.M.N.H. No. 89505 than on A.M.N.H. No. 89502.

The dental foramen is relatively far back on the ascending ramus,

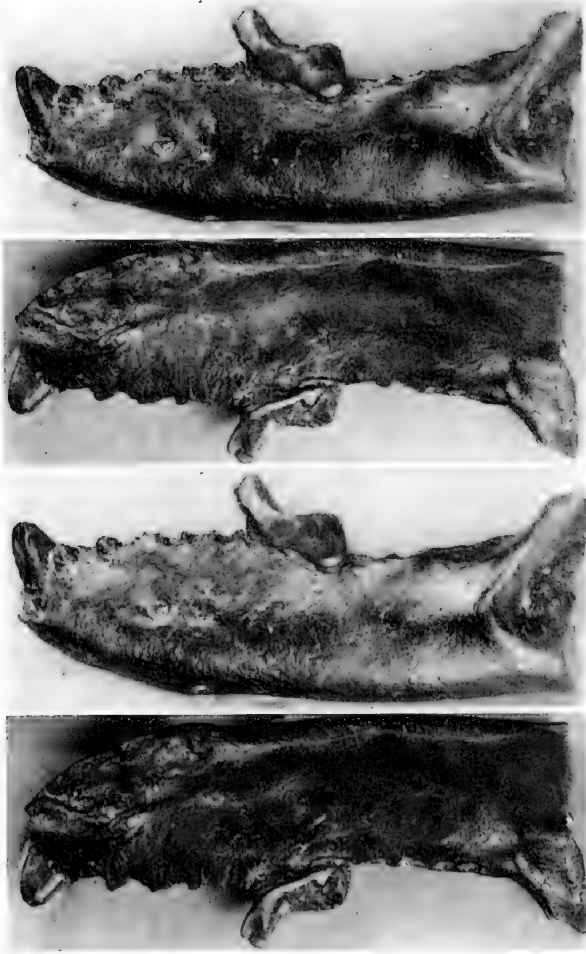


FIG. 8. *Picrodus silberlingi*, A.M.N.H. No. 89502, medial and lateral views of the horizontal ramus of the left dentary, with broken root of enlarged incisor and M₁; Swain Quarry.

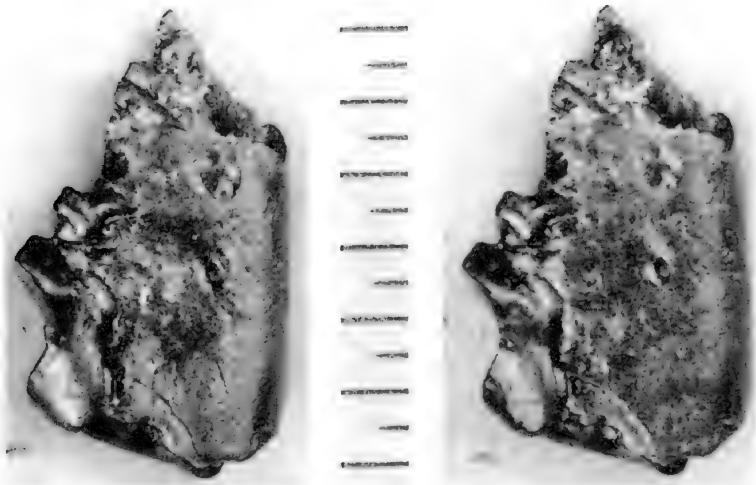


FIG. 9. *Picrodus silberlingi*, A.M.N.H. No. 89505, lateral view of anterior part of right dentary with P_4 - M_1 and alveoli for the antemolar dentition; Swain Quarry.

approximately equidistant from the base of the angle and the articular condyle itself. It is preserved only on A.M.N.H. Nos. 35453 and 35459. The large foramen is slitlike, and it opens posteroventrally.

LOWER ANTEMOLAR DENTITION: The most anterior tooth in the mandible, presumably an enlarged incisor (see discussion of homologies under Relationships, below), was greatly enlarged and extended posteriorly past the level of the large mental foramen, under P_4 . Inferred from the alveolus, immediately posterior and slightly lateral to the greatly enlarged anterior incisor there was a slim, procumbent tooth closely appressed to the first tooth; it was probably another incisor. This latter incisor, unlike the anterior one, was not enlarged. It is clear from A.M.N.H. No. 89505 that the slender root extended obliquely to the large mental foramen under P_3 . Unfortunately, no *in situ* incisors are known in the available collection. Simpson (1937, p. 137) described a tooth (illustrated in fig. 3 of this paper) as possibly in association with A.M.N.H. No. 9866 (M_1 of *P. silberlingi*). I have no confidence in this association. The tooth is unlike the enlarged lower incisor of any Paleocene primate known to me. Furthermore, its root is too large and bulky to fit any of the *Picrodus* mandibles. It might represent the lower canine of a small insectivore (possibly a pantolestid) or a palaeoryctoid.

Judged from the relation between the two alveoli posterior to the slight incisor and anterior to P_4 , it is doubtful that the two alveoli



FIG. 10. *Picrodus silberlingi*, U.S.N.M. No. 9626, medial view of incomplete right dentary, showing the posterior extent of the enlarged incisor; Lebo Formation.

represented a two-rooted tooth. If the two roots in these alveoli supported one tooth, then this tooth would have been almost twice as long as the double-rooted P_4 . I have no confidence in this possibility. It appears most probable to me that the relatively large, round alveolus anterior to P_4 (i.e., the tooth anterior to M_1) housed the single root of P_3 . The alveolus anterior to the presumed single-rooted P_3 was the root of a canine. Much of the pertinent discussion of the antemolar homologies of *P. silberlingi* is treated under Relationships, below. Neither a canine nor the tooth behind it (judged to be the P_3) is known in the available collections. The single alveolus of P_3 , however, judged from A.M.N.H. Nos. 89502 and 89505, was slightly more robust than either of the alveoli for P_4 .

The fourth lower premolar is well known in several specimens (A.M.N.H. Nos. 35454, 35459, and 89505). In comparison with the first molar posterior to it, the slightly procumbent P_4 is small and simple. The least crushed and most natural orientation of the tooth in the mandible is probably best preserved on A.M.N.H. No. 35454 (figs. 14 and 15). A faint protuberance on the anterolingual base of the protoconid indicates the presence of an incipient metaconid, although for all functional purposes this metaconid is largely unimportant. The



FIG. 11. *Picrodus silberlingi*, A.M.N.H. No. 35453, medial view of incomplete left dentary with M_{1-3} ; Lebo Formation.

homologue of the talonid on P_4 is a slight heel that fits under the small paraconid of M_1 .

LOWER MOLAR DENTITION: M_1 was thoroughly described by Simpson (1937, pp. 137-138); its redescription is not necessary. McGrew and Patterson (1962, p. 4) noted that the number of cuspsules on the cristid obliqua on specimens collected from the Lebo Formation varies from two to three. The Swain Quarry sample, which is larger and less badly weathered, shows these cuspsules to vary from two or three to as many as seven or eight. The more anterior cuspsules are essentially large rugosities, similar to those immediately lingual to them in the talonid basin. McGrew and Patterson reported that these cuspsules vary from four to nine on the first molars of the Shotgun local fauna sample. I have thoroughly examined the Lebo and Swain Quarry samples and the

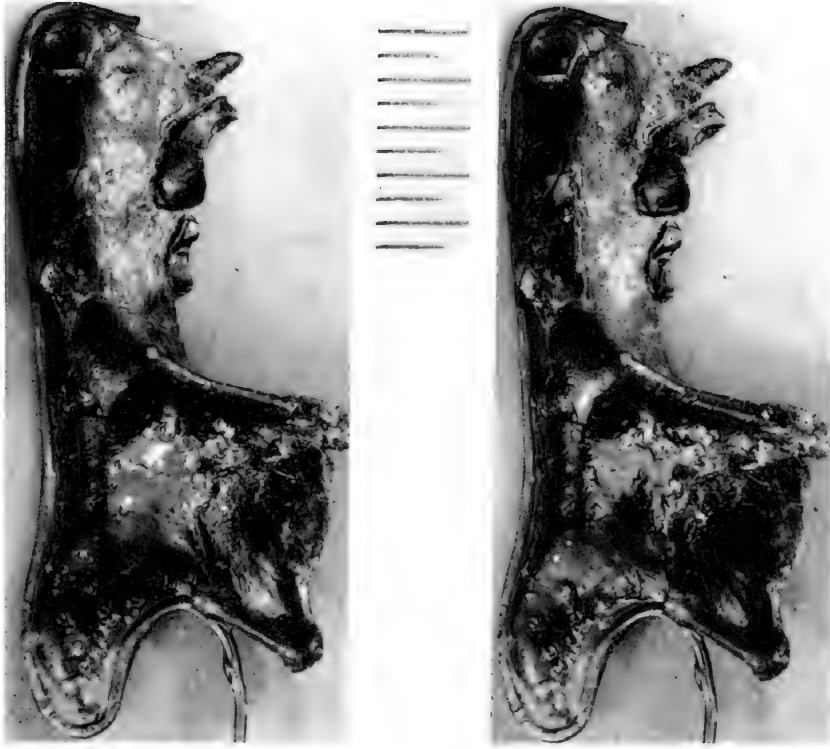


FIG. 12. *Picrodus silberlingi*, A.M.N.H. No. 35459, lateral view of incomplete left dentary with P₄-M₂; Lebo Formation.

stereophotographs of the two M₁'s published by McGrew and Patterson, and found that on all three samples there are two to three of these cusps on approximately the same posterobuccal segment of the cristid obliqua. These cusps are larger in size than the more variable, proliferated small to tiny protuberances on the more anterior segment of the cristid obliqua.

As McGrew and Patterson determined for the Shotgun sample, the two lingual cusps in the Swain Quarry sample are also highly variable in definition and size. The variation of the two cusps (the anterior one in the present report is called the entoconid and the one posterior to it the hypoconulid) can be thoroughly appreciated after a brief examination of figure 5. These nine isolated M₁'s from Swain Quarry also illustrate the diagnostic opening from the talonid basin, called a spout-like exit by Simpson (1937, p. 138). In addition to showing the wide size range for this tooth, this sample appears to show that the posterior

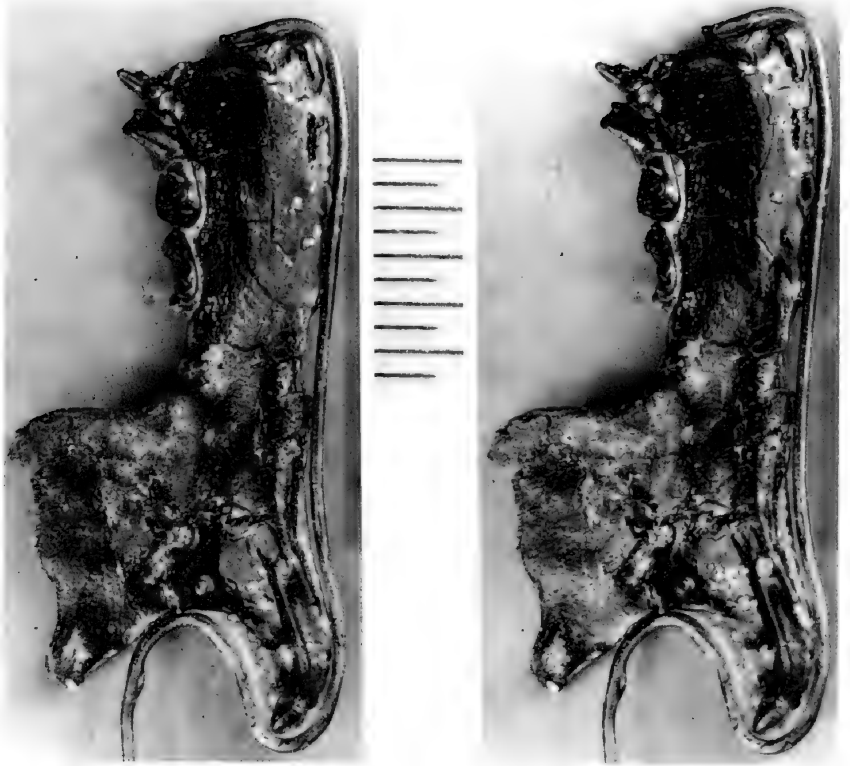


FIG. 13. *Picrodus silberlingi*, A.M.N.H. No. 35459, medial view of incomplete left dentary with P_4 - M_2 ; Lebo Formation.

face of the trigonid is unapillated as opposed to the talonid basin. There is no distinct line of demarcation, however, between the posterior face of the trigonid and the talonid basin. McGrew and Patterson (1962, p. 4) reported the paraconid to be invariably larger and higher than the metaconid in the Shotgun sample. Their figure 2b does not support this rigid distinction. I find the relative size and height of these two small cusps (compared to the large protoconid) quite variable in both the Lebo and Swain Quarry samples. This variation is partly real and partly the result of preservation and wear.

