

# DELTATHERIDIA, A NEW ORDER OF MAMMALS

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## INTRODUCTION

IN THE COURSE of studying the relationships of the arctocyoniid genus *Deltatherium*, I found that the early placental carnivores were poorly understood. As the deltatheridioids have been proposed by Matthew (1928), Simpson (1928), McKenna (1960a), and others to be close to the ancestry of the Carnivora, and as such a proposal excludes the arctocyoniids from being directly or nearly ancestral, a review of the deltatheridioids became desirable. The present paper deals with only the deltatheridioids and forms actually or supposedly related to them and is not intended as a comprehensive revision except for the Didelphodontinae and to some extent the other palaeoryctids. I have, however, attempted to allocate, insofar as is possible on presently available information, all genera referred to the Creodonta except *Creotarsus*, which is being studied by Peter Robinson; those genera referred to the Miacidae, which are being studied by Giles Mac Intyre; and those referred to the Arctocyoniidae and the Mesonychidae, which will be discussed in my revision of the Arctocyoniidae. I have nevertheless probably overlooked some of at least the ungulate and primate genera that have at one time or another been referred to the Creodonta. I have examined specimens wherever possible, and figures in the other cases, of all species of creodonts known to me. Lack of comment about a genus should be interpreted as tentative (not definitive) approval of the current arrangement.

A large collection of placental and other mammals from the late Cretaceous of the Hell Creek Formation at Bug Creek, Montana, was made by R. E. Sloan, W. Nelson, and myself in the summer of 1962 after the manuscript of the present paper had been submitted. A few statements must be modified as a result of this material (most important: the premolars of a genus similar to *Nyssodon* are remarkably like those of *Prodiacodon*, suggesting that leptictids may be more primitive than pantolestines), but the main conclusions are unchanged. The present paper was written in late 1961 and early 1962. Because of the delay in its publication, several papers written later and in

part based on it have now been published. These are Van Valen (1963b, 1963c, 1965); Clemens, McKenna, Russell, Sloan, and Van Valen (1964); Sloan and Van Valen (1965); and Mac Intyre (1966). An additional paper (Van Valen, in press) may also be published before the present one and gives a brief diagnosis of the Deltatheridia.

I wish to state explicitly that the use or lack of qualifications is deliberate; i.e., whenever I use such a word as "appear" or "perhaps," the situation is quite uncertain to me on present evidence and I am not merely hedging against future discoveries.

Horizons within the Willwood Formation have been estimated from the locality data for the specimens and from those for specimens of *Pelycodus* and *Oxyaena*, which were treated as stratigraphic markers. The lower Gray Bull of Van Houten (1945) appears to include level 1 of Sinclair and Granger (1911), and his middle and upper Gray Bull to correspond roughly to their levels 2 and 3.

All measurements were made with an ocular micrometer. Measurements of cusp heights were made perpendicular to the bone surface and were taken from the base of the enamel to the apex of the cusp, in the case of lower teeth from the level of the base of the enamel at the interradicular notch. Limits of approximately 90 per cent confidence intervals (not standard errors) for accuracy of measurement are indicated; if none is given the interval is estimated to be less than 0.05 mm. These confidence intervals were estimated while I was measuring and are only guesses, but serve to indicate the relative amount of error caused by crushing, breakage, wear, and angle of measurement. Corrections for these factors were introduced as necessary into the measurements, with corresponding increases in the approximate confidence intervals. These "confidence intervals" actually represent a Bayesian statistic known as the credible interval, but the difference is unimportant here. Measurements are given to the nearest twentieth of a millimeter; the terminal digit has no further significance.

Since the name "Deltatheridia" is used

before it is discussed, I should say that the order Deltatheridia consists mainly of the Deltatheridiidae, Palaeoryctidae, Hyaenodontidae, and Oxyaenidae of Simpson (1945).

I wish to thank especially Dr. M. C. McKenna for many stimulating conversations and for his criticisms of the manuscript. Dr. G. G. Simpson provided much useful criticism. Dr. G. T. MacIntyre and Mr. R. Van Frank took the photographs; Dr. MacIntyre also helped identify some probable miacids and provided various comments. Dr. J. S. Mellett has generously allowed me to use the results of his as yet unpublished study of the Didymoconidae. Mrs. S. R. Graham and Mr. R. E. Graham instructed me on the comparative anatomy of the skull of pinnipeds. Drs. M. R. Dawson, W. A. Clemens, D. E. Russell, and S. B. McDowell, Jr., provided useful comments. Dr. S. Polivanov directed my attention to and translated part of the paper of Novozhilov (1954). Professor B. Patterson and Dr. P. O. McGrew graciously relinquished description of *Pararyctes* and the Lostcabinian DeBeque specimen of *Didelphodus altidens*, and were helpful in arranging loans of specimens from the Chicago Natural History Museum and the Museum of Comparative Zoölogy, Harvard University. Professor Patterson also independently duplicated parts of this study; the fact is noted where appropriate, but I wish to thank him here for consenting to the incorporation of these sections in his paper, and for a number of valuable comments on the manuscript. Mr. C. Tarka, Mr. M. Insinna, and Dr. S. B. McDowell, Jr., gave advice on the illustrations. Drs. R. G. Van Gelder and K. R. Koopman helped in the collections of the Department of Mammalogy of the American Museum of Natural History. Drs. E. L. Simons, J. Ostrom, P. Robinson, and W. A. Clemens aided in various ways the search for the type of *Nyssodon punctidens*; these individuals also kindly permitted loans from the Yale Peabody Museum, the University of Colorado Museum, and the Natural History Museum of the University of Kansas. Dr. Clemens also generously permitted the use of his discovery that *Cimolestes* is a palaeoryctid. I am also grateful to the following individuals for aid in loans or other help with specimens in their care: Drs. C. L. Gazin and N. H. Hotton, III, of the United States

National Museum of the Smithsonian Institution; Drs. R. A. Stirton and G. T. James of the University of California Museum of Paleontology; Dr. R. W. Wilson of the South Dakota School of Mines; Mr. W. B. Turnbull of the Chicago Natural History Museum; Dr. C. C. Black of the Carnegie Museum; Dr. J. H. Madsen, Jr., of the University of Utah; Dr. A. J. Sutcliffe of the British Museum (Natural History); Dr. R. J. G. Savage of the University, Bristol; Prof. R. Dehm and Dr. T. zu Oettingen-Spielberg of the Bayerische Staatssammlung für Paläontologie und historische Geologie; Dr. H. Schaefer of the Naturhistorisches Museum, Basle; and Dr. D. Russell of the Institut de Paléontologie, Paris. M. P. Louis of Reims kindly allowed me to study part of his private collection. Drs. G. L. Jepsen and D. Baird permitted the examination of several type specimens in the Princeton University collection.

This study was made during my tenure of a Boese Postdoctoral Fellowship from Columbia University, with certain supplementary observations added in England during my tenure of a NATO postdoctoral fellowship.

The cost of publication of this monograph has been partially defrayed by a grant (GN-423) from the National Science Foundation.

The following abbreviations are used for institutional collections:

- A.M.N.H., the American Museum of Natural History
- B.M., British Museum (Natural History)
- B.S.P., Bayerische Staatssammlung für Paläontologie, Munich
- C.M., Carnegie Museum, Pittsburgh
- C.N.H.M., Chicago Natural History Museum
- M.C.Z., Museum of Comparative Zoölogy, Harvard University
- M.G.P., Museo Geologico di Padova
- M.N.H.N., Museum National d'Histoire Naturelle, Paris
- P.U., Princeton University
- R.A.M., Raymond Alf Museum of Natural History, Webb School of California, Claremont, California
- U.C.M., University of Colorado Museum
- U.C.M.P., University of California Museum of Paleontology
- U.K., University of Kansas Museum of Natural History
- U.S.N.M., United States National Museum, Smithsonian Institution
- U.W., University of Wyoming
- Y.P.M., Peabody Museum, Yale University

## TERMINOLOGY

## TEETH

The detailed description of teeth is cumbersome, with the use of only the conventional terms. Figure 1 shows the terminology used here for the upper and lower molars. Many of the terms are new, usually for structures not previously named. Their meanings should be obvious from the figures, and the terms are intended to be applicable to primitive therian teeth in general. Some of the structures named are absent from many or even most primitive therian molars. Geographical descriptions seem adequate for the remaining structures. An attempt has been made to use current names where these are not ambiguous or, sometimes, misleading. An alternative term for "talonid basin" is given with some hesitancy, but this structure is not always a basin, often being broadly open lingually. The term "postfossid" corresponds to the terms given to other similar structures.

Since developmental fields extend for a greater or less degree from molars to premolars (or vice versa) and in some cases even farther, I use the same terms for corresponding structures on molars and premolars on this developmental criterion of serial homology, rather than following strictly the often questionable historical criterion (cf. the accepted usage in equid upper premolars). This practice, however, does occasionally result in my calling historically homologous cusps of different groups by different names (the metaconid of rodent premolars is the protoconid of those of other placentals; cf. Wood, 1962). The philosophy of the hypocone will be discussed elsewhere; my preference, however, is to call a posterolingual cusp on an upper molariform cheek tooth a "hypocone" no matter what its origin, although qualifying adjectives are sometimes helpful. A cusp arising from the precingulum is a pericone (Rütimeyer, 1891; Stehlin, 1916; Simons, 1961; Anthony, 1961). In the following list parentheses enclose the names of structures apparently not primitive in therians:

## UPPER TOOTH

centrocrista (new term)  
ectocingulum (new term)  
ectoflexus (new term)  
(mesostyle)

metacingulum (new term)  
metacone  
metaconule  
metacrista (new term)  
metastyle  
paracingulum (new term)  
paracone  
paraconule [= protoconule]  
paracrista (new term)  
parastyle  
(postcingulum) (new term)  
postprotocrista (new term)  
(precingulum) (new term)  
preprotocrista (new term)  
protocone  
protofossa (new term)  
stylar shelf  
stylocone

## LOWER TOOTH

crista obliqua  
(ectostylid)  
entoconid  
entoconulid  
entocristid (new term)  
hypoconid  
hypoconulid  
hypoconid  
(mesoconid)  
metaconid  
(metacristid) (new term)  
(metastylid)  
paraconid  
paralophid  
postcristid (new term)  
postfossid (new term)  
prefossid (new term)  
protoconid  
protolophid  
(protostylid)  
talonid  
trigonid

Some terms not marked as new have previously been applied only to rodents or other specialized groups.

In addition, the terms "prevallum" and "postvallum" are proposed for, respectively, the anterior and posterior shearing surfaces of the upper teeth, i.e., the anterior face of the paracrista, paracone, and preprotocrista, and the posterior face of the metacrista, metacone, and postprotocrista, respectively. "Prevallid" and "postvallid" are used for the anterior and posterior walls, respectively, of the trigonid. "Paraconule wing" and "metaconule wing" are applied to the crests labial

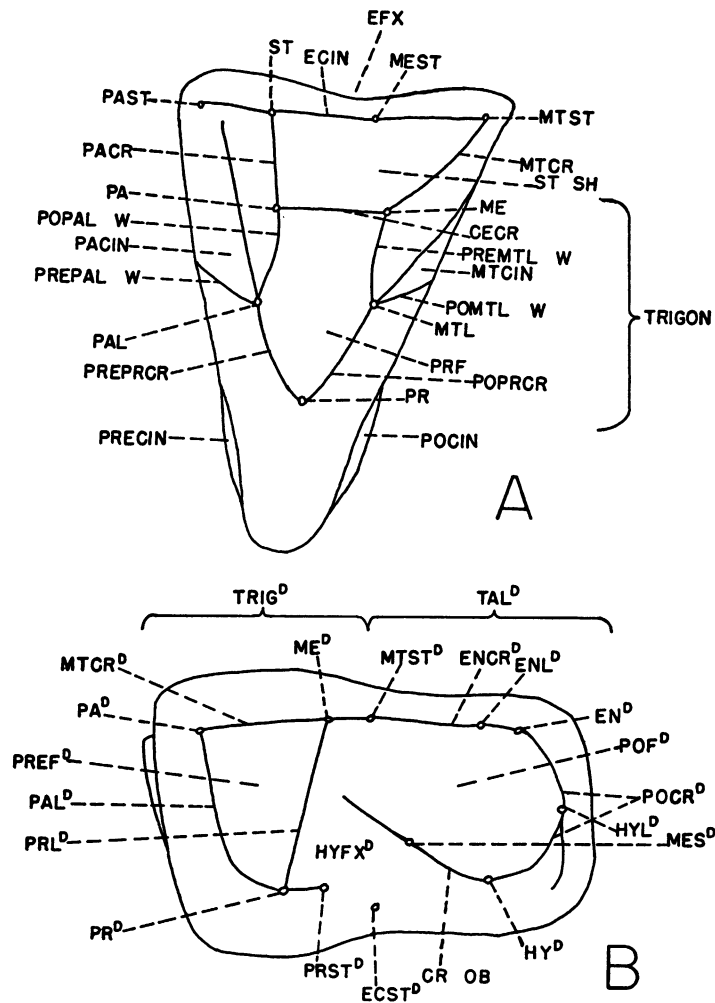


FIG. 1. Diagrams of therian molars, indicating the proposed terminology; anterior side to left.

A. Left upper molar. *Abbreviations:* cecr, centrocrista; ecin, ectocingulum; efx, ectoflexus; me, metacone; mest, mesostyle; mtcin, metacingulum; mtcrc, metacrista; mtl, metaconule; mtst, metastyle; pa, paracone; pacin, paracingulum; pacr, paracrista; pal, paraconule; past, parastyle; pocin, postcingulum; pomtl w, postmetaconule wing; popal w, postparaconule wing; popcr, postprotocrista; pr, protocone; premtl w, premetaconule wing; prepal w, preparaconule wing; preprcr, preprotocrista; precin, precingulum; prf, protofossa; st, stylocone; st sh, styler shelf.

B. Left lower molar. *Abbreviations:* cr ob, crista obliqua; ecstd, ectostylid; encrd, entocristid; end, entoconid; enld, entoconulid; hyd, hypoconid; hyfxd, hypoflexid; hyld, hypoconulid; med, metaconid; mesd, mesoconid; mtcrd, metacristid; mtstd, metastylid; pad, paraconid; palld, paralophid; pocrd, postcristid; pofd, postfossid; prd, protoconid; prefd, prefossid; prld, protolophid; prstd, protostylid; talld, talonid; trigd, trigonid.

to the paraconule and metaconule, respectively, including their extensions up the paracone and metacone. "Preparaconule wing" and similar constructions are more specific. Note that the preparaconule wing can be considered part of the paracingulum; the postmetaconule wing, part of the metacingulum. Similarly, the terms "precentrocrista" and "postcentrocrista" may be useful for the central part of the ectoloph in describing dilambdodont and selenodont teeth. The term "lingual cingula" applied to upper molariform teeth refers to the precingulum and postcingulum together.

The following directional terms are used:

**ANTERIOR:** Toward the front of the mouth, for cheek teeth; the term "mesial" is preferable because it is also applicable to incisors, but it is seldom used in paleontology.

**POSTERIOR:** Toward the rear of the mouth, for cheek teeth; the term "distal" is preferable because it is also applicable to incisors, but it is seldom used in paleontology.

**LINGUAL:** Toward the tongue or center of the mouth.

**LABIAL:** Toward the lips or side of the mouth.

**APICAL:** Away from the junction of the root and the crown, in a vertical direction.

**BASAL:** Toward the junction of the root and the crown, in a vertical direction.

**CENTRAL:** Toward the center of the tooth, in the occlusal plane.

**MARGINAL:** Away from the center of the tooth, in the occlusal plane.

#### INTERNAL CAROTID CIRCULATION

The probably primitive placental system of branches of the internal carotid artery (fig. 2) starts with a split near the postero-medial corner of the promontorium between a medial and a lateral branch.

The medial branch, here called the "medial entocarotid artery," passes into the braincase through the carotid foramen somewhere on the medial side of the promontorium and enters the circle of Willis. The lateral branch continues more or less anterolaterally over the promontorium, soon forking into an anterior (promontory artery) and a posterior (stapedial artery) branch.<sup>1</sup> The term "stape-

<sup>1</sup> Although the stapedial and promontory arteries are absent from all recent Carnivora known to me (unless the ascending pharyngeal artery of Davis and Story,

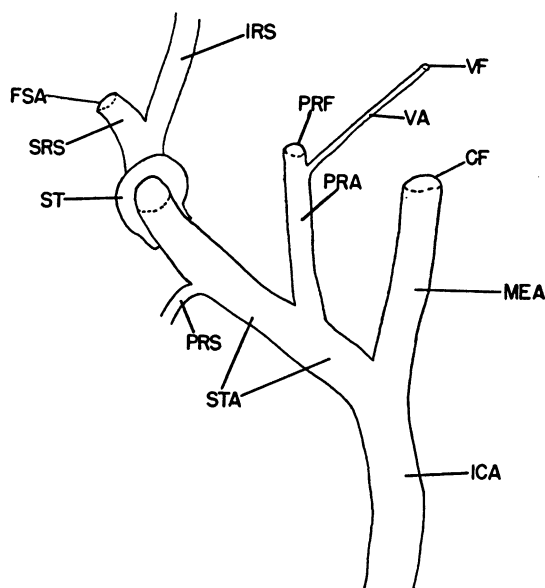


FIG. 2. Diagram of the major branches of the internal carotid artery in a primitive placental. The presence of a posterior ramus of the stapedial artery is uncertain, and the vidian artery may have originated from the medial entocarotid.

**Abbreviations:** cf, carotid foramen; fsa, foramen for stapedial artery; ica, internal carotid artery (undivided); irs, inferior ramus of stapedial artery; mea, medial entocarotid artery; pra, promontory artery; prf, promontory foramen; prs, posterior ramus of stapedial artery; srs, superior ramus of stapedial artery; st, stapes; sta, stapedial artery; va, vidian artery (of pterygoid canal); vf, vidian foramen.

dial artery" is here extended to include the main lateral branch before the fork.

1943, is the promontory artery), Matthew (1909) showed that they were present in both subfamilies of the Miacidae as well as in other groups. Hough (1948) implied that a stapedial artery is present in the viverrid *Nandinia*, but examination of skulls of that genus shows that she was mistaken and that *Nandinia* is not exceptional in this respect (Van Valen, 1963a). The presence of the stapedial artery is presumably a primitive mammalian trait, since it is well developed in at least some therapsids and in various Cenozoic mammals only distantly related to one another. Examination of a hemisected skull of *Manis* suggests that in the pangolin the internal carotid is reduced to the inferior ramus of the stapedial artery and that the circle of Willis is therefore supplied by only the vertebral artery, or possibly the external carotid. From the description of Wood (1962), it is probable that a stapedial artery was present in the paramyid rodent *Ischyrotomus*, as in recent rodents.

The promontory artery continues anteriorly over the promontorium, enters the braincase through the middle lacerate foramen or a separate promontory foramen, and joins the circle of Willis. Whether the vidian artery (of the pterygoid canal) was primitively a branch of the promontory artery, as it now usually is, or a branch of the medial entocarotid artery is not known.

The stapedia artery continues laterally across the promontorium and through the foramen in the stapes. A posterior ramus is in some cases given off before the stapes is reached. The stapedia artery then divides into a superior and an inferior ramus. The superior ramus enters the braincase and joins

(or becomes) the middle meningeal artery. The inferior ramus does not enter the braincase but continues anteriorly to a point near the foramen ovale where it joins (or becomes) the internal maxillary artery.

All or nearly all recent mammals have lost one or more of the branches of the internal carotid. The resulting arterial patterns, if used with sufficient regard to the obvious possibilities of convergence, provide a valuable taxonomic character.

All the branches mentioned above except, in some instances, the internal maxillary and middle meningeal arteries can be considered parts of the internal carotid system.

## SYSTEMATICS, MORPHOLOGY, AND EVOLUTION

### DELTATHERIDIA, NEW ORDER

#### SUPERFAMILY PALAEORYCTOIDEA

(WINGE, 1917)

#### FAMILY PALAEORYCTIDAE (WINGE, 1917)

##### SUBFAMILY DIDELPHODONTINAE

MATTHEW, 1918

The discussion of *Deltatheroides*, herein tentatively referred to the Didelphodontinae, can be found below, under the section entitled Other Palaeoryctidae.

#### PUERCOLESTES REYNOLDS, 1936

Plate 1, figure 7; table 1

*Puercolestes* REYNOLDS, 1936, p. 204.

TYPE AND ONLY KNOWN SPECIES: *Puercolestes simpsoni* Reynolds (1936, p. 204).

TYPE OF *P. simpsoni*: U.C.M.P. No. 36658, anterior two-thirds of skull with left  $P^4-M^1$ , roots of  $C-P^2$ ; right  $P^2$ ,  $M^{1-3}$ , roots of  $C-P^2$ ,  $P^4$ ; the trigonids and right  $P_4$  poorly figured by Reynolds have been lost.

KNOWN DISTRIBUTION OF *P. simpsoni*: Lower fossil level of Puerco, Tsosie Arroyo, San Juan Basin, New Mexico.

ILLUSTRATIONS: Reynolds (1936, pl. 25, fig. 1, photograph of right side of skull; pl. 25, fig. 2, photograph of palate; pl. 25, fig. 3,

photograph of lateral view of trigonids of right  $P_4-M_3$ ; text fig. 1, drawings of palate and lateral view of skull; text fig. 2, drawing of occlusal view of right upper teeth).

DISCUSSION: There are in addition several specimens obtained by the American Museum from washing the same locality in 1958, but these are probably not referable to *Puercolestes* and are at any rate of a smaller species. They are discussed below. No specimens of *P. simpsoni* were among the hundreds of all sizes collected in 1958, a fact that indicates its scarcity.

Reynolds (1936) assigned *Puercolestes* to the Deltatheridiidae but also considered it approximately ancestral to *Palaeoryctes*. It was placed in the Didelphodontinae by Simpson (1945).

#### NYSSODON SIMPSON, 1927

Plate 1, figures 3 and 4; table 2

*Nyssodon* SIMPSON, 1927, p. 124.

TYPE AND ONLY KNOWN SPECIES: *Nyssodon punctidens* Simpson (1927, p. 124).

TYPE OF *N. punctidens*: Y.P.M. No. 13654, left  $M^1$ .

KNOWN DISTRIBUTION OF *N. punctidens*: Latest Cretaceous, Lance Formation, Nio-

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Puercolestes simpsoni*, TYPE SPECIMEN (U.C.M.P. No. 36658)

	$P^3$	$P^4$	$M^1$	$M^2$	$M^3$	Series
Anterior tooth margin	2.30	3.60	4.40	5.80	5.15	—
Posterior tooth margin	2.10	4.75	4.90	$5.45 \pm 0.05$	4.05	—
Labial tooth margin	2.90	3.65	3.60	$3.55 \pm 0.15$	2.75	—
Length at paraconule	—	—	1.50	1.40	1.20	—
Horizontal distance of protocone apex from lingual margin of protocone	—	—	$1.00 \pm 0.10$	$1.10 \pm 0.10$	$1.35 \pm 0.05$	—
Posterior height of metacone	—	—	—	—	$2.05 \pm 0.15$	—
Posterior height of protocone	—	—	$3.00 \pm 0.20$	$3.20 \pm 0.15$	$2.35 \pm 0.10$	—
Labial height of paracone	$3.00 \pm 0.25$	—	—	—	—	—
Crown length						
$M^{1-3}$	—	—	—	—	—	$8.85 \pm 0.10$
Left $P^{2-4}$	—	—	—	—	—	$8.65 \pm 0.15$
Right $P^{2-4}$	—	—	—	—	—	$9.15 \pm 0.15$
Right $P^{1-4}$	—	—	—	—	—	$10.20 \pm 0.20$

TABLE 2  
MEASUREMENTS (IN MILLIMETERS) OF LEFT M<sup>2</sup>  
OF *Nyssodon punctidens*, TYPE SPECIMEN  
(Y.P.M. No. 13654)

Posterior margin	4.20 ± 0.20
Horizontal distance of apex of protocone from lingual margin of protocone	1.00 ± 0.25
Anterior height of paracone	2.90 ± 0.20
Posterior height of metacone	2.30 ± 0.10
Posterior height of protocone	2.45

brara County, Wyoming.

ILLUSTRATIONS: Simpson (1927, fig. 45H, drawings of occlusal and posterior views [reproduced in the present paper as pl. 1, figs. 3 and 4]; pl. 32, figs. 1 and 2, photographs of occlusal and posterior views).

DISCUSSION: *Nyssodon* is closely related to *Puercolestes*, but a generic distinction may be maintained, at least until *Nyssodon* is better known. *Nyssodon* was referred tentatively to the Pediomylinae by Simpson (1929a). See discussion under *Cimolestes*, below.

#### CIMOLESTES MARSH, 1889

*Cimolestes* MARSH, 1889, p. 89.

TYPE AND ONLY KNOWN SPECIES: *Cimolestes incisus* Marsh (1889, p. 89).

TYPE OF *C. incisus*: Y.P.M. No. 11775, left M<sub>1</sub>.

KNOWN DISTRIBUTION OF *C. incisus*: Latest Cretaceous, Lance Formation, Niobrara County, Wyoming, and Bug Creek Anthills Local Fauna, Hell Creek Formation, McCone County, Montana.

ILLUSTRATIONS: Marsh (1889, pl. 4, figs. 12–15, drawings of labial, lingual, and occlusal views of type). Simpson (1929a, fig. 50, drawing 1, lingual view of type).

DISCUSSION: W. A. Clemens (personal communication) has discovered that *Cimolestes* is a palaeoryctid and that there is a possibility that *Nyssodon* represents the upper teeth of *Cimolestes*. The latter possibility is not yet proved, and the genera may be retained as distinct pending Clemens' study of his new and better material.

The only identifiable tooth, other than the type, that was referred by Marsh to *C. incisus* (Marsh, 1892, pl. 10, fig. 5) is a P<sub>4</sub> of *Gypsonictops*. *Cimolestes curtus* Marsh, 1889, is a didelphid and was made the type of *Diaphorodon* by Simpson in 1927. *Cimolestes* was referred tentatively to the Pediomylinae by Simpson (1929a, 1951).

#### ACMEODON MATTHEW AND GRANGER, 1921

Plate 2, figure 1; text figure 3; tables 3 and 4

*Acmeodon* MATTHEW AND GRANGER, 1921, p. 3.

TYPE SPECIES: *Acmeodon secans* Matthew and Granger (1921, p. 3).

TYPE OF *A. secans*: A.M.N.H. No. 16599, left P<sub>1</sub>, P<sub>3</sub>–M<sub>1</sub>, talonid for M<sub>2</sub>, alveoli for C and P<sub>2</sub>.

REFERRED SPECIMENS: A.M.N.H. No. 4063, right P<sub>4</sub>–M<sub>2</sub>; A.M.N.H. No. 16600, left P<sub>4</sub>–M<sub>1</sub>, alveoli through M<sub>3</sub>; A.M.N.H. No. 16030, right M<sub>2</sub>–3, trigonids broken off; alveoli for right M<sub>1</sub> and P<sub>1</sub>–3; region of left dental foramen.

KNOWN DISTRIBUTION OF *A. secans*: Upper level of Torrejon, San Juan Basin, New Mexico. The levels of A.M.N.H. No. 4063 and A.M.N.H. No. 16030 are unknown, although these specimens are known to be from the Torrejon.

ILLUSTRATIONS: Matthew (1937, pl. 56, figs. 1a, b, c, photographs of occlusal, labial, and lingual views of type; pl. 56, figs. 2a, b,

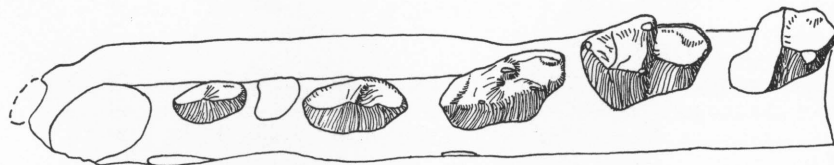


FIG. 3. Occlusal view of left mandible of *Acmeodon secans* Matthew and Granger, showing P<sub>1</sub> and P<sub>3</sub>–M<sub>2</sub>. There is some distortion in position of the posterior teeth. The mental foramina can be seen. Based on A.M.N.H. No. 16599, with the talonids of P<sub>4</sub> and M<sub>1</sub> completed from A.M.N.H. No. 16600. Torrejon. ×5.

TABLE 3  
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH AND JAWS OF *Acmeodon secans*  
AND OF Cf. *Acmeodon* Sp. FROM THE PUERCO

	<i>Acmeodon secans</i>			Cf. <i>Acmeodon</i> sp.
	A.M.N.H. No. 16030	A.M.N.H. No. 16599	A.M.N.H. No. 16600	A.M.N.H. No. 16413
Trigonid width				
P <sub>1</sub>	—	1.20	—	—
P <sub>3</sub>	—	1.55	—	—
P <sub>4</sub>	—	2.00±0.05	1.95	—
M <sub>1</sub>	—	2.50	2.45	—
M <sub>2</sub>	—	—	—	1.90±0.10
M <sub>3</sub>	2.20±0.05	—	—	—
Talonid width				
M <sub>1</sub>	—	2.00	2.30	1.80
M <sub>2</sub>	2.00	1.95	—	1.65
M <sub>3</sub>	1.50	—	—	—
Crown length				
P <sub>1</sub>	—	2.00	—	—
P <sub>3</sub>	—	3.15	—	—
P <sub>4</sub>	—	3.45±0.15	3.80	—
M <sub>1</sub>	—	3.45	3.70±0.05	—
Labial height of hypoconid				
P <sub>1</sub>	—	1.05±0.05	—	—
P <sub>3</sub>	—	1.55±0.05	—	—
P <sub>4</sub>	—	—	3.00±0.05	—
M <sub>1</sub>	—	2.00±0.05	2.20±0.05	—
Labial height of protoconid				
P <sub>1</sub>	2.80±0.05	2.80±0.05	—	—
P <sub>3</sub>	—	4.20±0.05	—	—
M <sub>1</sub>	—	3.70±0.15	—	—
Alveolar length of M <sub>1-3</sub>	10.30±0.05	—	10.20±0.15	8.90±0.10
Alveolar length, posterior edge of C through P <sub>4</sub>	—	11.20±0.55	—	—
Depth of mandible below M <sub>2</sub> protoconid	6.05±0.30	7.15±0.70	7.15±0.55	5.50±0.60

photographs of occlusal and labial views of A.M.N.H. No. 16600).

DISCUSSION: U.S.N.M. No. 15774, a possible P<sup>3</sup> from the Dragon described in a later section, may belong to *Acmeodon*. The presence of *Acmeodon* or of a very closely related genus in the Puerco is indicated by A.M.N.H.

No. 16413, a fragment of a left mandible with the talonids of M<sub>1-2</sub> and the alveolus of M<sub>3</sub>. It is from the upper level of the Puerco, 2 miles above Ojo Alamo, San Juan Basin, New Mexico. The small portion preserved is sufficiently similar to *A. secans* that no figure seems necessary. It is described below.

TABLE 4  
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Acmeodon secans* (A.M.N.H. No. 4063)

	P <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>
Anterior tooth margin	4.50±0.20	5.40±0.35	6.05±0.05
Posterior tooth margin	5.00±0.30	5.80±0.10	6.20±0.10
Labial tooth margin	3.80±0.15	4.60±0.20	3.80±0.05
Length at paraconule	—	2.10±0.10	2.05±0.05

A.M.N.H. No. 3609d, also from the Puerco, is a fragment of mandible with  $P_3$  and  $P_4$  of a larger species. It may be related to *Acmeodon* but more probably belongs to a pantolestid or hyopsodontid.

*Acmeodon* was referred by Matthew and Granger to the Leptictidae, still a fairly heterogeneous group, and this reference was retained and discussed by Matthew (1937). Simpson (1935, 1936a) followed Matthew in this respect, but in 1937 he showed that *Acmeodon* was related to *Gelastops* and thence to *Didelphodus*. In his classification of mammals (1945) he apparently inadvertently reverted to Matthew's arrangement, as did Gazin (1949).

**ABOLETYLESTES** DONALD E. RUSSELL, 1964

TYPE SPECIES: *Aboletylestes hypsilus* Donald E. Russell, 1964.

REFERRED SPECIES: *Aboletylestes* sp., late Paleocene of Cernay, France.

KNOWN DISTRIBUTION OF *A. hypsilus*:

Walbeck fissure-filling, middle Paleocene, Germany.

DISCUSSION: These species were described by Donald E. Russell (1964) two years after the present paper was written, and reference should be made to his paper for further information. *Gelastops* is the most similar American genus. The Cernay species differs from the Walbeck one in the lower dentition most noticeably in having a higher metaconid on  $P_4$ , broader molars, a higher paraconid on the molars, and slightly lower cusps. All these differences are possibly the result of an ancestral-descendant relationship.

**GELASTOPS** SIMPSON, 1935

Plate 2, figures 2-5; tables 5-8

*Gelastops* SIMPSON, 1935, p. 227.

*Emperodon* SIMPSON, 1935, p. 229.

TYPE SPECIES: *Gelastops parvus* Simpson (1935, p. 227) (synonym: *Emperodon acmeodontoides* Simpson, 1935, p. 229).

TYPE OF *G. parvus*: U.S.N.M. No. 6148,

TABLE 5  
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH AND JAWS OF *Gelastops parvus*

	A.M.N.H. No. 35224	A.M.N.H. No. 35225	A.M.N.H. No. 35226	A.M.N.H. No. 35227	A.M.N.H. No. 35228	U.S.N.M. No. 9446	U.S.N.M. No. 9601
Trigonid width							
$P_3$	—	—	1.55	—	1.30	—	—
$P_4$	1.80	—	1.80	1.70	1.55	—	—
$M_1$	2.15	2.05	2.20	2.05	2.00±0.05	—	—
$M_2$	—	2.20	—	2.15	—	2.10	2.30
$M_3$	—	1.95	—	—	—	—	1.95
Talonid width							
$M_1$	1.95	1.95	1.85	1.70	1.80	—	—
$M_2$	—	1.65	—	1.55	—	1.65	1.75
$M_3$	—	1.35	—	—	—	1.35	1.35
Crown length							
$P_3$	—	—	2.80	—	2.35	—	—
$P_4$	3.15	—	3.05	—	3.00	—	—
$M_1$	3.55±0.05	3.35	3.45	—	3.20±0.05	—	—
$M_2$	—	3.05	—	—	—	2.55±0.05	—
$M_3$	—	2.55	—	—	—	2.50±0.05	—
Height of C above antero-lingual border of alveolus	—	—	5.00±0.35	—	—	—	—
Alveolar length of $M_{1-3}$	8.70±0.20	9.20±0.05	—	8.55±0.15	—	—	9.15±0.20
Alveolar length, posterior edge of C through $P_4$	9.70±0.15	10.35	9.85±0.15	9.20±0.15	9.70±0.20	—	9.30±0.35
Depth of mandible below $M_2$ protoconid	5.85±0.50	6.80±0.50	—	5.70±0.35	—	5.45±0.70	5.70±0.55
Distance from posterior end of $M_3$ to dental foramen	—	—	—	—	—	7.45±0.25	—

TABLE 6  
MEASUREMENTS (IN MILLIMETERS) OF CUSP HEIGHTS OF LOWER TEETH OF  
*Gelastops parvus* (A.M.N.H. No. 35226)

	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>
Labial height of hypoconid	1.80	2.20	2.00 ± 0.05
Labial height of protoconid	3.70	3.50 ± 0.05	3.55 ± 0.05
Lingual height of protoconid	3.05 ± 0.10	3.00 ± 0.10	3.20 ± 0.20
Lingual height of paraconid	—	2.05	2.30 ± 0.05
Lingual height of metaconid	—	2.50	2.80 ± 0.05

right lower canine, M<sub>1</sub>, M<sub>3</sub>, alveoli posterior from at least I<sub>3</sub>.