M_2 is much smaller and less specialized than M_1 . An ectocingulid is present, although it is not very accentuated. This tooth has a relatively larger and lower trigonid than M_1 . The protoconid is the strongest cusp, and the reduced metaconid is slightly larger than the paraconid. The paracristid runs forward and slightly laterally and then very sharply

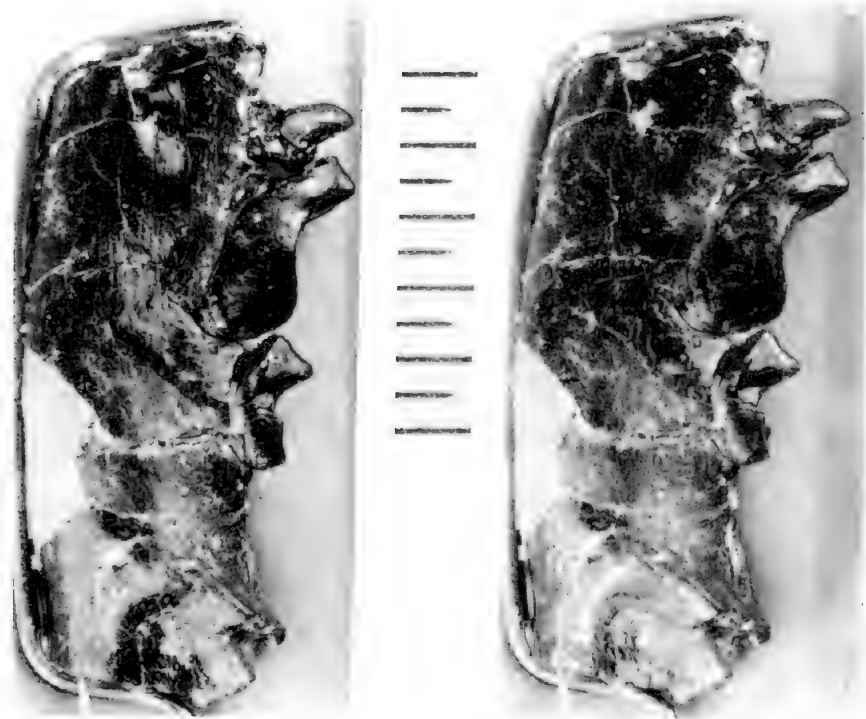


FIG. 14. *Picrodus silberlingi*, A.M.N.H. No. 35454, lateral view of part of left dentary with P₄-M₂; Lebo Formation.

turns posteromedially to join the small paraconid. The bulging base of the protoconid obliterates what has been the trigonid basin. In occlusal view the talonid is very rounded in appearance. It is papillated by the wrinkled enamel as is the talonid of M₁. The cristid obliqua joins the buccal part of the base of the protoconid. This condition holds true for most of the M₂'s from the Lebo Formation and Swain Quarry. An exception in the relatively very small known sample (about five M₂'s) is A.M.N.H. No. 35458 (see fig. 6) from Gidley Quarry. On this specimen the cristid obliqua turns more medially to join the posterior surface of the protoconid on M₂. The right M₂ figured by McGrew and Patterson (1962, fig. 2c, M.C.Z. No. 8422), from the Shotgun local fauna, shows the condition encountered on the majority of M₂'s. There is no discernible cusp either on the postcristid or on the cristid obliqua on any of the M₂'s known to me, except on A.M.N.H. No. 35458. On the M₂ of this specimen there are two faint cuspules, or rugosities, as on the postcristid and cristid obliqua of M₁'s. On the medial side of the talonid

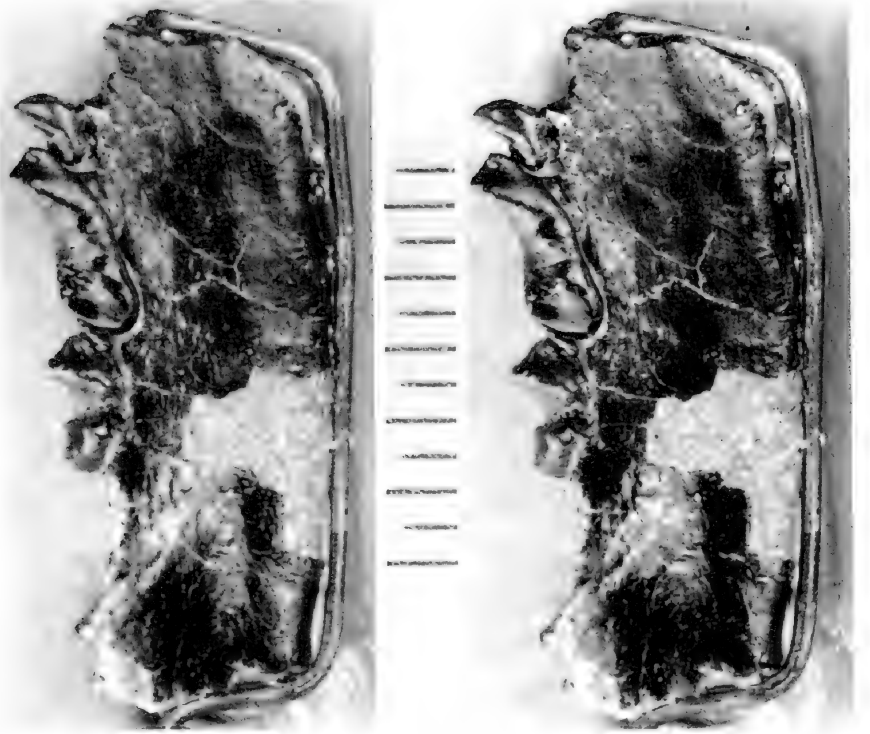


FIG. 15. *Picrodus silberlingi*, A.M.N.H. No. 35454, medial view of part of left dentary with P_4 - M_2 ; Lebo Formation.

the entoconid and hypoconulid are invariably present.

M_3 is known only from one specimen from the Lebo Formation. This specimen, A.M.N.H. No. 35453 (figs. 6 and 11), has not been reported or described before. The trigonid of this M_3 is strikingly different from that of both M_1 and M_2 . The paraconid is entirely absent; consequently the trigonid has lost its triangular outline. Immediately anterior to the protoconid, the paracristid turns lingually. Although it appears that the metaconid was larger and a higher cusp than the protoconid, the worn nature of the protoconid on the only known M_3 prevents a more certain assessment. At any rate, the metaconid on M_3 is relatively larger and distinctly taller than it is on M_2 . The trigonid notch, the cleft between the protoconid and the metaconid, is deep and separates these two cusps down to their bases. Although the trigonid of M_2 is distinctly longer than that of M_3 , the talonid of the last molar is about as long as that of the second. Of the talonid cusps on the only

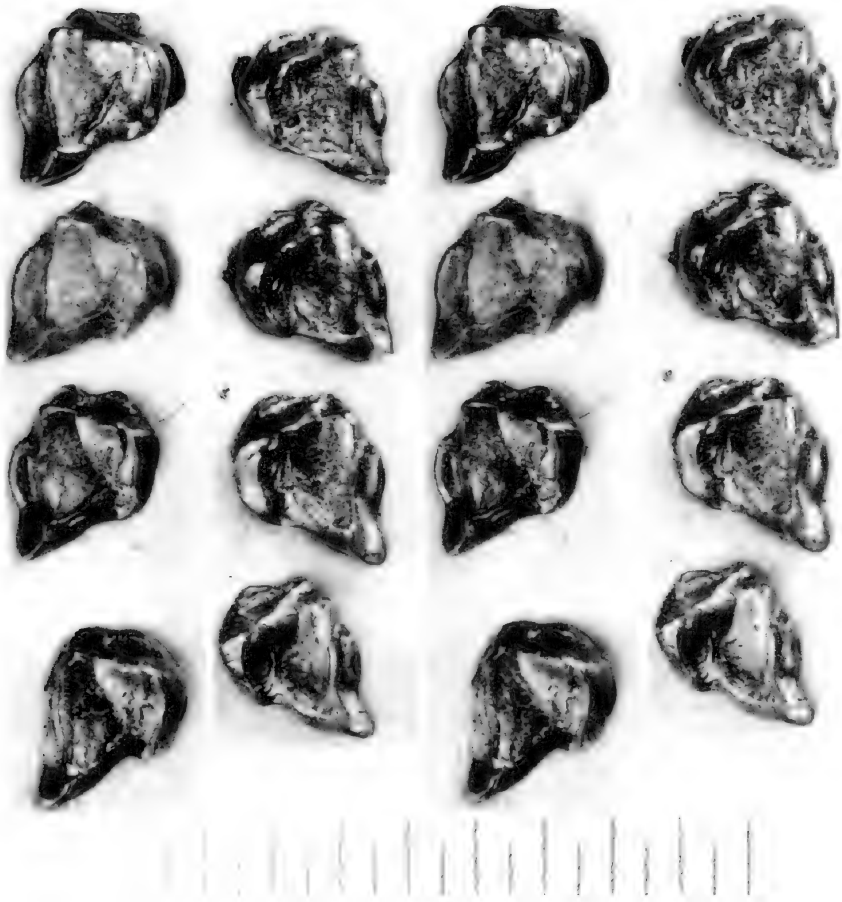


FIG. 16. *Picrodus silberlingi*, sample of M^1 's, showing variation and various stages of wear. *Left*: A.M.N.H. No. 89509. *Right*: A.M.N.H. No. 89510. Both Swain Quarry.

known specimen, only the lingual entoconid and hypoconulid are discernible. These two cusps are in the same approximate positions on the talonid as those on M_2 .

UPPER DENTITION: The first upper teeth of this species were reported by McGrew and Patterson. In addition to the M^1 's reported from the Shotgun local fauna, the Bison Basin Saddle locality yielded a left maxilla fragment with $M^{1,2}$ (U.W. No. 1780). This M^2 is the only one known; no M^3 's are known. Although a relatively large sample of first upper molars was found in the very large bulk of concentrate from Swain Quarry, no second or third upper molars were encountered. No

upper teeth are known in the collections from the Lebo Formation of the American Museum of Natural History or those of the United States National Museum.

The buccal planes of M^1 and M^2 illustrated by McGrew and Patterson form an angle of approximately 155 degrees.

M^1 is a peculiar tooth, and it is best characterized by its exceptionally reduced cusps and the chopped-off appearance of the parastylar area. In contrast to the complete absence of the anterobuccal corner of the tooth, there is a prominent posterobuccal wing. A short postmetacrista runs onto that wing from the metacone; the metacone itself is at the base of this posterobuccal wing. A relatively wide stylar shelf is present (probably as a result of the reduced paracone and metacone). On the most anterior and buccal corner of the stylar shelf there is a slight cuspule, topographically in the right position to be a mesostyle. The paracone and metacone are widely separated, and the centrocrista stretching between them is only barely divisible into a short postparacrista and a much longer premetacrista. A short crest (its homology is discussed under Relationships) runs lingually from the paracone. This crest is interrupted by a faint groove that leads into the trigon basin, then the crest continues as the preprotocrista. A presumed preparaconule crista runs anterolaterally from the preprotocrista slightly buccal to the protocone. The precingulum is strong, and it forms a large anterolingual pocket. The protocone is on the anterior half of the tooth, only slightly posterior to the imaginary direct line from the paracone to the palate. Posterobuccal to the protocone the postprotocrista is not directly connected to the cusp. In the proximity of the protocone the postprotocrista is faint and thin, but it becomes thicker as it runs posterobuccally, and it joins the crest formed on the lingual slope of the metacone. There appears to be a tiny remnant of the metaconule at the point where the postprotocrista turns more buccally or, rather, at the point where this crest is on the lingual slope of the metacone. Added to the trigon basin is the large pocket formed by the postcingulum (and the hypocone) from the protocone apex to the posterior border of the tooth. The enamel within the trigon basin and in the additional posterolingual area is as papillated as the talonid basins of the lower molars.

The prominent hypocone is essentially the large and bulging postcingulum. A faint but well-discernible fold is present between the most lingual extension of the postprotocrista and the anterior third of the postcingulum that runs onto the protocone.

A.M.N.H. No. 89508 from Swain Quarry (see fig. 17) consists of three left M^1 's. These three teeth, despite the different degrees of wear, clearly

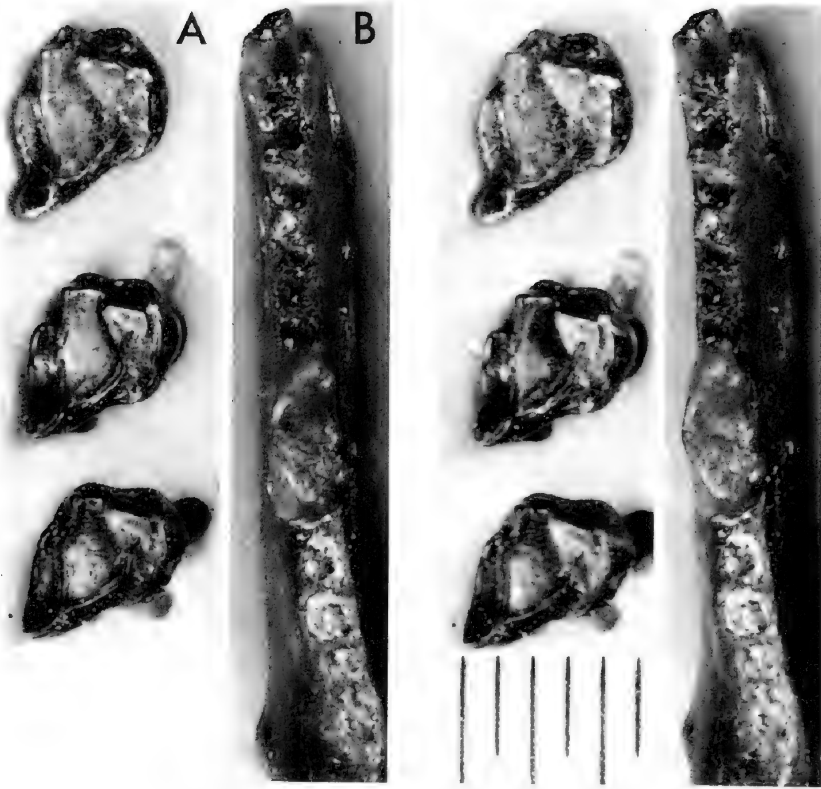


FIG. 17. *Picrodus silberlingi*. A. A.M.N.H. No. 89508, first upper molars. B. A.M.N.H. No. 89502, M_1 in dentary. Both occlusal views and both from Swain Quarry.

show the spectrum of intrademe variation of this tooth in the species. On the top of figure 17, at one extreme of the spectrum, the tooth is very elongated, showing all characteristic features accentuated to an extreme. This M^1 is relatively longer than the one shown on the bottom of the same figure. The elongation of the premetacrista in relation to the postparacrista and the enlargement of the hypocone are the observed extremes in the species on the M^1 on the top of the figure. The bottom tooth shows the minimum development of the features noted. Although these three teeth belonged to different individuals of the same deme, it is very likely that the M^1 on the bottom of the figure is structurally closer to a more primitive morphology.

The only second upper molar of *P. silberlingi* known to me is that of U.W. No. 1780 from the Bison Basin Saddle locality, illustrated by

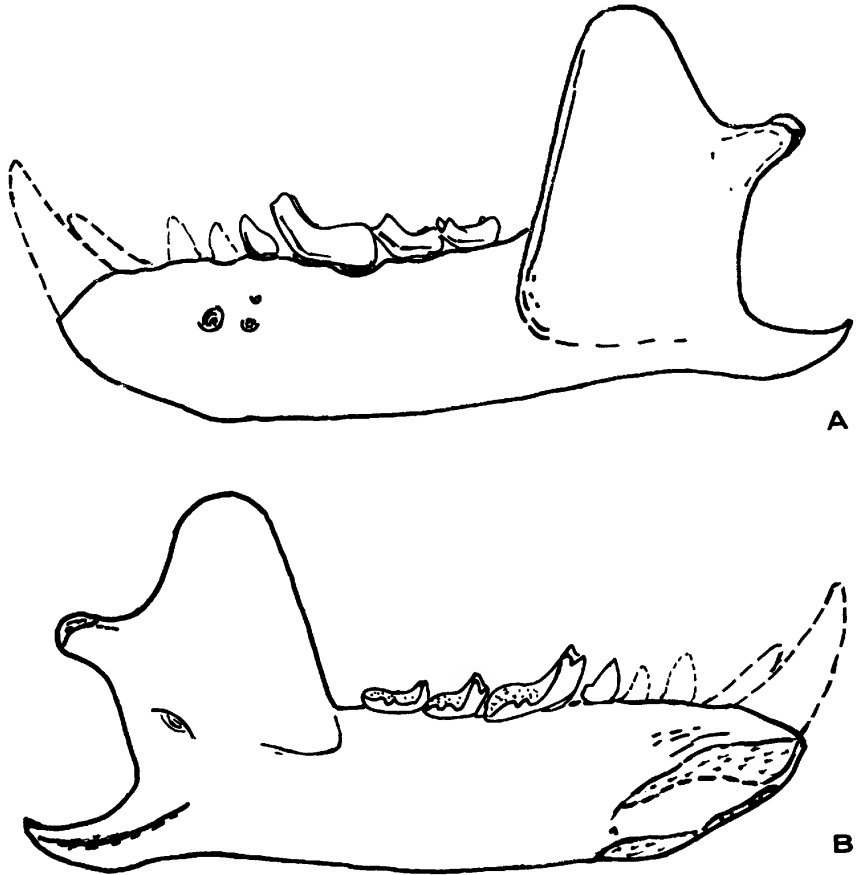


FIG. 18. Reconstructed dentary of *Picrodus silberlingi*. A. Lateral view. B. Medial view, $\times 6$.

McGrew and Patterson (1962, fig. 1a). The stylar shelf is wider buccal to the paracone than it is above the metacone. There is a faint, weak preparacrista. The protocone is well formed, almost directly lingual to the paracone. The preprotocrista appears to be continuous with the crest that is most likely the preparaconule crista. Judged from the stereophotographs published by McGrew and Patterson, the crest formed on the lingual slope of the paracone is not continuous, or is not directly in line, with the preprotocrista, unlike the situation on M^1 . The trigon basin and the depression formed between the postcingulum and post-protocrista (the latter completely obliterated) are continuous and represent a functional unit as on M^1 .

The third upper molar of this species is not known in any collection available to me.

DISCUSSION: On the basis of extensive comparisons of the published stereophotographs of McGrew and Patterson with the samples of *Picrodus silberlingi* from the Lebo Formation and the Swain Quarry, I find the fossils reported by these authors as *Picrodus* sp. cf. *P. silberlingi* to be conspecific on morphological criteria with *P. silberlingi*. Many homologous structures of the samples in question are lacking and only on the basis of additional specimens can the specific taxonomy be settled.

As quite correctly noted by McGrew and Patterson, *Picrodus* is more advanced, although it appears earlier on the record, than *Zanycteris*. This statement is based only on the morphology of the first upper molar; therefore additional specimens may alter this view. The morphology of the unknown lower teeth of *Zanycteris* will be crucial in a re-evaluation of the status of these two genera.

Simpson's (1937, p. 138) observed range for the oblique maximum diameter of M_1 (OMD, the distance from the tip of the paraconid to the posterolingual border of the talonid) from the Lebo Formation was given as 2.6–2.9 mm. The observed range of OMD for M_1 's of the Swain Quarry *Picrodus silberlingi* is 1.75–2.13, measured with an ocular micrometer and checked for accuracy with a Helios caliper calibrated to one-twentieth of a millimeter. Measured by these instruments, the Lebo sample in the American Museum showed an observed range within that of the Swain Quarry sample.

ZANYCTERIS MATTHEW, 1917

Zanycteris MATTHEW, 1917, p. 569.

Palaeonycteris WEBER AND ABEL, 1928, p. 159.

TYPE: *Zanycteris paleocenus* Matthew, 1917.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Tiffanian of Colorado.

DIAGNOSIS: Small picrodontids with posteriorly wide palate, probably one (?) enlarged upper incisor, three premolars, and three molars; first molar largest of three. Posterior half of palate much widened compared to muzzle. Characters differentiating *Zanycteris* from *Picrodus* listed under generic diagnosis of latter genus. Dental formula: $I^{(?)}$; C; $P^{2,3,4}$; $M^{1,2,3}$.

Zanycteris paleocenus Matthew, 1917

Figures 19–22; table 2

Zanycteris paleocenus MATTHEW, 1917, p. 569.

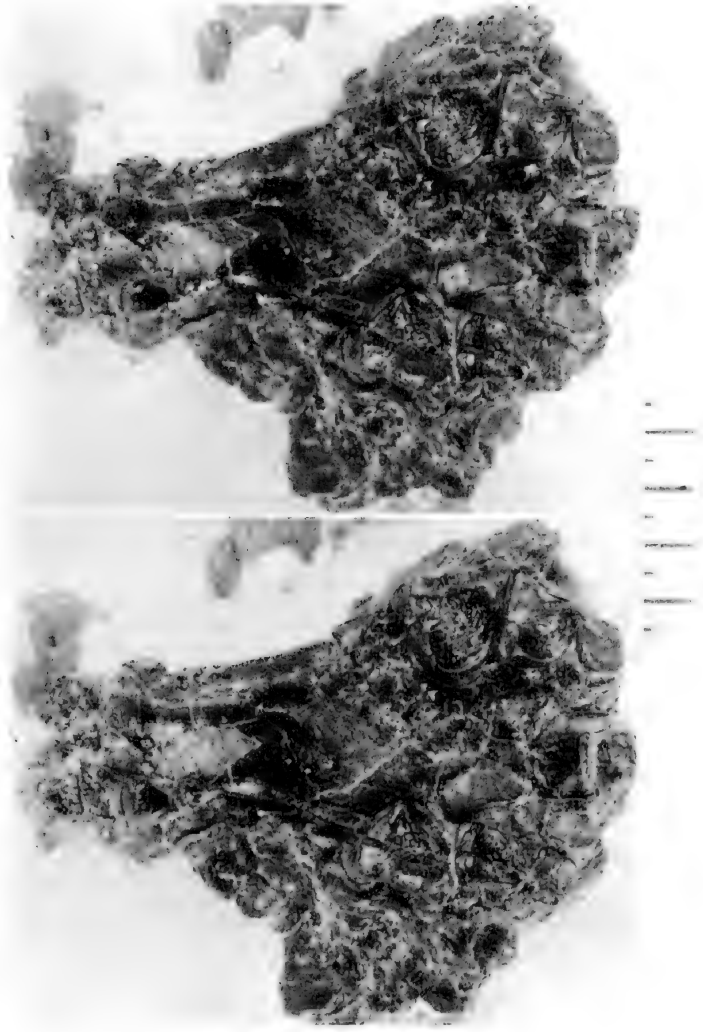


FIG. 19. *Zanycteris paleocenus*, A.M.N.H. No. 17180, ventral view of palate; Mason Pocket, Tiffany Formation.



FIG. 20. *Zanycteris paleocenus*, A.M.N.H. No. 17180, ventral view of right side of palate.

Palaeonycteris paleocenica WEBER AND ABEL, 1928, p. 159.

TYPE: A.M.N.H. No. 1780, crushed skull with the palate exposed; three molars on both sides and canine on right side preserved, other teeth missing. The type was collected from the Tiffany Formation, Mason Pocket, sect. 20, T. 33 N., R. 6 W., Ignacio, Colorado.

HYPODGM: Type only.

SPECIFIC DIAGNOSIS: Only known species of genus.

DESCRIPTION

No element of the lower jaw or lower teeth is known to me in any of the available collections.

PALATE: Figure 22 represents my attempt at reconstructing the palate of this species. A ready comparison can be made with the only known specimen, shown in figures 19–21. Reconstruction of the muzzle anterior to the canine is conjectural, although the anteriormost tip of the palate on the right side appears to be a worn stump of an enlarged incisor. The premaxilla-maxilla and maxilla-palatine sutures are highly conjectural parts of the reconstruction. There appears to be a faint suggestion from the broken left part of the palate, however, that the maxilla-palatine suture did not extend anterior to M^1 . The only known specimen is too badly twisted to show all important aspects of the crushed skull in one view. Several stereophotographs were needed to

TABLE 2
 NUMERICAL DATA OF THE TYPE OF *Zanycteris paleocenus*, A.M.N.H. No. 17180,
 FROM MASON POCKET, TIFFANY FORMATION, COLORADO
 (All measurements are in millimeters.)

	M^1		M^2		M^3	
	Left	Right	Left	Right	Left	Right
Length	2.05	2.13	1.25	1.25	0.85	0.82
Width	1.87	1.85	1.60	1.55	1.00	1.00
Distance between paracone and metacone	1.42	1.37	1.00	0.90	0.52	0.54
Distance between paracone and protocone	1.22	1.13	0.98	0.84	0.55	0.63
Distance between metacone and protocone	1.50	1.50	1.20	1.10	0.90	0.85

give satisfactory representation of the palatal and dental morphology.

On the left side of the palate there appears to be a broken-off, intact segment of the posterolateral part of the ventrally exposed palatine. This broken piece, with a rather thick palatine torus, may be interpreted as showing that the posterior edge of the palate was considerably posterior to M^3 . Because I am not certain where the posterior border of the secondary palate is lateral to the palatine torus, the reconstruction is a necessary compromise, as shown by broken lines on the figure.

INFRAORBITAL FORAMEN: The relatively high, slitlike infraorbital foramen is above P^4 . Although the foramen appears to be slitlike, it must be remembered that the type specimen is badly crushed. Only the base of the zygoma is preserved. It originated above the posterior half of M^1 and the entire length of M^2 .