REFERRED SPECIMENS: U.S.N.M. No. 9850, type of *Emperodon acmeodontoides*, right P<sub>4</sub>, M<sub>2</sub>, posterior part of P<sub>3</sub>, alveoli for M<sub>1</sub> and M<sub>3</sub>; U.S.N.M. No. 9446, right M<sub>2</sub>, talonid of M<sub>3</sub>, mandible to a little posterior to the dental foramen; U.S.N.M. No. 9554, left M<sup>2</sup>; U.S.N.M. No. 9601, right M<sub>2-3</sub>, alveoli from posterior half of canine; A.M.N.H. No. 35224, left P<sub>4</sub>-M<sub>1</sub>, alveoli for remaining teeth; A.M.N.H. No. 35225, left M<sub>1-3</sub>, alveoli for remaining teeth; A.M.N.H. No. 35226, right C, P<sub>3</sub>-M<sub>1</sub>, alveoli for P<sub>1-2</sub>; A.M.N.H. No. 35227, left P<sub>4</sub>-M<sub>2</sub>, alveoli from posterior canine through M<sub>3</sub>; A.M.N.H. No. 35228, right P<sub>3</sub>-M<sub>1</sub>, alveoli from posterior part of canine; A.M.N.H. No. 35229, unerupted right P<sub>4</sub>, alveoli for DP<sub>2-3</sub>.

KNOWN DISTRIBUTION OF *G. parvus*: Gidley Quarry and corresponding Torrejonian, Lebo Formation, Crazy Mountain Field, Montana.

ILLUSTRATIONS: Simpson (1937a, fig. 12,

labial view of U.S.N.M. No. 6148; fig. 13a, occlusal view of U.S.N.M. No. 9601; fig. 13b, lingual view of U.S.N.M. No. 9850).

DISCUSSION: I follow Simpson in referring the upper molar to *Gelastops* (and not to *Avunculus*) for the following reasons: its length is the same as or slightly less than that of M<sub>2</sub> in *Gelastops parvus*; its length is at least as great as that of M<sub>1</sub> in *Avunculus*; and M<sub>1</sub> in *Gelastops* is longer than M<sub>2</sub>. If the same relation holds in its relative, *Avunculus*, the upper molar would be too long to occlude properly. Direct manipulation shows that the upper molar occludes adequately with the M<sub>2</sub> of *Gelastops parvus*.

A second species (cf. *Gelastops*, sp. B) is represented by C.M. No. 8802, an isolated left M<sub>3</sub>, and by C.M. No. 8890, a right M<sup>2</sup>, both from the Tiffanian of the Dell Creek Local Fauna, Hoback Basin, Wyoming. It is not certain that these are conspecific or even congeneric, but there are no definite contraindications. The lower tooth was referred by Dorr (1958) to *Gelastops parvus*. (See fig. 4.)

TABLE 7  
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF CF. *Gelastops*, SPECIES B (C.M. No. 8802) AND *Gelastops* CF. *G. parvus* (U.S.N.M. FIELD No. K9-F1)

	Sp. B M <sub>3</sub>	Cf. <i>G. parvus</i>	
		Left M <sub>71</sub>	Right M <sub>71</sub>
Trigonid width	2.00 ± 0.05	2.55	2.55
Talonid width	1.35 ± 0.15	—	2.25
Crown length	2.70 ± 0.15	3.35 ± 0.10	3.45
Labial height of hypoconid	—	1.65 ± 0.05	1.55 ± 0.10
Labial height of protoconid	—	3.60 ± 0.15	3.95 ± 0.15
Lingual height of protoconid	—	3.70 ± 0.40	—
Lingual height of paraconid	—	2.90 ± 0.20 <sup>a</sup>	—
Lingual height of metaconid	—	3.10 ± 0.20 <sup>a</sup>	—

<sup>a</sup> The difference between the height of the paraconid and that of metaconid is 0.20 mm. with negligible error.

TABLE 8

MEASUREMENTS (IN MILLIMETERS) OF UPPER M<sup>2</sup>'S OF *Gelastops parvus* (U.S.N.M. No. 9554) AND CF. *Gelastops*, SPECIES B (C.M. No. 8890)

	<i>Gelastops parvus</i>	Cf. <i>Gelastops</i> , Sp. B
Anterior tooth margin	5.15	—
Posterior tooth margin	4.85	3.75 ± 0.15
Labial tooth margin	2.75	—
Length at paraconule	1.30	0.95
Horizontal distance of protocone apex from lingual margin of protocone	1.60 ± 0.05	0.85 ± 0.05
Anterior height of paracone	2.00 ± 0.05	2.20 ± 0.25
Posterior height of metacone	1.95 ± 0.05	—
Posterior height of protocone	2.20 ± 0.05	1.80 ± 0.10

No figure is given of the lower molar because it is distorted and the differences from *Gelastops parvus* should be clear from the later verbal comparison. Two additional specimens of *Gelastops* are represented by U.S.N.M. No. K9-F1 (field number), left M<sub>72</sub> and right M<sub>72</sub> of different individuals from the Shotgun member, "Fort Union Formation," northern Wind River Basin, Wyoming (Keefer, 1961). The fauna is about late Torrejonian in age. The specimens differ only slightly from *Gelastops parvus* and may be referable to that species, perhaps as a distinct subspecies, and

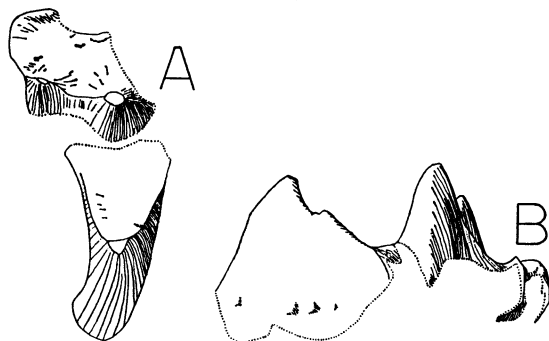


FIG. 4. Cf. *Gelastops*, sp. B, right M<sup>2</sup>, C.M. No. 8890; Dell Creek Local Fauna, Tiffanian. Dotted lines represent broken edges. A. Occlusal view. B. Anterior view. ×5.

are for convenience herein called *Gelastops* cf. *G. parvus*.

*Gelastops* was correctly referred by Simpson (1935) to the Didelphodontinae, but *Emperodon*, the type of which contained P<sub>4</sub>, was seen to be close to *Acmeodon*, so was put into the Leptictidae. The two genera and species were soon synonymized by Simpson (1937a). In his 1945 classification he inadvertently used his conclusions of 1935, as Gazin (1949) has pointed out although mistaking the original family reference.

#### AVUNCULUS, NEW GENUS

Plate 2, figure 6; text figure 5; table 9

TYPE AND ONLY KNOWN SPECIES: *Avunculus didelphodonti*, new species.

TYPE OF *A. didelphodonti*: A.M.N.H. No. 35297, left P<sub>3</sub>-M<sub>1</sub>, alveoli for P<sub>2</sub> and M<sub>2</sub>.

REFERRED SPECIMEN: A.M.N.H. No. 35296, left P<sub>2-4</sub>, alveoli through last lower incisor.

KNOWN DISTRIBUTION OF *A. didelphodonti*: Gidley Quarry, Torrejonian, Lebo Formation, Crazy Mountain Field, Montana.

TABLE 9

MEASUREMENTS (IN MILLIMETERS) OF LOWER JAWS AND TEETH OF *Avunculus didelphodonti*

	A.M.N.H. No. 35296	A.M.N.H. No. 35297
Trigonid width		
P <sub>2</sub>	1.00	—
P <sub>3</sub>	1.05	1.00
P <sub>4</sub>	1.30	1.35
M <sub>1</sub>	—	1.70
Talonid width of M <sub>1</sub>	—	1.65
Crown length		
P <sub>2</sub>	1.70	—
P <sub>3</sub>	1.80	1.65
P <sub>4</sub>	2.70 ± 0.05	2.45
M <sub>1</sub>	—	2.80
Labial height of protoconid of P <sub>3</sub>	—	2.50 ± 0.05
Lingual height of protoconid of P <sub>3</sub>	—	2.00 ± 0.05
Lingual height of paraconid		
P <sub>3</sub>	—	1.15
P <sub>4</sub>	—	1.55
Alveolar length, posterior edge of C through P <sub>4</sub>	7.80 ± 0.15	—

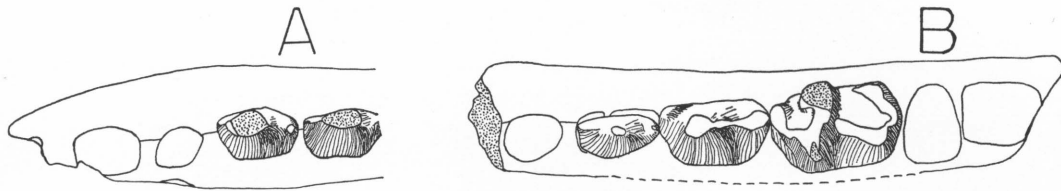


FIG. 5. *Avunculus didelphodonti*, new genus, new species; Gidley Quarry, Torrejonian. Occlusal views. Broken areas are stippled. A. Left mandible with  $P_{2-3}$ , A.M.N.H. No. 35296. B. Left mandible with  $P_3-M_1$ , A.M.N.H. No. 35297, type.  $\times 6$ .

**DIAGNOSIS:** Distinguished from other didelphodontines by following combination of characters, among others: alveolus for lower canine about half as long as that for  $P_4$ ,  $P_1$  one-rooted, paraconid present and relatively prominent on  $P_3$ , protostylid and metaconid absent from  $P_4$ , metacristid absent from at least  $M_1$ .

**ETYMOLOGY:** The name is given with reference to my belief that this genus is the closest, of those now known, to the ancestry of *Didelphodus*, although it is probably not directly ancestral (*avunculus*, Latin, uncle).

**DISCUSSION:** This genus was recognized by Simpson on the label as new, but he did not describe the American Museum material from the Gidley Quarry.

#### DIDELPHODUS COPE, 1882

*Didelphodus* COPE, 1882b, p. 522.

*Phenacops* MATTHEW, 1909, p. 535.

*Didelphyodus* WINGE, 1923, p. 194.

**TYPE SPECIES:** *Deltatherium absarokae* Cope.

#### *Didelphodus absarokae* (Cope, 1881)

Plate 1, figures 1, 2, 5, 6, 8, 9; plate 3, figures 1, 2; tables 10-14

*Deltatherium absarokae* COPE, 1881a, p. 669.

**TYPE SPECIMEN:** A.M.N.H. No. 4228, left  $I_1-C$ ,  $P_3$ ,  $M_3$ , roots of  $P_1-M_2$ ; right  $P_4$ , talonid of  $M_1$ , roots of  $C-P_3$ ; front half of crushed skull still partly obscured by hematite matrix, with left  $P^3-M^2$ , roots of  $C$ ,  $?I^{1-2}$ ; right  $P^2-M^3$ , roots of  $C-P^1$ ; Willwood Formation, Big Horn Basin, Wyoming.

**REFERRED SPECIMENS:** A.M.N.H. No. 4229, right  $M_{1-3}$ ; Willwood Formation. A.M.N.H. No. 15010, right  $M^2$ , partial alveoli for  $M^1$  and  $M^3$ ; upper Gray Bull. A.M.N.H. No. 15101, right  $M_{1-2}$ , alveoli for  $P_4$  and  $M_3$ ; middle Gray Bull. A.M.N.H. No.

15700, left  $M^{1-3}$ ; upper or possibly middle Gray Bull. A.M.N.H. No. 16237, left  $P_4-M_1$ , roots of  $P_{2-3}$ , alveoli for  $P_1$  and posterior part of canine; ?Almagre, possibly Largo. A.M.N.H. No. 16238, left  $P_4-M_2$ ,  $I_{73}$ , roots of  $C-P_3$ ; right  $P_{1-2}$ ,  $M_1$ , talonids of  $M_{2-3}$ , roots of  $I_{72-3}$ ,  $C$ ,  $P_{3-4}$ ; upper Almagre. A.M.N.H. No. 16240, right  $P_2$ ,  $M_1$ , left and right alveoli for  $P_1-M_3$  and posterior part of canine, right  $P^{3-4}$ ; Almagre. A.M.N.H. No. 16825, left  $P_4-M_3$ ; upper Gray Bull. A.M.N.H. No. 16826, left  $P_4-M_1$ , posterior root of  $P_3$ ; upper Gray Bull. A.M.N.H. No. 17007, left  $P_4-M_2$ , right  $P_4$ ; Sand Coulee. A.M.N.H. No. 48391, right  $M_{1-3}$ ; Almagre. A.M.N.H. No. 48392, right  $M^{1-3}$ , fragment of  $P^4$ ; Almagre; probably same individual as A.M.N.H. No. 48391. A.M.N.H. No. 48540, fragmentary right  $P^3-M^3$ ; Almagre. A.M.N.H. No. 48568, right  $P^4$ , trigonid of right  $M_1$ ; Almagre. A.M.N.H. No. 48579A, fragment of maxilla with right  $P^{3-4}$  and alveolus for  $M^1$ ; Almagre. A.M.N.H. No. 48600, labial half of left  $M^2$ ; Almagre. A.M.N.H. No. 59631, right  $M^2$ ; Four Mile. A.M.N.H. No. 80024, right  $M^1$ ; Almagre. A.M.N.H. No. 80025, left  $M^{2-3}$ ,  $C$ , alveoli for  $P^1$ ,  $P^3-M^1$ ; base of right  $C$ , alveoli for  $P^{2-3}$ ; Almagre. A.M.N.H. No. 80026, left  $M^1$ ; Willwood Formation. U.S.N.M. No. 18433, left  $M_2$ , roots of  $M_1$  and  $M_3$ ; Lost Cabin, Wind River Basin. U.S.N.M. No. 19458, left  $P_3-M_1$ , roots of  $C$  and  $P_2$ ; lower or possibly middle Gray Bull. U.C.M.P. Nos. 44027A, 44027B, left and right  $M^2$  of two individuals; Four Mile. U.C.M.P. No. 44307, right  $M_3$ ; Four Mile. U.C.M.P. No. 44916, left  $M^2$ ; Four Mile. U.C.M.P. No. 45965 (called 44965 by McKenna, 1960a), right  $M^3$ ; Four Mile. U.C.M.P. No. 46677, left  $M_3$ ; Four Mile. U.C.M.P. No. 58478, labial half of left  $M^1$ ; Four Mile. U.C.M.P. No. 58480, left  $M^2$  of two individuals, left  $M_1$ ; Four Mile. Possibly

TABLE 10

MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH AND JAWS OF *Didelphodus absarokae*  
FROM THE GRAY BULL AND LOST CABIN FAUNAS

	A.M.N.H. No. 4228	A.M.N.H. No. 4229	A.M.N.H. No. 15101	A.M.N.H. No. 16825	A.M.N.H. No. 16826	A.M.N.H. No. 17007	U.S.N.M. No. 19458	U.S.N.M. No. 18433
Trigonid width								
P <sub>3</sub>	2.05±0.05	—	—	—	—	—	2.20±0.05	—
P <sub>4</sub>	2.05	—	—	2.35	—	2.15	2.40	—
M <sub>1</sub>	—	2.55	2.50	2.35	2.20	—	2.65	—
M <sub>2</sub>	2.30±0.05	2.70	2.80	2.55	2.65	—	—	2.55
M <sub>3</sub>	—	2.30	—	2.20	—	—	—	—
Talonid width								
M <sub>1</sub>	—	2.30	2.05	2.15	2.30	—	2.20	—
M <sub>2</sub>	2.15	2.35	2.20	2.05	—	—	—	2.45
M <sub>3</sub>	1.85	1.95	—	1.80	—	—	—	—
Crown length								
P <sub>3</sub>	—	—	—	—	—	—	3.90	—
P <sub>4</sub>	3.70	—	—	3.50	3.65	4.60	3.75	—
M <sub>1</sub>	—	3.55±0.05	4.05±0.15	3.95	3.95±0.15	4.15±0.25	4.20±0.25	—
M <sub>2</sub>	—	3.70±0.05	4.05	3.80	—	—	—	3.80±0.05
M <sub>3</sub>	—	3.65	—	3.45±0.05	—	—	—	—
Labial height of hypoconid								
P <sub>4</sub>	2.00	—	—	—	—	—	—	—
M <sub>2</sub>	—	—	—	—	—	—	—	1.95
Labial height of protoconid								
C	8.55±0.70	—	—	—	—	—	—	—
P <sub>4</sub>	3.85	—	—	—	—	4.10±0.20	—	—
M <sub>2</sub>	—	—	—	3.80±0.05	—	—	—	3.15±0.05
Lingual height of protoconid								
P <sub>4</sub>	3.35±0.05	—	—	—	—	—	—	—
M <sub>2</sub>	—	—	—	—	—	—	—	2.80±0.05
Lingual height of paraconid								
P <sub>4</sub>	1.45±0.05	—	—	1.50	1.45	—	—	—
M <sub>2</sub>	—	—	—	—	—	—	—	1.45±0.05
Lingual height of metaconid								
P <sub>4</sub>	2.00±0.05	—	—	2.05	—	—	1.45	—
Alveolar length of M <sub>1-3</sub>	10.00±0.20	10.55±0.05	11.65±0.30	11.20±0.15	—	—	—	11.30±0.50
Alveolar length, posterior edge of C through P <sub>4</sub>	15.00±0.30	—	—	7.05±0.30	—	—	—	—
Depth of mandible below M <sub>2</sub> protoconid	7.30±0.40	7.30±0.30	7.85±0.70	7.05±0.30	—	—	—	—

C.M. No. 9696, left P<sup>3</sup>-M<sup>3</sup>, posterior alveolus for P<sup>2</sup>; DeBeque Formation, 8 miles west of Meeker, Rio Blanco County, Colorado. U.C.M.P. No. 44915, a left M<sup>2</sup>, and U.C.M.P. No. 46673, a left M<sup>1</sup> and two lower molars, additional specimens from the Four Mile referred by McKenna (1960a) to *Didelphodus absarokae*, were not seen.

KNOWN DISTRIBUTION OF *D. absarokae*: Earliest to late Wasatchian, northern New Mexico through northern Wyoming.

ILLUSTRATIONS: Cope (1884a, pl. 24e, fig. 13, palate of type; pl. 24e, fig. 13a, left view of

both rami of type). Matthew (1913, fig. 5, occlusal view of upper teeth and labial view [composite] of lower teeth, generally more accurate than his figures of 1918; 1918, fig. 10, lateral view of skull and mandible of type; fig. 11, top view of type skull; fig. 12, palatal view of type; fig. 13, occlusal view of all the teeth of the type; fig. 14, labial and occlusal views of type of "*Didelphodus absarokae secundus*"). McKenna (1960a, figs. 44b, c, occlusal views of M<sup>2</sup>, U.C.M.P. Nos. 44027A, 44027B, both mislabeled as to side of mouth). The figure in Gregory (1934, fig. 23V) is less

accurate than those listed.

DISCUSSION: A.M.N.H. No. 15102, a worn and fragmentary specimen referred to this species by Matthew (1918), is not a *Didelphodus*; Malcolm McKenna (personal communication) identifies it tentatively as *Palaeosinopa lutreola*. *Didelphodus absarokae* secun-

*dus* Matthew (1918, p. 584, type, A.M.N.H. No. 16825) is included in the above list. It can be surely recognized only by the larger metaconid and paraconid on P<sub>4</sub>, and this tooth is present in only A.M.N.H. No. 16825 and A.M.N.H. No. 16826 of the upper Gray Bull specimens. On the other hand, U.S.N.M. No.

TABLE 11  
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH AND JAWS OF *Didelphodus absarokae*  
FROM THE SAN JOSÉ FORMATION AND THE FOUR MILE FAUNA

	A.M.N.H. No. 16237	A.M.N.H. No. 16238	A.M.N.H. No. 16240	A.M.N.H. No. 48391	U.C.M.P. No. 44307	U.C.M.P. No. 46677	U.C.M.P. No. 58480
Trigonid width							
P <sub>2</sub>	—	1.80	1.85	—	—	—	—
P <sub>4</sub>	1.95	2.20	—	—	—	—	—
M <sub>1</sub>	2.15	2.35	2.30±0.05	2.50±0.05	—	—	2.55
M <sub>2</sub>	—	2.65	—	2.85	—	—	—
M <sub>3</sub>	—	2.35±0.05	—	2.60	2.40	2.45	—
Talonid width							
M <sub>1</sub>	2.00	2.20	2.05	2.25±0.15	—	—	2.40
M <sub>2</sub>	—	2.15	—	2.50±0.05	—	—	—
M <sub>3</sub>	—	1.80	—	2.05	1.80	1.90	—
Crown length							
P <sub>1</sub>	—	2.05±0.05	—	—	—	—	—
P <sub>2</sub>	—	3.05	3.00	—	—	—	—
P <sub>4</sub>	3.35	3.65	—	—	—	—	—
M <sub>1</sub>	3.50±0.20	3.50	3.55±0.15	4.10±0.05	—	—	3.55
M <sub>2</sub>	—	3.85	—	—	—	—	—
M <sub>3</sub>	—	—	—	4.30±0.10	3.85	3.85	—
Labial height of hypoconid							
M <sub>1</sub>	—	—	—	—	—	—	1.85
M <sub>3</sub>	—	—	—	—	1.95	2.00	—
Labial height of protoconid							
I <sub>7</sub>	—	1.00	—	—	—	—	—
P <sub>1</sub>	—	2.45±0.20	—	—	—	—	—
P <sub>2</sub>	—	3.85±0.15	—	—	—	—	—
P <sub>4</sub>	—	3.65±0.15	—	—	—	—	—
M <sub>1</sub>	—	—	—	—	—	—	3.25
M <sub>3</sub>	—	—	—	—	3.75	3.90±0.05	—
Lingual height of protoconid							
M <sub>1</sub>	—	—	—	—	—	—	2.45
M <sub>3</sub>	—	—	—	—	3.00±0.05	3.25±0.10	—
Lingual height of paraconid							
M <sub>1</sub>	—	—	—	—	—	—	1.85
M <sub>3</sub>	—	—	—	—	2.65	2.55	—
Lingual height of metaconid							
M <sub>1</sub>	—	—	—	—	—	—	2.20
M <sub>2</sub>	—	—	—	3.15±0.20	—	—	—
M <sub>3</sub>	—	—	—	2.80±0.20	2.80	2.85	—
Alveolar length of M <sub>1-3</sub>	—	10.85±0.35	10.05±0.20	—	—	—	—
Alveolar length, posterior edge of C through P <sub>4</sub>	13.70±0.55	14.65±0.70	12.85±0.15	—	—	—	—
Depth of mandible below M <sub>2</sub> protoconid	—	7.50±0.35 <sup>a</sup> 7.70±0.35 <sup>b</sup>	7.20±0.70	—	—	—	—

<sup>a</sup> Left side.

<sup>b</sup> Right side.

TABLE 12  
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Didelphodus absarokae*  
FROM THE WILLWOOD AND COLTON FORMATIONS

	A.M.N.H. No. 4228	A.M.N.H. No. 15010	A.M.N.H. No. 15700	A.M.N.H. No. 80026	C.M. No. 9696
<b>Anterior margin</b>					
P <sup>3</sup>	3.20±0.05	—	—	—	3.30±0.05
P <sup>4</sup>	3.80	—	—	—	4.55
M <sup>1</sup>	4.95	—	5.15	4.70	5.35
M <sup>2</sup>	5.05±0.20	5.20±0.15	5.50±0.15	—	6.05±0.15
M <sup>3</sup>	4.70±0.15	—	5.00	—	5.85±0.05
<b>Posterior margin</b>					
P <sup>3</sup>	3.35±0.05	—	—	—	3.65
P <sup>4</sup>	4.30	—	—	—	5.00
M <sup>1</sup>	5.35	—	5.55	5.05	5.70±0.05
M <sup>2</sup>	4.80	4.95	5.50	—	5.70±0.10
M <sup>3</sup>	3.30	—	3.50	—	4.15±0.05
<b>Labial margin</b>					
P <sup>2</sup>	2.85±0.35	—	—	—	—
P <sup>3</sup>	3.80±0.15	—	—	—	3.70±0.15
P <sup>4</sup>	3.85	—	—	—	4.00
M <sup>1</sup>	3.70	—	3.85	3.50	3.80±0.15
M <sup>2</sup>	3.45	3.50±0.15	3.55±0.15	—	3.80
M <sup>3</sup>	2.95	—	3.30±0.15	—	3.65±0.05
<b>Length at paracone</b>					
M <sup>1</sup>	1.70	—	1.80	1.70	2.00±0.05
M <sup>2</sup>	—	1.85	1.85	—	2.15±0.15
M <sup>3</sup>	1.55±0.05	—	1.80	—	1.80±0.05
<b>Horizontal distance of protocone apex from lingual margin of protocone</b>					
M <sup>1</sup>	1.05±0.05	—	1.50	1.15±0.15	1.15±0.10
M <sup>2</sup>	—	1.05	1.50	—	1.35±0.05
M <sup>3</sup>	0.85	—	1.05	—	0.85±0.05
<b>Anterior height of paracone</b>					
M <sup>2</sup>	—	2.30±0.15	—	—	—
M <sup>3</sup>	—	—	1.85	—	—
<b>Posterior height of metacone</b>					
M <sup>2</sup>	—	2.20	—	—	—
M <sup>3</sup>	—	—	1.70	—	1.55
<b>Posterior height of protocone</b>					
M <sup>2</sup>	—	2.00±0.05	2.05	—	—
M <sup>3</sup>	—	—	1.60	—	1.80±0.10
<b>Labial height of paracone</b>					
P <sup>3</sup>	3.50±0.05	—	—	—	—
P <sup>4</sup>	—	—	—	—	2.85±0.05
<b>Crown length of M<sup>1-3</sup></b>					
	10.00±0.35	—	9.70	—	10.70±0.40
<b>Crown length, posterior edge of C through P<sup>4</sup></b>					
	13.00±0.70	—	—	—	—

19458, from lower in the Gray Bull, has an even larger paraconid and talonid, although the metaconid is not quite so large. This fact indicates that both kinds of P<sub>4</sub> coexisted

through at least part of Graybullian time, and that *D. a. secundus* cannot be maintained as taxonomically distinct from *D. a. absarokae*. Van Houten (1945) questionably recorded

[illegible]

TABLE 14  
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Didelphodus absarokae*  
FROM THE FOUR MILE FAUNA

	A.M.N.H. No. 59631	U.C.M.P. No. 44027A	U.C.M.P. No. 44027B	U.C.M.P. No. 44916	U.C.M.P. No. 45965	U.C.M.P. No. 58478	U.C.M.P. No. 58480A	U.C.M.P. No. 58480B
Anterior margin								
M <sup>2</sup>	5.50	6.75	6.00	6.05	—	—	5.65	5.70
M <sup>3</sup>	—	—	—	—	6.00±0.30	—	—	—
Posterior margin								
M <sup>2</sup>	5.15	6.30	5.80	5.90±0.10	—	—	5.05	5.25
M <sup>3</sup>	—	—	—	—	3.60±0.10	—	—	—
Labial margin								
M <sup>1</sup>	—	—	—	—	—	4.10±0.05	—	—
M <sup>2</sup>	3.25	4.10	3.80	3.75±0.05	—	—	3.75	3.25
M <sup>3</sup>	—	—	—	—	4.10±0.30	—	—	—
Length at paraconule								
M <sup>2</sup>	1.65	2.05±0.05	1.95	2.20	—	—	1.90	1.85
M <sup>3</sup>	—	—	—	—	1.65	—	—	—
Horizontal distance of protocone apex from lingual margin of protocone								
M <sup>2</sup>	1.40	1.50±0.15	1.35	1.40	—	—	1.65	1.30
M <sup>3</sup>	—	—	—	—	1.10	—	—	—
Anterior height of para- cone of M <sup>2</sup>	2.40	2.45	2.35	—	—	—	2.35±0.05	2.10
Posterior height of meta- cone								
M <sup>1</sup>	—	—	—	—	—	2.30	—	—
M <sup>2</sup>	2.05	—	1.95	—	1.95	—	1.95	1.75
Posterior height of proto- cone								
M <sup>2</sup>	2.05	—	—	2.00±0.05	—	—	1.90	1.60±0.05
M <sup>3</sup>	—	—	—	—	1.75±0.05	—	—	—

*D. a. secundus* from the Willwood "Lysite," presumably because of a statement to this effect by Matthew (1918). I suspect that both known specimens are from a somewhat lower level.

The reference of U.S.N.M. No. 18433 to *Didelphodus absarokae* instead of to *D. ventanus*, as previously by White (1952), extends the range of *D. absarokae* to Lost Cabin time. However, the Lost Cabin form will probably deserve at least subspecific distinction when it is better known. The age of the Carnegie Museum specimen is indicated by its association under the same number with a mandible that compares closely with the type and other specimens of *Pelycodus trigonodus*, a more rapidly evolving species from about the middle Gray Bull (McKenna, 1960a, mentioned but did not figure or describe in detail speci-

mens of *Pelycodus* of the same size from the Four Mile).

***Didelphodus altidens* (Marsh, 1872)**

Plate 3, figure 3; plate 4, figures 1–3; tables 15–18

*Centetodon altidens* MARSH, 1872a, p. 214.

*Phenacops incerta* MATTHEW, 1909, p. 535.

*Didelphodus absarokae ventanus* MATTHEW, 1918, p. 585.

*Didelphodus ventanus* (Matthew) WHITE, 1952, p. 189.

*Didelphodus altidens* (Marsh) McKENNA, in McKenna, Robinson, and Taylor, 1962, p. 17.

TYPE SPECIMEN: Y.P.M. No. 13516, left M<sub>2</sub>, alveolus for M<sub>3</sub>; Bridger, "near Henry's Fork," so level C or possibly D.

REFERRED SPECIMENS: A.M.N.H. No. 12091, type of *Phenacops incerta*, very worn

TABLE 15  
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH AND JAWS OF *Didelphodus altidens*

	A.M.N.H. No. 12091	A.M.N.H. No. 14747	A.M.N.H. No. 56614	A.M.N.H. No. 56615	Y.P.M. No. 13516
Trigonid width					
P <sub>3</sub>	—	1.85	—	—	—
M <sub>1</sub>	2.15±0.10	—	—	1.95	—
M <sub>2</sub>	2.15±0.05	—	2.30	2.00	2.15
M <sub>3</sub>	—	—	1.85	1.95	—
Talonid width					
M <sub>1</sub>	1.95±0.15	—	—	1.65	—
M <sub>2</sub>	1.95±0.20	1.95	1.85	1.80	1.85
M <sub>3</sub>	—	1.70	—	1.55	—
Crown length					
P <sub>3</sub>	—	2.95	—	—	—
M <sub>1</sub>	—	—	—	3.35	—
M <sub>2</sub>	—	—	2.95	—	2.85
M <sub>3</sub>	—	—	—	3.20	—
Labial height of protoconid of P <sub>3</sub>	—	3.35±0.20	—	—	—
Lingual height of protoconid of P <sub>3</sub>	—	3.15±0.20	—	—	—
Lingual height of paraconid					
P <sub>3</sub>	—	1.05	—	—	—
M <sub>2</sub>	—	—	—	2.30±0.05	—
Lingual height of metaconid of M <sub>2</sub>	—	—	—	2.35±0.05	—
Alveolar length of M <sub>1-3</sub> <sup>a</sup>	8.70±0.05	10.30	—	9.15±0.35 <sup>b</sup>	—
Alveolar length, posterior edge of C through P <sub>4</sub>	9.55±0.20	12.15	—	—	—
Depth of mandible below M <sub>2</sub> protoconid	6.45±0.40	7.00±0.20	7.10±0.70	5.70±0.30	6.30±0.45
Distance from posterior end of M <sub>3</sub> to dental foramen	8.80±0.40	—	—	—	—

<sup>a</sup> U.S.N.M. 18369: 8.50±0.40.

<sup>b</sup> Estimated from both right and left sides.

left M<sub>1-3</sub>, roots of C–P<sub>4</sub>, mandible to shortly posterior to dental foramen (the P<sub>2</sub> and P<sub>3</sub> figured by Matthew have been lost); Bridger C<sub>4</sub>. A.M.N.H. No. 14747, type of *Didelphodus absarokae ventanus*, right P<sub>3</sub>, talonids of M<sub>2-3</sub>, alveoli from posterior part of canine, mandible almost to dental foramen; Lost Cabin, Wind River Basin. A.M.N.H. No. 55698, left M<sub>2</sub>; upper Bridger, Tabernacle Butte. A.M.N.H. No. 56614, right M<sub>2</sub>, alveolus for and trigonid of M<sub>3</sub>, posterior root of M<sub>1</sub>; Bridger, lower C. A.M.N.H. No. 56615, left M<sub>1-2</sub>, roots of P<sub>4</sub>; right M<sub>3</sub>, roots of M<sub>2</sub>; late Wasatchian, Cathedral Bluffs. U.S.N.M. No. 18369, crushed skull with basicranium and left P<sub>2</sub>–M<sub>3</sub>, isolated I<sub>2</sub>, both mandibular rami with alveoli for P<sub>3</sub>–M<sub>3</sub> and extending posteriorly to about the dental foramen; Lost

Cabin, Wind River Basin. M.C.Z. No. 3461, left C, P<sub>2</sub>, DP<sub>4</sub>–M<sub>2</sub>, unerupted M<sub>3</sub>, roots of I<sub>1</sub>–DP<sub>3</sub>; right C, P<sub>3</sub>, DP<sub>3</sub>–M<sub>2</sub>, unerupted M<sub>3</sub>, roots of I<sub>2</sub>–DP<sub>2</sub>; left I<sub>2</sub>, C, M<sub>1-2</sub>, roots of I<sub>1-3</sub>; right DP<sub>4</sub>–M<sub>1</sub>, isolated DP<sub>2</sub>; fragments of postcranial skeleton; Lost Cabin, Wind River Basin. M.C.Z. No. 7235, left maxilla with M<sup>1</sup> and alveoli for P<sup>3</sup>–M<sup>3</sup>; upper Bridger, Tabernacle Butte. C.N.H.M. No. P26864, badly crushed skull with right P<sup>4</sup>–M<sup>2</sup> and alveolus for M<sup>3</sup>; upper fossil level, DeBeque Formation, Nipple Hollow, Garfield County, Colorado.

KNOWN DISTRIBUTION OF *D. altidens*: Lostcabinian and Bridgerian, Wyoming and western Colorado.