ANTEMOLAR DENTITION: The most anterior tooth preserved on the

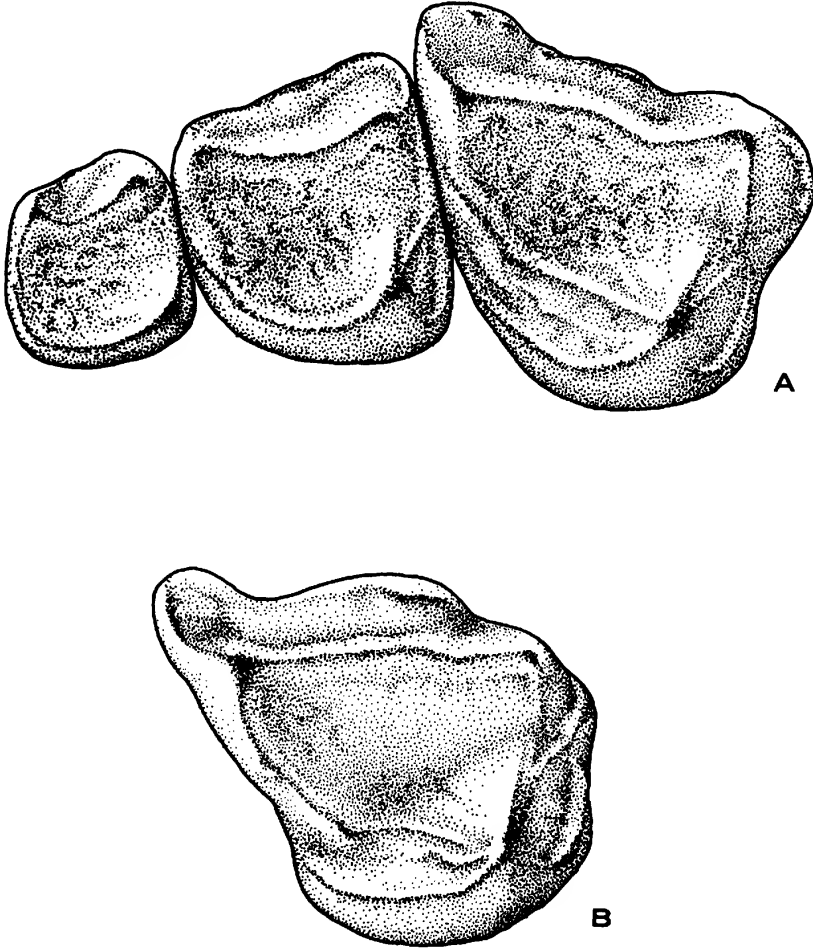


FIG. 21. A. *Zanycteris paleocenus*, A.M.N.H. No. 17180, M^{1-3} , occlusal view; Mason Pocket. B. *Picrodus silberlingi*, A.M.N.H. No. 89508, M^1 , occlusal view; Swain Quarry.

palate is a large, caniniform tooth on the right side. Judged from the suture that may be recognized anterior to it, the tooth is the canine. It is premolar-like in appearance; posterior to the main cusp, the paracone, the base of the tooth is lightly extended posteriorly in a premolar-like fashion.

There is a large diastema between the canine and the alveoli of the double-rooted premolar (known only from its alveoli) behind the canine. These faintly separated alveoli held a probably caniniform, elongated

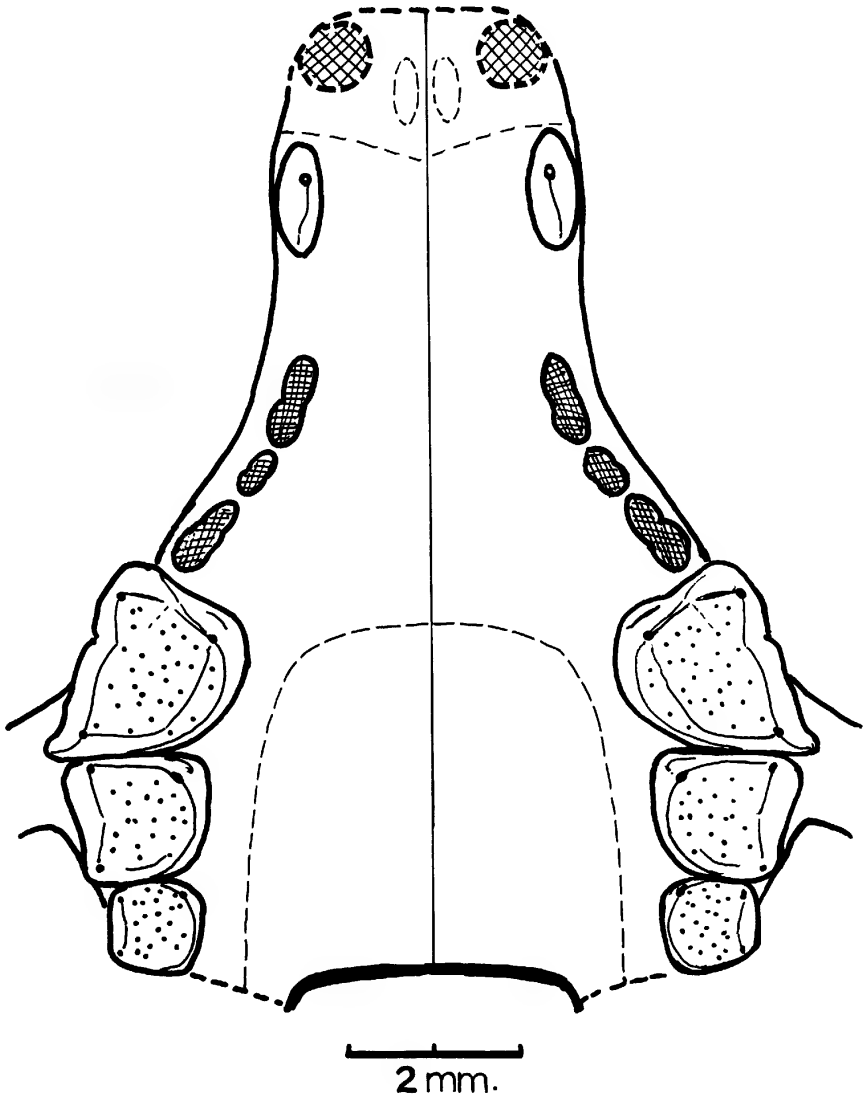


FIG. 22. Reconstructed palate of *Zanycteris paleocenus*.

P². Judged from their alveoli, both P³ and P⁴ were double-rooted, P⁴ lacking a third, lingual root. It appears that the posterior root of P⁴ was probably more robust than the anterior one.

MOLAR DENTITION: M¹ is distinctly the largest and most important of the upper molars. M² is considerably smaller, and M³ is the smallest

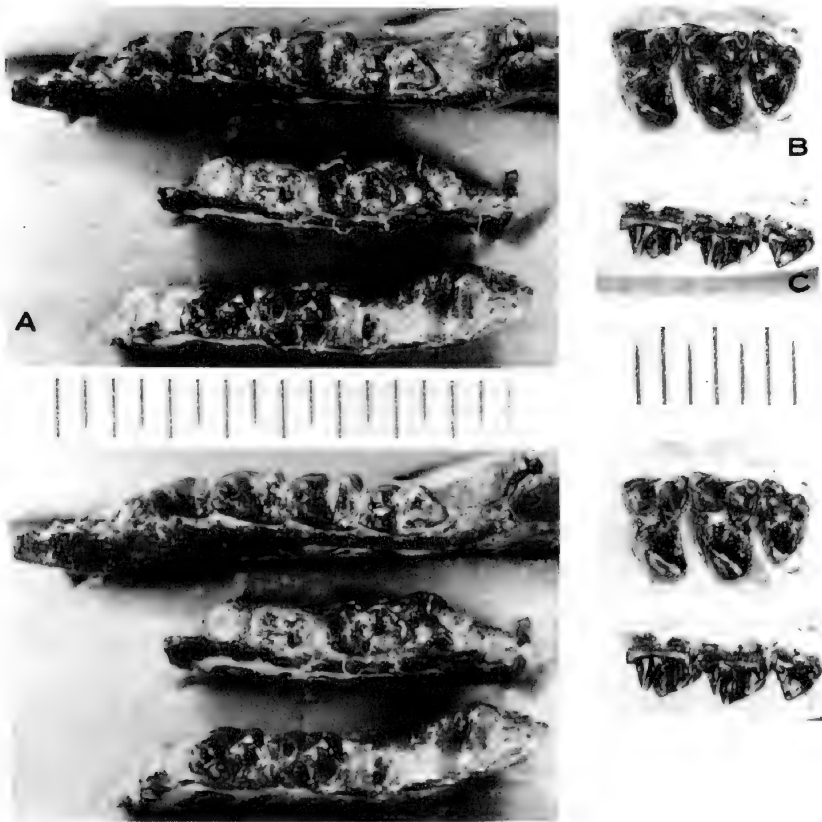


FIG. 23. *Palenochtha minor*. A (from top down). U.S.N.M. No. 9639, P_4 - M_3 ; U.S.N.M. No. 9632, M_3 ; U.S.N.M. No. 9647, M_{1-2} , occlusal views. B, C. U.S.N.M. No. 9590, composite M^{1-3} . B. Occlusal view. C. Buccal view. All from the Lebo Formation.

of the molar row. The buccal walls of M^1 and M^2 form an angle which measures 135–140 degrees lingually. Those of M^2 and M^3 form an obtuse angle of 150–155 degrees, measured on buccal limits of the teeth. The enamel on the trigon basins is papillated by fine wrinkles.

The paracone on M^1 is relatively large compared with the metacone. The postparacrista is distinctly shorter than the premetacrista. Although faintly, the postprotocrista is present all the way onto the apex of the low protocone. The parastylar area is relatively small, and the postero-buccal area of the tooth is drawn out and elongated. The precingulum is distinct, although not very extensive. A broad and important hypocone is essentially the much-expanded postcingulum. On M^2 the postcingulum (i.e., the hypocone also) is completely incorporated into the

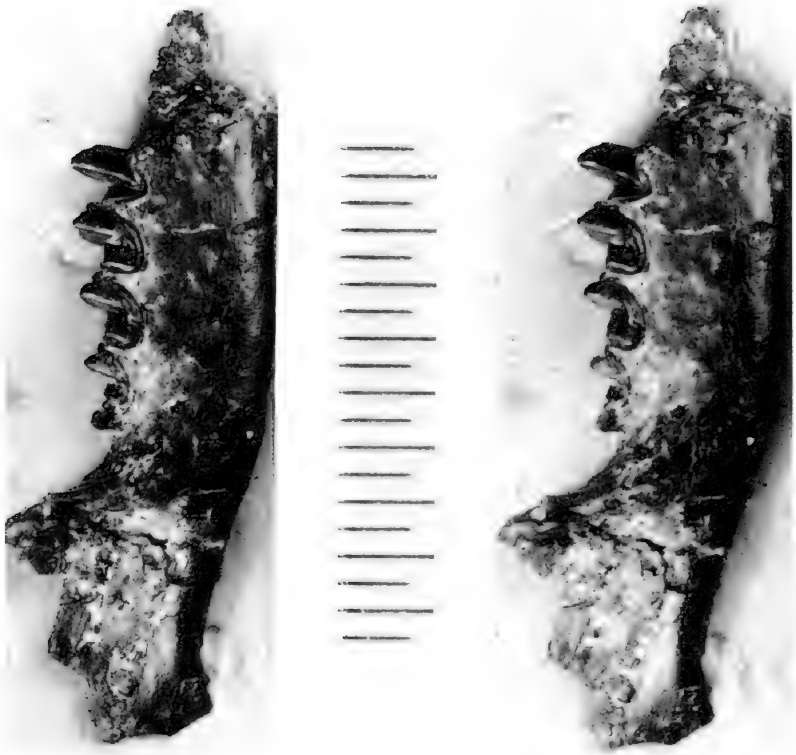


FIG. 24. *Palenochtha minor*, U.S.N.M. No. 9639 (type), incomplete right dentary with P₄-M₃, lateral view; Lebo Formation.

trigon basin. No traces of the postprotocrista or the postcingulum can be distinguished in that, or any other, area of the M². Adjacent to the posterior border on the buccal half of this tooth, a faint, short crest may be the remnant of one of the crests leading to the metaconule. Neither paraconule nor metaconule shows any traces.

The most distinguishing features of M³ are the equal-sized paracone and metacone, and the wide lingual half of the tooth. On M³ the lingual half of the tooth is wider than the buccal one. As on M², the postprotocrista is missing, and the hypocone is functionally incorporated into the trigon basin which forms a large, anteroposteriorly oriented trough.

DISCUSSION: *Zanycteris* is known from one specimen only. It appears to display a more primitive dental morphology than the earlier *Picrodus*, judged from the structure of M¹. Because the poorly known family is recorded by two genera only, almost all the available evidence has a



FIG. 25. *Palenochtha minor*, U.S.N.M. No. 9639 (type), medial view; Lebo Formation.

bearing on the broader affinities of the family. Much of what is known is discussed under Function and under Relationships, below.

RELATIONSHIPS

Extensive comparisons of the picrodontid material at my disposal to erinaceoids, mixodectids, apatemyids, leptictids, pantolestids, plagio-menids, some condylarths, paromomyids, carpolestids, plesiadapids, and phyllostomatid bats resulted in some fairly definite conclusions concerning the ordinal relationships of the Picrodontoidea. Detailed and lengthy comparisons with all of these groups would serve no useful purpose. Pertinent comments, however, in relation to some of the groups cited are given below, prior to a more thorough comparison with paromomyid primates.

Romer (1945, p. 612; 1966, p. 380) placed the Picrodontidae in the



FIG. 26. *Palaechthon alticuspis*, U.S.N.M. No. 9532 (type), incomplete right dentary with P_2 - M_2 , lateral view; Lebo Formation.

Insectivora, *incertae sedis* (1945) and in the Dermoptera, *incertae sedis* (1966). He stated (1966, p. 212) in the legend of figure 320 that *Zanycteris* is a possible relative of the modern colugos. Nowhere in the primary literature is there mention of such ties. In addition, the Paleocene plagiomenid *Planetetherium* bears no meaningful resemblance to picrodontids. I am acquainted with almost all collected specimens of the Paleocene as well as the Eocene dermopteran plagiomenids. In my opinion, there is nothing in either the upper or lower molar and antemolar dentitions of plagiomenids to suggest relationship with picrodontids.

There is no reason to discuss in detail the alleged chiropteran relationships of the Picrodontidae. I am in complete agreement with Simpson (1937, p. 136) and McGrew and Patterson (1962, pp. 7-8) that these Paleocene mammals are not bats. The latter authors present a perfectly convincing discussion on why picrodontids are merely convergent to phyllostomatid bats and not phylogenetically related to chiropterans.

Although Simpson has repeatedly emphasized that the similarity of picrodontids to phyllostomatids is adaptive, the alleged chiropteran ties of the Paleocene family managed to creep into one of his more widely

read¹ and quoted papers on primates. Simpson (1955, p. 436), in discussing ordinal characters among early primates, made the following statement: "It does make sense, for instance, to ask whether *Zanycteris* was really a bat or *Phenacodactylus* was really an artiodactyl. *Zanycteris* was really a bat if it had a wing (a point on which there is at present no real evidence)." Such a statement, of course, is not necessarily true. Even if picrodontids were to show adaptations to a flying mode of life, it would still not *de facto* or *de jure* prove bat relationships for *Picrodus* and its allies. Colugos, different groups of rodents, and marsupial phalangers evolved, convergently, an ability to glide and very similar mechanisms for gliding.

Both mixodectids and picrodontids have relatively heavy and deep mandibles, and two procumbent incisors, the more anterior being enlarged. The widespread presence of a mesostyle, the relatively long pre-paracrista, and the mode of hypocone formation among mixodectids make it very unlikely that picrodontids originated from the Mixodectidae.

As noted above, I also compared picrodontids with leptictids, pantolestids, and erinaceoids, but found no meaningful similarities worth discussing.

Ever since picrodontids have been known, there have been many vague, and some positive, opinions that these small Paleocene mammals were primates, allied to the known Paleocene prosimians. No one, however, previously has made detailed comparisons or discussed the pertinent evidence. Simpson (1937, p. 135) suggested broad, general similarities to the Insectivora, Chiroptera, and Primates. Although McGrew and Patterson (1962, p. 8) admitted the possibility that these mammals might be primates, they considered them Insectivora, with a query. Van Valen (1965, p. 435) regarded the picrodontids as primates. In his paper on the Deltatheridia (1966, p. 104), written prior to 1965, Van Valen stated that picrodontids ". . . may be bats or, more probably, primates." McKenna (in press), in his classification of prosimians, placed the Picrodontidae in the Prosimii, *incertae sedis*. I have considered (in press) this family to be primates, allied to the Paleocene prosimians.

At first glance, known picrodontids display such a unique morphology of both upper and lower molars that no meaningful resemblance to any other known group of the early Tertiary appears likely. As the mandible and the antemolar and molar dentitions of paromomyids and picrodontids are put under close scrutiny, however, a rather convincing com-

¹ See Buettner-Janusch's (1966, p. 98) discussion of early primates.

plex of subtle similarities emerges in spite of the obscuring effect of the peculiar picrodontid molar morphology. It is difficult to say which of the picrodontid upper molars is more altered, because the primitive ancestry is not known. Of the three upper molars the first one is the largest and shows the most complicated pattern.

The somewhat vague, but functionally real, hypocone is formed exactly the same way in both *Zanycteris* and *Picrodus*. The posterolingually expanded postcingulum becomes the hypocone, and the cingulum is connected to the apex of the protocone. The postcingulum expands to form a vague hypocone on the molars in the same manner in *Purgatorius*, *Palaechthon*, *Palenochtha*, *Paramomys*, *Pronothodectes*, *Plesiadapsis*, and some carpolestids. In all these Paleocene primates (except in plesiadapids) and in the two known genera of picrodontids the protocone is on the anterior half of the tooth, almost directly lingual to the paracone. In the earliest known plesiadapid, *Pronothodectes*, the protocone appears to be secondarily central lingually. The postcingulum, however, is almost connected or very closely approaches the apex of the protocone in the genera listed. The hypocone,¹ then, is formed in essentially the same way in picrodontids and paromomyids (and in some other families of early prosimians). This structure is not cusped in either family but merely an ill-defined expansion. The particular hypocone formation and the characteristically anteriorly skewed protocone of these families can be contrasted with those of leptictids and apatemyids, for example, which develop a more sharply defined, cusped hypocone. In all leptictids and early apatemyids known to me the protocone rises sharply away from the hypocone; the two structures can be easily delineated.

One of the outstanding morphological and inferred functional features of the early primates and condylarths is the marked reduction of shearing surfaces. This reduction is manifested in the loss of the preparacrista, transversely narrower upper molars, a transversely narrower trigonid, and a wider talonid (Szalay, in press). The almost complete

¹ In *Picrodus* there is a slim, distinct fold between the crest formed by the buccal border of the postcingulum and the postprotocrista. This may be similar to the *Nannopithecus*-fold of some primates. Like the *Nannopithecus*-fold of various genera, this fold on *Picrodus* does not form the hypocone or appear to give rise to the hypocone as claimed in various places in the literature for primates with a *Nannopithecus*-fold. The posterolingual extension of the protocone, i.e., the part bearing the postcingulum, expands and begins to form a functional, although morphologically vague, hypocone. This is certainly the case in *Palenochtha* illustrated in this paper, which has not developed a *Nannopithecus*-fold. I suspect that the latter fold is the result of the bulging and folding of the dentine and enamel of an enlarging hypocone, already developed prior to the appearance of the *Nannopithecus*-fold.

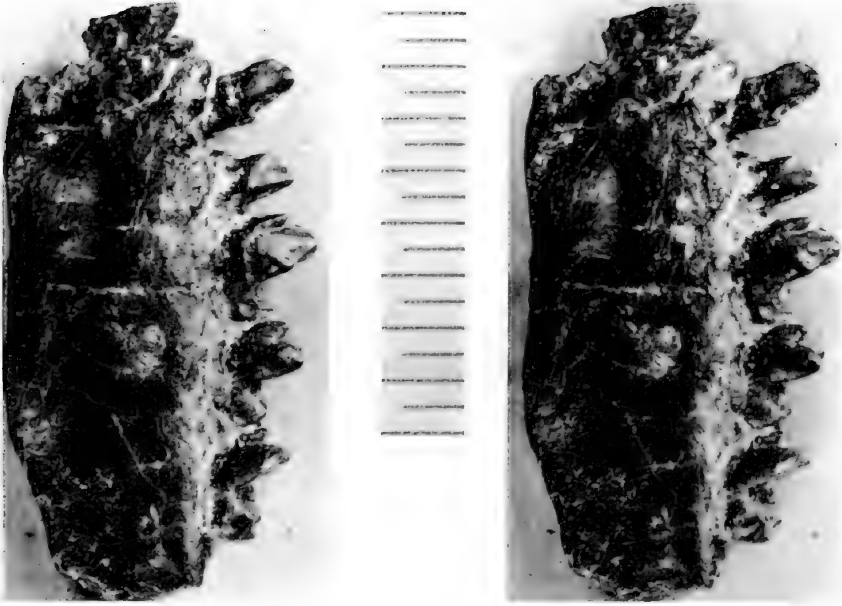


FIG. 27. *Palaeochthon alticuspis*, U.S.N.M. No. 9532 (type), medial view; Lebo Formation.

reduction of transverse shear along the prevallid-postvallum and postvallid-prevallum surfaces, and a shift to a mash-and-shear on the centrocrista and cristid obliqua, are more appropriately discussed under Function. Although some weight is placed here on the fact that shear was greatly reduced in all the earliest primates (and also the later ones), it must be noted that both leptictids and pantolestids show an early reduction of transverse shear.

No matter how modified the picrodontid trigonids are on any of the lower molars, one common feature is shared by all three in addition to the homologous cusps. This peculiar character is the angulate paracristid that characterizes all Paleocene primates and apatemyids. I am inclined to believe that on a trigonid as reduced in relative size and function as the picrodontid M_1 , the angulate paracristid would represent the retention of this feature from a relatively larger ancestral trigonid. It is difficult otherwise to explain the fact that such a distinct, peculiar character as the sharply bending paracristid would have independently evolved as the trigonid was being drastically reduced in size in relation to the talonid.

Picrodontids have, as anaptomorphids and omomyids do, distinct

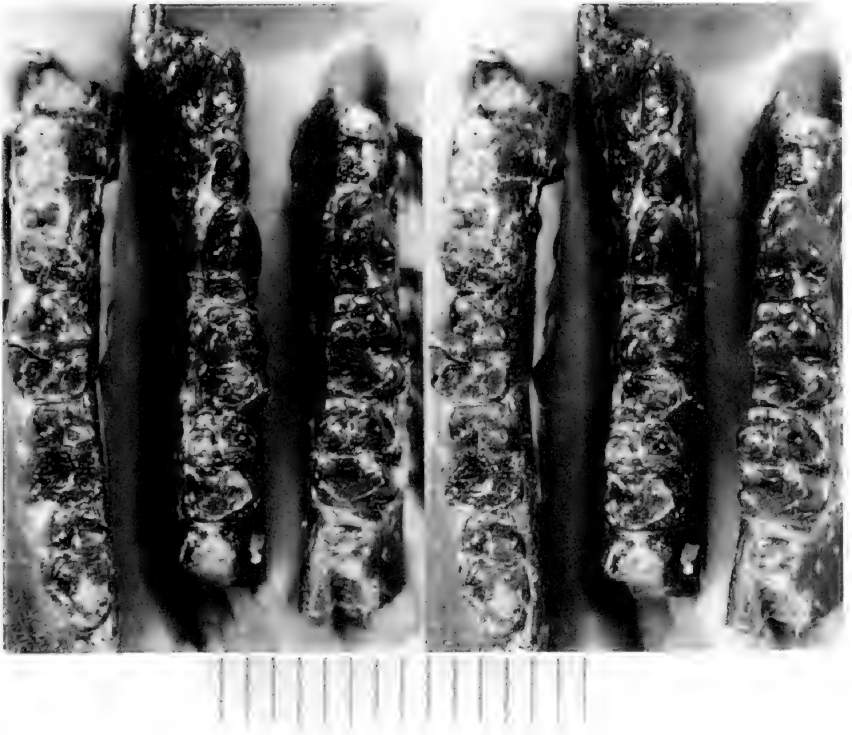


FIG. 28. *Palaechthon alticuspis*. Left to right: U.S.N.M. No. 9430, M_{1-3} ; U.S.-N.M. No. 9532, type, P_2-M_2 ; U.S.N.M. No. 9491, P_4-M_2 . All occlusal views and all from the Lebo Formation.

interradicular crests. Many isolated molars of *Paromomys* and *Palaechthon* that I have examined showed no traces of these crests. Most erinaeids, mixodectids, several specimens of leptictids known to me, and almost all microsypids have interradicular crests. This feature probably evolved many times independently; therefore its value in the assessing of relationships is necessarily very limited.