ILLUSTRATIONS: Matthew (1909, pl. 49, fig. 1, occlusal and labial views of type of

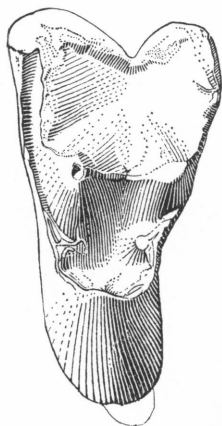


FIG. 6. Occlusal view of left  $M^2$  of *Didelphodus altidens* (Marsh), A.M.N.H. No. 55698; upper Bridger. Reproduced from McKenna, Robinson, and Taylor (1962).  $\times 10$ .

*Didelphodus absarokae ventanus*). White (1952, fig. 76, occlusal view of U.S.N.M. No. 18369). McKenna, in McKenna, Robinson, and Taylor (1962, fig. 6, occlusal view of A.M.N.H. No. 55698, reproduced in the present paper as text fig. 6).

DISCUSSION: As the DeBeque skull in the Chicago Museum is somewhat more similar to the Lost Cabin one than to the teeth from Tabernacle Butte, it can be tentatively dated as about Lostcabinian in age. Lostcabinian age of its horizon has been confirmed by Patterson (personal communication) on the basis of the other mammals present. In the absence of larger samples, no attempt is made herein to establish temporal subspecies.

Matthew (1918) recognized that *Phenacops* was probably related to *Didelphodus*, but it was not until recently (McKenna, in McKenna, Robinson, and Taylor, 1962) that the type of *Phenacops* was synonymized with Marsh's species, which McKenna transferred at the same time to *Didelphodus*. White (1952) raised Matthew's subspecies *D. absarokae ventanus* to specific rank, an action in which I follow him despite the name change and the fact that none of the characters mentioned by him as distinctive are valid except for the presence of a small parastyle on  $P^2$ . The most cogent reason for specific distinction from *D. absarokae* is the presence of the latter in the same fauna. Most of the specimens from the Four Mile local fauna referred

by McKenna (1960a) to *D. ventanus* actually represent a species of "*Peratherium*" (the size of and perhaps actually "*P.*" *comstocki*), which is identical with a maxilla (A.M.N.H. No. 48762) from the San José Formation. Such a possibility was first suggested by McKenna in conversation. There is an interradicular crest lingually between the paracone and metacone roots; such a situation is common in Lance marsupials. U.C.M.P. No. 44270, an  $M^3$  from the Four Mile also referred by McKenna (1960a) to *Didelphodus ventanus*, is a miacine, probably *Oodectes*.

Several other specimens have been or possibly could be referred to the Didelphodontinae. A.M.N.H. No. 2681, a fragment of mandible from the Huerfano, was considered by Osborn (1897) to be either "*Stypolophus*" (= *Sinopa* and *Prototomus*) or *Didelphodus*. Robinson (MS) considers it a miacid near *Oodectes*; I agree. *Proiverra americana* (= *Sinopa rapax* Osborn, Scott, and Speir, 1878, *non* Leidy) was mentioned as being possibly referable to *Didelphodus* by Scott (1892). I do not believe it belongs in that genus (see below). U.C.M. No 20802, a right lower molar from the Huerfano formation, locality 2 of Robinson (MS), may represent an advanced species of *Didelphodus*, but I believe it is an  $M_2$  of a primitive miacine. An upper molar poorly figured by Heller (1930, pl. 1, fig. 3) as an "Oxyaenide?" is possibly a didelphodontine, but is probably referable to the peculiar genus *Vulpavoides* Matthes (1952). U.C.M.P. No. 44772D, a large tooth from the Four Mile referred by McKenna (1960a) questionably to the Didelphodontinae, is apparently a didelphid, probably representing a new genus. (See the discussion below of the differences between didelphodontine and didelphine upper molars.) The  $P_4$  from Cernay described by Donald E. Russell (1964) as "*Adapisoriculus*-like" is also generally similar to the  $P_4$  of *Didelphodus absarokae*, the main difference being the reduced paraconid of the former.

Cope at first (1881b, 1882a, 1884a) placed *Didelphodus* (then included in *Deltatherium*) in the Leptictidae, a heterogeneous family the members of which are now distributed among four orders by vertical classification. The Leptictidae were part of his Creodonta. Shortly thereafter (1884b) Cope subdivided

TABLE 16  
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Didelphodus altidens*

	A.M.N.H. No. 55698	C.N.H.M. No. P26864	U.S.N.M. No. 18369	M.C.Z. No. 7235
Anterior margin				
P <sup>3</sup>	—	—	3.05	—
P <sup>4</sup>	—	—	3.55	—
M <sup>1</sup>	—	4.00	3.95	4.50
M <sup>2</sup>	5.35	4.65 ± 0.05	4.45 ± 0.15	—
M <sup>3</sup>	—	—	4.00	—
Posterior margin				
P <sup>2</sup>	—	—	1.35	—
P <sup>3</sup>	—	—	3.30	—
P <sup>4</sup>	—	—	4.00	—
M <sup>1</sup>	—	—	4.30	4.70
M <sup>2</sup>	5.20	4.50	4.55	—
M <sup>3</sup>	—	—	2.95	—
Labial margin				
P <sup>2</sup>	—	—	2.30	—
P <sup>3</sup>	—	—	3.05	—
P <sup>4</sup>	—	3.05	2.95	—
M <sup>1</sup>	—	—	3.15	3.45
M <sup>2</sup>	2.85	2.80	2.85 ± 0.05	—
M <sup>3</sup>	—	—	2.65	—
Length at paracone				
M <sup>1</sup>	—	1.50	1.50	1.60
M <sup>2</sup>	1.55	—	1.50	—
M <sup>3</sup>	—	—	1.50	—
Horizontal distance of protocone apex from lingual margin of protocone				
M <sup>1</sup>	—	0.95	1.15 ± 0.05	1.10 ± 0.20
M <sup>2</sup>	1.35	—	1.05	—
M <sup>3</sup>	—	—	0.85 ± 0.05	—
Anterior height of paracone of M <sup>2</sup>	1.85 ± 0.05	—	—	—
Posterior height of metacone of M <sup>2</sup>	1.70 ± 0.05	—	—	—
Posterior height of protocone of M <sup>2</sup>	1.70	1.70 ± 0.15	—	—
Crown length of M <sup>1-3</sup>	—	7.50 ± 0.15	8.20	—
Length of diastema between P <sup>2</sup> -P <sup>3</sup>	—	—	1.85	—

the Leptictidae, although retaining them as a family (in the first part of the same paper they were usually included in the Centetidae), and grouped *Didelphodus* with the genera then known of the group now known (see below) as the Proviverrini (plus *Prototomus*), separating it markedly from *Deltatherium*. I would also make this grouping with the genera that Cope knew. A member (*Esthonyx*) of an additional currently accepted order was added at the same time to the family, and another one (*Peratherium*) was removed. Schlosser (1886, 1887) established the more or less current classification of creodonts,

placing *Didelphodus* in the Proviverridae (which, however, also included *Deltatherium* and *Triisodon*). Scott (1892) followed Schlosser in this action. Matthew (1901), in establishing his groupings by carnassiality, was rightly puzzled by *Didelphodus* and placed it in the Hyaenodontidae (including the Proviverridae) for lack of a better place. In 1918 he hesitantly returned it to the Leptictidae, establishing for it the new subfamily Didelphodontinae. A special similarity to *Deltatheridium* was recognized by Gregory and Simpson (1926) and especially by Simpson (1928, 1945), who placed *Didelphodus* and

TABLE 17

MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Didelphodus altidens* (M.C.Z. No. 3461)

	C	P <sub>2</sub>	P <sub>3</sub>	DP <sub>3</sub>	DP <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	Other
Trigonid width	—	—	—	1.70	1.95	2.40	2.50	2.05±0.05	—
Talonid width	—	—	—	—	1.85	2.15	2.15	—	—
Crown length	—	2.60±0.20	2.95	3.30	3.30	3.45	3.50	—	—
Labial height of hypoconid	—	—	—	—	2.00±0.10	2.40±0.05	2.35±0.20	—	—
Labial height of protoconid	7.00±0.50	—	—	2.95±0.05	—	4.05	4.30	—	—
Lingual height of protoconid	6.50±0.20	—	3.55±0.10	2.75±0.05	—	3.30±0.40	3.40±0.30	—	—
Lingual height of paraconid	—	—	0.80	1.30±0.05	2.10±0.10	2.60±0.05	2.75±0.10	—	—
Lingual height of metaconid	—	—	—	—	2.55	3.05±0.05	2.95±0.10	—	—
Depth of mandible below M <sub>2</sub> protoconid	—	—	—	—	—	—	—	—	5.55±0.20

*Deltatheridium* in separate subfamilies of the Deltatheridiidae. The addition of *Palaeoryctes* to this family by McDowell (1958) resulted in a change in the family name, based on the mistaken belief that the name "Palaeoryctidae" was proposed before the name "Deltatheridiidae." This change was tentatively accepted by McKenna (1960a).

#### RECOGNITION OF GENERA

The figures of teeth should be consulted for the relative terms that are used in the following discussion.

The upper molars of *Puercolestes* and *Nyssodon* are most easily recognized by their relatively narrow (transversely) stylar shelf, relatively connate paracone and metacone, a low parastyle, and large conules. *Didelphodus* has a wide stylar shelf, less connate paracone

and metacone, a low parastyle, and moderately large conules. *Gelastops* has a relatively narrow (transversely) stylar shelf, moderately connate paracone and metacone, a tall parastyle, and vestigial conules. *Acmeodon* has a moderately narrow stylar shelf, moderately connate paracone and metacone, a prominent and probably tall parastyle, and moderately large conules. *Nyssodon* differs from *Puercolestes* (in addition to being of smaller size) in having somewhat closer and taller cusps. The upper molars of *Avunculus* are unknown.

The P<sup>4</sup> of *Puercolestes* has a relatively anterior protocone; a metacone is clearly present, and a small preprotocrista is present. In *Didelphodus* the protocone is more posterior, a metacone is nearly or quite absent, and the preprotocrista is nearly absent. In *Acmeodon*

TABLE 18

MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Didelphodus altidens* (M.C.Z. No. 3461)

	DI <sup>2</sup>	DP <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>
Anterior margin	1.10±0.05	2.75	—	—
Posterior margin	—	3.45±0.05	5.20	4.90
Labial margin	1.15	3.55±0.05	3.50±0.15	2.65±0.05
Length at paraconule	—	—	2.00±0.10	1.95±0.10
Horizontal distance of apex of protocone from lingual border of protocone	—	—	1.25±0.05	1.40±0.05
Posterior height of metacone	—	—	2.10±0.05	1.95±0.05
Posterior height of protocone	—	—	1.85±0.05	1.70±0.05

the protocone is even more posterior, the presence of a metacone is uncertain, and the preprotocrista is very high. The  $P^4$ 's of *Gelastops* and *Avunculus* are unknown.

From *Cimolestes* (probably the lower molars of *Nyssodon*) a metacristid is absent; the paraconid is much lower than the metaconid but about as anterior as in *Didelphodus*. From *Didelphodus* a metacristid is absent or it is poorly developed, but the lingual border of the prefossid is no lower than the center; the paraconid is not much lower than the metaconid. In *Gelastops* a metacristid is present on at least  $M_1$ , and the paraconid is more posterior than in *Didelphodus* but not much lower than the metaconid. In *Acmeodon* a metacristid is present, and the paraconid is more anterior than in *Didelphodus* but not much lower than the metaconid. In *Avunculus* the lingual border of the prefossid is lower than the center (as in *Cimolestes*), and the paraconid is similar in position to that of *Didelphodus*. The lower molars of *Puercolestes* are unknown but are probably generally similar to those of *Cimolestes*.

The  $P_4$  of *Cimolestes* has a low paraconid and no trace of a metaconid or protostylid. In *Didelphodus* the paraconid is low, a metaconid is more or less distinctly detectable on the lingual surface of the protoconid, and there is no protostylid. In *Gelastops* the paraconid is high, a metaconid is present on the lingual surface of the protoconid, and a strong protostylid crest is present without a differentiated protostylid. In *Acmeodon* the paraconid is high, a metaconid is present on the posterolingual face of the protoconid, and a strong protostylid is present. In *Avunculus* the paraconid is high, and neither a metaconid nor a protostylid is present. The  $P_4$  of *Puercolestes* is unknown.

Additional characters are presented in the descriptions of teeth in the next section.

#### INTERDEME VARIATION IN *Didelphodus*

Although specimens of *Didelphodus altidens* range from the Lost Cabin to the upper Bridger and show normal variation, no secular change can be detected in the lower teeth or in size without larger samples.  $M^2$  is discussed below.

In  $P_4$ , the two specimens of "*Didelphodus absarokae secundus*" differ from the others in

the following respects: the paraconid is larger and slightly more lingual (see table 10), the metaconid is larger, the tooth is even broader, and the entocristid is conspicuous. One specimen has a weak anterior cingulum. The lower molars differ (in the known sample) in having a slightly less labial slope on the hypoconid, producing a slightly narrower talonid, and in having a somewhat more lingual hypoconulid on the first two molars. All these differences can be accounted for by a greater development of the lingual side of the lower teeth. As mentioned above, it is very probable, however, that this is a case of discrete or even gradational polymorphism.

The only possibility of difference between samples of *Didelphodus absarokae* of different ages has to do with the Lost Cabin specimen U.S.N.M. No. 18433. This tooth is most similar to the only Four Mile anterior lower molar available. These teeth and A.M.N.H. No. 15101 differ from the Almagre and upper Gray Bull specimens especially in having a less differentiated talonid rim, but such is clearly not a secular trend, as the latter group is surrounded in time by the former. I also do not believe that these groups are specifically distinct. Sampling error, reversal of the direction of change, and shifting of subspecies back and forth with time are the remaining possibilities. One characteristic of the Lost Cabin tooth is, however, markedly different from any other specimen. The paraconid projects forward, with only a slight vertical component in the slope of the posterior face; the curvature of the lingual margin of the tooth also exceeds that found elsewhere (although the closest approach is in specimens from the Four Mile).

Aside from the situations mentioned above, I can detect no consistent differences whatever among the samples of *Didelphodus absarokae* from the Four Mile, Gray Bull, and Almagre, in either upper or lower teeth. The Carnegie Museum DeBeque specimen, of Graybullian age, is, however, rather different. The metacrista of  $M^2$  is slightly less demarcated from the stylar shelf than is the paracrista, the apex of the protocone is relatively more lingual, the metaconule is somewhat larger (the paraconule is not preserved), and the parastyle is smaller and less projecting.  $M^1$  is partly broken. All the differences are among

those separating *D. altidens* from *D. absarokae*, but the specimen is very probably not appreciably later than middle Graybullian and is geographically and temporally surrounded by typical *D. absarokae*. I interpret this situation as most likely indicating subspecific differentiation within *D. absarokae*, quite possibly with shifting boundaries, the subspecies represented by the Carnegie Museum specimen giving rise to *D. altidens*. It is also possible that the specimen is the earliest known example of *D. altidens*, reproductively and ecologically isolated from *D. absarokae* at this time; it is in any event the same size as typical *D. absarokae* and is much closer to it than is typical *D. altidens*. This difference in interpretation rests on the present lack of information as to gene flow, a gap that further collecting may fill.

#### MORPHOLOGY

##### LOWER TEETH

There are three crowded lower incisors in *Didelphodus absarokae* (A.M.N.H. No. 4228). They form a continuous arc between the canines of opposite sides and extend medially and somewhat anteriorly from a point just anterior to each canine. The incisors are of about equal size,  $I_2$  being slightly the largest. The width of all three together is somewhat less than the anteroposterior length of the canine. The crown of  $I_3$  (A.M.N.H. No. 16238) is elliptical and somewhat linguolabially elongate at its base, expanding somewhat laterally and becoming subspatulate near the tip. There is a moderate wear facet mediolingually. An incisor of *D. altidens* of unknown position in the mouth is present in U.S.N.M. No. 18369 and is of similar form. The incisor roots of M.C.Z. No. 3461 are similar to those of *D. absarokae*.

There is a moderately large alveolus directly in front of the canine in *Avunculus*, about the size of the alveolus for  $P_1$ . There was apparently none more posteriorly and little room for any more anteromedially. *Acmeodon* has an alveolus in front of the medial part of the canine, almost as long as that for  $P_1$ ; there is room for another alveolus anteromedial to it.

In *Gelastops parvus*, A.M.N.H. No. 35226 and U.S.N.M. No. 6148 show an apparently

moderately large incisor alveolus (about as large as the alveolus for  $P_1$ ) equidistant from the canine and the symphysis, anteromedial to the canine. The other incisors are absent or much smaller. A.M.N.H. No. 35225 shows two apparent alveoli, the more anterior corresponding to the one above, the more posterior in front of the canine and less projecting. (There is some chance, although unlikely, that one or both of the alveoli in A.M.N.H. No. 35225 are fortuitous breaks in the bone.)

A complete lower canine is preserved in *Gelastops parvus* (A.M.N.H. No. 35226 and the type). It is nearly vertical, expanding posterolingually near the base. Its cross section is oval. There is a prominent anterior crest on the upper half and a weak posterior crest on the upper two-thirds, the latter merging with an incipient talonid. The height of the canine is about three halves of the height of the premolars and molars; its alveolar length is about the same as that of  $P_4$ . The latter statement is also true for *Acmeodon*, which has a similar basal cross section. *Avunculus* differs from all others in the subfamily in that the alveolar length of the canine is only about half of that of  $P_4$ .

In *Didelphodus absarokae*, the posterior face of the canine is curved, without a marked expansion near the base. The anterior crest is even more sharply demarcated lingually than that in *Gelastops* and extends nearly to the bone level (it is presumably an anterior extension of the paralophid, as it has the same shape, direction, and position). A moderately weak midlabial concavity also extends nearly to the bone level. There is a weak posterior crest on all the tooth that is preserved; a talonid is absent. The height is uncertain, and the alveolar length is about the same as that of  $P_4$ . The canine of *D. altidens* is similar to that of *D. absarokae*; it is nearly twice the height of the premolars and molars.

In each genus represented by an undistorted jaw, the tooth row is straight from the canine posteriorly, appearing to become more lingual posteriorly as the mandible recedes labially from the symphysis and expands labially toward the masseteric fossa.

Contrary to previous interpretations, the first postcanine tooth preserved in the type of *Acmeodon secans* is  $P_1$ , not  $P_2$ . Further preparation under ultraviolet light has dis-

closed an alveolus between it and  $P_3$ . This interpretation is supported by A.M.N.H. No. 16030, which has alveoli for four premolars, although the first is in this specimen one-rooted. In the type it is definitely two-rooted. The talonid is relatively even larger than that of  $P_3$ , and more lingual; the paraconid is also slightly larger. The protostylid crest merges into the labial border of the talonid; a moderate entocristid leads to the side of the protoconid. The protoconid apex is over the anterior root, and the paraconid projects distinctly forward. Possibly the former situation is due to the tooth's being loose at one time and pushed slightly forward, but even so, the paraconid still projects.

Seven specimens of *Gelastops parvus* each have  $P_1$  one-rooted. In U.S.N.M. No. 9601 it is somewhat compressed and displaced labially by the canine. The  $P_1$  of *Avunculus* is also one-rooted. In *Didelphodus absarokae* three specimens show a two-rooted condition, while in A.M.N.H. No. 16240  $P_1$  is apparently one-rooted on the left side (or possibly two-rooted, the anterior root smaller and pushed labially by the canine) and absent or having one minute root on the right. The anterior root is clearly pushed labially by the canine on one or both sides of two additional specimens. The shape of the tooth is similar to that of  $P_2$  except that the posterior slope is more gradual. In *D. altidens*  $P_1$  is two-rooted in two Lost Cabin specimens and one-rooted in a Bridger one; a trend is possible but is not really indicated.

$P_2$  in *Acmeodon* is one-rooted, but the alveolus is subdivided incipiently in A.M.N.H. No. 16030. The type either displays this condition or is two-rooted. In *Gelastops parvus*  $P_2$  is two-rooted in all six specimens in which the alveolus is preserved. In *Avunculus* and *Didelphodus* it is also two-rooted. The two specimens of *Didelphodus absarokae* differ somewhat. In A.M.N.H. No. 16238 there is a tall protoconid, nearly the height of  $P_3$ , the apex of which turns somewhat linguallly. A weak paralophid is present, but no paraconid. A trace of a talonid shelf is present, but this does not extend even so far posteriorly as the top of the posterior root. The only other feature is a faint protostylid ridge. A.M.N.H. No. 16230 differs in the following respects: It is a little broader medially

and posteriorly. A distinct but small paraconid, scarcely if at all projecting, is present at a point one-third to one-fourth of the lingual height of the tooth, at the end of a stronger paralophid. The protostylid ridge is stronger and leads into a single-cusped talonid that projects somewhat posteriorly. *Avunculus* differs from the latter specimen in that the paraconid, although weaker, is at a point about two-fifths of the lingual height of the tooth, and this region projects forward markedly. The protostylid crest meets the talonid centrally; the latter is also somewhat higher on the tooth and may be a little larger. In *Didelphodus altidens* the anterior root is pushed labial to  $P_1$  in one specimen. From the figure of Matthew (1909) no difference can be detected in the crown of A.M.N.H. No. 16240.

The remaining comparisons are with *Didelphodus absarokae* unless specifically indicated otherwise.

The  $P_3$  of *Didelphodus absarokae* (A.M.N.H. No. 4228) is larger and relatively broader than  $P_2$ , and somewhat higher than  $P_4$ . It differs from the  $P_2$  of A.M.N.H. No. 16240 in having the paraconid lower on the tooth (only one-fourth or one-fifth of the lingual height) and a lingual cuspule on the somewhat broader and longer talonid, and by a bulge suggesting an incipient metaconid immediately lingual to the protoconid. The entocristid presumably continues to the base of this bulge. In U.S.N.M. No. 19458 the paraconid is markedly larger and a little more lingual than in A.M.N.H. No. 19458; the protoconid is distinctly concave above it. The talonid is also much larger, a condition formed by a more vertical postvallid. The lingual talonid cuspule is only an entocristid here. In *D. altidens* the tooth is relatively shorter, the paraconid is slightly larger than in A.M.N.H. No. 4228, and the talonid is more projecting but has only one main cusp (an entoconid is differentiated in M.C.Z. No. 3461). *Acmeodon* differs in that the tooth is somewhat narrower, and much narrower posteriorly; therefore the paralophid is sharper. The weak paraconid is one-third of the lingual height of the tooth. The protostylid crest is sharper, and a protostylid is weakly differentiated from it halfway up. The talonid is larger and more projecting; the anterior border is narrower and steeper

because of the width of the tooth. There is no lingual talonid cusp and also no trace of a metaconid, although there is a broad median vertical ridge on the labial side of the protoconid that is continuous with the entocristid. The tooth is much higher than  $P_4$ .

*Gelastops parvus* also has a narrower  $P_3$ , especially posteriorly, and a sharper paralophid. There is no paraconid. The protostylid crest is sharper, but there is no trace of a protostylid. The talonid is larger and more projecting, its anterior part is steeper, and the entocristid is more developed. There is only a trace of a lingual talonid cusp and no trace of a metaconid. The talonid is about half of the labial height of the tooth, as contrasted with a fourth or a third for that of the genera discussed above. The tooth is somewhat higher than  $P_4$ . *Avunculus* has an even narrower  $P_3$ ; the paraconid is at least half of the lingual height of the tooth. The talonid is even less developed and is one-cusped; the protostylid crest meets it almost in the midline of the tooth. There is no entocristid or metaconid. The tooth is slightly lower than  $P_4$ .

$DP_3$  is known only in *Didelphodus altidens* (M.C.Z. No. 3461). It is considerably lower and apparently slightly narrower than the  $P_3$  visible beneath it, but is about the same length as  $P_3$ . As is usual in a deciduous tooth, the roots diverge around the protoconid of  $P_3$ . The paraconid is similar to but larger than that of  $P_3$ , extends a little more lingually, and is confluent with a moderately weak anterolabial cingulum. There is no expansion of the lingual side of the protoconid, but on the contrary a moderately distinct metaconid emerges on the lingual margin of the posterior face of the protoconid, at about three-quarters of the lingual height of the protoconid. An entocristid proceeds from the metaconid to form the lingual margin of the postfossid; an entocristid is present but weaker than that of  $P_3$ . The talonid is lower and a little longer than that of  $P_3$ . Its most anterior point is labial, not lingual as on  $P_3$ , because a protostylid crest is completely absent. A hypoconulid is present on the midline of the tooth; the labial edge of the postfossid extends only slightly more labially than this and does not appear to have borne a pronounced hypoconid. The labial wall of the talonid slopes obliquely

down. The widest point of the tooth is just anterior to the talonid.

$P_4$  is the most distinctive single tooth. In *Didelphodus absarokae* ("*D. a. secundus*" is described above) a moderately sharp paralophid and protostylid crest extend in opposite directions from the lingual side of the apex of the central protoconid, delimiting lingually a rounded median ridge. The paraconid and talonid are of equal height, about one-third of the lingual height and two-fifths of the labial height of the tooth. The paraconid is fairly lingual and is a distinct cuspule; there is no more ventral anterior cingulum. No protostylid is developed. The talonid has one or two cusps, and lingually it is one-fourth of the length of the tooth. The postcristid is more or less well elevated above the postfossid. The latter may or may not be bounded lingually by an entocristid. A very weak hypoflexid is present. A moderately distinct metaconid is developed at half of the lingual height of the tooth immediately lingual to the protoconid apex; weak but broad crests extend nearly symmetrically down its anterior and posterior ends. The protoconid is roughly as tall as that of the molars. The tooth is widest just posterior to the protoconid apex; the labial height is slightly greater than the length. All that can be said of the  $P_4$  of *D. altidens* is that the talonid had an entocristid in one specimen.

$DP_4$  is known only in *Didelphodus altidens* (M.C.Z. No. 3461). It is completely molari-form, differing from the molars in only a few respects. It is narrower than the molars and a little lower-crowned; because of the former difference the paraconid is somewhat more anterior relative to the trigonid width, and the crista obliqua is less transverse. There is no trace of a metacristid, unlike the molars of this specimen, and the roots appear to be a little more divergent.

The  $P_4$  of *Acmeodon* is a low tooth, considerably lower than either  $P_3$  or the molars. The protoconid apex is not much more than a third of the way from the front of the tooth and from its lingual part sends a strong paralophid forward and an equally strong protostylid crest backward. A weak to strong paraconid emerges lingually from the paralophid at two-thirds to three-fourths of the proto-

conid height. An anterior cingulum is developed ventrolabial to the paraconid. A strong protostylid is present, nearly as high as the protoconid, its posterior edge dropping abruptly to the labial wall of the talonid. A well-demarcated protolophid extends medially and somewhat posteriorly from the protoconid; a moderately strong metaconid is developed from its posterior edge but does not extend so far posteriorly as does the protostylid. The talonid is well developed and basined and lingually is a little more than one-third of the length of the tooth. There is a well-developed cusp posterior and slightly lingual to the protostylid, about four-fifths as high labially as the protoconid; a weaker entoconid is lingual to it. The entocristid meets the lingual base of the metaconid. There is no trace of a hypoflexid. The widest point of the tooth is at the level of the protostylid; the labial height is less than the length.

The  $P_4$  of *Gelastops parvus* is only slightly lower than  $P_3$  and  $M_1$ . It differs from the  $P_4$  of *Acmeodon* in several ways. The paraconid is slightly more lingual and usually larger and more distinct. A distinct protostylid is not developed, and the protostylid crest, although prominent, does not extend so far posteriorly. The metaconid is somewhat higher, but the labial talonid cusp is only two-thirds as high as the protoconid. The entoconid region of the talonid is not so well developed; the entoconid is more anterior and scarcely or not at all differentiated, and the entocristid is lower. The talonid is lingually about two-fifths of the length of the tooth. There is a fairly pronounced hypoflexid. The widest point of the tooth is at the level of the protoconid apex; the labial height is about the same as or slightly greater than the length.

The  $P_4$  in *Avunculus* is about as tall as  $M_1$  and markedly taller than  $P_3$ . It differs from that of *Didelphodus absarokae* in the following respects: It is somewhat narrower and has a weaker paralophid that leads to a paraconid half or three-fifths of the lingual protoconid height. There is a weak anterior cingulum. The paralophid and weak protostylid ridge originate from the lingual side of the protoconid. The talonid has one cusp, and lingually is a little less than one-third of the length of the tooth. There is no entocristid, metaconid,

or protolophid. The tooth is widest somewhat posterior to the level of the protoconid apex. The hypoconid is two-fifths or one-half of the labial height of the protoconid; the labial height is distinctly less than the length.

The lower molars of *Didelphodus absarokae* are sufficiently similar that they can be described together. "*Didelphodus a. secundus*" and the Lost Cabin tooth (U.S.N.M. No. 18433) are omitted. The trigonid is moderately tall; its cusps are triangular and flat-sided. The paraconid ranges in position from a point almost in front of the metaconid to one nearly central, but it is usually slightly median to the metaconid. It projects somewhat anteriorly and has ventrally a moderately strong anterior cingulum. The paralophid and protolophid are both V-shaped in profile, nearly straight, and with a more or less well-developed notch in the middle. There is no metacristid or only a trace of one, but the lingual border of the prefossid is at least as high as the center. The protoconid is clearly the highest cusp, the metaconid is next, and the paraconid is lowest but still well developed. The paraconid is somewhat more anterior on  $M_1$  than on  $M_2$ . There are occasionally slits at the deepest point of the paralophid and the entocristid. The crista obliqua extends from below or somewhat lingual to the protolophid notch and bears a more or less conspicuous hypoconid that is about half of the labial height of the protoconid. The hypoconulid is well to vaguely differentiated; any of the talonid cusps may be highest, but none is ever conspicuously so. The postfossid is rather deep, and the entocristid is almost or quite as tall as the crista obliqua; the entocristid may continue vaguely up the lower part of the metaconid. The most anterior point of the hypoconulid (when this is differentiated) is by the entoconid or at the same level as its labial edge. The talonid of  $M_1$  tends to be wider than that of  $M_2$  relative to both its length and the trigonid width. The trigonid is invariably slightly wider than the talonid.  $M_3$  differs from  $M_1$  and  $M_2$  in the following ways: the hypoconulid and its posterior slope are both larger, and the former tends to be more lingual; the trigonid and especially the talonid are both relatively narrower.

*Didelphodus altidens* differs in having a tendency for a narrower talonid, a higher hypoconulid, and a less-differentiated hypoconulid and entoconid, but individual specimens of lower molars cannot be surely identified except by the smaller size. The only character not overlapping is the more convex paraconid face of  $M_3$  in *D. altidens*, but this character is known in only two specimens of one species and three of the other and seems of little predictive value for future specimens.

In *Acmeodon secans* the paraconid is more anterior, the protoconid is relatively higher, and a metacristid is distinctly developed. The postvallid is somewhat more transverse. The crista obliqua usually has a vertical slit in its lowest point; the entocristid is relatively lower. The hypoconulid is somewhat more labial; its most anterior point is by the hypoconid. The entoconid is the weakest cusp but is nevertheless differentiated. The talonids of cf. *Acmeodon* sp. from the Puerco (A.M.N.H. No. 16413) differ from those of *A. secans* only in having a slightly more differentiated hypoconulid and in having the deepest part of the postfossid concentrated a little more lingually.

In *Gelastops parvus* the paraconid is somewhat lower and somewhat more posterior, directly in front of the metaconid and on  $M_2$  and  $M_3$  closely appressed against it. A metacristid is present on at least  $M_1$ . The postvallid is somewhat more transverse. The entocristid is markedly lower; the postfossid is shallower. The talonid of  $M_3$  is relatively shorter, making the entoconid there more transverse. The most anterior part of the hypoconulid is by the hypoconid or at the same level as the lingual side. The entoconid is quite variable in size, shape, and position.

*Gelastops* sp. B. differs from *Gelastops parvus* in several respects. The paraconid is more medial and much smaller; therefore the trigonid is relatively even shorter. The protoconid is sharper. The metaconid is about as tall as the protoconid (it is shorter on  $M_1$  of *G. parvus*). The hypoconid is much smaller, and the hypoconulid is even taller and perhaps more labial. The crista obliqua may be more oblique.

*Gelastops* cf. *G. parvus* (Shotgun specimens) differs from *G. parvus* as follows: It is slightly larger, the hypoconulid is slightly more

labial, the paraconid is a little taller relative to the metaconid, and the walls of the pre-fossid are a little more bulbous. If the teeth are  $M_2$  the paraconid is slightly more anterior and the talonid is relatively broader; if they are  $M_1$  these two differences are in the opposite direction.

*Avunculus* differs from *Didelphodus absarokae* only in having a slightly higher trigonid, perhaps a slightly shorter paraconid, a somewhat lower entocristid, and a complete absence of the metacristid, the prefossid sloping smoothly into the lingual wall of the trigonid. The postvallid is also slightly more transverse. In the single lower molar available, the paraconid is slightly more medial than usual and the hypoconulid is strictly transverse or with perhaps a slight tendency to be more anterior near the entoconid.

From the photograph of the trigonids of *Puercolestes*, it is possible to say only that they were tall, and that the protoconid was probably the highest cusp, the metaconid being intermediate and the paraconid being considerably lower. The paraconid was directed more anteriorly on  $M_1$  than on  $M_2$ .

#### UPPER TEETH

Two alveoli for incisors are apparently present on the left side of the skull in A.M.N.H. No. 4228, the type of *Didelphodus absarokae*. They are about the anteroposterior length of the canine in front of the canine and as much lingual to it, but there is some distortion. The medial one ( $I^2$ ) is about twice as large in linear dimensions as the lateral one ( $I^3$ ) and is adjacent to it; the bone is then broken away.

There is apparently a fossa to receive the lower canine in front of the upper canine in the same specimen. There is evidence of a similar fossa in *Puercolestes*. The heights of these fossae are unknown.

In *D. altidens* (M.C.Z. No. 3461) the root of  $I^2$  is about twice as large linearly as the roots of  $I^1$  and  $I^3$ , which are adjacent to it. The crown of  $I^2$  is preserved. Its height is markedly higher than that of the known lower incisors. It is similar to these lower incisors in other respects, except that its anterior face is moderately curved toward the occlusal end and the sides of the tooth extend backward to form the apical side of a parabolic cylinder.

The upper canine is adequately preserved only in the specimen A.M.N.H. No. 80025 of *Didelphodus absarokae*, in which the tip is broken off. Its features are not different from the parts preserved in A.M.N.H. No. 4228 or the Colton specimen (C.M. No. 9696). The tooth is moderately tall, its height being probably somewhat more than the anterior width of  $M^2$ . It has an anteroposteriorly oval cross section, widest four-tenths of the anteroposterior length of the tooth from the front of the tooth; the anteroposterior length at the alveolar surface is similar to the crown length of  $M^2$ . The tooth is longest anteroposteriorly slightly below the level of the bone. It tapers gradually distally and is slightly curved posteriorly. A slight metacrista is present as the only surface feature, although there is a moderate corner anterolingually. In *D. altidens* (M.C.Z. No. 3461) the canine is similar. The canine roots are present in *Puercolestes*; the only difference detectable is that the anteroposterior length at the alveolar surface is slightly shorter than the crown length of  $M^2$ .

In *Didelphodus* and *Puercolestes*, the only genera for which the character is determinable, the upper tooth rows diverge only slightly from the canine to  $P^8$ . In *Puercolestes*  $P^3$  and, to a lesser extent,  $P^4$  diverge more strongly than the more anterior teeth, the molars forming a small arc of a circle, with the parastyles of  $M^2$  and  $M^3$  the most labial points. The protocones of the molars are the same distance from the midline of the palate, but the protocone of  $P^4$  is slightly more lingual. *Didelphodus* is similar except that the divergence of  $P^3$ - $P^4$  is not quite so great, and the molar protocones also appear to diverge slightly.

The crown of  $P^1$  is unknown in any didelphodontine. However, two alveoli are present for it bilaterally in *Didelphodus absarokae* (A.M.N.H. No. 80025). On the right side, but not on the left, the posterior root is displaced lingually, although  $P^2$  is at the usual distance posteriorly.  $P^1$  is as long as  $P^2$ . This fact forces a change in the dental formula that dates from Cope (1882b), who recognized only three upper premolars. But even in the type specimen there is an alveolus on the right side slightly lingual to the space between  $P^2$  and what I presume to be the alveolus for the canine. If the latter identification is correct,

there is not room for a second alveolus unless this is even more lingual than the one observed. In the type of *Puercolestes simpsoni*  $P^1$  is apparently absent from the left side and is one-rooted on the right. The anterior post-canine alveolus on the left is the shape of the anterior  $P^2$  alveolus on the right and not the shape of the  $P^1$  alveolus. There is evidence that the left  $P^1$  never formed in this individual: partly, on the left side the anterior alveolus for  $P^2$  is close to the alveolus for the canine and, partly, the left  $P^2$  is somewhat larger than the right one as a compensation.

$P^2$  in *Didelphodus absarokae* is two-rooted. The paracone is nearly or quite as tall as  $P^3$  and  $P^4$  and probably nearly as long. It is adjacent to  $P^3$  and about three halves as long as wide. The protocone is small or absent, the paracrista and metacrista are weak, and a parastyle is absent. Other aspects are covered by the matrix or broken off. There is a diastema in *D. altidens* between  $P^2$  and  $P^3$ , about as long as  $P^2$ . Although most of the paracone is broken off  $P^2$  in U.S.N.M. No. 8369, the only specimen with this tooth present, it is possible to see that there is a slight parastylar area, which continues to a weak ectocingulum which in turn continues to a weak metastylar area. A weak cingulum turns lingually and somewhat anteriorly from the metastylar area, ending in the region corresponding to the metaconule on the molars. A protocone is absent; the widest part of the tooth is one-fourth of the length of the tooth anterior to the posterior end of the tooth. There is no diastema between  $P^1$  and  $P^3$ , or at most a very short one, in the Colton specimen.  $P^2$  in the type of *Puercolestes simpsoni* is broken off near and below the base of the crown. It is two-rooted, the posterior root larger than the anterior one, but not so much so as in *Didelphodus altidens*. A metastyle was apparently present.

$DP^{72}$  in *D. altidens* is an elongate tooth with two widely divergent roots. Anterior and posterior crests extend from the apex of the paracone to basal cuspsules.

The  $P^3$  of *Didelphodus absarokae* from the Willwood and San José differs from  $P^4$  (described below) in several respects. The paracone is somewhat longer than wide and has somewhat steeper labial and posterior faces. A metacone is absent, and the metastyle and

parastyle are smaller. The protocone is much smaller, being only a third of the height (from the base of the enamel) and a fourth of the width of the paracone; therefore the tooth is narrower. The protocone is anteroposteriorly elongate and equidistant from the anterior and posterior ends of the tooth; therefore both anterior and posterior borders of the tooth are concave. The ectocingulum is even smaller, and the paracingulum is also smaller. The Graybullian DeBeque specimen differs from the preceding in that the metastyle of  $P^3$  is even smaller and the paracone is about as wide as long.  $P^3$  of *D. altidens* differs from that of the typical *D. absarokae* in having a wider parastylar shelf, much more pronounced cingula, a paracone slightly more compressed posteriorly, and a much wider protocone. The latter is six-tenths of the width of the paracone. It is slightly anterior to the midline of the tooth, but both anterior and posterior concavities are more pronounced. *Puercolestes* differs in that the protocone is only a small projection low on the tooth, two-thirds of the way posteriorly, so the tooth is markedly longer than broad. The lingual root is not separate from the posterolabial root. The metastyle is much more prominent, and there is a slight indication of a metacone. The paracingulum is less developed, and an ectocingulum is absent.

In *Didelphodus absarokae* of the Willwood and San José, the paracone is much the tallest cusp on  $P^4$ . It is elongate anteroposteriorly near the top and widens to a cross section, near the bottom, that is somewhat between a circle and an equilateral triangle. Its apex is somewhat posterior to the middle of the tooth. A metacrista and paracrista are present, the former farther from the labial margin of the tooth and with a hint of a metacone halfway down. A metastyle and parastyle are present as small cusps on their respective corners of the tooth, sharply defined from the paracone. The protocone is subconical, with low protocristae. The preprotocrista is more labial than the postprotocrista; the two crests continue into a weak paracingulum and metacingulum, respectively. There are no conules. The height from the base of the enamel of the protocone is five- to six-tenths of that of the paracone, its width about half of that of the paracone. It is above a distinct lingual root.

The ectocingulum is weak, continuous, and markedly lower in the middle than at either end, where it rises to meet the styles. The labial and posterior margins of the tooth are about straight; the anterior is somewhat concave because the apex of the protocone is distinctly anterior to the level of the apex of the paracone. This last condition is involved with the development of the postvallum for shearing against the  $M_1$  prevallid.

*Didelphodus altidens* differs from *D. absarokae* in the following respects: the metastyle and parastyle are not so distinct, so the ectocingulum is less raised anteriorly and posteriorly; the protocone is decidedly more transverse (its width is almost equal to that of the paracone) and slightly lower; the paracone is somewhat lower; and the apex of the paracone is about equidistant from the anterior and posterior ends of the tooth. The paracone is also slightly more compressed posteriorly. The Graybullian DeBeque specimen also differs from typical *D. absarokae* in several respects. The metastyle and parastyle are absent as distinct cusps, so the ectocingulum is not raised anteriorly and posteriorly. The metacrista is stronger, apparently more labial, and has no trace of a metacone. The paracone is somewhat less rounded near the base, and its apex is equidistant from the anterior and posterior ends of the tooth.

*Puercolestes* is even less similar to *Didelphodus absarokae*, but in other ways. The protocone is taller, shorter anteroposteriorly, and more anterior, so there is an even more marked anterior concavity. The parastyle is slightly more projecting. The paracrista is slightly less developed, but the metacone is slightly larger, and the metastyle is apparently slightly more prominent. The labial surface of the paracone is more vertical. The protocristae are well developed, the preprotocrista forming a prominent angle, and a metaconule is slightly differentiated. The paracingulum is less developed.

The  $P^4$  of *Acmeodon* is particularly distinctive in having a very tall preprotocrista; the apex of the protocone has apparently shifted anterolabially onto it. The postprotocrista is now incomplete but was lower; a well-marked protofossa is present. The lingual lobe of the tooth is about as wide transversely as the paracone and is about as long as wide. The

paracone is elongate posterolabially, perhaps suggesting the presence of a moderately differentiated metacone. All three borders of the tooth are moderately concave. A weak paracingulum and metacingulum continue the protocristae to the stylar areas. Breakage obscures further details.

DP<sup>4</sup> is known only in *Didelphodus altidens* (M.C.Z. No. 3461). Unlike DP<sub>4</sub>, it is not fully molariform; in fact it is no more molariform than P<sup>4</sup>, although in different respects. The anterolingual part of the paracone is broken away. This tooth may be DP<sup>3</sup> rather than DP<sup>4</sup>.

The tooth is longer than broad; all three roots diverge markedly from one another. The height of the paracone is uncertain, but it probably was slightly lower than that of P<sup>4</sup> in U.S.N.M. No. 9696. A rather weak metacone projects from the posterior edge of the paracone; a typical metacrista extends posterolabially. A small parastyle is present. A protocone was apparently not present as a distinct cusp; the lingual face of the paracone, although mostly absent, appears to have continued to the lingual margin of the tooth. The lingual root is very slightly anterior to the midline of the tooth; both the anterior and posterior margins of the tooth are slightly concave, the former apparently more so than the latter. The labial margin is slightly convex.

The upper molars are best considered by first describing the sample of M<sup>2</sup>'s of *Didelphodus absarokae* from the Four Mile, much the best sample of a single upper tooth. Inter-individual differences are considerable (see tables 11 and 14 of this paper, and the figures in McKenna, 1960a), but they are not explicable by the occurrence of the sample in three different quarries. There is no indication of any difference among the samples of teeth of *Didelphodus* from East Alheit, West Alheit, and Timberlake quarries of the Four Mile.

The tooth is transverse. There is a marked ectoflexus, the deepest point of which is 0.55 to 0.70 of the length of the tooth from the front and about labial to the paracone-metacone junction. It is variably angular or rounded and divides the labial part of the stylar area into two lobes. The distance from the apex of the paracone to the anterolabial corner of the tooth is the same as or slightly greater than that from the apex of the meta-

cone to the posterolabial corner of the tooth. The paracone and metacone are six- to seven-tenths of the anterior width of the tooth from the lingual edge of the protocone and are connate for about half of the height of the paracone. The paracone is wider and, especially, higher than the metacone. Both cusps are longer than wide near the top and wider than long near the bottom. They are usually separated from each other and from the paracrista and metacrista by sharp, narrow notches. They are subconical except for the paracrista, centrocrista, and metacrista.

The paracrista is prominent, extending labially and slightly anteriorly from the anterior corner of the paracone to near the labial margin of the tooth, where it merges with the ectocingulum to form a slight eminence (absent from one specimen) possibly homologous to the stylocone. Its posterior slope gradually merges with the stylar shelf. The parastylar area is just anterior to the eminence mentioned above; it does not bear a distinct parastyle. This area is a slight to fairly pronounced enlargement of the paracingulum where this rises to meet the ectocingulum. The metacrista is slightly lower than the paracrista, but somewhat more sharply demarcated from the stylar shelf. It extends labially (in different individuals with a slight anterior or posterior trend) from the posterior corner of the metacone to the posterolabial corner of the tooth. It makes a rather sharp angle in occlusal view where it leaves the metacone. No metastyle is developed. The ectocingulum is low, formed from an overturning of the labial edge of the tooth. One or two low to rather prominent cuspules are usually developed on different parts of it, but there is no tendency for the development of a mesostyle. The ectocingulum turns more lingually on the parastylar area, exposing the labial face of the tooth.

The protocone is prominent. Its apex is 0.25 to 0.35 of the anterior width of the tooth from the lingual edge of the protocone and is moderately anterior, three- to four-tenths of the way from the anterior edge of the tooth. The protocristae are fairly sharp, the two crests meeting in either a parabolic curve or nearly at an angle. A broader ridge extends labially from the apex of the protocone into the protofossa, vanishing at the

bottom of the latter. The labial slope of the protocone is thus roughly flat, not markedly convex or concave as a whole. The deepest point of the protofossa is distinctly posterior to the midline of the tooth at this point. The paraconule is larger, higher, and more lingual than the metaconule, and is three- to four-tenths of the horizontal distance from the apex of the protocone to the apex of the paracone but slightly anterior to the latter. A slight crest runs from it to the paracone. The paracingulum runs from its apex so that it resembles an enlargement on the lingual end of the paracingulum. The paracingulum is distinct, somewhat wider lingually and labially than centrally. With the base of the enamel used as a horizontal standard, it gradually becomes lower from the paraconule until just labial to the notch in the paracrista, then begins to rise somewhat more steeply. The metaconule is moderately rounded, with only a weak ridge to the metacone, or none at all. A weak metacingulum continues labially from its apex, proceeds lower on the tooth fairly steeply, and vanishes at a point that varies posterior to the metacone. There are very slight to no traces of a precingulum and postcingulum, at a level a third of the height of the protocone.

The parastylar area projects forward slightly, producing a gentle concavity lingual to it. The lingual part of the protocone is curved posteriorly, producing a gentle concavity that reaches nearly to the apex of the metacone. The outline is convex otherwise except for the ectoflexus. The anterior face of the paracone and paracrista is flat and nearly vertical down to the paracingulum. The anterior face of the protocone is flat and has a slope of about 80 degrees, becoming vertical and then projecting out, as well as becoming somewhat more rounded, as the parastylar area is approached. The posterior face of the metacrista, metacone, and metaconule ranges from 75 degrees to 90 degrees and is slightly rounded. It becomes less steep, 60 degrees to 75 degrees, as the protocone is reached. The lingual face of the protocone has a slope of 45 degrees to 55 degrees and is flat in anterior or posterior view until near the base. The labial margin of the tooth overhangs and is generally vertical but rounded.

The lingual root is transverse. Its vertical

lingual face extends to a depth about one and a half times the height of the enamel on the protocone. Its labial border is 50 degrees to 60 degrees to the horizontal, nearly flat in anterior or posterior view, and reaches to a point under the lingual part of the paracone. The anteroposterior length is about the same for each depth, but perhaps slightly more near the base and tip than in the middle. The slope is about 10 degrees posterior to the vertical. The anterior surface is nearly flat, the posterior somewhat rounded. In cross section the lingual face is rounded, but the labial edge is nearly angular. The anterolabial and posterolabial roots are also transverse. The former extends from the parastylar area to about the apex of the paracone, remaining under the paracrista. It has a 70-degree to 80-degree slope on its lingual and labial borders. Its anterior face is flat; the others are rounded except for a slight angularity on the lingual side. Its depth is unknown. The posterolabial root extends from the posterolabial part of the metacrista to the lingual part of the metacone. The roots do not touch each other, and interradicular crests are absent. A slight interradicular crest is, however, present on the only  $M^1$  for which this character is determinable (U.C.M.P. No. 58478), here extending only between the two labial roots on their lingual side.

I present in this paragraph the differences of specimens from other areas not in the belief that they represent real interdeme differences but because they expand the observed range. The greater and apparently genuine differences of the Graybullian DeBeque specimen are discussed above. A.M.N.H. No. 15700, from the Gray Bull, differs in having the paraconule not larger than the metaconule, although it is higher on the tooth, and in that the lingual face of the protocone has about a 60-degree slope and is slightly rounded near the tip. The other Gray Bull specimens are similar to the Four Mile sample in all respects. In A.M.N.H. No. 48392, from the Almagre, the paracingulum is obsolete below the paracrista on  $M^3$  and nearly so on  $M^2$ ; the condition on  $M^1$  is unknown. In A.M.N.H. No. 80025 the protocone is slightly rounded near the apex and is slightly longer anteroposteriorly; the latter situation is also true in A.M.N.H. No. 80024.

M<sup>1</sup> of *Didelphodus absarokae* differs from M<sup>2</sup> in the following ways: the ectoflexus is 0.45 to 0.60 of the length of the tooth from the front; the distance from the apex of the paracone to the anterolabial corner of the tooth is distinctly less than the distance from the apex of the metacone to the posterolabial corner of the tooth; the cuspules on the ectocingulum tend to be more developed; the apex of the protocone is two- to three-tenths of the anterior width of the tooth from the lingual edge of the protocone; the anterior border of the tooth is largely concave; the anterior and posterior slopes of the protocone vary from 70 degrees to 80 degrees, and the lingual slope varies from 50 degrees to 70 degrees. M<sup>3</sup> differs from M<sup>2</sup> in the following ways: the metastylar area is greatly reduced, so the labial border of the tooth is straight and trends markedly posterolingually; all cusps are lower; the protocone apex is 0.15 to 0.25 of the anterior width of the tooth from the lingual edge of the protocone; and the lingual slope of the protocone varies from about 40 degrees to 50 degrees.

As for *Didelphodus altidens*, the Bridger M<sup>2</sup> (A.M.N.H. No. 55698) differs structurally from typical *D. absarokae* in several respects. It is even more transverse, being relatively shorter anteroposteriorly, especially labially. The paracone and metacone are 0.55 of the anterior width of the tooth from the lingual edge of the protocone; the paracone is only slightly wider and higher than the metacone. All the cusps and crests are somewhat lower and therefore appear slightly more separate. There is no anterior component to the direction of the paracrista, which is as low as the metacrista; both merge gradually into the stylar shelf. The metacone merges gradually into the metacrista; the latter has no sharp angle. There is no tendency for cuspule development on the ectocingulum, which itself is virtually absent. The metaconule is as large as the paraconule, which is smaller than in *D. absarokae*. The metacingulum is less developed. The parastylar area is smaller and does not project forward; the only marginal concavities are the ectoflexus and one posterior to the metaconule. The lingual face of the protocone is somewhat rounded. The stylar area is flatter than in *D. absarokae*. The lingual root is less wide transversely, reaching

a point under the paraconule only; it is slightly longest anteroposteriorly at its middle depth.

The Bridger M<sup>1</sup> (M.C.Z. No. 7235) differs from typical *D. absarokae* in the same ways that M<sup>2</sup> does, except as follows: the paracone and metacone are two-thirds of the anterior width of the tooth from the lingual edge of the protocone, and the paracone appears to have been distinctly higher than the metacone in the unworn tooth. There are several indistinct cuspules on the ectocingulum. The relative size of the conules is not known because of wear. The parastylar area is similar to that of *D. absarokae*, as is the width of the lingual root.

Although all the cusps and crests are well worn and the conules are worn away, there are a number of differences detectable between the DeBeque M<sup>2</sup> (C.N.H.M. No. P26864) and typical *D. absarokae*. M<sup>1</sup> of the DeBeque specimen is even more worn and partly broken; no structural differences are observable on it. On M<sup>2</sup>, the paracone and metacone are 0.55 of the width of the tooth from the lingual margin of the protocone. The metacrista is even less sharply demarcated from the stylar shelf than is the paracrista. The stylar area is flatter, and the ectocingulum is virtually absent. The protocone is more lingual, its apex being about two-tenths of the anterior width of the tooth from the lingual edge of the protocone. The metacingulum is apparently absent. The labial part of the tooth is relatively shorter anteroposteriorly; the parastylar area is smaller and less projecting. The anterior face of the protocone is slightly rounded and is steeper than the anterior face of the paracrista, the slopes being, respectively, about 85 degrees and 75 degrees. The lingual face of the protocone is slightly rounded and has a slope of about 70 degrees.

A Lost Cabin specimen (U.S.N.M. No. 18369), from which much of the stylar area on M<sup>2</sup> is broken away, shows rather fewer differences from *D. absarokae* than do the preceding specimens. The metacrista is not lower or more sharply demarcated than the paracrista; both are low and merge with the stylar shelf. The apex of the protocone is 0.20 to 0.25 of the anterior width of the tooth from the lingual border of the protocone. The para-

conule is smaller, and not larger, than the metaconule. There is no sharp angle on the metacrista at the base of the metacone. There is a large stylar cusp, fully as large as the metacone of  $M^3$ , posterior to the ectoflexus; this cusp is absent from  $M^1$  and  $M^2$ . The paracingulum is absent below part of the paracrista. This absence of a paracingulum also characterizes  $M^1$  but not  $M^2$ . A *D. absarokae* specimen (A.M.N.H. No. 48392), described above, shows an obsolete paracingulum on  $M^3$  but one rather less so on  $M^2$ . Except for this character, the only differences detectable on  $M^1$  are that the ectocrista cusps are less developed (note the contrast with  $M^2$ ), the paracrista is lower, and all the stylar area is flatter and more regular.

The other Lost Cabin specimen (M.C.Z. No. 3461) differs from *D. absarokae* in being more compressed anteroposteriorly, having a somewhat shallower ectoflexus and a somewhat lower paracone and metacone, and in virtually lacking a metacingulum.

As for differences from *Didelphodus altidens*, there appears to be some tendency for an evolutionary shift away from the condition of *D. absarokae*. The Lostcabinian DeBeque specimen (C.N.H.M. No. P26864) is at about the same level of change as the Lost Cabin ones from the Wind River Basin (U.S.N.M. No. 18369 and M.C.Z. No. 3461): the ectocingulum is weaker than in *D. absarokae*, and  $M^2$  (probably  $M^1$  also) is slightly shorter labially, but the metacrista has a sharp angle at the base of the metacone. The metacingulum is apparently absent, and the lingual face of the protocone is somewhat steeper. However, the Bridger specimens (A.M.N.H. No. 55698 and M.C.Z. No. 7235) differ from the DeBeque one in the following presently detectable ways: they are somewhat more transverse, the protocone is slightly less lingual, the lingual face of the protocone is less steep, and the anterior face of the paracrista is slightly steeper. Presently detectable differences from both Lost Cabin specimens are in being more transverse; in having a smaller parastylar area; in having a less cuspidate ectocingulum (but compare  $M^1$  and  $M^3$  of U.S.N.M. No. 18369); in having all cusps lower, especially the conules; and in having a smaller lingual slope on the protocone.

*Puercolestes simpsoni* has an  $M^1$  rather

different from that of *Didelphodus absarokae*. The parastylar area projects much more anteriorly; the paracrista is weaker, as is the metacrista. The stylar area is narrower; the paracone and metacone are about seven-tenths of the anterior width of the tooth from the lingual edge of the protocone and have a steeper lingual face. The paracone and metacone are more connate (but much less so than in *Palaeoryctes*), higher, and somewhat more posterior. The paraconule is somewhat larger. The tooth is shorter anteroposteriorly lingual to the stylar area. The protocone is more lingual and somewhat taller; it is almost as tall as the paracone. Its lingual and, especially, anterior faces are more vertical. (Therefore prevallum shear is better developed at the expense of postvallum shear.) The lingual slope of the protocone is about 80 degrees. The paracingulum is slightly wider. The deepest point between the paracone and metacone is somewhat on the posterior half of the tooth. The lingual root extends only to a point slightly labial to the paraconule.  $M^2$  has similar differences, except that there is a sharper ectoflexus. The same is true of  $M^3$ , the cause here being a relatively larger metastylar area. On  $M^3$  the lingual face of the protocone has a smaller slope than on  $M^{1-2}$ , only about 60 degrees, while in *Didelphodus absarokae* the slope is usually similar on all three molars. *Nyssodon* differs from *Puercolestes* in having somewhat higher and closer cusps.

The upper molar of *Gelastops parvus* is generally more similar to that of *Puercolestes* than to that of *Didelphodus*. Comparison is made first with the former. All parts of the tooth are even shorter anteroposteriorly (the tooth is more transverse); almost all cusps and crests are somewhat lower. The parastyle is much taller. The metacone is turned more posterolabially, so the low metacrista does not turn when it reaches the base of the metacone. The conules are markedly smaller; the metaconule is a scarcely visible swelling in the postprotocrista, and the paraconule has no ridge to the paracone. The protocone apex is much more labial; therefore the lingual slope of the protocone is only about 45 degrees.

*Gelastops parvus* differs from *Didelphodus absarokae* in the following respects: All parts of the tooth are shorter anteroposteriorly; almost all cusps are somewhat lower. The

parastyle is much taller. The paracrista and metacrista are much smaller; the stylar area is markedly narrower. The paraconule and especially the metaconule are less developed. The lingual, labial, and anterior faces of the protofossa are steeper. The labial face of the protocone is distinctly concave, and the protocone itself is relatively taller, being nearly the height of the paracone. The lingual root extends labially to a point almost or quite under the apex of the paracone.

The upper molar of cf. *Gelastops*, sp. B., differs from that of *G. parvus* in several ways. It is smaller, and the cusps are taller relative to the width of the tooth. The metacrista is more developed and has an angle at the base of the metacone. The paraconule is even smaller and is more lingual. The metaconule and posterior protocrista are higher (but not more developed) and much more lingual. The protocone apex is somewhat more lingual, and the lingual slope of the protocone is about 75 degrees. The lingual half of the protofossa is not so steeply bounded; the protofossa itself is not so deep.

The ectoflexus in the molars of *Acmeodon* is deeper than in *Didelphodus*. The paracone and metacone are seven-tenths of the anterior width of the tooth from the lingual edge of the protocone and are a little more connate than in *D. absarokae*. A parastyle was probably present. The metacrista is almost straight in occlusal view from the apex of the metacone to the posterolabial corner of the tooth. A weak mesostyle is present at or near the lingualmost part of the ectoflexus.

The apex of the protocone is two-tenths of the anterior width of the tooth on  $M^2$  and three-tenths on  $M^1$ , from the lingual edge of the protocone. The protocristae are quite tall, especially the preprotocrista; the apex of the protocone is slightly anterolabial to the lingualmost point of the postprotocrista. The protofossa is deep, and its deepest point is only slightly posterior of the midline of the tooth.

The parastylar area projects markedly forward. The lingual part of the protocone is not curved posteriorly. The anterior and posterior borders of the tooth are nearly parallel between the conules and the paracone and metacone.

Various growth fields could be described in

several species for characters varying in expression along the tooth row, but none are unusual and too little is known of the family to indicate trends in their evolution. Certain of these fields are implied in the discussion.

I present the following differences of the Four Mile "*Peratherium*" from *Didelphodus absarokae* in part to support its transfer from *Didelphodus* but mainly to indicate the differences in morphology between the molars of early didelphines and those of didelphodontines, which have a generally similar appearance. The large majority of the differences are common to most early species of *Peratherium* and *Peradectes*.

The teeth of the Four Mile "*Peratherium*" are markedly less transverse. The paracone is shorter and the metacone taller, but their relations vary; they are not quite so connate and each bears a sharp lingual ridge. The paracrista is smaller than the metacrista; there is a distinct posterior component in the direction of the latter from the metacone. The ectocingulum does not turn lingually on the parastylar area. The protocone apex is only 0.15 to 0.20 of the anterior width of the tooth from the lingual edge of the protocone. The labial face of the protocone is flat except that the apex of the protocone is turned upward. The paraconule and metaconule are vestigial; the latter is at least as lingual and high on the tooth as the former. The paraconule is more posterior than the apex of the paracone. The lowest point of the paracingulum is just anterior to the apex of the paracone; the metacingulum is even smaller than in *Didelphodus*. The lingual slope of the protocone is about 70 degrees. The posterolabial root nearly reaches the lingual root; an interdicular crest is present between the lingual parts of the two labial roots.

#### MANDIBLE

The mandible in all didelphodontines is moderately shallow, of almost the same depth from  $M_3$  to about  $P_3$ . At about  $P_3$  the ventral margin gradually rises toward the front. The condyle and the coronoid process are unknown, but the glenoid fossa of *Didelphodus* suggests that the former was relatively narrow.

The symphysis is unfused in all 17 specimens that preserve it, indicating the possibil-

ity of a small amount of independent movement of the mandibular rami. There is in every specimen a weak to moderate groove about a third of the way from the bottom of the mandible, extending on the lingual side almost from the symphysis to the end of the tooth row or a little beyond. It forms an area of weakness, together with the infradental canal, and the bone is often bent somewhat there, by crushing. It is, however, also present on apparently uncrushed specimens and is in no case on the labial surface. It is not so pronounced as in *Solenodon*. I interpret it as for the origin of the mylohyoid (cf. Fiedler, 1953; Reighard, Jennings, and Elliott, 1935). The type of "*Didelphodus ventianus*" has a somewhat flattened area on the posterior part of the ventrolingual face of the mandible, marked off by a faint ridge extending posteriorly and somewhat dorsally from the ventral surface below  $M_3$ . This is probably the area of insertion of the digastric. The ventral border of the ramus also curves somewhat dorsally on all specimens in this area, providing a better attachment.

The masseteric fossa is somewhat variable and is subdivided to a greater or lesser extent by a ridge. This ridge is stronger ventrally, and this part is the only part preserved in some cases. It originates posteriorly at or near the ventral margin of the fossa, continues anteriorly and somewhat dorsally to a point several millimeters from the anterior end of the fossa, then turns sharply posterodorsally nearly parallel to the masseteric ridge but slightly converging toward it. Its dorsal end is unknown. It appears to indicate a subdivision of the masseter.

The masseteric fossa in *Didelphodus absarokae* is shallow and poorly demarcated anteriorly and ventrally. Its anterior border is below, to a third of the alveolar length of  $M_3$  behind, the posterior end of the alveoli for  $M_3$ . The intrafossa ridge is present and of moderate strength. *Didelphodus altidens* is similar except that the intrafossa ridge is somewhat stronger and the fossa in some cases extends to a point under the posterior end of  $M_3$ . In *Acmeodon* (both Puerco and Torrejon specimens) the fossa is of moderate depth and is rather sharply demarcated anteriorly and a little less so ventrally. Its anterior border is as in *Didelphodus absarokae*. The intrafossa

ridge is weak and developed only postero-ventrally. In *Gelastops parvus* the fossa is deep and is sharply demarcated anteriorly and somewhat so ventrally. Its anterior border is the alveolar length of  $M_3$  or a little more posterior to the alveoli for  $M_3$ . The intrafossa ridge is very weak and present only ventrally.

The masseteric ridge, the anterior border of the masseteric fossa, is well developed in all genera. Although strictly speaking it is a curved surface, its angle with the plane of the tooth row in lateral view can be approximated. This is between 45 degrees and 60 degrees in *Didelphodus absarokae*, *D. altidens*, and *Acmeodon* and is 70 degrees in *Gelastops parvus*. The masseteric ridge ends anteroventrally at about a fourth to a half of the height of the mandible. The anterior extent of any significant bulge is somewhat variable. In *Didelphodus absarokae* and *D. altidens* it varies from the posterior root of  $M_3$  to the posterior end of  $M_2$ ; in *Acmeodon* it varies from the anterior border of  $M_3$  to just posterior to that tooth; and in *Gelastops parvus* it is at the posterior end of or just posterior to  $M_3$ , in accordance with its more vertical position in this genus.

Between  $M_3$  and the ascending ramus there is a horizontal area of zero to half of the length of  $M_3$  in *Didelphodus*. A ridge three- to five-fourths as broad as the posterior alveolus for  $M_3$  extends along this area. It is moderately well demarcated in *D. absarokae* and continues up the ascending ramus for at least 3 mm. (as much as is preserved). It is moderately well to poorly demarcated in *D. altidens* and does not continue up the ascending ramus. The level area is a fourth of the length of  $M_3$  in *Acmeodon* (both Puerco and Torrejon specimens.). The ridge in this genus is poorly demarcated and two-thirds of, to fully as broad as, the posterior alveolus for  $M_3$ . In *Gelastops parvus* the level area continues from a half of to the length of  $M_3$ . The ridge is narrower and sharply demarcated, is about half as broad as the posterior alveolus for  $M_3$ , and does not continue up the ascending ramus.

In *Gelastops parvus*, *Acmeodon secans*, and both species of *Didelphodus* (the condition is unknown in the other species) there is evidence for an excavation of moderate depth on

the medial side of the coronoid process. The ventral border of this excavation is at the level of the dorsal border of the horizontal ramus. This excavation, for the insertion of the deeper part of the temporalis muscle, seems, from the small part preserved, to be about as deep as in *Tenrec* and shallower than in *Apternodus*, *Solenodon*, and *Nesophontes*.

The posterior border of the symphysis also offers certain characters. In *Didelphodus absarokae* the border is abrupt, with little or no emargination, and extends to about the  $P_2$ - $P_3$  interval. A minute nutrient foramen is occasionally present by the surface. In *D. altidens* the border is abrupt to moderately gradational, with no or only a little emargination, and extends to the front of  $P_3$ . No foramen is present in any specimen. A.M.N.H. No. 12091 and M.C.Z. No. 3461 show two paired foramina near the midline of the ventral surface, below the canine. The existence of these foramina in other species is uncertain. In *Acmeodon* the border is fairly gradational, with no or little emargination, and extends to the front of  $P_3$ . A foramen is absent from one specimen (A.M.N.H. No. 16599) but rather well developed in the other (A.M.N.H. No. 16030). In *Gelastops parvus* the border is gradational and has a marked emargination. It ends posteriorly at some point under  $P_3$ . A small foramen is present. It is possible in this case to say that there is no association of the degree of development of the emargination with age, as estimated by tooth wear. In *Avunculus* the border is very gradational, without emargination, and extends to the middle of  $P_3$ . There is no foramen in either individual.

There is a strong thickening below the dental foramen in *Acmeodon*, halfway to the ventral margin (poorly developed in or absent from the Puerco specimen, A.M.N.H. No. 16413). The dorsal border of this thickening is sharply demarcated. The lingual margin of the foramen is nearly flush with the rest of the mandible, so there was presumably a deep groove posterior to it. The ventral margin of the mandible turns somewhat ventrally (in the posterior direction) in this region in the Torrejon specimen (A.M.N.H. No. 16030), while the bend is a little more anterior in the Puerco one (A.M.N.H. No. 16413). In *Gelastops parvus* the thickening is absent. The

lingual margin of the foramen distinctly projects out from the rest of the bone, so there was at most only a slight groove posterior to it. The ventral margin of the mandible turns ventrally more gradually than in *Acmeodon* and somewhat more anteriorly. In *Didelphodus altidens* the thickening is present but not so pronounced as in *Acmeodon* and is somewhat more ventral and posterior than in that genus. Its dorsal border is not so sharply demarcated. The lingual margin of the dental foramen projects only slightly, and on M.C.Z. No. 3461 it can be seen that there is a deep groove here also. The ventral margin of the mandible does not turn ventrally here.

The two (typically) mental foramina are small to moderate in size, situated at two-fifths to two-thirds of the height of the mandible. In *Didelphodus absarokae* and *D. altidens* the posterior one is situated below the  $P_3$ - $P_4$  interval or the posterior root or interradicular interval of  $P_3$ , the anterior one below the posterior root or middle of  $P_1$ . In the type of "*D. ventanus*" the posterior foramen is divided into three, which extend from the posterior root of  $P_2$  to the anterior root of  $P_4$ . In *Acmeodon* the positions are below the posterior root of  $P_3$  and below  $P_1$  or the C- $P_1$  interval. In *Gelastops parvus* the posterior one ranges from below the interradicular interval of  $P_3$  to that of  $P_4$ , the anterior one below  $P_1$  or the anterior root of  $P_2$ . The anterior foramen is absent from one specimen (A.M.N.H. No. 35227). In *Avunculus* the foramina are below the posterior root of  $P_4$  and below  $P_1$ .

#### ANTERIOR PART OF SKULL

The general appearance of the skull of *Puercolestes* can be seen from the photographs given by Reynolds (1936). The skull narrows rapidly anteriorly from the zygoma to about the posterior part of  $P^2$ , where a moderately long, straight-sided muzzle begins. The interorbital area is about three halves as wide as the muzzle. The dorsal curvature was probably similar to that of *Deltatheridium* (see Gregory and Simpson, 1926). As in all palaeoryctids and some other mammals, there are depressions in the maxilla in front of  $P^4$  to  $M^3$  inclusive, to receive the respective trigonids in the shearing mode.