The complex, interwoven series of similarities revealed by a close comparison of paromomyids and picrodontids cannot be considered proof of relationship in the same sense as an intermediate genus between the two families would be. Nevertheless, the presently available evidence is judged to be adequate for the derivation of picrodontids from early primates, and not from any of the known groups of Paleocene insectivores, deltatheridians, or bats. The lack of intermediates between picrodontids and their presumed ancestors is another strong reminder that

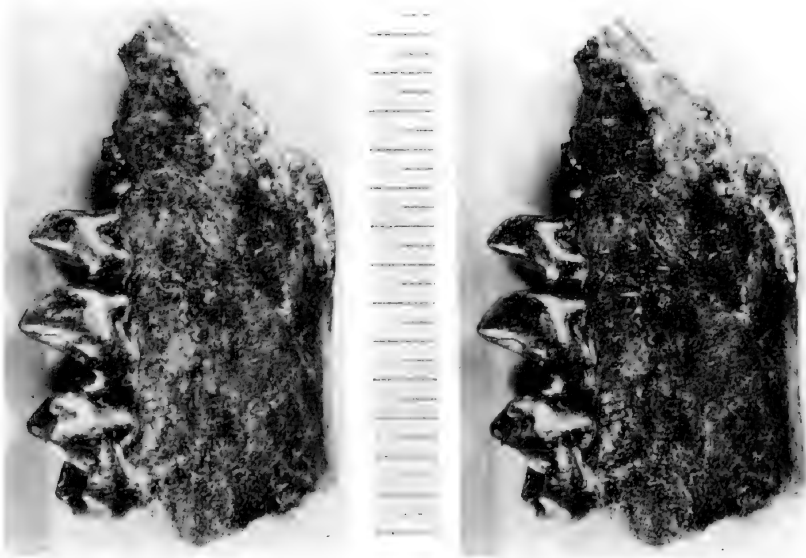


FIG. 29. *Paromomys maurus*, A.M.N.H. No. 89501, incomplete left dentary with P_3 - M_1 , medial view; Swain Quarry.

many habitats and facies of the Paleocene have never been sampled.

Because the known picrodontid lower dentition is well reduced at its time of appearance, an attempt to adduce evidence for picrodontid-paromomyid ties from the antemolar dentition seems to be an example of circular reasoning. Nevertheless, such an avenue may be explored more profitably than at first suspected. Before we can proceed, however, the lower dental formula of paromomyids reported in the literature must be briefly reviewed and revised.

The lower dental formula of *Palenochtha minor* was given by Simpson (1937, p. 159) as 1.1.2.3. Van Valen (1965, pp. 435-436) reported an additional antemolar tooth. He gave the lower formula as 1.1.3.3., and claimed, incorrectly I believe, that the dental formula and the homologies of the teeth are very probably the same as those of *Paromomys*. In A.M.N.H. No. 35451, a specimen of *Palenochtha minor* from Gidley Quarry, the most anterior of the preserved teeth (P_2 of Van Valen) has a tiny posterior elongation, essentially a barely incipient talonid. Probably this feature of the erectly implanted tooth prompted Van Valen to call it a P_2 , rather than a canine. The two alveoli on the same specimen anterior to the erect tooth are procumbent, as are those in *Palaechthon*, *Paromomys*, and *Picrodus*. The procumbent nature of these alveoli strongly

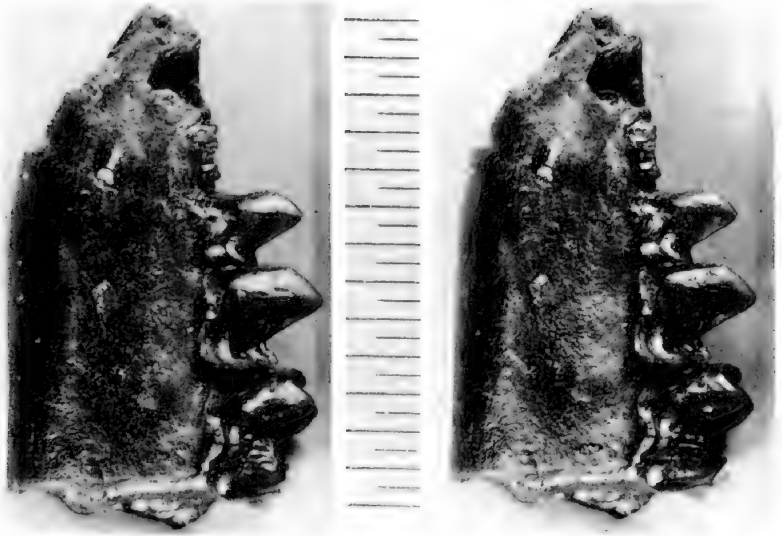


FIG. 30. *Paromomys maurus*, A.M.N.H. No. 89501, lateral view; Swain Quarry.

suggests that they held incisors (for further discussion on the incisor homologies, see paragraph below). An additional dentary fragment of *Palenochtha minor*, A.M.N.H. No. 89511, clearly shows that there were five antemolar teeth, as Van Valen noted. From the relative size of the alveoli, however, it appears equally clear that there were two double-rooted premolars (probably P_4 and P_3), an erectly implanted single-rooted canine, and two procumbent incisors. The unusually large mental foramen of this specimen under P_3 opens dorsally and slightly anteriorly.

For *Paromomys*, Simpson (1937, p. 148) gave the lower dental formula as 1.1.3.3. In his 1955 paper on the Phenacolemuridae he again published the same formula. Van Valen (1965, pp. 435–436) confirmed this, as indirectly noted in the paragraph above. Available evidence strongly contradicts the interpretation of Simpson and of Van Valen. A.M.N.H. No. 89501 (figs. 29–31) is the anterior fragment of a left dentary, with clearly identifiable P_3 , P_4 , and M_1 , of *Paromomys maurus*. Anterior to the first molar there were unmistakably six antemolar teeth and not five. The three premolars anterior to M_1 are double-rooted and decrease in size from P_4 to P_2 . Anterior to the double-rooted P_2 there is a large alveolus sunk directly into the dentary. This alveolus is distinctly larger than the two combined alveoli of P_2 . I have little doubt that the large round alveolus housed the canine. There is every reason to believe that

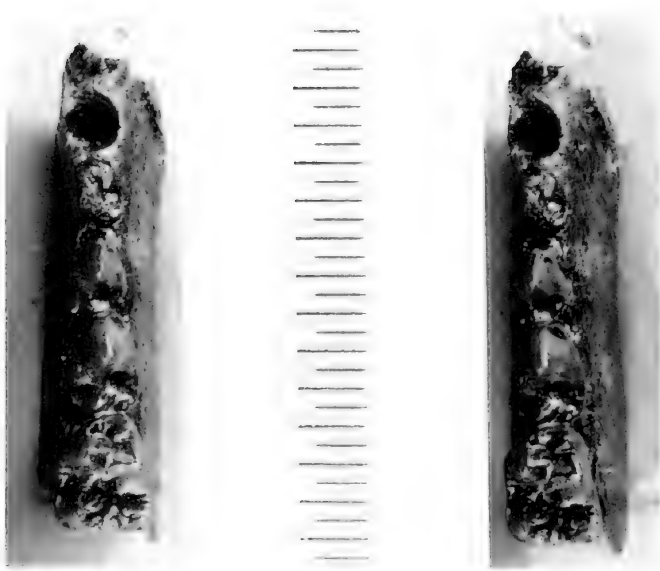


FIG. 31. *Paromomys maurus*, A.M.N.H. No. 89501, occlusal view; Swain Quarry.

the size discrepancy between the P_2 and the tooth anterior to it represents the primitive size discrepancy between the most anterior premolar (not P_2 , of course) and the distinctly larger canine of the primitive therian dentition.

In known Paleocene and Eocene primates, in addition to the reduction of some of the incisors, the first and then the second premolars invariably precede the reduction of the canines. As in *Paromomys*, although in different proportions, the Wasatchian anaptomorphid *Absarokius* or the Bridgerian omomyid *Omomy*s shows the size difference of the canine (following the two procumbent incisors) and the relatively smaller P_2 behind it.

Anterior to the large canine alveolus of *Paromomys*, there were two incisors. The root of the posterior incisor is preserved in the alveolus in A.M.N.H. No. 89501. This transversely flattened root (transverse in relation to the sagittal plane of the symphysis and skull) indicates a slightly enlarged, procumbent tooth. This incisor was closely, posterolaterally flattened against the greatly enlarged anterior incisor. That these two incisors represent I_1 and I_2 is merely a guess at present, based on the supposition that incisor reduction proceeded from back to front.

Simpson (1937, p. 156) interpreted the lower dental formula of *Palaechthon alticuspis* as probably 1.1.3.3. In 1955 (p. 419) Simpson ac-

cepted this formula apparently without any doubt. As Van Valen (1965) noted, there are six and not five antemolar teeth, and the correct lower dental formula is 2.1.3.3. This is best observed in A.M.N.H. No. 35478. The three premolars are double-rooted, as in *Paromomys*, but the single-rooted canine is relatively smaller (see figs. 26–28) in relation to the premolars than it is in *Paromomys*. The enlargement of the anterior incisor, as indicated by the alveoli, is similar to the condition seen in *Paromomys*.

The homologies and the number of antemolar teeth of *Picrodus silberlingi* are partly treated under the description of this species. As did *Palenochtha minor*, this species had five lower antemolar teeth. The reduced but paromomyid-like P_4 of *Picrodus* is two-rooted, as noted in the description. The homology of the single-rooted tooth anterior to P_3 and posterior to the two procumbent incisors may be disputed, although I believe it to be the canine. Judged from the alveolus, it was a larger tooth than the P_3 behind it—a very suggestive, but of course not fully proved, criterion for the usual anterior premolar-canine size relationship noted above. The size relationship of the two incisors of *Picrodus* is astonishingly similar to the condition of these teeth in *Paromomys*, as far as it can be judged from the alveoli. This is best appreciated by comparing A.M.N.H. No. 89505, *Picrodus* (fig. 9), with A.M.N.H. No. 89501, *Paromomys* (figs. 30–31). I consider the two incisors in both these genera homologous and enlarged probably in a similar manner.¹ In summary, concerning the antemolar dentition of picrodontids and paromomyids, I have no reasonable doubts that the antemolar dentition of *Palenochtha* and that of *Picrodus* are homologous. Although *Palaechthon* and *Paromomys* retain a P_2 that is absent from *Palenochtha* and *Picrodus*, the homologies of the remaining antemolar dentition of the two former genera are probably the same as those of the latter two.

Paromomys, as does *Picrodus*, displays the larger of the two mental foramina, the anterior one, under P_3 . In *Palaechthon*, the larger anterior foramen is slightly anterior to P_3 . On the type mandible of *Palenochtha minor* and on A.M.N.H. No. 89511 there is a large mental foramen under the area where P_3 was implanted. Thus, a comparison of the position of the mental foramina of *Palenochtha*, *Palaechthon*, *Paromomys*,

¹ In the large Swain Quarry sample I have encountered entirely *Paromomys*- and carolestid-like enlarged incisors which have a much more likely "size relationship" with *P. silberlingi* than with the other four species of primates occurring in the quarry. These four species of paromomyids are the very rare *Palenochtha minor*, the abundant *Palaechthon alticuspis*, the rare *Paromomys depressidens*, and the very abundant *Paromomys maturus*. This point is yet to be proved by incisors associated with the molar dentition.

and *Picrodus* also suggests paromomyid-picrodontid ties.

The angles of the dentaries in *Picrodus*, *Palenochtha*, *Palaechthon*, and *Navajovius*¹ are very similar, displaying a conspicuous internal pterygoid crest on the medial surface of the angle. The sharing of this character between *Picrodus* and the other genera listed may, however, mean nothing more than a primitive retention of this feature from a remote Cretaceous ancestor. The evidence derived from the dentition indicates otherwise.

FUNCTION

WEAR FACETS

Figure 32 and table 3 present concise summaries of the wear facets on the first upper and first lower molars of *Picrodus silberlingi*. There is no single upper or lower molar that clearly shows all the wear facets described and illustrated. Nevertheless, when all the specimens are studied, the wear facets shown can be recognized. There is no reason at present to describe and analyze the wear facets on the upper dentition of *Zanycteris*. Lack of known lower molars would prevent meaningful evaluation. The known wear surfaces on the only specimen of *Zanycteris paleocena* appear to be very similar to those of *P. silberlingi*.

Interesting wear can be observed on the P₄ of *P. silberlingi* (A.M.-N.H. No. 89505, fig. 4). The protoconid is worn halfway down, and the wear surface points anterolingually.

MASTICATION AND OCCLUSION

NOTES ON MANDIBULAR MECHANICS: In the following discussion emphasis is placed on the mandible of *Picrodus*, whatever inferences the available specimens permit in regard to the musculature and its function. Because complete mandibles or skulls of related genera (or of *Picrodus*) are not known, a force-vector analysis without the appropriate comparative taxa would not be very meaningful. Analysis of the mandibular mechanics of one species is of little use in a study of phyletic changes. Even the essentially static (from an evolutionary viewpoint) force analysis to decipher the dynamics of mastication is prevented by lack of good cranial material.

¹ Shortly after my paper on mixodectids and microsypids (Szalay, in press) was submitted for publication, in which I advocated probable microsypid affinities for *Navajovius*, my views on this interesting genus shifted slightly. Paromomyid derivation of *Navajovius* and a formal classification within that family appear to be more meaningful and desirable.

TABLE 3
 HOMOLOGOUS WEAR FACETS OF THE FIRST UPPER AND FIRST LOWER MOLARS OF *Picrodus silberlingi*
 (On several specimens many of the wear facets may be continuous.)

Wear on M ¹	Wear on M ₁
On anterior two-thirds of centrocrista and a broad band lingual to it	Cristid obliqua and a narrow strip lingual to crest
Large area anterobuccal to protocone, posteriorly limited by crista running lingually from paracone and preprotocrista	Almost entire posterior face of trigonid
Area posterior to protocone between postprotocrista and anterior segment of postcingulum	Tip and lingual surface of entoconid
Ill-defined area between vestigial metaconule and postcingulum	Tip and lingual face of hypoconulid
Narrow band anterior and posterior to mid-segment of postmetaconule crista (?)	Postero-buccal part of cristid obliqua and postcristid
Posterior part of postcingulum	Ill-defined area in spoutlike exit of talonid
Postero-buccal segment above postcingulum; this facet a result of M ₂ paraconid wear on M ¹ (a remnant of primitive prevallid-postvallum shear between M ₂ and M ¹)	—

Judged from the medial crest of the angle, the internal pterygoid probably was not a very powerful muscle. Its action, along with that of the superficial masseter, probably resulted in a propalinal component of mastication, judged from wear on the molars. The presumed extent of this propalinal component can be seen in the relative position of M_1 in figure 33A and 33B. Until a complete skull and an intact mandible are collected, however, the extent of propalinal motion during mastication can only be guessed.

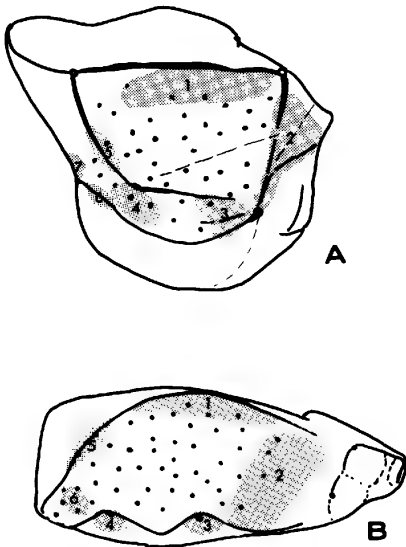


FIG. 32. Diagrammatic outline of homologous wear facets in *Picrodus silberlingi*. A. M^1 . B. M_1 . Buccal is to the top of the page, and anterior is to the right.

Without a skull that would show muscle scars on the posterolateral part of the palate and on the zygoma, the alignment of the internal pterygoid and the superficial masseter cannot be learned. The same lack of data prevents our understanding the orientation of the deep masseter and the temporalis complex. Judged from the relatively deep pit at the anteroventral part of the masseteric fossa, the zygomaticomandibularis and the deep masseter were powerful and the former probably inserted into this area by a tendon. This depression in the masseteric fossa is best shown on A.M.N.H. No. 35459 (fig. 12). The very large coronoid process and the strong, distinct crista coronoidea on the important ascending ramus indicate an unusually strong temporal muscle complex. Unlike the situation in most primarily insectivorous groups (judged from the high-cusped and shearing molars of these forms), such as erinaceoids and paleoryctids of the Paleocene, the picrodontid man-

dible was deep and massive. The relatively deep mandible may be indicative of a powerfully developed tongue musculature, although I found no adequate muscle scars on the known species to support such an interpretation. The large and important ascending ramus, in comparison with the relatively small angle, strongly suggests that propalinal jaw motion was relatively unimportant compared with the role of orthal and ectental components in picodontid mastication.

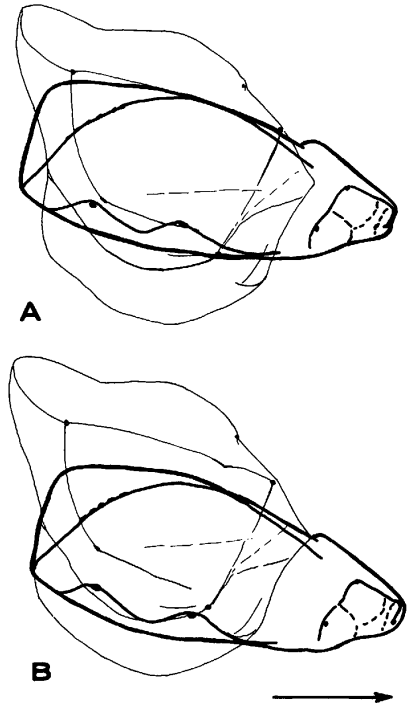


FIG. 33. Occlusal diagrams of M^1 and M_1 of *Picrodus silberlingi*. A. Buccal phase. B. Centric occlusion. The arrow is lingual to the teeth and points anteriorly. The plane of the shaft of the arrow represents the orientation but not the relative position of the palatine suture in relation to M^1 in both A and B.

DEFINITION OF PHASES OF OCCLUSION: The buccal phase is understood here as the most buccal point of occlusion at the lateral excursion of the mandible. Note that the mandibular movement is referred to separately from the occlusal movements of superimposed teeth.

The lingual phase of occlusion is understood here as the occlusal interaction of the teeth after they meet in the buccal phase of occlusion. This means the motion of the lower molars across the surface of the upper ones during the medial excursion of the mandible until the medial palatine suture and the imaginary longitudinal axis of the mandibles are aligned. The centric occlusion of most authors is a static moment of the lingual phase, as used here, when the longitudinal axes noted above align with each other.

Whether the lingual phase of occlusion ends with centric occlusion and thus coincides with the medial excursion of the mandible probably depends on the fused or unfused nature of the dentaries and the species-specific habits of the animals involved. Strict definitions are meaningless, because both buccal and lingual phases, as defined here, are part of a continuum. The two terms are useful, but they merely facilitate the description of occlusal dynamics.

The lingual phase of some authors (e.g., see Mills, 1955, in particular and references therein) restricts this phase to occlusion of the molars when the lower molars are pulled lingual to their position in centric occlusion. I believe that, whether this additional lingual excursion follows while in occlusion or not, past centric occlusion is largely a factor of a fused or unfused symphysis. The recent primates that Mills studied have fused symphyses, or at least the analysis was based on that assumption. Starting from a centric position of a species with fused symphysis, if the right mandible begins a lateral excursion, the left one is also pulled medially. A rigidly fused symphysis would not allow separation of the dentaries. The motion of one dentary thus has full effect on that of the other one. This rigid action of the dentaries, acting as one unit, results in a distinct lingual phase past centric occlusion, and may even begin active occlusion on the opposite side by motion of the lower molar across the upper one in a buccal direction. In the case of a mobile symphysis, however, I suspect that neither mandible followed completely the motion of the one opposite it. Except during centric occlusion, when the forces acting on the two dentaries were in balance, forces acting on either of the dentaries could not be fully transmitted to the other. The mobile symphysis, unlike a fused one, passively opposed transmission of forces from one dentary to the other. In essence, then, as a generalization, which may have many exceptions, I suspect that mammals with mobile symphyses [see Scapino's (1965) fine study on the mobile symphysis of *Canis*] do not have a lingual phase in the sense of Mills (1955), i.e., significantly more lingual than centric occlusion. It may be, although it does not necessarily follow, that the motion of the lower teeth across the upper ones is mostly in a lingual direction from a point of occlusion that is defined in this paper as the buccal phase. Extremes in size may have an additional influence on mastication. Unfortunately, modern studies on mastication of living small mammals are lacking.

OCCCLUSION: Judged from the unfused dentaries of *Picrodus*, the orientation of the wear facets, and, as circumstantial but important evidence, the orientation of M¹ on the palate of *Zanycteris*, the dentaries were

separated during the lateral excursion of either dentary. As the dentary was pulled laterally, the articular joint probably also allowed some lateral motion, a point entirely unconfirmed by lack of glenoid areas of the skull. All the lateral and possibly posterior components of M_1 occluding with the static M^1 are interpreted in figure 33.¹

Both the buccal and lingual phases of occlusion (as defined and used in this paper) attempt to describe dynamic parts of the total occlusion during mastication. Figure 33A and B portrays only two static moments in this continuum. Figure 33A shows the buccal phase (the first moment of occlusion at the end of the lateral excursion of the mandible); figure 33B, the presumed end moment of the lingual phase, the teeth in centric occlusion. M_1 moved across the surface of M^1 (from fig. 33A to fig. 33B) in an anterolingual direction as the dentary was pulled medially during the medial excursion of the left mandible. The arrow on the lower right corner of the figure represents the alleged spatial orientation (but not relative position) of the palatine suture. It represents for both phases the orientation of the anteroposterior axis of the skull in relation to the upper molar and presumably also for the lower molar.

Judged from the wear facets on the upper and lower molars, after the left dentary made its lateral excursion, the lower molar met the upper one in occlusion presumably as shown in figure 33A. The cristid obliqua of M_1 aligned with the anterior half of the centrocrista, and the posterobuccal cuspules of M_1 made contact with the anterolingual slope of the metacone. At that moment the posterior face of the trigonid was in contact with part of the upper molar anterior to the preprotocrista and to the crista running lingually from the paracone. The entoconid was posterobuccal to the protocone, and the hypoconulid was in contact with the vestigial metaconule. Approximately from the occlusal position described above, the first lower molar moved across, presumably in an anterolingual direction, as the left mandible was pulled into rest position. As the mandible was pulled medially into rest position, the molars reached the presumably most lingual point in their occlusal contact. This is the centric position, portrayed in figure 33B. It is quite possible that the lower molar may have been slightly more

¹ Because the first molars are the best-known teeth of *Picrodus*, mainly their occlusal relationships are analyzed. Lack of *Zanycteris* lower molars prohibits a similar evaluation of that genus. As already noted, *Picrodus* is somewhat more advanced than *Zanycteris* in several features of M^1 . Discovery of *Zanycteris* lower molars will undoubtedly stimulate important insights concerning the direction of occlusal evolution from a primitively tritubercular ancestry.

lingual to the upper than is shown on the figure. At centric occlusion the entoconid occluded slightly posterolingual to the protocone, and the hypoconulid was lingual to the vestigial metaconule. It is almost certain that the lower molars were moved more lingually than shown in centric occlusion, but during this lingual displacement occlusion was probably not maintained as the dentary was passively pulled medially during the lateral excursion of the opposite dentary. On page 45 an attempt is made to explain how a mobile symphysis, as in *Picrodus*, probably prohibited tight occlusal contact between the teeth on one side past centric occlusion, as the opposite dentary began its lateral excursion.

It is quite possible that there was more propalinal jaw motion in addition to the total anteroposterior travel shown for M_1 in figure 33 from A to B. If this additional anterior motion took place, then the entoconid would have been pulled slightly anteriorly to the protocone and the spoutlike talonid exit would have been closer to the metaconule at the end of the lingual phase.

Largely as a result of the propalinal component of mastication, the hypoconulid wears a deep groove between the postprotocrista and the crest of the postcingulum. This trough is worn all the way to the dentine on many specimens illustrated.

The wear on P_4 of A.M.N.H. No. 89505, noted under Wear Facets, may be tentatively explained as follows: As the lingual phase began, P_4 was opposed against the posterior (or posterolateral) face of P^3 . Part of the wear exhibited on P_4 is undoubtedly caused by food held between the opposing premolars.

EVOLUTIONARY TRENDS

No one disputes the fact that, to interpret the known morphology of a group of fossils, we must understand the evolutionary trends that led to them. In bare essentials, the steps followed for deciphering the trends leading to the peculiar dental morphology of picrodontids are outlined here.

What caused a certain adaptive¹ change? To answer this broad question, the inquiry into the nature of the change must be broken down onto several levels. Once the raw data are carefully studied, the first question is directed to explaining the picrodontid tooth structure in terms of occlusion. Whatever changes occurred in the molar dentition

¹For present purposes it is assumed that all observed morphological changes had some adaptive value.

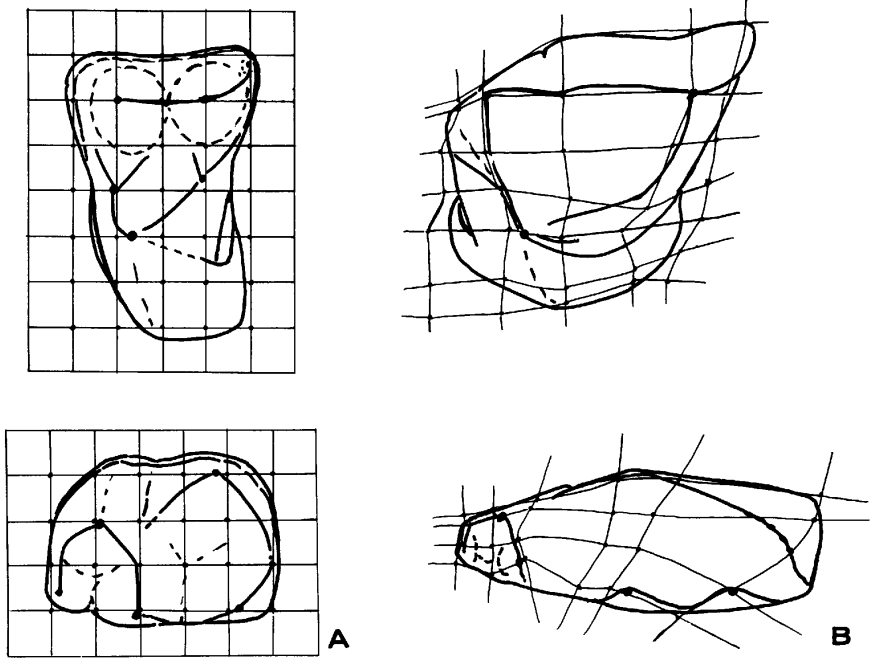


FIG. 34. Comparison of the first upper and first lower molars by deformed coordinates. A. *Palenochtha minor*. B. *Picrodus silberlingi*. This method illustrates the changes in proportion from a presumed structural ancestor similar to *Palenochtha*, to *Picrodus*. This graphic presentation is intended simply to show the probable changes outlined in the discussion of trends and by no means as proof for early paromomyid origins of the picrodontids.

of picrodontids from that of their alleged tritubercular ancestors, they must have been in accord (at least at the time of the origin of the picrodontids) with the occlusal requirements of these ancestors. So, at this first level, answers are sought concerning the morphology of the upper and lower molars in terms of the interdependence between the occlusion of the ancestors and that of picrodontids.