All detectable sutures are open or moderately so; none are clearly fused, although the

animal was mature, as determined by tooth wear. The premaxilla overlaps the maxilla somewhat along the entire suture. The surface suture extends posterodorsally from the anterolateral part of the alveolus for the canine, but the maxilla extends medial to the premaxilla at least to the fossa for the lower canine. The nasomaxillary suture extends horizontally and slightly upward from the nasal-maxilla-premaxilla junction nearly to the orbit, at which point the nasals have their maximum width. They are only moderately expanded. It is not certain whether a frontomaxillary or a nasolacrimal contact is made, but whichever one exists is short. The nasals then contract posteriorly to the midline just median to the postorbital processes. The facial exposure of the lacrimal is relatively small. It begins somewhat anterodorsally to the anteroventral corner of the orbit and continues as a thin band anterodorsally to somewhere near the anterodorsal corner of the orbit. This latter area is too crushed on both sides for the situation to be determined, but a lacrimojugal contact is made. It is not known whether the palatine extends to the lacrimal, but the distribution of cracks suggests that it does. The palatine extends anteriorly to the level of the posterior part of  $P^4$ .

A weak postorbital process is present dorsal to  $M^3$ . A weak temporal crest curves medially from this to a point some distance behind the posterior end of the nasals, where the bilateral crests merge to form a low sagittal crest. There is a weak extension of the temporal crest for 3 or 4 mm. posteroventrally from the postorbital process. A postpalatine torus is present and moderately pronounced, especially on its lateral corners; it has a slight posterior expansion in the middle. The interpterygoid canal extends to the anterior part of the protocone of  $M^3$ . Its anterior width is roughly half of that of the palate between the protocones of  $M^3$ ; posteriorly its width is only about four-fifths of its anterior width. There is no or little concavity in the palatine between the pterygoid process and  $M^3$ . The orbit extends anteriorly to above the posterior end of  $P^4$ . A concavity between the zygoma and the palate extends anteriorly to the level of the middle part of  $M^3$ .

The infraorbital foramen is vertical, above the  $P^3$ - $P^4$  interval. It is fairly large, its diam-

eter being about the length of  $P^3$ . The posterior opening of the infraorbital canal is on the floor of the orbit, above the  $M^1$ - $M^2$  interval. It is apparently more transverse than the anterior opening, even when crushing is allowed for, and is slightly higher above the palate. The enlarged lacrimal foramen is above  $M^1$ , higher on the skull than and about half of the diameter of the infraorbital foramen, being 1.9 or 2.0 mm. tall. It is relatively about the size of that in *Solenodon* and smaller than that in *Apternodus* and *Geolabis*. (*Nesophontes* has a small lacrimal foramen.) It is inside the orbit, separated from the border of the orbit only by a thin lamina of the lacrimal. Aside from two or three minor nutrient foramina in the maxilla anterior to the infraorbital foramen, no other foramina are detectable on the specimen.

As far as comparable regions are known, the general outline of the skull of *Didelphodus* is similar to that of *Puercolestes*. It is perhaps somewhat wider, possibly entirely a result of crushing. Because of this crushing no sutures are detectable, not even the premaxilla-maxilla suture figured by Matthew (1918). The orbit is more anterior, reaching to a point above the posterior end of  $P^3$ . The concavity between the zygoma and palate variably reaches to the levels of the middle part of  $M^3$  or the  $M^2$ - $M^3$  border. The postorbital process is dorsal to  $M^1$ ; a weak temporal ridge curves posteromedially and joins its fellow at or slightly posterior to the level of  $M^3$ , forming a sagittal crest that is moderately weak for the few millimeters that are preserved. The postpalatine torus is as in *Puercolestes* but stronger. The anterior width of the interpterygoid fossa is half to three-fifths of the width of the palate between the protocones of  $M^3$ ; the fossa extends anteriorly to an uncertain point close to the level of  $M^3$ . There is in one specimen (A.M.N.H. No. 4228) no excavation of the posterior edge of the palate between the pterygoid process and  $M^3$ . In another specimen (A.M.N.H. No. 48392) there is an approach to such an excavation, but the border of the palate does not extend more anteriorly than its level on the posterolateral corner.

The infraorbital foramen of *Didelphodus absarokae* is above the anterior part of  $P^3$ . Its diameter is somewhat greater than the length

of  $P^3$ , and its dorsal part is anterior to its ventral part. The "infraorbital foramen" figured by Matthew (1918) was a depression in the original limy matrix, now removed, which revealed a bit of the inner hematite matrix. It was, nevertheless, in about the right place. The posterior opening of the infraorbital canal is at the level of the  $P^4$ - $M^1$  interval. It is more transverse than the anterior opening and not or only slightly higher above the palate. No other foramina are detectable.

The Graybullian DeBeque specimen (C.M. No. 18369) is similar to the ones on which the preceding statements were based in the anterior extent of the orbit, the posterolateral border of the palate, the indentation between the zygoma and the palate, and the infraorbital foramen, except that the infraorbital foramen is apparently vertical. In the two specimens of *Didelphodus altidens* (C.N.H.M. No. 26864 and M.C.Z. No. 7235) showing the anterior part of the skull, the indentation between the zygoma and the palate extends only to the posterior or middle part of  $M^3$ , the orbit extends to at least the middle of  $P^4$ , the anterior opening of the infraorbital canal is above the middle of  $P^3$ , and the posterior opening is above the middle of  $P^4$ . A moderate sagittal crest is present. There is also a low ridge posteroventrally from the post-orbital process, marking the anterior border there of the temporal musculature.

The (?)sphenopalatine foramen in the maxilla is at the base of the orbit, just medial to the posterior opening of the infraorbital canal. A canal enclosed in bone continues from it medial and parallel to the infraorbital canal and opens into the base of the nasal chamber above the anterior end of  $P^3$ . Possibly this canal contained a branch of the infraorbital artery which functionally replaced the sphenopalatine artery.

#### POSTERIOR PART OF SKULL

The posterior part of the skull is known only in *Didelphodus altidens*. The two specimens available (C.N.H.M. No. P26824 and U.S.N.M. No. 18369) both show the presence of a moderately strong sagittal crest, extending posteriorly to the equally strong nuchal crests. At the intersection of these three crests there is evidence for a posteriorly directed

bony process as in *Canis*, which does not, however, continue ventrally except as an almost imperceptible midoccipital thickening of the bone. There is a horizontal torus midway between the dorsal projection and the foramen magnum, and from this torus to the foramen magnum is a somewhat less pronounced and wider vertical torus. There are thus three fossae in the dorsal part of the occiput (the more ventral part is not preserved), the upper one presumably for the insertion of the rectus capitis posterior and the lower ones presumably for the obliquus capitis superior. A parietal foramen for a tributary of the superior sagittal sinus is present 4 mm. from the sagittal crest and at least 5 mm. from the nuchal crest. From the angle of 40 degrees made by the lateral surface of the mastoid with the ventral surface, and to a lesser extent from the roughened lateral surface of the mastoid, it is probable that this bone was covered laterally by the squamosal. The posterolateral part of the squamosal is broken off anterior to the mastoid. From the angle of the mastoid it is doubtful, but nevertheless possible, that the lateral surface of the braincase met the dorsal surface at an angle. No sutures are detectable with certainty on either specimen.

The following description of the ear region is based on only the specimen in the United States National Museum (see pl. 5, figs. 1-3, and text figs. 7, 8). The promontorium of the petrosal is oval and conspicuous, without trace of attachment for a bulla or a tympanic ring. Both promontoria are present, the left one in normal or nearly normal position, the right one displaced 90 degrees vertically, almost touching the left one, and with its medial side projecting through the skull roof. I have prepared the entire basicranium myself and can assert that none of the grooves or pits described are artifacts of preparation or handling. In my opinion a short groove extending posteriorly from the hypoglossal foramen and a small chip from the anteromedial quadrant of the left promontorium are the only such artifacts.

The fenestra rotunda is elongate, clearly visible in ventral view, about a third of the way medially from the lateral edge of the promontorium. There are no bony processes in its immediate vicinity. The fenestra ovalis

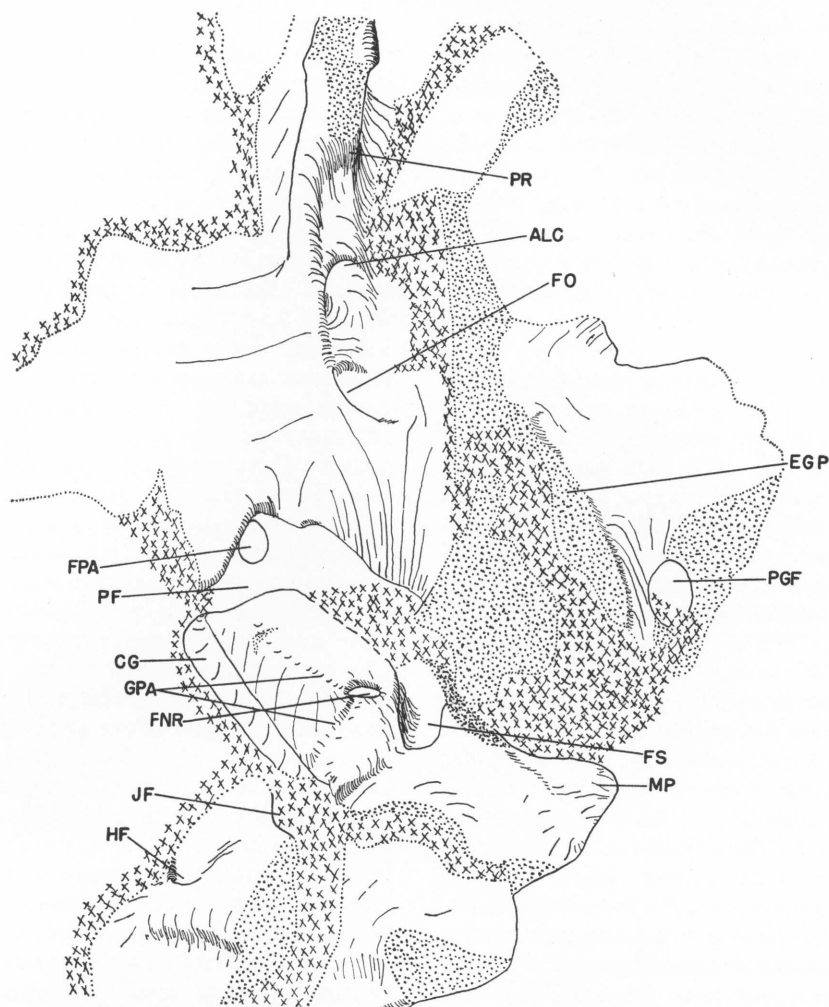


FIG. 7. Map of ventral view of crushed left basicranium of *Didelphodus altidens* (Marsh), U.S.N.M. No. 18369. Compare with plate 5. Broken parts are shown by stippling and dotted lines; matrix is indicated by X; and a reconstructed area is shown by the dashed line.  $\times 7$ .

*Abbreviations:* alc, posterior opening of alisphenoid canal; cg, groove for medial entocarotid artery; egp, entoglenoid process; fnr, fenestra rotunda; fo, foramen ovale; fpa, promontory foramen; fs, fossa for stapedius muscle; gpa, groove for promontory artery; hf, hypoglossal foramen; jf, jugular foramen; mp, mastoid process; pf, pyriform fenestra; pgf, postglenoid foramen; pr, pterygoid ridge.

is almost round, is dorsolateral and only slightly anterior to the fenestra rotunda, and also has no bony process. A deep pocket for the origin of the stapedius muscle lies just posterolateral to the promontorium. A foramen for the hypoglossal nerve is present medial and a little posterior to the jugular

foramen. Three conspicuous grooves radiate from the posteromedial corner of the promontorium. The most posterior of these bounds the promontorium posteriorly and is directed laterally toward the fossa for the stapedius. It clearly contained a nerve or blood vessel, probably the auricular nerve (a

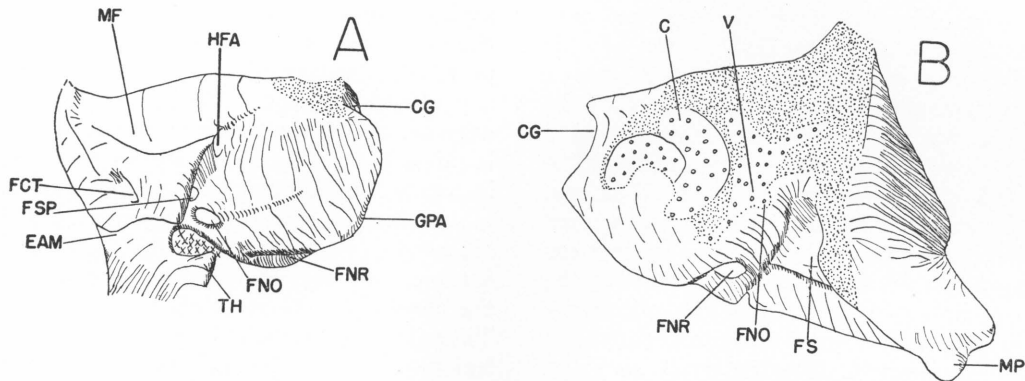


FIG. 8. Parts of basicranium of *Didelphodus altidens* (Marsh), U.S.N.M. No. 18369. Broken parts are shown by stippling; matrix is marked by X; the exposed endocast of the labyrinth is shown in areas marked with small circles. A. Ventral and somewhat anterolateral view of right promontorium and adjacent structures. B. Anterior view of left petrosal and mastoid.  $\times 7$ .

**Abbreviations:** c, cochlea; cg, groove for medial entocarotid artery; eam, external auditory meatus; fct, foramen possibly for chorda tympani; fno, fenestra ovalis; fnr, fenestra rotunda; fs, fossa for stapedius muscle; fsp, foramen stylomastoideum primitivum; gpa, groove for promontory artery; hfa, hiatus facialis; mf, mesotympanic fossa; mp, mastoid process; th, tympanohyal; v, vestibule.

branch of the vagus). The middle groove extends to the middle of the fenestra rotunda and clearly carried a lateral branch of the internal carotid artery. At the medial side of the fenestra rotunda a groove for the promontory branch turns sharply forward from the groove just described and continues anteriorly and somewhat medially to near the anteromedial corner of the promontorium. There is no trace of a groove from the fenestra rotunda to the fenestra ovalis, but a stapedial branch of the internal carotid may, nevertheless, have been present there. The third major groove runs anteriorly on the medial side of the promontorium and continues dorsolaterally into what appears to be the carotid foramen, which is situated directly anterior to the anteromedial corner of the promontorium. The dorsal wall of this foramen is visible almost until it enters the braincase just anterior to the cochlea. From the continuity and regular curvature of the groove and foramen, it is probable that they carried a fairly large medial entocarotid artery. At least the anterolateral part of this groove was clearly not a groove for an adjacent bone, because there was no bone there. A very similar groove is present in *Prolimnocyon atavus* (A.M.N.H. No. 15171). A shallow groove, slightly deeper than that for

the promontory artery, extends medially and slightly anteriorly from the fenestra ovalis, where it is deepest. It continues for about half of the width of the promontorium. I suspect that this groove was for the stapedial artery (although it may not have been). By this interpretation the stapedial artery diverged from the promontory artery at a sharp angle and much more anteriorly than usual; it then had made two sharp bends since reaching the promontorium. However, I cannot otherwise account for this groove.

The tympanohyal is fused to the posterolateral wall of the fossa for the stapedius and extends, diminishing rapidly in width, to a point 0.2 mm. from the promontorium, nearly enclosing a small opening for the facial nerve (sometimes known as the foramen stylomastoideum primitivum). The facial nerve emerges from the petrosal lateral and a little anterior to the fenestra ovalis, in the anterodorsal margin of the epitympanic recess. This opening also possibly received the stapedial artery; this artery, if present, could also have proceeded anteromedially in a vague groove medial to a strong flange of bone in front of the epitympanic recess. This strong flange overhangs the foramen stylomastoideum primitivum and continues anterior to it, separating the lateral part of the mesotym-

panic fossa sharply from the epitympanic recess. On the anteromedial corner of this partition is a small foramen with a groove running anteromedially from it. I tentatively interpret this foramen as the hiatus facialis for the superficial petrosal nerve, although it is possible that it carried the stapedial artery. On the ventral surface of the partition is an additional small foramen with a groove extending anterolaterally from it. This could be for the chorda tympani, but, if it is, the posterior opening of the canal is more dorsal than would be expected. The external auditory meatus is immediately posterior to the lateral part of the flange, extending externally from the ridge of bone between the fenestra ovalis and the external opening of the facial canal. A small mastoid process is present, projecting more laterally than ventrally and connected to the tympanohyal by a ridge.

The internal auditory meatus is visible on the right petrosal, opposite the center of the promontorium. It is divided, somewhat below the level of its rim, by a bar of bone that sets off the internal opening of the facial canal, a foramen a little smaller than the internal auditory meatus proper. Both foramina are nearly circular. The facial canal appears to continue for a short distance straight to its external opening. Posterodorsal to this double foramen, as usual, is the fossa for the appendicular lobe of the cerebellum.

An endocast of the labyrinth is partly exposed by a fortuitous crack. The cochlea has almost precisely two full turns and is partly involute; it is twice as broad as tall. The semicircular canals are in their usual positions; all three are visible in one or both petrosals.

The mesotympanic fossa is covered posterolaterally with matrix which it would be dangerous to remove. Examination and preparation of the anteromedial part under ultraviolet light disclosed a surface that is not bone but also is not the usual matrix, since it fluoresces differently from either. Its consistency is also different. A fairly large foramen is present in this material anteromedially which I interpret as for the promontory artery, showing the latter to be moderately large and of about the same size as the medial entocarotid. The most likely interpretation for the surface in this region seems to be a

replacement of non-osseous connective tissue that covered an unossified area between the petrosal, alisphenoid, and basisphenoid, i.e., a pyriform fenestra (McDowell, 1958). The edge of at least the latter two bones, however, is thick and well marked, unlike the situation in *Solenodon*, *Blarina*, and *Apternodus*.

A vidian foramen is not preserved as such, although it may have been confluent with the foramen for the promontory artery or with the carotid foramen, or obscured by a crack. There is no positive indication of a ramus inferior of the stapedial artery, but it may, nevertheless, have been present, underlying the pyriform fenestra. There is a wide, shallow groove on the anterolateral wall of the mesotympanic fossa. A similar groove medial to it and separated from it by a low posterior continuation of the pterygoid process was presumably for the Eustachian tube. The foramen ovale is just lateral to the pterygoid process and has no smaller foramen in its anterior border. The posterior opening of the alisphenoid canal is anterior to and nearly as large as the foramen ovale; they are not in the same fossa. The canal opens anteriorly lateral to a posterior expansion of the pterygoid process; this opening appears to be confluent with the orbital fissure, which probably contains also the foramen rotundum.

Much of the glenoid fossa is preserved. It is almost flat, with no preglenoid process and apparently not a strong postglenoid one. Presumably in life it faced anteroventrally more or less as preserved. There is a distinct groove just medial to the postglenoid process, presumably for the auriculotemporalis nerve (a posteriorly directed branch of the mandibular division of the trigeminal nerve), the chorda tympani, or probably both. A postglenoid foramen, a little larger than the foramen ovale, is present just lateral to this Glaserian fissure and just posterior to the postglenoid process. An entoglenoid process (a term discussed by McDowell, 1958) is present but was apparently low. The broken lateral edge of the zygomatic process of the squamosal is quite thin, indicating in itself that the zygomatic arch may have been incomplete, but perhaps present but weak, as in talpids. However, M.C.Z. No. 7235 preserves the zygomatic process of the maxilla, which is of moderate size and onto which

broadly overlapped the jugal. The masseteric fossa on the mandible is not particularly shallow.

#### POSTCRANIAL SKELETON

Postcranial fragments are known for only *Didelphodus altidens* (M.C.Z. No. 3461). Even in this case the association is not certain, since an incisor clearly not didelphodontine and tentatively identified by M. C. McKenna as apatemyid is present with the *Didelphodus* teeth. This incisor, however, is quite worn, and the *Didelphodus* specimen is young, so some separation is possible.

The only identifiable bones, aside from small fragments of vertebrae, are phalanges. Two of these, an apparently proximal one and an ungual, deserve mention. The former is about two and a third times as long as its proximal breadth and has an epiphysis remaining on its proximal end. The latter does not now have an epiphysis, but the transversely convex shape of its proximal surface is evidence that it probably had one at death. In addition, its size is not disproportionate to the proximal phalanx. I therefore believe that the ungual phalanx is probably referable to *Didelphodus*.

This ungual phalanx (fig. 9) is remarkably



FIG. 9. Lateral view of ungual phalanx probably of *Didelphodus altidens* (Marsh), M.C.Z. No. 3461. The dotted line represents a broken edge.  $\times 4$ .

low and broad, fully as broad (relatively) as that of *Mesonyx* and more so than that of *Patriofelis* (cf. Matthew, 1909). Although it is broken distally, a conspicuous groove comparable to that of *Patriofelis* is evident. The distal three-fourths of the ventral surface is flat, the proximal fourth slightly tilted up and bearing the paired nutrient foramen.

#### TOOTH OCCLUSION

As with many other mammals with triangular teeth (e.g., the Pentacodontinae: Van Valen and McKenna, MS), the occlusion of the teeth of *Didelphodus* can conveniently be divided into two modes, termed shearing and

grinding. The separation between them is not absolute; they are based on the relative position of the teeth. The shearing mode occurs when the talonid is thrust onto the protocone and the trigonid into the interdental embrasure (if this is present), often creating embrasure shearing by the action of the prevallid and postvallid against the postvallum and prevallum, respectively. Some crushing and piercing are produced by the cusps. In addition, some grinding may occur by transverse movement of the mandible when the teeth are appressed. In the grinding mode, the trigonid moves across the trigon in various ways. The relative importance and precise method of employment of these modes differ from species to species, individual to individual, and also with age. Nevertheless the wear facets produced are sometimes useful as taxonomic characters. In younger individuals the shearing mode is more important, while the reverse is true in older ones. In older individuals, in fact, little shearing surface may remain, and the trigonid grinding may spread to part or all of the talonid. Transverse grinding itself acts as a kind of shear, more efficient than pounding (Shaw, 1917). Gregory (1934, fig. 23V) gave a somewhat inaccurate figure of the occlusion of *Didelphodus absarokae* in the shearing mode.

The terms "opisthotome mastication" and "proterotome mastication" proposed by Cope (1889) appear to correspond to prevallum (postvallid) shear and postvallum (prevallid) shear, respectively. It is important to note that the terms "shearing mode" and "grinding mode" refer only to the relative positions of the upper and lower teeth, although the names are derived from their most characteristic functions.

The wear facet on the prevallid produced by shearing extends down to the oblique anterior cingulum, which is also worn and in some individuals is worn away. This cingulum occludes against the apical part of the metacone; the main shearing on the postvallum is in the metacone region. On the prevallum, the main shear involves the paracone and the lingual part of the paracrista, ending on the paracingulum, but the paraconule and preprotocrista are also usually involved. The various notches on the upper molar and on the trigonid improve the efficiency of shear

(Shaw, 1917; Simpson, 1933). The one commonly present in the centrocrista may be a morphogenetic byproduct of the functional ones anterior and posterior to it. The paracone produces a characteristic facet, sometimes entering the dentine, low in the hypoflexid.<sup>1</sup> When the paracone is making this contact, the protocone occludes at or near the entoconid; the metacone, outside the hypoconid; the paraconule, on the crista obliqua; and the metaconule on the hypoconid. This occlusion is why the paraconule is higher on the tooth than the metaconule, and the paracone higher than the metacone. Short lateral movements, perhaps as a final component of the major vertical<sup>2</sup> one, would account for all the talonid wear facets.

The grinding mode is especially variable. The relations of the canines seem to prevent much anteroposterior movement. In some cases the mandible is moved slightly anteriorly or posteriorly and the transverse component in or following this movement produces anteriorly and posteriorly sloping facets on the trigonid and corresponding ones on the anterior and posterior sides of the cusps and crests (except on the most labial part of the tooth) on the opposing upper tooth. In other cases the mandible is moved posteriorly, and the entire trigonid occludes at once with the trigon and paracrista.

In the shearing mode, almost the entire postvallum of  $P^4$  (including the apex of the protocone) slices by the prevallid of  $M_1$ , but

this shear is usually less important than the  $M^1$ - $M_2$  one.  $P^4$ - $P_4$  shear is even less important, as is that of the more anterior premolars. In the grinding mode the lower premolars move posteriorly with the rest of the mandible, and wear from the upper premolars occurs sometimes for a considerable distance down either the labial or the lingual side of the tooth, but not on both in the specimens available. The only bilateral specimen shows lingual wear on both sides of the mouth.

There is no consistent difference in wear pattern between the species of *Didelphodus*. *Acmeodon* is generally similar except that there is relatively less shear. The protostylid, metaconid, and protoconid are worn about equally on  $P_4$ , indicating some function in the grinding mode. *Avunculus* is generally similar to *Didelphodus* except that there is an additional crushing modification of the shearing mode, in which the molar paracone is plunged onto the top of the crista obliqua and the  $P^4$  paracone down the protostylid ridge. *Gelastops* is similar to *Didelphodus* except that  $P_4$  is included in the grinding mode, as is also true of *Puercolestes*. However, *Didelphodus* also occasionally shows this situation.

In at least *Didelphodus altidens*,  $DP^4$  occludes as does  $M^1$  except for its lack of a protocone.  $DP_4$ , and even more strongly  $DP_3$ , show the facet in the hypoflexid caused by the paracone in the shearing mode. The wear on  $DP_4$  is identical to that normally found on  $M_1$  except for the absence of any wear on the entocristid, as expected. Only postvallid shear is indicated for  $DP_3$ , except for some transverse movement on the crista obliqua.  $DP^{?2}$  has only one face, presumably anterior, worn.

Cope (1884a) remarked of *Didelphodus* that "its delicately acute teeth indicate a diet of insects." Although I would not quarrel with this statement, it must remain speculative in view of the diverse diets of recent mammals with teeth generally alike.

Some degree of habitat differentiation within the Didelphodontinae, at least in the middle Paleocene, is indicated by the fact that any two species are usually found in different places. Only at Gidley Quarry and in the rather diverse Lost Cabin beds are any two species found together.

<sup>1</sup> This facet occurs regularly in all species of *Didelphodus*, *Gelastops*, and *Avunculus* and in cf. *Acmeodon* sp. from the Puerco, is absent from *Acmeodon secans*, *Palaeoryctes*, *Pararyctes*, and *Micropternodus*, and cannot be determined in the other genera of the family. It is emphasized by Patterson (1956, p. 56) for *Amphitherium* and zalambdodonts, and also occurs regularly in *Sinopa*, *Prolimmocyon*, *Oxyaena*, and miacids, but is absent from didelphids, carnivorous marsupials, condylarths (including most Arctocyoniidae), many insectivores, and mesonychids, except for sporadic occurrences in mesonychids, where it is farther posterior on the talonid. It is apparently related to well-developed shear with a tall paracone, an apparently primitive trait in eutherians. Its absence from *Palaeoryctes* is perhaps due to the piercing rather than shearing adaptations of the teeth in this genus.

<sup>2</sup> Numerous striations show that the shear moves apparently ventrolabially on the lower teeth and dorso-lingually on the upper ones, but this fact merely indicates the true vertical position of the teeth.

## PHYLOGENY

A tentative phylogeny is presented in figure 10. *Puercolestes* could well be, but for lack of intermediates cannot at present be demonstrated to be, ancestral to the rest of the subfamily. *Puercolestes simpsoni* probably is not because of the reduction of P<sup>1</sup>. Of the other genera, *Avunculus* has the fewest characters that appear to preclude it from the ancestry of *Didelphodus*, whence its name and position in the phylogeny. Of these characters the most striking are the height on the tooth of the premolar paraconids and the reduction of the canine. *Acmeodon*, *Gelastops*, and *Avun-*

*culus* are separated from *Didelphodus* mainly because of the high premolar paraconids, and *Gelastops* and *Acmeodon* are separated from *Avunculus* mainly because of the greater development of the protostylid crest on P<sub>4</sub>, although other characters are also involved in all these decisions.

Despite this probable phylogeny, *Gelastops parvus* is structurally closer to *Avunculus* than it is to *Acmeodon*, suggesting a relatively more rapid rate of evolution in the phyletic line leading to the latter. The alternative to this suggestion is to invoke parallel evolution and have *Acmeodon* branch off *Avunculus* or

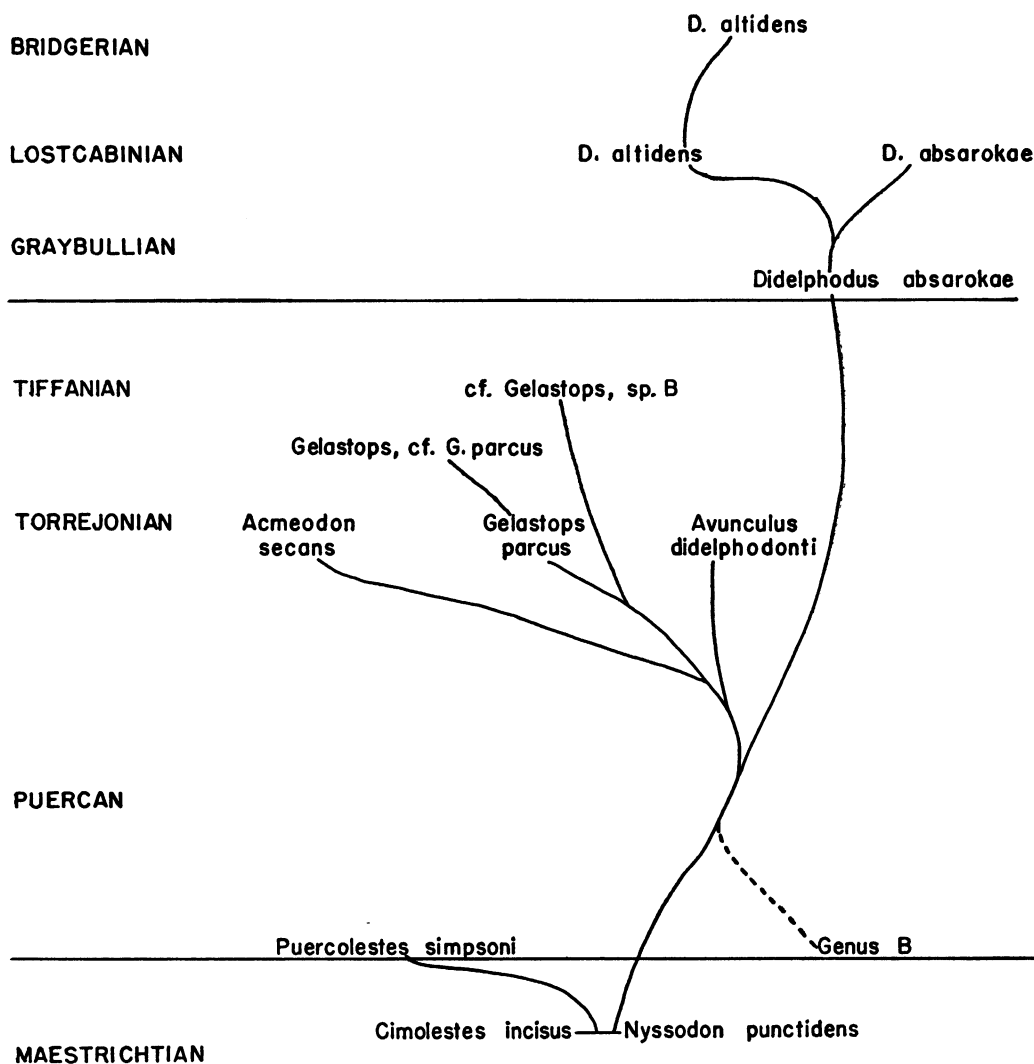


FIG. 10. Tentative phylogeny of the known North American Didelphodontinae.

the immediate ancestor of the latter; this second alternative is perhaps supported by the presence of cf. *Acmeodon* sp. in the Puerco. In 1965 it appears that *Gelastops* or *Aboletylestes* may best indicate the primitive structure of the Didelphodontinae, although these genera are in some ways specialized.

#### OTHER PALAEORYCTIDAE

##### DELTATHERIDIUM AND DELTATHEROIDES

GREGORY AND SIMPSON, 1926

The following remarks are intended to supplement the description and figures of Gregory and Simpson (1926) and should be read in conjunction with that paper. Their lateral figure of the skull of *Deltatheridium* shows it somewhat (one-tenth or two-tenths) too high relative to its length. The middle part of the postpalatine border was probably straight. The pterygoid crests are incomplete posteriorly, and the median ridge shown in the narial trough is one of these crests displaced. In other respects, except for a few aspects of the teeth (see below), the figures are accurate.

The internasal and nasomaxillary sutures are open in *Deltatheridium* (A.M.N.H. No. 21706); the others are closed. The amount of facial exposure of the lacrimal is not known, but it touches the abruptly expanded posterior wing of the nasal, thus excluding the frontal from the border of the maxilla. The nasals extend posteriorly to the level of the postorbital process, which is present but weak dorsal to  $M^3$ . Very faint temporal crests curve to a moderately weak sagittal crest. The postpalatine torus is low; its configuration is not known. The width of the narial trough is about five- to six-tenths of the palatal width between the protocones of  $M^3$ . The indentation between the zygoma and the palate extends anteriorly to at least the middle of  $M^3$ . There is no excavation of the posterior border of the palate between the pterygoid process and  $M^3$ ; this is a smooth curve, as figured. The infraorbital foramen is above the middle of  $P^4$  and is  $1.4 \pm 0.1$  mm. tall, only about half of the length of  $M^1$ . The nature of the border of this foramen is not known. The posterior opening of the infraorbital canal is above the posterior end of  $M^1$ . The orbit extends anteriorly to the middle or posterior part of  $M^1$ , depending on the amount of breakage present.

Under strong ultraviolet light of 3660 Å the bone and teeth are markedly distinct, by visual observation of fluorescence, from the matrix. This shows that the lingual lobe figured on  $P^4$  of the type specimen of *Deltatheridium* is really matrix; the tooth was in reality simple. In addition, there is no alveolus in this position in the referred specimen (A.M.N.H. No. 21706). The talonid of  $M_3$  is really as large as figured; this is not matrix. Slight additional preparation under ultraviolet light has disclosed the presence in A.M.N.H. No. 21706 of alveoli for four upper incisors, a number previously unknown in postembryonic placental mammals. (Ärnback-Christie-Lind, 1912a, 1912b, reported *Anlagen* of four or probably five upper incisors in fetuses of *Sorex*, but in a more comprehensive study Kindahl [1959] found evidence for only three upper incisors in the same species.) The alveoli in *Deltatheridium* are nearly round, with a slight linguolabial elongation.  $I^3$  is the largest and measures 0.9 mm. linguolabially. The alveolus for  $I^4$  measures about 0.8 mm.; that for  $I^2$ , about 0.6 mm.; and that for  $I^1$ , roughly 0.4 mm.  $I^4$  was nearly or quite vertical, and  $I^1$  was apparently quite procumbent;  $I^2$  and  $I^3$  were intermediate.

In A.M.N.H. No. 21706 there are apparently only two lower incisors. The anterior one is moderately large, about half of the diameter of the canine, and the lateral one is half of the diameter of the anterior one. They are situated only slightly in front of the canine. In this specimen  $P_2$  is two-rooted, while in the type it is one-rooted on the right (although the exposure of the pulp cavity simulates two roots) and the condition on the left is unknown. The talonid of each of the three molars seems to be distinctly higher posteriorly than anteriorly. The trigonid of  $M_1$  is distinctly narrower and somewhat more elongate than that of  $M_2$ , and the change in the angle of the postvallid (more transverse posteriorly) is the reverse of that shown in figure 4 of Gregory and Simpson (1926). The metaconid of  $M_3$  is even slightly anterior to the protoconid.

Mental foramina are situated below  $P_1$  and  $P_4$ . The masseteric ridge has an angle of about 50 degrees with the horizontal ramus; the masseteric fossa is somewhat sharply demarcated ventrally and, especially, ante-

riorly. The symphysis continues to the posterior part of  $P_3$  or the anterior part of  $P_4$ .

In the only known specimen of *Deltatheroides* there are no sutures detectable, at least in part a result of poor preservation. The orbit extends to the anterior part of  $M^1$ . The infraorbital foramen is above the middle of  $P^3$  and its border apparently tilts slightly forward dorsally. There seems to be no post-orbital process, but a weak temporal ridge is present.

Matthew (1928) gave an inaccurate figure of reconstructed teeth of *Deltatheroides*, labeling it "after Gregory and Simpson." The figure of the latter, however, is different and accurate. The only dental features not observable on the latter figure are that there is a strong metacrista on  $M^1$  and probably on  $M^2$ , and that on  $M^1$  the metacone appears to be like that in *Potamogale velox*. There is, however, some possibility that this cusp in *Deltatheroides* is merely part of the metacrista.<sup>1</sup>

Novozhilov (1954; cf. also Orlov, 1962, p. 47; Thenius, 1959; and Rozhdestvensky, 1957) has stated that the mammals supposedly found in the Djadochta of Mongolia actually came from the Gashato, which over-rides it. This claim, based on new field work, cannot be dismissed lightly. In view of this doubt as to the stratigraphic provenance of *Deltatheridium* and its associated mammalian fauna, I propose the name "Shabarakh Usu Fauna" for this assemblage so that it can be referred to unambiguously. The mammals were found in concretions apparently at the base of the cliffs, and similar nodules also

occur in the Gashato of Mongolia. However, Berkey and Morris (1927), Morris (MS), and Granger (MS) noted the occurrence of such nodules in the Djadochta, and Simpson (in conversation) stated that Granger told him that the Gashato is not exposed at the top of the cliffs where the mammals were found. The matrix is more similar to that around *Protoceratops* than to that around the Gashato mammals, no Shabarakh Usu mammals were found in the Gashato, no Gashato mammals were found in the Djadochta, and no Shabarakh Usu mammals have been reported by the Russians. It is possible, as Novozhilov suggested, that the Shabarakh Usu mammals are from a lower part of the Gashato Formation than are the fossils known to be from this formation. Novozhilov wrote that this lower part of the Gashato was redeposited from the Djadochta and separated from it by only a disconformity. It is possible that this includes the "Djadochta" nodule zones of Berkey, Morris, and Granger. It is also possible that the Shabarakh Usu Fauna came from a part of the Djadochta Formation deposited significantly later than that at the base of the cliffs.

Although paleontologically the peculiar Shabarakh Usu mammalian fauna could be of an age as late as late Paleocene even better than late Cretaceous, there is no proof at present, and the question must remain open until Shabarakh Usu mammals are found in place. In this paper I very tentatively consider the Shabarakh Usu mammals as of early Paleocene age, a possible age and one intermediate between other possibilities. Faunal breaks were hypothesized by Novozhilov above and below the redeposited Djadochta sediments; if the Shabarakh Usu mammals came from such a stratum their age could be anything from Campanian to Clarkforkian.

#### HYOTHERIDIUM GREGORY AND SIMPSON, 1926

In the only known specimen of *Hyotheridium* (A.M.N.H. No. 21702) the internasal is the only clearly visible open suture. The nasals are of about the same width at different levels anteriorly, but a broad posterior expansion begins above  $P^2$ . Their maximum width occurs at the level of the anterior border of the orbit, and they extend to the

<sup>1</sup> Despite the assertion of McDowell (1958, p. 180), both *Micropotamogale ruwenzorii* and *M. lamottei* have an indication of a metacone, at least on  $M^1$  (Heim de Balsac and Bourlière, 1955; de Witte and Frechkop, 1955; Guth, Heim de Balsac, and Lamotte, 1959). It is quite possible that both the metacone and the protocone of *Potamogale velox* are secondarily enlarged, and it is quite unknown in which direction the changes in molar pattern proceeded in the Potamogalinae (Guth, Heim de Balsac, and Lamotte, 1959, 1960). If the metacone became larger, it is also unknown whether it was once totally absent. But even if it was once absent, the morphogenetic competence to produce it was probably retained, and in the evocation of this competence *Potamogale velox* can be considered primitive, whether by retention or by reversion. In this developmental sense, and quite possibly historically as well, the metacone of *Potamogale* can be considered homologous to that of other therians (cf. Sondhi, 1962).

level of the postorbital process. The sutures of the lacrimal are obscure. It is, at the present time, impossible to confirm the statement of Gregory and Simpson (1926) that there is "a good nasolacrimal contact." It is possible nevertheless that there is one, but the most likely suture line to give it would place the postorbital process on the lacrimal. A precanine flange of the maxilla passes over the premaxilla as in *Deltatheridium*.

The postorbital process is weak and is situated dorsal to  $M^3$ . The orbit extends anteriorly to the level of the middle of  $M^1$ . The lacrimal foramen is not detectable, but enough of the bone surface is preserved to indicate that it was either quite small or well within the orbit; the latter seems more probable. The infraorbital foramen is moderately small (1.3 mm. in height) and is above the anterior part of  $P^3$ . Its dorsal margin is inclined somewhat anteriorly.

Examination under ultraviolet light has shown that three nearly equal alveoli for upper incisors are present in front of the fossa for the lower canine. Not all three can be seen on one side. A gap in the bone anteromedial to them is clearly not a result of crushing, and none of the incisors belonging to the known alveoli would meet in front of the lower incisors, so it is possible but highly speculative that one or even two additional pairs of upper incisors were present. There could, however, easily have been a horny pad on the median part of the premaxilla.

There is a large median pair of lower incisors, and apparently only one smaller pair lateral to them. This condition is similar to that of *Deltatheridium* but more specialized. The more posterior upper incisor occluded against the lateral lower incisor, while the two anterior upper incisors occluded against the side of the median lower incisor.

The upper molars have a paracone and metacone that are connate, although to an unknown degree. The styler shelf is somewhat narrower than that of *Deltatheridium*, especially that of  $M^1$ ; that of  $M^3$  is apparently fully as wide as that of  $M^1$ . The most external part of the tooth row is between  $M^2$  and  $M^3$ , but not much more external than the junction between  $M^1$  and  $M^2$ . There is a strong metacrista on at least  $M^2$ . Despite the statement by Gregory and Simpson (1926),

there is no evidence as to the relative height of the paracone on  $P^3$  and  $P^4$  as compared to  $M^1$ ,  $M^2$ , and  $M^3$ . There is not room for so long a talonid on  $M_3$  as that of *Deltatheridium*. The jaws are locked in the shearing mode.

#### *Palaeoryctes puercensis* Matthew, 1913

The redescription of the skull of *Palaeoryctes puercensis* (from the Torrejon, not the Puerco as stated by McDowell, 1958) is presented mainly because I disagree in several points with the interpretation of McDowell. Bryan Patterson also prepared some notes on the specimen, which I did not see until much of the present work was done. As we agree on most points, he has generously relinquished publication to me. An additional specimen (U.K. No. 7748) preserves the anterior half of the skull and is being described by R. W. Wilson. McDowell's figure (1958, fig. 26) is accurate on all points shown except the "epihyal." Certain features, however, were omitted. At the time he drew the specimen (which is very fragile), it had to be examined through a glass box. (See pl. 7, fig. 1; text fig. 11; tables 19 and 20.)

The intermaxillary, interpalatine, and palatomaxillary sutures, and the postero-medial and posterior sutures of the alisphenoid, are the only ventral sutures that are unfused. The palatines extend forward to the level of the posterior part of  $P^4$ . A posterior palatine foramen is present on the palatomaxillary suture lingual to the  $M^1$ - $M^2$  embrasure. There is only a weak postpalatine torus. The posterior border of the palate is almost a straight line except for the pterygoid processes. Immediately dorsal to the lateral end of the palate, and posteromedial to the protocone of  $M^3$ , is the posterior opening of the postpalatine canal. The sphenopalatine foramen is either merged with it, not adjacent to it, or lost.

The pterygoid processes are not divided into a lateral and a medial portion. They extend posteriorly and are high to a point at almost the level of the foramen ovale, at which point a continuation of the ridge extends posterolaterally to the glenoid fossa. The latter, contrary to the statement of McDowell, is present to a considerable extent on the right side; perhaps only the lateral margin is broken off. It is nearly flat and had

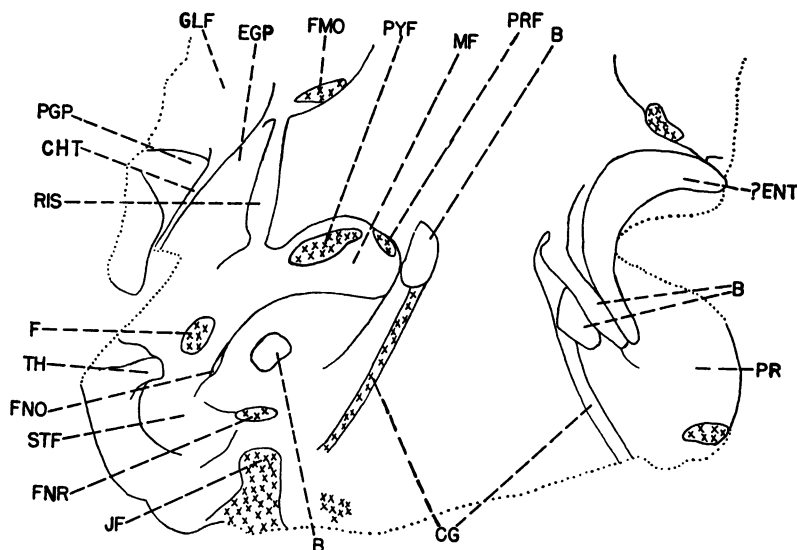


FIG. 11. Map of the basicranium of *Palaeoryctes puericensis* Matthew, A.M.N.H. No. 15923; Torrejon. Compare with plate 6, figure 1. Dotted lines are broken edges; areas marked by X are matrix.  $\times 10$ .

**Abbreviations:** b, bone fragments of uncertain identity; cg, groove for medial entocarotid artery; cht, groove for chorda tympani; egp, entoglenoid process; ?ent, entotympanic or tympanic; f, foramen stylomastoidum primitivum; fmo, foramen ovale; fnr, fenestra rotunda; fo, fenestra ovalis; glf, glenoid fossa; jf, jugular foramen; mf, mesotympanic fossa; pgp, postglenoid process; pr, promontorium; prf, promontory foramen; pyf, pyriform fenestra (stapedial foramen); ris, groove for ramus inferior of stapedial artery; stf, fossa for stapedius muscle; th, tympanohyal.

no preglenoid process, or only a faint one. The postglenoid process is relatively weak and continues as an entoglenoid process onto the medial side of the fossa, where it becomes obsolete anteriorly. Patterson (unpublished) noted that "the base of the condyle is preserved in the right mandible and this part suggests a rather small rounded condyle in keeping with the size and shape of the glenoid surface."

A groove stated by McDowell to be for the chorda tympani demarcates the entoglenoid process from the postglenoid process; it extends posterolaterally from near the center of the posterior rim of the glenoid fossa. There is no groove immediately medial to the glenoid fossa. The postglenoid foramen figured by McDowell is in the position of a small crack and, although it cannot be positively said to be absent, mentally fitting the pieces together appears to give a small depression (perhaps an artifact) with a solid floor of bone. The piece of bone posterior to the crack was

labeled "?tympanic" by McDowell; there is no evidence that it is. The object in his figure 28 (1958) just posterior to the fenestra ovalis, also labeled "?tympanic," and shown on the right side of his figure 26, is not now present as bone; a piece of wire holding the specimen and covered by glue is in about the same position. I do not know whether the fragment of bulla present is entotympanic, as proposed by McDowell, or tympanic, as claimed by Matthew.

A small area bilaterally obscured anterolateral to the foramen ovale may represent a distinct foramen rotundum, but that it is is quite doubtful. Contrary to Matthew and McDowell, the alisphenoid canal is complete, bridged on the right side of the skull and possibly originally so on the left, although the canal on the left side is open ventrally and the exposed bone surfaces are smooth, indicating a possible asymmetry in this condition. The internal surface of the canal is complete. The posterior opening is anteromedial to the

TABLE 19  
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH AND MANDIBLE OF  
*Palaeoryctes puercensis*, TYPE SPECIMEN

	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	Others
Trigonid width	0.65	0.45	0.65	0.80	1.25	1.30	1.15	—
Talonid width	—	—	—	—	1.00	0.90	0.75	—
Crown length	0.85	0.45	1.05	1.50	1.60	1.45	1.40	—
Labial height of hypoconid	—	—	0.70±0.05	0.90±0.05	1.05±0.05	1.00±0.05	0.95±0.10	—
Labial height of protoconid	—	—	1.40±0.10	2.10±0.05	2.60±0.10	2.55±0.05	2.30	—
Lingual height of protoconid	—	—	1.05±0.05	1.70±0.05	2.25±0.15	2.30±0.10	2.05±0.05	—
Lingual height of paraconid	—	—	—	—	1.45±0.10	1.45±0.10	1.35±0.05	—
Lingual height of metaconid	—	—	—	—	1.85±0.10	1.90±0.10	1.60±0.10	—
Alveolar length from posterior edge of C to P <sub>1</sub>	—	—	—	—	—	—	—	4.20±0.05
Alveolar length of M <sub>1-3</sub>	—	—	—	—	—	—	—	4.10±0.05
Depth of mandible below M <sub>2</sub> protoconid	—	—	—	—	—	—	—	2.00±0.15
Distance from M <sub>3</sub> to mental foramen	—	—	—	—	—	—	—	3.90

foramen ovale; they are not in a common fossa. The anterior opening is confluent with the orbital fissure. In other deltatheridians, an alisphenoid canal is present in oxyaenids, limnocyonines, and *Didelphodus*; it is probably absent from hyaenodontines and proviverrines. Matthew (1906) figured an alisphenoid canal in *Sinopa grangeri*, but from A.M.N.H. No. 13142, a specimen probably referable to the same species, it is probably absent (a small bilaterally asymmetrical foramen lateral to the usual position may represent its entrance). In *Tritemnodon agilis* (Y.P.M. No. 10073), as well as in *Hyaenodon*, a small foramen is present shortly in front of

the foramen ovale. I interpret this foramen as for the middle meningeal artery or perhaps for an anastomotic branch of it or for a vein, rather than for the larger internal maxillary artery.

The basioccipital bears a small median ridge. It is not now possible to be sure that this bone ended at the point shown in McDowell's (1958) figure 26, as a small part has been broken off. The "hypoglossal foramen" shown on his figure 28 is a small patch of matrix on the right side which may or may not cover a foramen.

The promontorium is conspicuous. The fenestra rotunda opens on its posteroventro-

TABLE 20  
MEASUREMENTS (IN MILLIMETERS) OF SKULL AND UPPER TEETH OF  
*Palaeoryctes puercensis*, TYPE SPECIMEN

	P <sup>2</sup>	P <sup>3</sup>	P <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	Others
Anterior margin	—	0.75	1.55±0.05	—	2.70±0.10	2.45±0.05	—
Posterior margin	—	1.00	2.00±0.05	2.70±0.20	2.50±0.10	1.70±0.05	—
Labial margin	0.55	1.15	1.55	1.60±0.20	1.45	1.25	—
Length at paraconule	—	—	—	0.55±0.05	0.50±0.05	0.45±0.05	—
Horizontal distance from apex of protocone to lingual margin of protocone	—	—	0.40±0.05	0.55±0.10	0.65±0.20	0.40±0.10	—
Anterior height of paracone	—	—	—	—	1.80±0.20	—	—
Posterior height of protocone	—	—	1.00±0.05	1.40±0.20	1.45±0.15	1.15±0.10	—
Labial height of paracone	—	1.30	1.60±0.05	—	—	—	—
Crown length, M <sup>1-3</sup>	—	—	—	—	—	—	3.80±0.15
Distance from posterior border of M <sup>3</sup> to posterior border of promontorium	—	—	—	—	—	—	11.10±0.10

lateral surface and, judged by the undisturbed left side, had no process posterior to it. The fenestra ovalis opens on the lateral side, anterolateral to the fenestra rotunda; just anterolateral to the fenestra rotunda is the opening of the facial canal. The medial part of the roof of the epitympanic recess is present lateral to this foramen. The tympanohyal is fused to the petrosal and is apparently broken on its medial surface; the surrounding bone in this region is continuous and apparently in its original configuration. The facial nerve passed dorsal to the tympanohyal and emerged just posterior to it. A fossa of average depth for the stapedial muscle lies between the tympanohyal and the fenestra rotunda, anterolateral to a large jugular foramen.

McDowell (1958) is correct in stating that there are no grooves on the promontorium that can be assigned with confidence to branches of the internal carotid artery. A faint groove bilaterally present lateral to the apex of the cochlea may be for the tensor tympani. There is, however, good evidence for the presence of the complete primitive number of branches of the internal carotid (a situation now known but not in every case published for members of Group M,<sup>1</sup> the Condylarthra, Deltatheridia, and Fissipeda; see Matthew, 1909, p. 451).

A foramen bilaterally present in the antero-medial corner of the mesotympanic fossa is

surely for the promontory artery. There is a broad and indefinitely marked groove extending from it posterolaterally in the direction of the fenestra rotunda. This may have contained the promontory artery, although, topographically, it is for the most part simply the space between the apex of the cochlea and a prominent anteromedial ridge on the promontorium that formed the base of the bulla in this region. The promontory artery could, on the other hand, have been on the lateral surface of the promontorium, where matrix covers what may be a groove.

A somewhat larger foramen just lateral to the one for the promontory artery presumably contained the ramus superior of the stapedial artery. Its borders are not certainly known on any but the medial side, but they may well have been as now preserved. This foramen is presumably homologous with the pyriform fenestra of *Didelphodus*, *Apternodus*, Soricidae, Vespertilionidae, and others (cf. McDowell, 1958). Figure 26 of McDowell (1958) does not show the bar of bone between the pyriform fenestra and the promontory foramen in *Palaeoryctes*. A groove on the alisphenoid, from the point where the preotic crest meets the entoglenoid process and extending in the direction of the fenestra ovalis, presumably housed the ramus inferior of the stapedial artery, which could easily have joined (or formed) the internal maxillary artery and proceeded into the alisphenoid canal.

The groove noted by Matthew and McDowell for the medial entocarotid (grooving both the basioccipital and the petrosal) is also present, although filled with matrix on the right side and containing a small longitudinal crack on the left. The carotid foramen, if present, is covered by matrix or scraps of loose bone on both sides. This medial entocarotid appears to have been rather smaller than either the promontory or the stapedial, the opposite situation from that of *Didelphodus* and the hyaenodontoids.

The anterior face of the mesotympanic fossa is abruptly vertical. I believe that such is the original condition, since bone is visible on the wall in places and both the lateral and, especially, the medial boundaries are continuous bone with no clear indication of displacement.

<sup>1</sup> The name "Group M" is used here (cf. the usage of "Menotyphla" by McDowell, 1958, and McKenna, 1960a) because no valid name has been proposed for the probably natural but probably undefinable (by characters-in-common) group of Insectivora that includes the Pantolestidae, Mixodectidae, Leptictidae, Zalambdalestidae, probably the Apatemyidae and *Endotherium*, and possibly the Tupaiidae. Note that the Macroscelididae, an essential component of Haeckel's Menotyphla, are not included, and the Tupaiidae, the other original family of the Menotyphla, are only doubtfully referred. Contrary to statements still often made, the caecum is small and is in some cases absent from the Tupaiidae (Chapman, 1904; Lyon, 1913; and references cited in these papers). The families in the above list have been shown to be related by the work of Butler, McDowell, McKenna, and others. A designation by letter is given because otherwise the misleading name "Menotyphla" would have to be used until an adequate name is proposed. "Group M" can be defined as the stem placental and those families not subordinally distinct from the stem placental.

***Palaeoryctes punctatus*, new species**

Plate 6, figure 2; table 21

TYPE AND ONLY KNOWN SPECIMEN: A.M.N.H. No. 15850, fragment of right mandible with most of  $M_2$  and  $M_3$  and the ventrolabial parts of  $P_4$  and  $M_1$ , fragment of right maxilla with broken  $M^{1-3}$ , distal end of left humerus, proximal end of ulna.

KNOWN DISTRIBUTION: Latest Paleocene or perhaps earliest Eocene, "blue beds," near the head of Big Sand Coulee, Bighorn Basin region, Wyoming.

DISCUSSION AND DESCRIPTION: The teeth are unworn. Simpson (1937b) said that the specimen is "suggestive of *Nyctitherium*" and referred it tentatively to the Nyctitheriidae; this family reference was accepted without Simpson's question mark by Van Houten (1945). The specimen was first identified as *Palaeoryctes* by P. Robinson and M. C. McKenna.

In addition to being almost a third larger than *P. puercensis*, this species, probably from the Clark Fork, differs from the one from the Torrejon as follows: The anterior cingulum is more pronounced and less vertical on  $M_1$ , more pronounced but no less vertical on  $M_2$ , and apparently similar to that of *P. puercensis* on  $M_3$ . The paralophid extends more anteriorly on  $M_1$  and  $M_2$  but perhaps not on  $M_3$ , and the postvallid is slightly oblique on  $M_1$ , not strictly transverse as on  $M_3$  of this specimen and all teeth of *P. puercensis*. The hypoconid of  $M_3$ , but probably not that of  $M_1$ , is relatively taller than that of *P. puercensis*. The structure of the paraconid is known only on  $M_2$ , where it is a little higher but appar-

ently slightly more reduced than that of *P. puercensis*. The talonid of  $P_4$  extends farther labially, perhaps indicating a slightly more molariform condition. The protoconid of  $M_3$  (and that of  $M_2$ , as far as preserved) and the hypoflexids of the molars are identical to those of *P. puercensis*. The mandible is relatively slightly deeper and does not have a mental foramen below the posterior part of  $P_4$ , as in *P. puercensis*. There also appears to be no space between the ascending ramus and  $M_3$  as in that species. All other structures of the lower jaw and teeth are broken away or too damaged for comparisons.

The metacone is somewhat more distinct from the paracone on  $M^1$  but not on  $M^2$ .  $M^1$  and  $M^2$  appear to be longer anteroposteriorly relative to the anteroposterior length of the paracone. The styler area is somewhat narrower; there is only a slight ectoflexus, so the labial border of the tooth is nearly straight. The paracrista of  $M^2$  leads not to a partly distinct stylocone but to the parastyle. The metastylar area of  $M^3$  is not so reduced as in *P. puercensis*; the posterolabial root is distinctly posterior to and not much more lingual than the anterolabial root. There are no lingual cingula on  $M^1$ , and the metacrista of  $M^2$  seems about as tall and distinct as in *P. puercensis*. Aside from these features the upper teeth of one or both species are too damaged for comparisons. Most of the labial area of  $M^1$  is preserved on the Clark Fork specimen, and shows a small stylocone posterior to a parastyle of similar size.

The distal end of the humerus (fig. 12) is missing laterally; the anterior face is exposed.

TABLE 21

MEASUREMENTS (IN MILLIMETERS) OF TEETH OF TYPE SPECIMEN OF *Palaeoryctes punctatus* (A.M.N.H. No. 15850)

	$M^1$	$M^2$	$P_4$	$M_1$	$M_2$	$M_3$	Other
Labial margin	1.95	1.65	—	—	—	—	—
Crown length	—	—	$1.45 \pm 0.05$	$2.00 \pm 0.05$	$2.10 \pm 0.15$	$1.65 \pm 0.05$	—
Labial height of hypoconid	—	—	—	$0.90 \pm 0.10$	—	$0.90 \pm 0.10$	—
Labial height of protoconid	—	—	—	—	—	$2.15 \pm 0.10$	—
Alveolar length of $M_{1-3}$	—	—	—	—	—	—	$5.50 \pm 0.10$

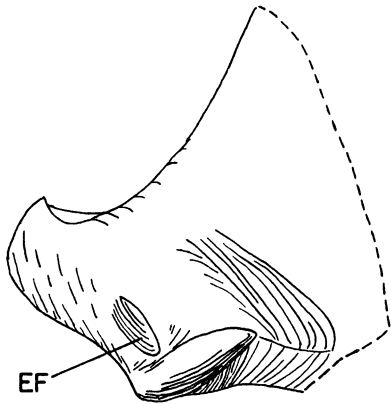


FIG. 12. Anterior view of distal end of left humerus of *Palaeoryctes punctatus*, new species, A.M.N.H. No. 15850. The broken line indicates a broken edge.  $\times 20$ .

Abbreviation: ef, entepicondylar foramen.

The entepicondyle (medial epicondyle) is moderately large, with a hook-shaped process such as is found in most shrews (especially *Blarina* and *Sorex*) and moles (not *Uropsilus*; see Campbell, 1939). The entepicondylar (supracondyloid) foramen is fairly small and unusually distal. The trochlea is relatively long, the lateral part of it more rounded than the medial part and continuous with a small but moderately deep fossa. This fossa extends proximomedially to a rounded ridge that there forms the medial border of the bone.

The preserved part of the humerus is most similar to that of shrews, *Tenrec*, and to some extent *Solenodon*, but is considerably different from any humerus known to me. The expanded entepicondyle and the distal position of the entepicondylar foramen are the most striking features, and both are common in burrowing animals (in both the "terrier" and "mole" types of Campbell, 1938). Specifically, these features are well displayed in *Palaeonodon*, *Myrmecophaga*, *Tamandua*, *Tachyglossus*, a humerus referred to *Ceratogaulus* by Matthew (1902), *Necrolestes* (Scott, 1903–1905, pl. 64; cf. Patterson, 1958), Talpidae (except *Uropsilus*), *Cryptoryctes* (Charles A. Reed, 1954), *Arctoryctes* (Charles A. Reed, 1956), and a humerus of an unidentified fossorial Paleocene mammal (Charles A. Reed, 1954). To some extent they are present in *Chrysochloris*, *Manis*, *Aplodontia*, *Dasyurus*, and the Miocene humerus described by Reed

and Downs (1958), but they are poorly or not represented in *Taxidea*, *Orycteropus*, *Meta-cheiromys*, *Pentapassalus* (Gazin, 1952), *Myrmecobius*, *Phascolomis*, and *Mylagaulus* (Fagan, 1960). Many other digging mammals (especially rodents) have lost the entepicondylar foramen, but almost all have the entepicondyle expanded to a greater or less degree.

The region of the entepicondyle that is expanded in *Palaeoryctes* is in shrews and moles the origin of the pronator radii teres and the epitrochleo-anconeus muscles (Charles A. Reed, 1951), both of which are more developed in moles than in shrews. There is in *Palaeoryctes* no fossa for the origin of the ligament to the muscle that flexes the digits and is tightened by rotation of the humerus (Charles A. Reed, 1954); this fossa is present on all known humeri with action of the mole type. Because of the lack of this fossa and the similarity in outline to the humeri of shrews, it is probable that *Palaeoryctes* dug by action of the "terrier type" (but cf. Reed and Downs, 1958). It is, nevertheless, possible that *Palaeoryctes* was ancestral to *Cryptoryctes* and thence to *Arctoryctes* (but cf. Katherine M. Reed, 1961). Such a possibility is, however, merely permitted by the evidence available and should not be used as evidence for either the reference of these humeri to the Apternodontidae or *Micropternodus* (Dale Russell, 1960) or the allocation of *Palaeoryctes* to the ancestry of either of these taxa.

The name *Palaeoryctes* ("early digger") now appears to be excellently suited to its owner.

#### PARARYCTES, NEW GENUS

Plate 7, figures 1–5; tables 22 and 23

TYPE SPECIES: *Pararyctes pattersoni*, new species.

TYPE OF *P. pattersoni*: U.W. No. 2002, left M.<sup>1</sup>

KNOWN DISTRIBUTION OF *P. pattersoni*: Tiffanian (late but not latest Paleocene), Saddle Locality of Gazin (1956), Bison Basin, Wyoming.

REFERRED SPECIMENS: U.W. Nos. 2003, right lower molar; 2004, left lower molar; 2005, fragment of left maxilla with P<sup>4</sup> and the labial half of M<sup>1</sup>; and 2006, labial half of right M<sup>1</sup>.

TABLE 22  
MEASUREMENTS (IN MILLIMETERS) OF LOWER  
TEETH OF *Pararyctes pattersoni* FROM THE  
TIFFANIAN OF THE BISON BASIN

	U.W. No. 2004 Left M <sub>71</sub>	U.W. No. 2003 Right M <sub>71</sub>
Trigonid width	1.30	1.25
Talonid width	1.15	1.10
Crown length	1.65	1.55
Labial height of protoconid	2.35 ± 0.10	—
Labial height of hypoconid	1.10	1.10 ± 0.05
Lingual height of protoconid	1.85 ± 0.15	—
Lingual height of paraconid	1.00 ± 0.10	0.90 ± 0.10
Lingual height of metaconid	—	1.50 ± 0.25

DIAGNOSIS: Differing from all other palaeoryctids in having both a precingulum and a postcingulum distinctly developed on the upper molars. (See description for further characters.)

DISCUSSION AND DESCRIPTION: The six teeth now known of this species were collected by Patterson and McGrew. An upper molar from the Paskapoo, probably referable to *Pararyctes*, was figured by Loris S. Russell (1932, fig. 10).

Two lower teeth are present in the Bison Basin sample, a right one (U.W. No. 2003) and a left one (U.W. No. 2004). The former lacks the metaconid, and the latter lacks the

apices of the protoconid and metaconid. Because of the forward placement of the paraconid and the relative width of the talonid (almost as wide as the trigonid), I hesitantly identify both these teeth as M<sub>1</sub>. They are about the same size as M<sub>1</sub> of *Palaeoryctes puericensis*, but differ from it in a number of respects.

The most striking difference from *Palaeoryctes puericensis* in the lower teeth is the distinctly greater height of the talonid and the slightly reduced height of the trigonid. The anterior cingulum extends a little higher on the tooth. The paraconid is relatively larger, higher relative to the other cusps but lower relative to the base of the enamel, less transverse, and more forwardly placed than in *Palaeoryctes puericensis*. In conjunction with this, the anterolingual face of the protoconid faces more lingually. The protoconid and especially the metaconid are also longer anteroposteriorly. The prefossid does not descend smoothly into the lingual border of the trigonid but is demarcated by an incipient metacristid. The postvallid is distinctly oblique. The talonid is wider, but differs consistently otherwise only in having the hypoflexid deeper ventrally. As in *Palaeoryctes*, but better shown in *Pararyctes*, the hypoconulid is very close to the hypoconid and is nearly twinned with it; both cusps, however, are rather poorly demarcated. There is a marked anterior rise in the base of the enamel on both sides of the tooth, similar to the situation in *Palaeoryctes* but unlike that in the Didelphodontinae.

The upper teeth differ from those of

TABLE 23  
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Pararyctes pattersoni* FROM  
THE TIFFANIAN OF THE BISON BASIN

	U.W. No. 2002 Left M <sup>1</sup>	U.W. No. 2006 Right M <sup>2</sup>	U.W. No. 2005 P <sup>4</sup>	U.W. No. 2005 M <sup>1</sup>
Anterior margin	2.90	—	1.80	—
Posterior margin	3.10	—	2.50	—
Labial margin	1.80 ± 0.05	1.80 ± 0.05	1.95	1.75
Length at paraconule	1.00	—	—	—
Anterior height of paracone	—	1.85 ± 0.20	—	—
Posterior height of metacone	—	1.60 ± 0.10	—	—
Maximum anteroposterior length of postcingulum	0.25	—	—	—

*Palaeoryctes puericensis* most importantly in the presence of pronounced precingula and postcingula on the molars. The precingulum is roughly a fourth, and the postcingulum roughly a third, of the protocone height. Although the postcingulum is scarcely higher than the precingulum, the apex of the protocone is markedly anterior to the midline of the base of the tooth (it is in fact over the anterior edge of the lingual root), so the lingual part of the prevallum is steeper and has a smaller enamel height than the lingual part of the postvallum. The precingulum extends from near the lingual limit of the tooth to a point slightly lingual to the paracone. It is roughly half as wide at its widest point as is the postcingulum; its widest point is at about its middle. The posterolingual corner of the postcingulum is broken off, but enough is preserved of the basal part of the enamel to indicate that the cingulum did not extend much beyond its present horizontal limits. It is widest on its lingual third and continues to the level of the lingual border of the paracone. Lingually it extends slightly beyond the base of the protocone.

The apices of the paracone and metacone and the entire labial surface of the protocone are removed by wear on all teeth that have these parts preserved. The position of the apex of the protocone is unknown, but it was probably not far from a third of the width of the tooth labially from the lingual border of the protocone. It may have been somewhat more lingual but very probably not so lingual as in *Palaeoryctes puericensis*. The locations of the paraconule and metaconule are worn away; if present, however, they were not large. The paracingulum gradually narrows labially and becomes indistinct anterior to the paracone. The parastylar area is a separate widening of the anterior border of the tooth, not a continuation of the paracingulum as in *Palaeoryctes puericensis* and most other mammals. A parastyle is not well differentiated. The metacingulum is broad, in fact broader than the paracingulum, and extends labially to about the level of the labial edge of the metacone, where it ends more or less abruptly under the metacrista. The paracone and metacone are strongly connate, but the metacone is not so strongly reduced as that in *Palaeoryctes puericensis*. The metacone is comparable to

that of M<sup>1</sup> of *Palaeoryctes punctatus*. There is no trace lingually, and only a slight trace labially, of a groove between the paracone and metacone until near the apex of the metacone. The paracone is decidedly higher and broader than the metacone. The stylar shelf is narrower than that in *Palaeoryctes puericensis*, but about the same as that in *P. punctatus*. A low paracrista extends labially and a little anteriorly from the paracone; a weak stylocone is variably present at its labial end. A strong metacrista, which, however, is poorly demarcated from the stylar shelf, extends posterolabially from the metacone. Its crest somewhat overhangs its posterior surface. At the metacone it makes a bend of about 45 degrees, and at this position in one specimen there is a distinct carnassial notch as in the University of Kansas specimen of *Palaeoryctes puericensis* (U.K. No. 7748). I do not believe that this difference between the Bison Basin specimens and some other differences that are observable indicate that two species are present. The degree of morphological variation is less than that of, e.g., the Four Mile sample of *Didelphodus absarokae*, and the University of Kansas specimen of *Palaeoryctes puericensis* differs quite as much from the type as these Bison Basin specimens do among themselves. There is a low ecto- cingulum with no accessory cusps. Especially because of the weaker development of the parastylar area, the ectoflexus is less pronounced than it is in *Palaeoryctes puericensis* (but it is similar to that of *P. punctatus*.) The basal enamel limits of both the anterior and posterior sides of the tooth rise sharply just lingual to the level of the paracone, as in *Puercolestes* and various other mammals. The lingual root is transverse; the labial ones are less so. The lingual root extends to about the lingual border of the paracone. There are no interradicular crests.