Once the first inquiry is completed, the second question is posed to reveal what were the selective advantages that allowed the changes to occur. On this second level an attempt is made to explain the functional adaptation in terms of the selective premium it conferred on the evolving group. To phrase this somewhat differently: Why was it advantageous for the picrodontids to evolve the dentition they did, and have it function the way it did?

In reality the changes or the reasons for them occurred in the reverse

order of the questions. Certain morphology is selected for, because it performs a function advantageous for a species with certain behavioral attributes. This morphology, and its function, change either because new behavioral attributes¹ place new requirements on the morphology and function of the species, or because selection further improves the existing function for the same (i.e., the old) mode of life. It is probably invariably altered behavior that results in change in function, which further changes the morphology of a species. The functional attributes of a group probably closely channel the possible avenues open for evolution in a broad direction best suited for this ancestral group, e.g., it is more likely that a group of omnivorous-frugivorous mammals would be ancestors of specialized frugivores than of specialized carnivores.

The evolutionary trends from a paromomyine ancestor (or, at any rate, from a tritubercular ancestor with reduced transverse shear) to the striking specializations of picrodontids are treated under the two general categories of the question asked above: (a) to explain the change from the morphology and function of the alleged ancestry to those of the picrodontids, and (b) to determine the selective advantages of this change in terms of broad habitus and the feeding mechanism.

Intermediates are not known between an alleged tritubercular² ancestor (e.g., a form probably similar to *Palaechthon* in structure and function) and picrodontids. Nevertheless, I believe that an attempt to explain picrodontid evolution from such a hypothetical ancestor is warranted on the basis of a paromomyid-picrodontid similarity, which is discussed under Relationships, above.

The important major changes on the first upper and lower molars from the alleged paromomyid ancestor are first summarized and then discussed. With the use of *Palaechthon* as a structural but not real ancestor, the method of deformed coordinates in figure 34 helps to demonstrate these inferred changes on *Picrodus*.

SUMMARY OF MAJOR CHANGES ON M¹: Reduction in relative size of trigon cusps; obliteration of conules. Extensive enlargement and elongation of postero-buccal corner of tooth; general area of metacone spread out to occupy almost one-third of total tooth surface. General elongation of trigon posterior to para-

¹ This new behavior may be the result of exploratory behavior and later an adaptive answer to a changed environment.

² I follow Patterson's (1956, pp. 32-33) use of the terms "tritubercular," "dilambdodont," and "zalambdodont" as descriptively useful for conditions of therian molars that were derived from what Patterson (originally Simpson) referred to as a tribosphenic structure (e.g., that of the Albian *Pappotherium* or the early Tertiary *Didelphodus*). Adherence to Patterson's crystal-clear delineation of these terms can only clarify meaning and increasingly improve communication among students of therian mammal evolution.

cone and protocone.

SUMMARY OF MAJOR CHANGES ON M_1 : Drastic reduction in relative size of trigonid; reduction of hypoconid. Extensive enlargement and elongation of posterobuccal area of talonid and consequent anterolingual shift of entoconid and hypoconulid. General elongation of tooth, particularly talonid.

Some quantitative evidence supplies confirmation of the change inferred from morphology, namely, that the most drastic alterations in proportion in the upper teeth involved the posterobuccal area of the first upper molar. From the morphology, for example, it can be seen that the premetacrista is relatively much longer than the postparacrista in both *Zanycteris* and *Picrodus*. In all tritubercular small mammals known to me, and in various insectivores, primates, and deltatheridians, the postparacrista and premetacrista are approximately the same length. It follows that the elongation of the centrocrista in the manner carried out by picrodontids was a morphological and functional innovation. Some quantitative data on the first upper molars of *Picrodus* show that the coefficient of variation of the distance between the apex of the paracone and that of the metacone is 9.11 as contrasted with 5.58 for that of the distance between the apex of the paracone and that of the protocone. This contrast in the variation in the different parts of the same molars can even be appreciated visually in figure 17A. Guthrie's (1965) penetrating and revealing studies on variability in characters undergoing rapid evolution¹ (he studied the molars of fossil and Recent samples of *Microtus*) gave strong evidence that quantitative characters maintain and usually increase phenotypic variation rather than show decline.

A change closely correlated with the elongated centrocrista is the elongation of the cristid obliqua and the postcristid (the crest between the hypoconid, reduced in picrodontids, and the hypoconulid). Just as the premetacrista component of the centrocrista was relatively more elongated than the postparacrista, so the posterior part of the cristid obliqua and of the postcristid was more "stretched-out" than the anterior part of the cristid obliqua. The functional importance of the centrocrista and the buccal crest of the first lower molar is rather clear. The changes allowed a peculiar, very extensive, horizontal "shear" on

¹Partly from the known record of paromomyids and partly from the large variation in what I believe to be crucial morphological modifications of picrodontids, I think that the latter family may have undergone a very rapid evolution and differentiation from paromomyids. The family may have been distinct by middle or late Puercan time and have resulted in advanced genera such as *Picrodus* as early as middle-late Torrejonian.

these surfaces of the upper and lower molars. I suspect that the extreme anterolingual position of the entoconid and the hypoconulid is the direct result of the extensive phyletic growth of the buccal crest of the molar. As the result of the maintained occlusion, as the crest was gradually increased along with the functionally interrelated centrocrista, the entoconid maintained its primitive position and distance from the trigonid. The position of the anteriorly skewed protocone in relation to the paracone did not change much from a similar position seen in paromomyids. In relation to the entire tooth, however, this cusp is far anterior on the molar. As the protocone and entoconid occlusion is rather rigidly controlled in most groups of therians, the entoconid maintained its occlusal contact with the protocone. The rather unorthodox position of the entoconid is then really a manifestation of the drastically elongated posterobuccal corner of the talonid. The position of the hypoconulid posterior to the entoconid, rather than posterobuccal to it as in more orthodox eutherians, can also be explained in terms of its occlusion with the metaconule and the peculiar elongation of the talonid.

In a more simplified form, the above paragraph may be summarized as follows: Because of the initial unique change on the posterobuccal corner of the molars and the subsequent selective premium for a long centrocrista and the functionally correlated long buccal crest on the talonid, the entoconid and hypoconulid had to remain stationary to maintain their occlusal contact with the protocone and metaconule.

The hypocone increased in size on all three upper molars, and the additional pocket formed became incorporated into the trigon basin. The increase and posterolingual expansion of the hypocone and the reduction of the relative size of the trigonid must have occurred concurrently. As the hypocone expanded, there was progressively less room between the upper molars for the trigonid of M_2 and that of M_3 . Although almost all prevallid-postvallum shear was eliminated, occlusal contact between the posterior face of the very procumbent trigonids and the anterior face of the upper trigons remained. As the posterior face of the trigonid became a gently sloping continuation of the talonid basin on M_1 , this surface could pull across the anterolingual face of the opposing M^1 . Thus the postvallid-prevallum shear of the ancestors was molded into an efficient squashing mechanism in picrodontids.

A striking feature of M_3 , contrasted with the other lower molars, is the relatively tall and acute metaconid compared with the smaller protoconid. What possible function could this cusp serve in contrast to the reduced, bulbous trigonid cusps of M_1 and M_2 ? It is possible that no selective advantage is attached to this type of trigonid on M_3 and that

it merely represents the more primitive cusp structure, less influenced by the genetic field affecting M_1 and M_2 . A relatively drastic modification of the talonids, that of the position of the entoconid and hypoconulid, is, however, shared to the same degree by all three lower molars. Also, the reduction of the paraconid is even more drastic than it is on the first and second molars. The entirely "chopped-off" paraconid on M_3 may be explained as follows: The space between the large, squared-off, trigon basin (and the hypocone) on the posterolingual area of M^2 and the anteriorly skewed protocone on M^3 (unfortunately known only in *Zanycteris*) barely leaves room for the M_3 trigonid to occlude. The reduction of the paraconid is explicable as a direct consequence of the posterolingual expansion of M^2 . The persistently tall metaconid on M_3 , however, may be explained by the inferred frugivorous habitus of picrodontids. A tall and acute cusp, somewhat removed from the area of most intensive mashing, that between the first two pairs of molars, may confer a slight selective premium on the species, by being able to pierce and open tough-skinned juicy berries or other small fruits.

The known paromomyine dental morphology and its function are ideal as a starting point for explaining the origins and direction of the picrodontid molars and their occlusion. In every known way the North American paromomyids were ideally preadapted to give rise to the Picrodontidae. Already in the Cretaceous they had begun the reduction of transverse shear and the accentuation of horizontal shear. In the earliest paromomyids the trigonids were slightly tilted forward and, correspondingly, the protocone was slightly skewed anteriorly. The procumbency of the trigonid and the anterior migration of the protocone occurred simultaneously to maintain contact between the posterior face of the trigonid (the postvallid) and the anterior face of the occluding upper molar (the prevallum).¹ We can only speculate on what may have prompted this very minor but potentially very important change. As the relative heights of the trigon and trigonid cusps were reduced in the earliest primates (see Szalay, in press), the former prevallum-postvallid may have been utilized as two opposing surfaces between which to squash and grind food, as we see it best in picrodontids, for example, rather than as a slicing apparatus. From this early primate stage it was merely a matter of time and intensity of selection for the

¹ In addition to piercing, the cusps of the primitive therian dentition supported, between them, the crests and the vertical tooth surfaces. Thus, even in groups that came to utilize some of the cusps for pounding and crushing, the migration of a cusp may have been a mechanism for shifting opposing shearing surfaces.

depressing of the trigonid and making its posterior face essentially continuous with the talonid basin, as seen in picrodontids.

This extreme increase of horizontal shear (or rather occlusal contact, since shear in the primitively insectivorous-carnivorous sense was not involved) is not unique among early primates. One glance at the molars of *Phenacolemur*, particularly a species such as *P. jepseni* (see Simpson, 1955, pl. 30), reveals at once the adaptive similarity between *Phenacolemur* and picrodontids. A closer examination, however, shows that the adaptively similar phenotypes are the results of different evolutionary trends. *Phenacolemur* can be easily derived from a structural ancestor similar to *Paromomys*, and the latter from a primitive paromomyid, by a simple flattening out and squaring off of the teeth. Although this picture is a grossly simplified one, it can be safely said that through this structural sequence of all the intermediate taxa, the various areas of the molar teeth were evenly altered. The genetic change must not have been very extensive for *Phenacolemur* to evolve from a *Palaechthon*-like ancestor. In picrodontids, however, the flattening out of the molars and the increase of transverse occlusal contact were realized through a relatively drastic genetic innovation. The teeth were elongated not by an even spreading out of the embryonic material available from the tooth germ, but rather by the disproportionate enlargement of the posterobuccal areas of the first upper and first lower molars. As a consequence, the topography of the molar teeth had to be drastically altered to obey the demands of rigidly controlled occlusion. What *Phenacolemur* could achieve by relatively minor changes required complicated and involved alterations for the picrodontids.

Unfortunately, the step-by-step changes in the picrodontid molar pattern cannot as yet be studied. If the evolution of this group was indeed rapid, then we may never collect the complete record. Any intermediates, however, will further stimulate inquiry into the evolution of mammalian occlusion.

Now we can answer the second question posed, that concerning the selective advantage for the evolution of the picrodontid feeding mechanism. It is difficult to see how insects or leaves could have been efficiently masticated. Contrasted with other Paleocene primates, picrodontids, *Phenacolemur*, and more advanced carpolestids show extreme specializations in the dentition. It is reasonable to assume that these specializations represent direct responses to feeding on a restricted diet, although carpolestids were clearly adapted to a different staple diet than picrodontids.

I am in close agreement with Matthew and with McGrew and Patterson, who suggested that the picrodontid molars, judged from their flattened, low crowns and papillated enamel, reflect a frugivorous diet. From the alleged direction of change and the occlusal function of the molars, it appears that these mammals could feed efficiently only on fruits or other juicy vegetable matter.

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