There are no traces of lingual cingula on P<sup>4</sup>. The protocone is relatively lower than on the molars, and its apex is apparently somewhat more lingual; the apex is not anterior, as on the molars, but central. The protocone extends nearly as far anteriorly as does the parastylar area, an extension that produces a marked concavity in the anterior margin of the tooth, while the postvallum is virtually straight. Unlike the situation in *Palaeoryctes puericensis*

a slight ectoflexus is present. The protocone lobe is even shorter anteroposteriorly than that in *Palaeoryctes puercensis*; its anterior and posterior margins are strictly parallel in occlusal view for most of their extent. The parastyle is larger than that of *Palaeoryctes*, about the size of that of *Puercolestes*. It is a distinct cusp and is connected to the protocone by a weak paracingulum. The meta-cingulum and metacrista are as on the molars. A moderately distinct metacone is present, as in *Puercolestes*; a metacone is absent from later didelphodontines, *Palaeoryctes puercensis*, and *Deltatheridium*. The combined paracone and metacone are longer anteroposteriorly than those of  $M^1$ . There is no stylar area or ectocingulum labial to the paracone, although a weak ectocingulum is present in the metastylar area.

The  $P^4$  differs from that of *Palaeoryctes puercensis* in the following ways: the protocone lobe is wider transversely and extends a little farther forward; the paracone is narrower; the parastyle is larger; an ectoflexus and metacone are present; and the meta-cingulum is larger. It differs from the  $P^4$  of *Puercolestes simpsoni* in having a more transverse and more anterior protocone lobe, a lower protocone, no crest between the protocone and paracone, a larger metacingulum, a more labial metacone, and perhaps a narrower paracone. It is no more similar to that of the Puerco genus B (see below) than it is to that of *Puercolestes*.

There are embrasure pits in the maxilla in front of at least  $P^4$  through  $M^2$ , for the trigonids of the lower teeth in the shearing mode. These pits are pierced by small foramina. The infraorbital foramen is 1.20 mm. high and 0.25 mm. wide. It is immediately dorsal to the space between  $P^3$  and  $P^4$ , as in *Puercolestes*, a little more anterior than in *Palaeoryctes*. Its dorsal border is more anterior than its ventral one. The lacrimal foramen is somewhat higher on the skull, as usual in mammals but not as in *Apternodus*. The infraorbital canal becomes a little more ventral as it continues posteriorly; by  $M^1$  it is separated from the buccal cavity by only a thin lamina of bone. The sphenopalatine artery grooves the maxilla as far anteriorly as  $P^3$ . It does not seem to come from a position internal to the infraorbital canal and certainly

does not run parallel and adjacent to it (see *Didelphodus altidens*).

#### SARCODON MATTHEW AND GRANGER, 1925

The type and only known specimen of *Sarcodon pygmaeus*, A.M.N.H. No. 20427, is a single left upper molar from the Gashato Formation of Mongolia. The parastylar area is broken off, although probably not much more was present originally than is present now. This breakage was not mentioned by the describers, Matthew and Granger (1925); their description and figures are in other respects correct. I believe the tooth is  $M^1$ , although it could conceivably be  $M^2$ . There are no interradicular crests.

*Sarcodon* was compared by Matthew and Granger (1925) to the Limnocyoninae, Proviverrinae, Leptictidae, Borhyaenidae, "Cimolestidae," *Didymoconus*, and the Mustelidae, and tentatively referred to either the Oxyaenoidea or the Borhyaenoidea. Simpson did not mention it in his classification of mammals (1945). The connate paracone and metacone, the transverse shape of the tooth, and the amount of metastylar area with the heavy wear on the metacrista suggest the Oxyaenoidea or the Palaeoryctidae, but these groups are not otherwise known to develop the hypocone that is present here.

*Paracyctes* is the closest genus to *Sarcodon* yet discovered. They are similar in a large number of features, of which the most important are the transverse nature of the tooth, the appression of the paracone and metacone, and the development of a moderately large postcingulum. This combination of features is not present in any other genus of mammals known to me. The similarity supports the identification of the *Sarcodon* tooth as  $M^1$ . The two genera differ, however, in several respects. *Sarcodon* is about one and a half times as large as *Paracyctes*, linearly. Its metacrista is more prolonged and a little more posteriorly directed, while the parastylar area is much reduced. The postcingulum is much larger and bears a distinct hypocone; a precingulum is lacking. The metacingulum is smaller, of normal palaeoryctid size. The metacone is somewhat larger than that of *Paracyctes* and slightly more separate from the hypocone. A well-developed paraconule is

present, larger than is possible in *Pararyctes*; the metaconule is probably also larger.

Except for *Micropternodus* (see below), the closest approach to *Sarcodon* among other genera is by *Gypsonictops* from the late Cretaceous of North America. This similarity may indicate some relationship, but in *Gypsonictops* the paracone and metacone are not so nearly united, the teeth are less transverse and possess interradicular crests, the relative emphasis of parastyle and metastyle is reversed (but not quite so much so as is indicated by fig. 3 of Simpson, 1951; the tip of the metastylar area is broken off A.M.N.H. No. 39595, the M<sup>1</sup> used), and there are other differences. I am inclined to agree with Simpson (1951), McKenna (1960b), and Dale Russell (1960) that *Gypsonictops* is closer to the erinaceids.

The age of the mammalian fauna from the Gashato is uncertain. The multituberculates are very possibly survivors in an ecologically or probably geographically isolated area that had not yet, whatever its age, acquired rodents (the order Rodentia is unknown in all of Asia before the late Eocene), and *Prodinoceras*, as one moderately primitive genus, is really insufficient evidence for adequate dating, particularly in view of the occurrence of *Mongolotherium* and *Haplolambda* in the Eocene of Mongolia. The presence of *Sarcodon* (more specialized than *Pararyctes*) somewhat suggests early Eocene age. The rest of the fauna is too peculiar or too little understood to be useful for correlation.

#### MICROPTERNODUS MATTHEW, 1903

*Micropternodus* shows considerable similarity to *Sarcodon* in both general configuration and details, as was noted by McKenna (1960a) in a discussion of a then unidentified insectivore tooth. Prominent among these similarities are the development of the meta-crista and the general configuration of the hypocone region. *Micropternodus* is an unusual genus in that P<sup>4</sup> is fully zalambdodont (except for the lack of a paracrista), M<sup>1</sup> has a tall paracone and metacone twinned to about the same degree as in *Sarcodon* and more than in *Didelphodus*, and M<sup>2</sup> is a more or less typical dilambdodont tooth. Since *Micropternodus* cannot have descended from both erinaceid-like and palaeoryctid-like close

ancestors,<sup>1</sup> its special similarities to either *Sarcodon* (and *Pararyctes* and *Palaeoryctes*) or *Scenopagus* and *Gypsonictops* (Dale Russell, 1960) must be convergent.

The upper molars of *Geolabis* (see McKenna, 1960b) also show an appression of the paracone and metacone, although without the gradient in its expression present in *Micropternodus*. Since this appression in *Geolabis* is greater than in its earlier relatives *Gypsonictops* and especially *Scenopagus*, probably this protozalambdodont condition evolved in part within the Geolabidinae. Possibly the incipient zalambdodonty of *Micropternodus* was a parallel development within the Erinaceoidea, but, unless the common ancestor of *Micropternodus* and *Geolabis* was protozalambdodont (unlikely because *Scenopagus* is more similar to *Geolabis* than is *Micropternodus*), the closeness of the paracone and metacone does not in itself indicate special relationship.

*Sarcodon*, known from a single upper molar, shows a number of resemblances to the M<sup>1</sup> of *Micropternodus*. The trigon region is transverse. The paracone and metacone are conate for most of their height. A strong meta-crista extends far posterolabially and is heavily worn in the shearing mode. The parastylar area projects slightly forward, but no parastyle is present. There is only a slight ectoflexus. The lingual slope of the paracone and metacone is steeper than the labial slope. The protocone apex is lingual. A precingulum is absent, but a long postcingulum expands from the lingual half of the posterior border of the tooth and bears a hypocone in the form of a rather tall transverse crest on its posterolingual corner. A broad transverse groove separates the hypocone from the trigon.

As pointed out to me by McKenna in conversation and as suggested as a possibility by McDowell (1958), both P<sub>1</sub> and P<sub>2</sub> are present in *Micropternodus* and are single-rooted, in contrast to the interpretations of Matthew

<sup>1</sup> It is possible but doubtful that the dilambdodont Lipotyphla are closer phyletically to the Deltatheridia than to Group M (see p. 55, footnote 1). In any event the latest common ancestor of the first two groups must have been in the Cretaceous, since both groups are known in the Lance and Hell Creek. *Micropternodus* shows similarities to both these groups, but many of these similarities are restricted to one group or the other.

(1903) and Schlaikjer (1933). The alveolus for  $P_1$  is about three times as long and twice as wide as that for  $P_2$ . Normally the posterior root of a lower premolar is longer than the anterior one; this fact is well shown on the next succeeding tooth,  $P_3$ , of *Micropternodus*. This enlargement of  $P_1$  and reduction of  $P_2$  are present also in *Palaeoryctes puericensis*.<sup>1</sup> The short, somewhat narrow, and apparently moderately low talonid (particularly that of  $P_4$ , with the lingual position of the talonid cusp), the excavation in the hypoflexid, the size and almost the entire configuration of  $P_3$ , the degree of the steep rise of the base of the enamel from both sides of the tooth under the paraconid on the molars (a characteristic feature of *Palaeoryctes* and *Pararyctes* but not even of other palaeoryctids), the shallow mandible, a small hump on the anterolingual side of the coronoid process where it meets the horizontal ramus, the fact that the mental foramen is below the anterior part of  $P_3$ , and the many similarities in the upper molars to *Sarcodon* and thence through *Pararyctes* to *Palaeoryctes* all suggest a palaeoryctid ancestry. There are no traces of interradicular crests in the figure of the alveoli of  $P^3$  given by Dale Russell (1960); these crests are characteristic of erinaceoids, among other groups. The large infraorbital foramen close to the

orbit and the depression of the skull are the only important differences from palaeoryctids. I strongly suspect, but am not quite convinced, that *Micropternodus* was derived from a palaeoryctid. If it lacks interradicular crests on the molars I would be convinced, but this character is not now determinable. Saban (1954, 1958) derived *Micropternodus* from *Palaeoryctes*, because he believed it to be zalambdodont and ancestral to *Solenodon*, as Matthew (1919) had suggested. *Clinopternodus* is possibly related to *Micropternodus*, but such relationship is not certain on the basis of the published evidence (Scott and Jepsen, 1936; John Clark, 1937). The very tall talonids of *Clinopternodus* are not in keeping with the usual palaeoryctid occlusion.

#### GENUS B, PUERCO

Plate 7, figures 6–9; table 24

Two  $P_4$ 's and three other specimens from the lower level of the Puerco, collected in 1958 by washing, are pertinent to the present paper. One of the  $P_4$ 's (A.M.N.H. No. 58409) is probably that of a viverravine. It has been described by Mac Intyre (1966) in his revision of the Miacidae. The other (A.M.N.H. No. 59910) is a moderately slender tooth, with only three cusps. The paraconid is rather small but distinct, situated on the anterolingual corner of the tooth. A moderately weak paralophid connects it with the apex of

TABLE 24  
MEASUREMENTS (IN MILLIMETERS) OF TEETH FROM THE PUERCO REFERRED TO GENUS B

	A.M.N.H. No. 59910 $P_4$	A.M.N.H. No. 59896 $P^4$	A.M.N.H. No. 59893 ?M, Upper	A.M.N.H. No. 59901 ?DP <sup>4</sup>
Trigonid width	1.30 ± 0.05	—	—	—
Talonid width	1.30	—	—	—
Crown length	2.55	—	—	—
Lingual height of protoconid	2.50 ± 0.10	—	—	—
Lingual height of paraconid	1.10	—	—	—
Anterior margin	—	2.45 ± 0.05	—	—
Posterior margin	—	3.10 ± 0.15	—	—
Labial margin	—	2.75	—	—
Labial height of paracone	—	2.25 ± 0.10	—	—
Posterior height of protocone	—	—	1.70	1.75 ± 0.05
Length at paraconule	—	—	1.10	1.35 ± 0.05
Horizontal distance of apex of protocone from lingual margin of protocone	—	—	1.10	1.10

<sup>1</sup> In *Palaeoryctes* there is an alveolus for an even larger tooth, which I believe is the canine, just in front of  $P_1$ .

the protoconid; there is a distinct notch on the paralophid between the paraconid and the protoconid. There is no trace of a metaconid. The paraconid is about a third of the lingual height, and about half of the labial height, of the protoconid. There is no anterior cingulum. The anterior surface of the protoconid is somewhat convex in lateral view; the posterior surface is nearly flat. A weak postprotoconid crest terminates ventrally somewhat labial to the midline of the tooth. A notch separates it from the crista obliqua, which continues posterodorsally to the single tall talonid cusp. This cusp is on or slightly labial to the midline of the tooth, is two-fifths or a little more of the labial height of the protoconid, and projects slightly posteriorly. A weak postcristid and entocristid connect it to the ventrolingual corner of the protoconid but do not enclose a distinct basin.

Among the didelphodontines (aside from the virtually unknown  $P_4$  of *Puercolestes*) the closest approach of this tooth is to teeth of *Didelphodus absarokae* and *Avunculus didelphodonti*. It differs from the  $P_4$  of the former in lacking a metaconid and in having a slightly higher paraconid and trigonid; the paraconid is also weaker. It differs from the  $P_4$  of *Avunculus* most importantly in having a lower and weaker paraconid. It differs from the  $P_4$  of *Prolimnocyon atavus* only in having a higher and slightly stronger paraconid (the paraconid is weaker than that of A.M.N.H. No. 16111, but there is some possibility that this specimen is not conspecific with the type of *P. atavus* but a member of the population ancestral to the type of *Sinopa mordax*, if these species are separable). The greater height of the paraconid is the only consistent difference from Wasatchian specimens of *Sinopa*. From early species of *Oxyaena* it differs in having a higher and somewhat stronger paraconid, a lower talonid, and a protoconid that does not lean posteriorly. As all the latter specializations of *Oxyaena* except the height of the talonid are matched in one or more specimens of *Sinopa*, the species to which A.M.N.H. No. 59910 belongs is a possible ancestor for both the Didelphodontinae and the Oxyaenoidea. The small size of the paraconid is perhaps not expected for a primitive didelphodontine, and the height of the paraconid is perhaps unexpected for an

oxyaenoid ancestor, but both these suppositions (particularly the latter) are based on analogies with other groups and may easily be wrong.

The  $P_4$  of *Palaeosinopa veterrima* is in general aspect also similar to that of *Sinopa* and the Puerco specimen under discussion, but differs in several respects. The protoconid is somewhat shorter and stouter and has a distinct posterolabial crest. The talonid cusp is clearly on the lingual half of the tooth, while in the palaeoryctids and oxyaenoids it is labial or occasionally central, in accordance with its shearing function. *Bessoecetor diluculi* is about as similar, but differs from the Puerco specimen in having a larger and lower paraconid, a lower and less slender protoconid, a more lingual and lower talonid cusp, and in various details of crests. Most of these differences are also true for *Oxyclaenus cuspidatus*, which has the most primitive  $P_4$  known in the Arctocyonidae. I know of no other mammalian teeth that need explicit comparison. Thus, although an isolated tooth is insufficient evidence to be conclusive, A.M.N.H. No. 59910 is probably a palaeoryctid and perhaps ancestral to the Oxyaenoidea.

The virtual absence of Paleocene oxyaenoids in North America may be real or it may be due to their being small, scarce, or their having lived in habitats that are not, or are only poorly, represented in the known fossil localities. The fragmentary specimens described in this paper suggest, but emphatically do not prove, that oxyaenoids or their ancestors were present in North America throughout the Paleocene. Even if they were present in North America throughout this time they could have undergone their major evolution elsewhere. For such a possibility there is no positive and little negative evidence.

A.M.N.H. No. 59896 is a  $P^4$  from the Puerco, lacking the protocone (see pl. 7, figs. 8, 9; table 24). A small parastyle is present, but a paracrista is scarcely detectable. The paracone is fairly tall and somewhat longer than wide, with a sharp metacrista that continues into a moderately well-developed metastyle, which is, however, not more than a fourth of the labial length of the tooth. The postvallum is well developed in this region, and there is a notch (V-shaped, not a slit as in

most carnivores) in the metacrista by the paracone. The anterior face of the paracone is less vertical than the posterior face. The protocone was anterolingual to the paracone, but its apex was not so far anterior as the parastyle. The protocone was apparently fairly small and was connected to the base of the paracone by a low median crest. The length of the tooth in the commissure between the paracone and protocone is about half of the labial length. Weak cingula surround the preserved part of the tooth except the labial part of the postvallum. The tooth was about as wide as long when complete.

This P<sup>4</sup> could be pantolestine, miacine, or deltatheridian. Its relative width, small parastyle, short metastylar length, not greatly anterior protocone, lack of a carnassial slit, and the crest between the paracone and protocone, together with the flatness of this commissure area, suggest deltatheridian or possibly pantolestine affinities, but it is impossible to say than an early Paleocene miacine would not also possess these characters. Nevertheless none of these features is found in any miacid known to me, and all are common (but not all are universal) in deltatheridians and to some extent in pantolestines.

The tooth differs from that of either species of *Bessoecetor*, especially in its longer, higher, and more shearing metastyle, but also in the fact that the protocone is smaller, so the postvallum is more transverse; the metacrista has a slight angle at the base of the metacone; the dorsal part of the metacrista is not marked off from the rest of the paracone; the paracone leans more posteriorly; the parastyle is smaller; and the precingulum and especially the postcingulum are less pronounced (in conjunction with shearing adaptations), but the ectocingulum is somewhat larger.

From *Puercolestes simpsoni* the following differences are detectable: the parastyle is somewhat smaller, there is no trace of a metacone, the paracone leans somewhat more posteriorly, the cingula are less developed, and the protocone is apparently less transverse, relatively longer anteroposteriorly, apparently not quite so anterior, and probably smaller. Each of these differences can, however, be matched in other early deltatheridians.

The tooth is not that of an arctocyoniid or other condylarth. It differs from the P<sup>4</sup> of *Oxyclaenus cuspidatus*, the most primitive condylarth in respect to this tooth, in having a much smaller and more anterior protocone, a much smaller parastyle, a more pronounced metacrista, a narrower paracone, a flatter paracone-protocone commissure, and in a number of other features.

This Puerco P<sup>4</sup> probably belongs to the same species as A.M.N.H. No. 59910; this taxon may be referred to as genus (and species) B. It is of a similar size difference from *Puercolestes simpsoni*, being about eight-tenths as long. It is slightly longer than the P<sub>4</sub>, as is usual in deltatheridians. This difference is even more pronounced in miacids, but the P<sup>4</sup> is only seven-tenths as long as the Puerco miacid P<sub>4</sub>. In addition, the Miacinae are not known in any of the numerous Paleocene faunas of North America.

Two fragments of upper molars from the Puerco (A.M.N.H. No. 59893 and A.M.N.H. No. 59901) also probably represent genus B. Both specimens lack the paracone, metacone, and stylar region. There is a slight possibility that they are marsupials or some unrecognized placental, but *Puercolestes* is very similar to them, much more so than any other genus I have examined. They differ from *Puercolestes* and *Nyssodon* as follows, in addition to smaller size: the preprotocrista is scarcely higher than the postprotocrista; the conules may be slightly larger than those in *Puercolestes*, but this situation is variable; and the lingual root is slightly less transverse. In addition, A.M.N.H. No. 59901 is less transverse than any tooth of *Puercolestes*; it is possibly a deciduous tooth (the only respect in which it differs from A.M.N.H. No. 59893).

#### OCCLUSION IN THE PALAEORYCTIDAE

The normal functions of the teeth of mammals can conveniently be grouped into five categories: grasping, piercing, slicing, pounding, and grinding. These names are merely suggestive of the major kinds of functions and are not intended as definitions: thus gnawing is similar to slicing, and munching is a combination of weak pounding and grinding, often with some slicing. (Other functions, such as fur combing for incisors of lemurs and the straining of crustaceans for the cheek teeth of

*Lobodon*, do occur sporadically.) Most evolutionary modifications of the structure of mammalian teeth can be related in some detail to one or more of these functions. Not all are present in all mammals, and different ones are emphasized in different mammals (in some instances also in different ages and different individuals of the same species). It is well known that the primary differentiation of regions of the tooth row, and the various kinds of evolutionary dedifferentiation and redifferentiation that occur, are also related to efficient performance of these functions.

With the exception of *Hyotheridium*, in which there may be a component of slicing, the incisors of palaeoryctids are not known to have any function other than grasping. The canines are moderately large in all known cases except probably *Avunculus*, and presumably retained their usual functions of piercing, grasping, and slicing. The anterior premolars are in several cases reduced and appear to serve only for relatively minor slicing and perhaps grasping. In all palaeoryctids the molars and at least  $P^4$  retain the primitive variety of slicing known as embrasure shear, although this is reduced in *Palaeoryctes*. The posterior teeth in *Palaeoryctes* appear to have had little function other than piercing and presumably preventing the escape of prey. In the other genera pounding and grinding are more or less developed, most so in *Micropternodus*.

In *Palaeoryctes puercensis* the grinding mode (see Didelphodontinae) is not present, but two forms of the shearing mode are. In the first the crista obliqua and anterior hypoconid of the molars occlude against the posterolabial surface of the protocone and the posterior protocrista. There are no other unambiguous indications of wear on the talonid, the postvallid, or the prevallid. At the same time the anterolingual part of the talonid of  $P_4$  meets the posterolabial side of the protocone of  $P^4$ , and the posterior face of the protoconid of  $P_4$  shears more labially against the anterior protocrista of  $P^4$ . In the second form of the shearing mode the anterolingual side of the protoconid of the molars, together with the parolophid and the anterolingual side of the paraconid, occludes past the posterior face of the merged paracone and metacone of  $P^4$ ,  $M^1$ , and  $M^2$ . On  $P^4$  this second occlusion

includes the metacrista also. Since the protocone is somewhat anterior to the paracone and metacone, a simple lateral movement is all that is necessary for the transition between the two forms of occlusion in *Palaeoryctes*. It is tempting to think that one side of the mouth used one form at the same time as the other side used the other form, but there may have been some degree of independent movement of the jaws. Occlusion in *Palaeoryctes* is vertical, without more than a slight transverse component. Certain facets, particularly that on the labial face of the metaconid, are not explicable by crest-on-crest action.

The shearing mode was used exclusively in *Pararyctes* also. In it there were both prevallum and postvallum shear, the latter being of more importance. Some transverse movement took place at the end of a shearing stroke, as indicated by corresponding facets on the paraconid and postcingulum. The labial face of the protocone and the apices of the paracone and metacone are the most heavily worn surfaces of  $P^4$  and the upper molars, apparently because of occlusion at the beginning of a shearing stroke, as indicated by the lower molars. This situation is not greatly removed from the action in a grinding mode. Wear on the largely vertical protolophid suggests some anteroposterior movement. There is no wear from the hypoconid or protoconid on the lingual side of the paracone and metacone. A peculiar fact is the continuation on two of the three specimens of the wear facet on the posterior side of the metacristid, onto the posterior corner of the labial margin of the tooth. This posterolabial continuation is set at an angle to the more normal metacristid facet and probably was not caused by the shearing mode. There is a corresponding facet on the parastylar area. It is probable that, as in horses and various other mammals, movement of adjacent teeth in the same jaw relative to one another causes some wear between them, although this mechanism may not entirely explain these facets in *Pararyctes*.

The occlusion of *Sarcodon* was similar to that of *Pararyctes* as far as determinable, except that postvallum shear was even more pronounced and the wear facet on the metacrista does not continue labially.

In *Micropternodus* the shearing mode is

dominant and perhaps the only mode present in some individuals. Both prevallum and postvallum shear are present, and some transverse movement apparently occurred at the end of a vertical stroke. The type specimen of *Micropternodus borealis* (A.M.N.H. No. 9602), however, shows a deep and broad anteroposterior grooving of the trigonids of the molars that could have been produced only by anteroposterior movement, presumably against the protocone, but not necessarily so. Neither of the figured specimens of upper teeth (Dale Russell, 1960; White, 1954) shows wear facets that correspond to this movement, which may be unique to this specimen, particularly as it shows little evidence of shear. A roughly similar wear is combined with heavy shearing on U.S.N.M. No. 22817 and was probably derived from the early phase of a shearing stroke. The occlusion of *Micropternodus* is generally similar to that of *Sarcodon* and *Pararyctes* but not to that of such primitive erinaceoids as *Gypsonictops* and *Scenopagus*, which have a rather well-developed grinding mode.

A proper occlusal analysis is impossible in the Shabarakh Usu mammals, because wear surfaces are undetectable on their abominably preserved teeth.

The occlusion of *Geolabis* is similar to that of *Micropternodus*, and differs from that of other primitive erinaceoids (including other geolabidines), in apparently lacking the grinding mode. This fact is probably related to its protozalambdodonty, and the situation in other geolabidines is a small piece of additional evidence for the independent evolution of protozalambdodonty in the two genera named. The occlusal analysis given here is based on the skull and jaws described by McKenna (1960b), R.A.M. No. 4514.

Shear was well developed in *Geolabis*, and a facet from the paracone is present on the labial slope of the hypoconid. There was some transverse movement in the shearing mode, producing well-marked hypoconid-protocone and paraconid-hypocone facets on the molars. The protoconid and metaconid of  $P_4$  occluded against the protocone of  $P_4$ . The more anterior premolars are worn with nearly a flat, horizontal surface, suggesting action by food in crushing. But, despite the relatively small size of these premolars, there

is evidence that tooth-on-tooth action was responsible for at least much of this wear. The supernumerary tooth on the left side, which does not occlude with any lower tooth directly, has a wear facet not on its tip but on its anterior face. The maxilla bends down in the region of the anterior premolars, permitting occlusion.

It is of course evident that animals normally have food in their mouths when they chew and that this food is often the immediate cause of wear facets. But the common existence of corresponding wear facets on upper and lower teeth strongly suggests that wear is often directed by pressure, if not always by direct tooth contact, on dental elements that occlude when the mouth is empty.

#### PALAEORYCTIDAE: SYNTHESIS

The three best-known early palaeoryctids are *Puercolestes*, *Palaeoryctes*, and *Deltatheridium*. Each pair of these three has several characteristics in common that are not shared by the third. *Puercolestes* differs from the others in still having a metacone and a fairly pronounced parastyle on  $P^4$ , a less reduced posterolabial area on  $M^3$ , only a low paracrista on the molars (the metacrista was probably larger in *Puercolestes* than as now preserved, as it is broken off on every molar), and a more anterior and somewhat larger infraorbital foramen. *Deltatheridium* is different from the other two in having a wider styler area (i.e., a more lingual paracone and metacone), the metacrista larger than the paracrista, the paraconid on the lower molars larger than the metaconid, reduced premolars (their total length is less than the total length of the molars, contrary to the situation in all other deltatheridians), a more anterior paracone on the molars, a reduced or possibly absent paracingulum, and an enlarged talonid on  $M_3$ , and in lacking a protocone on  $P^4$ . *Palaeoryctes* differs in having an almost fused paracone and metacone, more transverse upper molars, a  $P_1$  that is larger than  $P_2$ , and reduced molar talonids.

*Puercolestes* (together with *Nyssodon* and *Cimolestes*) is both the most primitive and perhaps the oldest known deltatheridian. Since of known genera those referred to the Didelphodontinae most closely approach it in structure, I follow Simpson (1945) in includ-

ing it in that subfamily, but this allocation should not be taken as an argument against its nearly central place in the order.

Although several divergent lines are present in the Palaeoryctidae, only three of them (together with the Didymoconidae: see below) seem at present to warrant taxonomic recognition. These are the Palaeoryctinae, including *Palaeoryctes* and *Pararyctes*; the Micropternodontinae, including *Sarcodon* and *Micropternodus*; and the Deltatheridiinae, including *Deltatheridium* and probably *Hyotheridium*. The Didelphodontinae may be expanded to include the remaining genera.

Separation of the didymoconids from the palaeoryctids at the family level may not be justified but is done pending the revision of this group by J. S. Mellett. He discovered their relation to *Palaeoryctes*. The Didymoconidae seem about as divergent from the Palaeoryctinae and Didelphodontinae as do the Micropternodontinae.

Although the name "Palaeoryctidae" was established later (Simpson, 1931) than the name "Deltatheridiidae" (Gregory and Simpson, 1926), the name "Palaeoryctae" was used at the level of a tribe by Winge (1917), and according to Article 36 of the International Code of Zoological Nomenclature *Palaeoryctes* must therefore be the type genus of any family-group taxon that includes it. The name "Palaeoryctidae" has been used in the present inclusive sense by McDowell (1958), McKenna (1960a), McKenna, in McKenna, Robinson, and Taylor (1962), and Donald E. Russell (1964), i.e., by all authors who have combined the families Palaeoryctidae and Deltatheridiidae.

The family Cimolestidae was established by Marsh (1889). This name was last used in Hay in 1930 (as Cimolestinae) and therefore is the correct name for the family here called Palaeoryctidae. However, the latter name has always been the one used for the present family grouping (*Cimolestes* is so similar to *Puercolestes* that its addition causes no change in the concept of the family). Furthermore, the name "Cimolestidae" (or Cimolestinae) has always referred to a group of supposed and true marsupials. Even in this usage it has been completely replaced in the literature since 1930 by the name "Pediomyinae." For these reasons the International Commission

on Zoological Nomenclature has been requested to suppress the name Cimolestidae, and by Article 80 of the Code the name Palaeoryctidae may be used until any contrary decision is published.

The Deltatheridiinae are best characterized by the presence of only two lower incisors, the first of which is enlarged. This subfamily is not certainly monophyletic, but the grouping is current and possible. *Deltatheroides*, as far as known, shows no special similarity to *Deltatheridium* and *Hyotheridium* and is herein removed to the Didelphodontinae.

The Palaeoryctinae may be defined as palaeoryctids that have a tall trigonid, relatively small talonid, low paraconid, and sharp anterior rise of the base of the enamel on the lower molars; have a strongly connate paracone and metacone on the strongly transverse upper molars; and lack the grinding mode in occlusion.

The Didelphodontinae are a difficult group to define by the method of individually distinctive characters-in-common, since *Acmeodon secans* shares few characters with *Didelphodus absarokae* that are not also shared by *Deltatheridium* or *Palaeoryctes*.<sup>1</sup> The unity of the subfamily is, however, attested by their forming a sequence in the technical sense of Simpson (1961, p. 95), in this case a sequence with branches. An additional difficulty is that certain teeth and part of the mandible are the only parts of the animal known for most of the genera. As I prefer to base definitions on characters that are known in most or all the taxa included in, and of the rank next below, the taxon being defined, such a restriction drastically limits the possible characters. Although probably the best definition at present is one by the method of enumeration, i.e., simply specifying which taxa of lower rank

<sup>1</sup> A partial improvement of this method of definition is the common one of making the definition the intersection of a number of characters, i.e., something is an A if and only if it has all the characteristics a, b, c, d, . . . , even though B and C may each have some of these characteristics also. This type of definition suffers, however, even more than the stricter one in being relatively unlikely to apply to discoveries made in the future, except in the special case in which some of the characteristics define a more inclusive group and the rest of the characteristics are individually distinctive characters-in-common of the group really being defined.

are to be included, I give the following supplementary definition:

As presently known, the Didelphodontinae are palaeoryctids that have an incompletely connate paracone and metacone and a wide stylar shelf on the upper molars, a metaconid on the lower molars that is larger than the paraconid, small lower incisors, a rudimentary postcingulum or none, a grinding mode in occlusion, and in general lack the particular specializations of the other genera of palaeoryctids. *Deltatheroides* fits this definition, as far as is known, and may in fact be a didelphodontine. It is, in any event, here placed in the ancestral, heterogeneous subfamily.

#### SUBFAMILY MICROPTERNODONTINAE

STIRTON AND RENSBERGER, 1964

Since *Sarcodon* appears to be intermediate between ordinary palaeoryctids and *Micropternodus*, these two genera may well be included in the same subfamily. Although *Sarcodon* is more similar to *Pararyctes* than to *Micropternodus*, *Pararyctes* is too close to *Palaeoryctes* to warrant subfamily separation at this time. The Micropternodontinae are palaeoryctids that have an expanded postcingulum with a hypocone. The appression of paracone and metacone on M<sup>1</sup> and the strongly developed postvallum shear on M<sup>1</sup> also distinguish the subfamily from various non-palaeoryctid genera. Stirton and Rensberger (1964) have recently placed *Micropternodus* in a family of its own, Micropternodidae (*sic*), and have argued for a relationship with erinaceoids. The total evidence is ambiguous when the present discussion is added to theirs, and I see no necessity at present to abandon my arrangement in light of their work.

#### FAMILY DIDYMOCONIDAE KRETZOI, 1943

##### MONGOLORYCTES, NEW GENUS

TYPE SPECIES: ?*Hapalodectes auctus* Matthew and Granger (1925b, p. 3).

KNOWN DISTRIBUTION OF *M. auctus*: Late Eocene of Mongolia, Irdin Manha Formation.

DIAGNOSIS: As given by Matthew and Granger (1925b) for ?*Hapalodectes acutus*. Distinguished from *Ardynictis* especially by greater size and more transverse M<sup>1</sup>. (The only known tooth is possibly P<sup>4</sup> or even DP<sup>4</sup>,

but it compares more closely with M<sup>1</sup>, and the same differences are true whatever its homology.)

ILLUSTRATION: The figure in Matthew and Granger (1925b, fig. 2) is correct except for the depiction of the wear facets. (See table 25 of the present paper.)

ETYMOLOGY: Mongolia, and an analogy with *Palaeoryctes*.

TABLE 25

MEASUREMENTS (IN MILLIMETERS) OF THE TYPE SPECIMEN OF *Mongoloryctes auctus* (A.M.N.H. No. 20130), PROBABLY M<sup>1</sup>

Anterior margin	11.7
Posterior margin	14.9 ± 0.3
Labial margin	10.1 ± 0.1
Length at paraconule	5.2
Horizontal distance of protocone apex	
from lingual margin of protocone	4.4 ± 0.3
Posterior height of metacone	7.1 ± 0.2
Posterior height of protocone	7.7 ± 0.1

DISCUSSION: When Matthew and Granger described *M. auctus*, the upper teeth of the peculiar mesonychid genus *Hapalodectes* were unknown, and to my knowledge still are, and reference to the family as well as the genus was only tentative.

The only known specimen (A.M.N.H. No. 20130) is probably not a mesonychid but a derivative of the palaeoryctids. The tooth is quite transverse, with the protocone widely separated from the paracone and metacone, unlike that of any known mesonychid. Reference to the genus *Hapalodectes* is unlikely, since *Hapalodectes* is specialized by having transversely compressed lower teeth which, however, have only the wear facets that are present in other mesonychids: on the apices of the cusps and crests, and occasionally on the anterolabial and posterolabial sides of the tooth.<sup>1</sup> By analogy with the lower teeth of *Palaeoryctes* and *Ardynictis* (see below), those of *Mongoloryctes auctus* would be expected to

<sup>1</sup> This statement is based on an examination of 11 specimens in the American Museum of Natural History and the United States National Museum, in all of which, unlike all other mesonychid species, the wear facets do not or barely do pass through the enamel. In conjunction with the small size and compressed teeth of *Hapalodectes*, this difference seems to indicate food habits different from those of other mesonychids, perhaps a diet mainly of small, soft invertebrates.

have relatively wide and tall trigonids, a condition opposite to that in *Hapalodectes*. There are, however, no wear facets on the specimen (there are solution pits in a number of places), so this condition of the lower teeth cannot be conclusively shown at present. Although *M. auctus* is about the same size as *Propterodon irdinensis*, the roots do not fit the alveoli for the latter, and the specimen shows no or little indication of the specializations (pronounced metacrista, anterior and subangular protocone) that characterize the upper molars of hyaenodontids.

Among Eocene or earlier species the closest resemblance of *Mongoloryctes* is to *Palaeoryctes punctatus*. The only differences detectable from the crushed specimen of the latter species are a somewhat larger and higher metacone, a somewhat narrower stylar area, from which the ectocingulum is virtually absent, and the fact that the paracrista extends anteriorly to the parastyle, not anterolabially to a separate cuspule. Differences from the lingual side of  $M^1$  of *Palaeoryctes puercensis* are less anteroposterior compression, a more distinct protocone, and the fact that the protofossa is concave anteroposteriorly, not convex, between the protocristae.

Differences of *Mongoloryctes* from *Puercolestes* and *Nyssodon* are the following: The labial border of the tooth is more convex, the stylar area is narrower, and the paracrista does not extend to the parastyle. The metacrista is much weaker, and the parastyle is a little more lingual. The conules, paracingulum, and metacingulum are weaker, and the protocone is apparently more distinct. The preprotocrista is not appreciably higher than the postprotocrista.

*Mongoloryctes* is probably descended from a genus close to *Palaeoryctes*, possibly even *Palaeoryctes* itself. It is, however, even more closely related to *Ardynictis*, a matter that will be discussed by James S. Mellett in his review of the Didymoconidae.

#### SUPERFAMILY OXYAENOIDEA (COPE, 1887)

##### FAMILY HYAENODONTIDAE LEIDY, 1869

##### SUBFAMILY HYAENODONTINAE LEIDY, 1869

##### PROTOTOMUS COPE, 1874

The genus *Prototomus* Cope (1874) has as its type species *Prototomus viverrinus*, the type specimen of which originally consisted

of a partial skull with most of the upper dentition and various skeletal fragments. Since a mandible in the same nodule as the skull was not believed by Cope (1877) to pertain to the same genus, the association of the skeletal material is questionable. The diagnostic upper dentition has been lost, according to Gazin (1962), but the figure, measurements, and perfunctory description by Cope (1877), if accurate, are sufficient to eliminate many possibilities. It is from the Wasatchian of the San José Formation of New Mexico.

The identification of the individual teeth is not entirely certain. The second preserved tooth from the front has a distinct but fairly small protocone exactly midway between the anterior and posterior ends of the tooth; this condition is both described and figured. Such a situation is much more common on  $P^3$  than on  $P^4$ , probably because postvallum shear is uncommon on  $P^3$ , but a  $P^4$  generally similar to that of *Prototomus* is present in some moderately advanced proviverrines (*Tritemnodon agilis* and *Propterodon minutus*). As the paracoid of  $M_1$  is normally more anteriorly placed than that of  $M_2$ , if the tooth in question is a  $P^4$  with postvallum shear the protocone should be even more anterior than that of the next posterior tooth. In fact it is considerably more posterior, indicating both by its position and by its lack of a well-developed postvallum that it did not shear against a prevallid.

If this tooth is  $P^3$ , *Prototomus* is either an oxyaenid or a miacid, more probably the latter (G. T. Mac Intyre, in conversation, informs me that Cope, at the time he described *Prototomus*, did not know the  $P^4$  of any miacid). If it is an oxyaenid the meta-stylar area of the tooth then interpreted as  $M^1$  is expanded, and under this supposition the paracone and metacone would be moderately separated, a condition unknown in any oxyaenid. An incipient to small protocone occurs sporadically in the present position on  $P^3$  in various genera of miacids, although it in no case so well developed as in *Prototomus*. Certain species of miacids, e.g., *Miacis exiguus* from the Gray Bull and A.M.N.H. No. 56504, a primitive species of *Oodectes* from the lower Huerfano, have only small lingual cingula on the molars. I have examined the fairly extensive collections from the San José made by Simpson and have found only one

tooth that is possibly (but far from certainly) referable to *Prototomus*. It is an  $M^1$  probably referable to *Miacis*, close to *M. exiguus* but perhaps more primitive. Cope's figure (1877) of the possible  $P^4$  of *Prototomus* is not diagnostically miacid, but it cannot be said to exclude it completely from this family.

*Prototomus* is not a limnocyonine and synonymous with *Prolimnocyon*, as McKenna (1960a) believed. His best specimen (U.C.-M.P. No. 44864) falls within the observed range of variation of *Prolimnocyon atavus*. Although  $M^1$  of *Prototomus* is similar to that of *Prolimnocyon*, and  $M^2$  is also, if the more lingual of the two possible labial borders shown is accepted,  $M^3$  is too wide, and  $P^4$  is much different in its central and relatively small protocone and its apparently central paracone. The shape of the middle of the skull is not diagnostic. *Tritemnodon* and *Sinopa* have a skull generally similar to that of *Limnocyon* and *Thinocyon* in this region; the only difference in shape in the front half of the skull is a somewhat longer rostrum in the proviverrines.

Cope (1877) synonymized *Prototomus* with "*Stypolophus*" (= *Sinopa* and *Tritemnodon*), and he has been followed in this action by almost all subsequent authors (e.g., Matthew, 1901, 1915; Gazin, 1962). This allocation is possible and is in my opinion the most probable one, but it has the difficulty that the metastylar region of  $M^2$  would have to be assumed to have been broken away. That such may have happened is indicated by the allocation of *Prototomus* by Cope and Matthew, the only authors known actually to have seen the specimen. Until comparable upper teeth are found the species is indeterminate; the reference of lower jaws to *P. viverrinus* on the basis of size is indefensible. *Sinopa minor*, from the Bridger, is of about the same size but has a rather different  $P^3$ . In 1963 I submitted a proposal to the International Commission on Zoological Nomenclature to designate as neotype of *P. viverrinus* the mandible figured by Gazin (1962), U.S.N.M. No. 22456.

**PROLIMNOCYON MATTHEW, 1915, AND  
SINOPE LEIDA, 1871**

*Prolimnocyon* and *Sinopa* are quite difficult to distinguish in the Graybullian, and I sus-

pect, as did Denison (1938), that in the Clarkforkian or almost certainly the Tiffanian they were not yet differentiated. The only adequate distinctions are the greater reduction of  $M^3$  and the more anterior labialmost point in the upper molar series in *Prolimnocyon*. As suggested by Butler (1946), this sort of difference could easily have been the result of an anterior or posterior shift in the fields of molarization; it could also be due to independent derivation from a less specialized ancestor (Gazin, 1946). Because of the great structural similarity of the two genera and the importance of postvallum shear in carnivores, I believe the former alternative is more likely. A shift in the anterior rather than the posterior direction is suggested by two lines of argument. First, reduction of  $M^3$  leads in the Limnocyoninae to its loss; as a moderately large  $M^3$  was surely ultimately primitive, a reversal of this important trend would be required if a posterior shift occurred. Second, several species of *Sinopa* (e.g., *S. vulpecula*) have  $M^3$  smaller than  $M^2$ .

*Prolimnocyon robustus* cannot be distinguished (with the scanty material available) from *Sinopa mordax* except by the greater reduction of  $M^3$  in the former; their similarity was noted by McKenna (1960a). It is quite possible that these two forms were conspecific, but such conspecificity cannot be well demonstrated at present. The type of *Sinopa mordax* (A.M.N.H. No. 16157, from the early Gray Bull) is apparently conspecific with A.M.N.H. No. 16155, from the middle Gray Bull, in which  $M^3$  is larger than  $M^2$ . In addition, A.M.N.H. No. 15248, from the middle Gray Bull, and U.C.M.P. No. 43597, from the Four Mile, in both of which  $M^3$  is at least as large as  $M^2$ , are quite possibly conspecific with A.M.N.H. No. 16230, from the Almagre, in which  $M^3$  is of moderate size but smaller than  $M^2$  (about the size of that of *Prolimnocyon robustus*), and with *Prolimnocyon atavus*. There are no clear differences in the structure of  $P^4$  or  $M^2$  ( $M^1$  is absent from the Gray Bull specimen) or in size. The same could also be true of A.M.N.H. No. 17006, from the Gray Bull, which has part of a large  $M^3$ . It is possible but doubtful that U.S.N.M. No. 22456, referred by Gazin (1962) to "*Sinopa viverrina*," is conspecific with these. It is also quite possible that U.S.N.M. No. 1025, the type of

*Sinopa secundaria*, is conspecific with or close to *Prolimnocyon atavus*, but such a conclusion is not provable and will not be until a stratigraphically controlled detailed variation study is made.

Specimens referred by Matthew (1915 and on labels) to *Prolimnocyon atavus* are quite variable in size and structure, but I see no distinct gap in the series, and there is no clear correlation with stratigraphic position, although U.C.M.P. No. 46642, from the Four Mile, is considerably the smallest  $M^1$  (labial length only 5.3 mm.) and U.C.M.P. Nos. 44864 and 47153, also from the Four Mile, are two of the smaller lower jaws (and have relatively large  $M_3$ 's). This range appears to include all characteristics (except perhaps the reduced hypoconulid and the slightly reduced paraconid on  $M_1$ ) of the two teeth ( $P_4$  and  $M_1$ ) preserved of the type specimen of *Protoproviverra palaeonictides*, the earliest European proviverrine. This statement is based on a cast in the American Museum and later examination of the type in Paris. Reduction in size and complexity of  $M_3$  are positively but far from perfectly associated in Wasatchian *Prolimnocyon*.  $M_3$  in *Prolimnocyon robustus* is absolutely and relatively larger, but has a less-developed paraconid and metaconid, than is usual in *Prolimnocyon atavus*. Wasatchian specimens of *Sinopa* are also variable, although probably more than one lineage is involved.

From the evidence given above it is probable that the condition of *Prolimnocyon* (at least in the lower teeth) evolved more than once. *Sinopa* is simply the name given to all primitive American proviverrines (as most used in practice, oxyaenoids with a fairly large  $M_3$  that has a non-vestigial metaconid and talonid), while *Prolimnocyon* is the name given to specimens that would be called *Sinopa* if they had a larger  $M_3$ . Upper teeth provide a better criterion ( $M^2$  and  $M^3$  are recognizable at a glance by their shape) but are much less common. I use these generic names in the accepted sense for the sake of convenience without intending to imply approval of the current generic separation of specimens. A stratigraphically controlled revision of all available specimens (the first step being to determine the number of species present in each local fauna) is greatly needed.

The teeth in *Prolimnocyon* appear to have about the same relation to the skull as in *Sinopa*, as far as can be determined: the orbit extends to about the anterior part of  $M^1$  in both genera. The posterolateral border of the palate is more anterior in *Prolimnocyon*, but this is apparently also more anterior in relation to the orbit, so does not indicate a change in tooth position. The anterior position of the posterolateral border of the palate results merely from the reduction of  $M^3$ . Therefore there is a change from *Sinopa* to *Prolimnocyon* in the moment distribution of lever action in the jaw movement, in relation to the mean point of application of shear. Butler (1946) has pointed out that all early oxyaenoids had more than one tooth in which the shearing function was accentuated. There is a rather strong positive association in all the subfamilies of oxyaenoids between the degree of specialization for shearing and restriction of this specialization to fewer teeth. This association is true also for the ancestral family Palaeoryctidae, in which all the posterior cheek teeth were used for shearing but none is particularly specialized for this function. A forward shift in the mean shear would at first place it farther from the fulcrum of mandibular movement and thus permit greater speed in slicing with the same application of force. Conceivably this shift could in some cases more than offset adaptively the loss in power resulting from it.

This kind of argument should not be used to indicate adaptive differences between, e.g., the proviverrines, the limnocyonines, and the miacids, each of which emphasized a different pair of teeth as the main carnassials. Adaptive differences were undoubtedly present between different species<sup>1</sup> and quite possibly between most or all members of the three lineages considered, but the difference in

<sup>1</sup> Because population control of these sizable mammals could not well have been entirely by (1) direct effects of weather when refuges are absent or equally available to each species, (2) different predators or parasites for each species, (3) the same predators or parasites but for which the probability of attack on a species varies with the relative frequency of this species, or (4) decrease of reproduction or increase of mortality when at high conspecific densities but not when competing species are at high densities (if indeed any species is completely controlled by these factors indefinitely), competitive exclusion operated in some form.

carnassials does not give more than vaguely suggestive evidence on this point. Although it is quite possible (but far from certain) that the same carnassial lever system would be optimal for all selection operates on the entire animal, not just on one aspect independently of the rest. Therefore a species or group less well adapted in one way than another species or group may nevertheless replace the latter because it is better adapted in other ways, or coexist because of niche differentiation and the threshold difficulty of expanding into an already occupied niche. For example, we cannot validly say without direct investigation that the marsupial reproductive system (or dental formula or any other character) is poorer than that of placentals, although this may nevertheless be true; all that we can say is that most marsupials are adaptively inferior to most placentals.

The type of *Prolimnocyon elisabethae* is not much different in size from the type of *P. antiquus*, a nearly edentulous jaw (see Gazin, 1962). Since both are from beds of Lostcabinian age I suspect that these names refer to the same species. The depth of jaw, as well as tooth length and relative tooth width, is rather variable in Lostcabinian specimens of *Prolimnocyon* and these characters do not vary entirely concordantly. There are, at least to some degree, gradations and intermediates in all three characters even in the few specimens now available. But in the present chaotic state of the systematics of *Prolimnocyon* and *Sinopa*, I prefer not to make any formal changes. Contrary to the statement of Gazin (1952), a paraconid is in some cases well developed on the lower premolars of *Prolimnocyon atavus* (e.g., in A.M.N.H. No. 16111). The variation present in the Gray Bull in this character and in tooth width could easily have continued into Lostcabinian time.

What is probably a left DP<sup>4</sup> of *Prolimnocyon atavus* is represented by U.C.M.P. No. 44772A, from the Four Mile (pl. 7, figs. 10 and 11). The roots are missing. It differs from M<sup>1</sup> especially in being less transverse (the labial length is about 6.1 mm., the anterior border only 5.0 mm.), particularly in the lingual lobe. The metacingulum is weak, and the lingual cingula are virtually absent. The paracone and metacone are a little less con-

nate. There is some wear from the apices of all the cusps and some shear on the metacrista, but there is little or no anterior shear and none on the lingual side of the paracone and metacone.

#### EUROPEAN PROVIVERRINI

Despite the existence of most of a skull and much of the dentition, *Proviverra* is a poorly known genus. There is only one species certainly referable to it (see below), *P. typica* from the middle Eocene of Egerkingen. The only figures of it known to me are the careless, partly unrecognizable, and partly inconsistent ones given by Rüttimeyer (1862, 1891). The brief descriptions do not add much information. Schlosser (1887) referred to this species a mandibular fragment with M<sub>2-3</sub>, from the Phosphorites, but it is not clear that this specimen is closely related to the specimens from Egerkingen (cf. Schlosser, 1911, p. 76, footnote, and Martin, 1906, p. 420). This specimen may not even be a hyaenodontid.

Lemoine (1880; 1891, p. 272; and perhaps also in 1881 in the Bulletin of the Société d'Histoire Naturelle de Reims, the relevant volume of which is not available in England or North America) described a species from the early Eocene, *Proviverra palaeonictides*, that he referred to the same genus. In 1891 (p. 265 only, not elsewhere in the paper) he gave this species a second name, *P. pomeli*, based on the same specimen, and referred both to a new genus, *Protoproviverra*. Teilhard (1921) used the invalid synonym *P. pomeli* and abandoned the questionable genus *Protoproviverra*. A specimen of *Protoproviverra* in the collection of P. Louis, Reims, has M<sub>2</sub> and M<sub>3</sub> preserved. These teeth are similar in size and structure, thus eliminating the possibility that *Protoproviverra* was a limnocyonine. *Protoproviverra* is surely congeneric with at least many American Wasatchian specimens of *Sinopa*, but the pertinence of these specimens to *Sinopa* is not established beyond reasonable doubt.

The type of *P. palaeonictides* (M.N.H.N. No. AL-5155) consists of a fragment of mandible with P<sub>4</sub> and M<sub>1</sub>. A P<sub>3</sub> of a different individual is associated, but this tooth is only doubtfully conspecific. The P<sub>4</sub> is nearly unworn. On the M<sub>1</sub> the protoconid is worn moderately, from the apex, as is the meta-

conid to a lesser extent. The paraconid is worn from the apex and somewhat anterolabially. There is moderate wear on the basolabial surface of the hypoflexid; a separate facet, presumably from the metaconid, is present basoposterolabially from the hypoconid. There is a slight truncating wear on the hypoconid. The hypoconulid is moderately worn or else broken. There is slight shear on the prevallid and postvallid.

Scott (1892) named a maxillary fragment with  $P^3$  and  $P^4$ , from the Bridger, *Proviverra americanus*. It had previously been described by Osborn, Scott, and Speir (1878) and referred to Leidy's species *Sinopa rapax*. The type of *P. americana* has recently been found in the Princeton collection and numbered as P.U. No. 17888. It is an artiodactyl. The lack of any indication of a shearing metacrista on  $P^4$  and the heavy wear on the prevallum of this tooth are features unknown to me in any carnivorous mammal except to a slight degree in *Deltatherium* (if *Deltatherium* was particularly carnivorous, as I doubt).

A genus *Galethylax*, with the species *G. blainvillei*, from the Phosphorites (Gypse de Bicêtre) is said (e.g., Trouessart, 1897) to have been established by Gervais in 1850; I have not seen this publication. On pages 220 and 221 of the second edition of the same book (1859) Gervais figured this species and placed it among the carnivores. Subsequent authors have considered it close to *Proviverra* for reasons (other than its apparent primitiveness) not indicated. Piveteau (1935) referred it to *Cynohyaenodon*, also without justifying this placement.

The type of *G. blainvillei*, now in Paris, is a partial right mandible. Only the lingual surface and most of the dorsal surface are visible; the remainder is still embedded in matrix. The horizontal ramus and the lower part of the ascending ramus are preserved, as are  $I_3$ , C,  $P_{1-2}$ ,  $P_4$  (much broken), and  $M_1$  (root only). The dental formula was

$$I_3^?, C_1^?, P_4^?, M_3^?,$$

showing that the specimen is not a marsupial. The molar talonids were apparently about as wide as the trigonids. The alveoli of  $M_3$  are about the size of those of  $M_{1-2}$  (and those of  $P_{2-4}$ ), except that they are slightly narrower. No structure is visible on  $P_4$  because of the

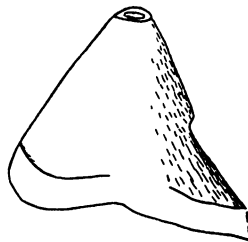


FIG. 13. *Galethylax blainvillei*, lingual view of right  $P_2$  of type specimen. The dotted line represents a broken edge.  $\times 6$ .

breakage.  $P_2$  is the most posterior tooth for which the structure can be determined (fig. 13). It is a simple tooth, except for the presence of a weak but distinct metaconid halfway down the posterior crest of the protoconid.  $P_1$  is only slightly shorter than  $P_2$ , but its height is only about half as great. Its structure is similar except that the weak metaconid is absent. The canine is scarcely taller than  $P_2$ . Because of the complete emergence of  $M_3$ , it is improbable that the deciduous dentition is present. Therefore these characters must be ascribed to the permanent teeth. The alveolar length of  $M_{1-3}$  is  $13.5 \pm 0.1$  mm. (approximate 95% confidence interval), and of  $P_{1-4}$   $17.8 \pm 0.3$  mm. The length of the preserved part of  $P_2$  is 5.2 mm. The distance from the posterior edge of the alveolus for  $M_3$  to the posterior edge of the condyle (which is about at the occlusal plane) is  $19.3 \pm 2.0$  mm.

The presence of weak metaconid on  $P_2$  and the small size of the canine are characters sufficiently unexpected in a hyaenodontid (although not in a palaeoryctid) that the reference of *Galethylax* to the Hyaenodontidae is called into question. I cannot, however, determine its correct allocation. A comprehensive faunal and biostratigraphic study of the Phosphorites is much needed.

The genus *Pseudosinopa* was established by Depéret (1917) for a proviverrine from Egerkingen referred by Rüttimeyer (1891) to *Stypolophus*. *Pseudosinopa* is not clearly distinct from *Cynohyaenodon*, but a presumptive case for their synonymy does not yet exist.

In 1891 Rüttimeyer described a new genus and species, *Prorhyaena* (not "*Prorhizaena*") *egerkingiae*, from the middle Eocene of Swit-

zerland. Apparently on the basis of Rüttimeyer's comparison with *Suricata*, Matthew (1909) believed *Prorhyzaena* had reduced premolars and a short face. There is no published evidence for this statement; the character of even the preserved and figured  $P^4$  is uncertain. *Prorhyzaena* appears to be closest to *Palaeosinopa* and *Pantolestes* but may well be at least generically distinct. It apparently differs from proviverrines (if the figure is reasonably accurate) in having a labial paracone and metacone and a more posterior protocone on the molars and a smaller protocone on  $P^4$ . As its name implies, *Palaeosinopa* was also referred to the Proviverrinae when first described (Matthew, 1901). Martin (1906, p. 417) referred *Prorhyzaena* to *Cynohyaenodon* for unknown reasons.

Matthes (1952) established four new genera of Proviverrinae from the middle Eocene of Geiseltal: *Prodissopsalis*, *Imperatoria*, *Leonhardtina*, and *Geiselotherium*. The first two of these are definitely proviverrines, and *Geiselotherium* is probably referable to this group (cf. also Matthes, 1954). *Prodissopsalis* and *Imperatoria* may justifiably be regarded as synonyms until they are shown to be different.

Without exception the genera mentioned above have never been adequately figured. The only European proviverrine genera that are really identifiable from published information are *Cynohyaenodon*, *Quercitherium* (the only proviverrine genus surely not a senior or junior synonym), and to a large extent *Paracynohyaenodon*. (As figured by Martin, 1906, *Paracynohyaenodon* differs from *Cynohyaenodon* especially in its larger  $M_3$  and smaller molar metaconids, both of which differences are in the direction of the Hyaenodontini.) In this chaotic situation no revisionary work can be done until the genera are better known. It is very probable that some, possibly even most, of the described genera of proviverrines are invalid. *Galethylax*, *Geiselotherium*, and *Prorhyzaena* may not even be referable to the Proviverrini. *Cynohyaenodon* resembles the American genus *Tritemnodon* and should perhaps not be separated from it (but on the other hand Schlosser in 1923 synonymized *Cynohyaenodon* with *Proviverra*). The same is true of *Protoproviverra* and possibly *Proviverra* (cf. Teil-

hard, 1921) with the *Sinopa-Prolimnocyon* complex (see above).

#### QUERCITHERIUM FILHOL, 1882

*Quercitherium* is a proviverrine that has greatly enlarged, crushing premolars and relatively small molars. As with *Apternodus*, such an anterior position of crushing teeth seems rather inefficient. An analysis of muscular forces like that of Maynard Smith and Savage (1959) could be illuminating for both these genera. In each of these genera, shear was retained on the molars. In primitive placentals the premolars have little shear; most of their wear is often from the apex (cf. discussion of *Geolabis* with *Micropternodus*). Therefore, if crushing and slicing were both important, the premolars rather than the more efficient molars would be expected to be the teeth modified for crushing. Other explanations are, however, possible.

The following additions can be made to the description of the basicranium by Piveteau (1935). There is no clear indication of a promontory artery, although there is a large middle lacerate foramen, and a shallow longitudinal depression is present on the middle of the promontorium. A stapedial artery was probably present, as indicated by a moderately large foramen in the mesotympanic fossa lateral to the middle lacerate foramen. A groove between the fenestra rotunda and the fenestra ovalis may have carried the stapedial artery. A deep groove between the fenestra rotunda and the jugular foramen, apparently going into the latter, may also have partly housed the stapedial artery; it probably also carried the tympanic and perhaps the auricular nerves. A groove from the anterolateral part of the tympanic fossa toward the posterior foramen of the alisphenoid canal may have been formed by an inferior ramus of the stapedial artery. A vidian foramen is present in the postero-medial end of the pterygoid ridge. A moderately large foramen, just medial to the middle of the promontorium, undoubtedly carried the medial entocarotid artery. A tympanic (and possibly entotympanic) bulla was probably present, as indicated by an articular surface on the basioccipital and the fact that the promontorium is sunken.

**METASINOPA** OSBORN, 1909, AND  
**PROPTERODON** MARTIN, 1906

*Metasinopa* is on almost the same grade of carnassial specialization as *Pterodon* and is apparently closely related to it. *Sinopa aethiopica* Andrews (1906) is clearly referable to *Metasinopa*; it differs from *M. fraasi* only in being smaller and probably in having a larger metaconid (see Schlosser, 1911). These two species probably form a phyletic series; the former is from the lower, and the latter from the upper, Fluvio-marine Beds. A relationship to *Paracynohyaenodon* (not certainly separable on the generic level) is also indicated.

*Propterodon* Martin (1906, p. 455) was originally based on an unnamed fragmentary mandible with one broken tooth, figured by Rüttimeyer (1892). The type species of *Propterodon* is *P. irdinensis* Matthew and Granger (1925b) by Article 69 (a) (ii) (2) of the International Code of Zoological Nomenclature. *Hyaenodon minutus* Douglass is probably congeneric with *Propterodon irdinensis*, if an upper jaw (A.M.N.H. No. 9623; cf. Matthew, 1903) is correctly referred to this species, and may be placed provisionally in *Propterodon*. The specimen figured by Rüttimeyer is doubtfully distinct from *Pterodon*, as this genus is now delimited.

The species of *Pterodon* and *Hyaenodon*, especially those of the Old World, badly need revision, as do the species of *Thinocyon*, but this is beyond the scope of the present paper. M. C. McKenna (in McKenna, Robinson, and Taylor, 1962) has discovered that the type of *Entomodon comptus* Marsh (1872), Y.P.M. No. 13506, is referable to *Thinocyon*.

**SUBFAMILY LIMNOCYONINAE** WORTMAN, 1902

**THEREUTHERIUM** FILHOL, 1877

Piveteau (1935) figured a skull of the European limnocyonine *Thereutherium* in which the lateral branches of the internal carotid are restored (the promontory artery, which is unusually medial for a limnocyonine, enters the skull through the middle lacerate foramen), but there is no visible evidence of a medial entocarotid. This situation, if it were actually the case, would be unique in the Deltatheridia. Although Matthew (1909) could not find evidence for the presence of

a medial entocarotid in *Thinocyon velox*, he noted its presence in *T. medius* and believed it was present in both species. Slight additional preparation in *T. velox* (A.M.N.H. No. 13081) has disclosed a groove for it on the medial side of the promontorium, as in *T. medius*, *Didelphodus*, and other genera, which passes into a carotid foramen at the anteromedial corner of the promontorium.

I have examined the figured skull of *Thereutherium* in Paris and present the following remarks supplementary to those of Piveteau (1935). There is a distinct groove, deep and fairly broad, between the promontorium and the basioccipital and grooving both, as does the smaller groove in *Palaeoryctes*. This groove leads into the carotid foramen at the anteromedial corner of the promontorium and presumably carried a large medial entocarotid artery. A groove for the vidian artery and nerve extends anteromedially from the carotid foramen to the vidian foramen, which is slightly medial to the pterygoid crest. There is no definite indication of a ramus inferior of the stapedial artery, although it could have passed through the unusually large groove for the chorda tympani and the auriculotemporalis nerve. A moderately small foramen anteromedial to the foramen stylomastoideum primitivum and anterior to the fenestra rotunda presumably carried the superior ramus of the stapedial artery.

A foramen in the anterior margin of the jugular foramen presumably contained the inferior petrosal sinus. This fact is positive evidence that this sinus did not occupy the groove interpreted as for the medial entocarotid. A wide, shallow groove extends laterally from the jugular foramen, narrowing laterally and passing over the fenestra rotunda. It may have carried the auricular nerve or nothing at all. A minute tunnel extends laterally from the border of the jugular foramen, posterior to the fenestra rotunda; its lateral entrance is underhung by a small flange of bone. This tunnel is perhaps a more likely site for the auricular nerve, or it may have housed the tympanic nerve (a branch of the glossopharyngeal, and therefore emerging from the jugular foramen more anteriorly than the auricular nerve). A tunnel extending from the lateral margin of the

jugular foramen into the vestibule presumably carried the cochlear aqueduct.

A moderately large epitympanic recess is present just lateral to the foramen stylomastoideum primitivum. The mastoid is exposed laterally for all its length, but the exposure is narrow vertically. There is no trace of an attachment for a bulla.<sup>1</sup>

**?*Oxyaenodon wortmani*, new species**

TYPE: A.M.N.H. 1893, fragment of mandible.

HORIZON: Uinta B, Utah.

DIAGNOSIS: Differing from *O. dysodus* by having alveolar length from the posterior end of the canine through  $M_3$  54 mm.

DISCUSSION: In June, 1899, Wortman described as a new genus and species, *Oxyaenodon dysodus* from the Uinta C. However, in March of 1899 Matthew had published the same name in a faunal list of the Uinta, with the following footnote: "Unpublished. See Osborn, Bull. Am. Mus. Nat. Hist., 1896, fig. 3 (*Hyaenodon*)." Although it is clear from the word "unpublished" that Matthew had no intention of establishing a new name, this is in itself insufficient under the International Code of Zoological Nomenclature to debar him from authorship. However, I believe it is clear that the reference to Osborn's figure was intended only to show the general aspect of the form in a paper already published and that this essentially edentulous mandibular fragment was not intended as the type. Since Matthew knew of Wortman's name, he surely knew of the previously collected skull and jaws that Wortman used for a type three months later. It is therefore apparent that Matthew's name was intended as a synonym of Wortman's, and therefore is not available by Article 11 (d) of the Code.

This situation is particularly unfortunate in that the specimens mentioned by Matthew and Wortman are different in size, and Hay (1902) proposed the name *Oxyaenodon dysclerus* for Wortman's species. Although to my

knowledge only Wortman has used *O. dysodus* in the sense of Wortman since that time, I believe this usage is correct. *Oxyaenodon dysclerus* is therefore an objective synonym of *O. dysodus* Wortman. A new name is required for the species represented by Osborn's figure, whether or not Wortman's and Matthew's species are distinct, by Article 60 of the Code, which does not permit discretion to be used in such cases. Although A.M.N.H. No. 1893 is inadequate as a type specimen and I would prefer to leave this doubtful species nameless at present, I follow Article 60 and give it a name. Its generic reference is uncertain (cf. Peterson, 1919), although most probably the species belongs to *Oxyaenodon*. It is probably but not certainly specifically distinct from *O. dysodus* Wortman. A.M.N.H. No. 1894, from the Uinta B, contains an isolated trigonid that is the size of A.M.N.H. No. 1893 and is apparently better referable to *Oxyaenodon* than to *Limnocyon*.

**FAMILY OXYAENIDAE COPE, 1887**

It is sometimes difficult to distinguish an isolated tooth of an oxyaenine from one of *Sinopa* or *Prolimnocyon*. I present the following discussion partly as an aid to such identification and partly as background for the succeeding discussion of occlusion, which also gives characters that may be useful for identification. Comparison of a large number of specimens, particularly of *Sinopa*, is necessary to appreciate the variation within each group.

On the  $P_4$  of *Oxyaena* the lingual height of the talonid (i.e., the hypoconid) is more than half of the lingual height of the protoconid from the base of the enamel, and the width of the tooth is at least half of its length. In *Dipsalidictides*, *Sinopa*, and *Prolimnocyon* the hypoconid is less than half of the lingual height of the protoconid, and the width of the tooth is usually not more than half of its length (it is slightly more in one specimen of "*Sinopa shoshoniensis*," A.M.N.H. No. 15747). Apparently all other characters overlap. Even the convexity of the anterior surface of the protoconid is no more in the type of *Oxyaena gulo* than in a specimen of "*Sinopa multicuspis*" (A.M.N.H. No. 16156).

I do not detect any consistent differences

<sup>1</sup> In both *Thinocyon medius* (A.M.N.H. No. 12154) and *T. velox* (A.M.N.H. No. 13081) a flat depression in the petrosal in the place of the remaining bulla fragment of *Palaeoryctes* suggests the presence of at least a cartilaginous bulla in *Thinocyon*. The depression is not for the promontory artery, which occupied a more lateral, rounded groove.

on  $M_1$  and  $M_2$ , but the hypoconid is lower than the entoconid in *Oxyaena* and usually higher in *Sinopa* and *Prolimnocyon*. In the  $M_2$  of *Dipsalidictides* the hypoconid is markedly lower than the entoconid; the hypoconid is completely worn away on  $M_1$ .

The mandible is shorter and deeper anteriorly in oxyaenids, with a greater reduction of the anterior premolars. The depth of the mandible at the anterior end of  $P_2$  is more than the distance from the anterior end of  $P_2$  to the posterior end of  $P_3$  in oxyaenids and less than this distance in *Sinopa* and *Prolimnocyon*.

In *Oxyaena* and *Dipsalidictides* the metacrista of  $P^4$  is both more than a third of the labial length of the tooth and clearly more than half of the labial height of the paracone. In *Sinopa* and *Prolimnocyon* the metacrista is less than a third of the labial length of  $P^4$  and is less than or equal to half of the labial height of the paracone; the parastyle is also usually smaller than in oxyaenids.

On  $M^1$  the angle of the anterior and labial margins of the tooth at the parastyle tends to be sharper in *Sinopa*, *Prolimnocyon*, and *Dipsalidictides* than in *Oxyaena*, and the paracone and metacone are transversely wider, and usually more connate, in *Oxyaena* than in *Prolimnocyon* and *Sinopa*. In *Dipsalidictides* the paracone and metacone are relatively tall and connate but also relatively narrow. The lingual cingula are not less than half of the height of the protocone in *Oxyaena*, not more than half of the protocone height in *Sinopa* and *Prolimnocyon*. The precingulum and postcingulum of *Dipsalidictides* are less than half of the protocone height, but the commissure between them is higher. The height of the metacrista above the base of the tooth is distinctly less than that of the protocone in *Prolimnocyon* and especially *Sinopa*, but more than the height of the protocone in *Oxyaena*, although in this genus they may be almost the same. In *Dipsalidictides* the situation is uncertain, but more probably than not similar to that of *Oxyaena*.

The best distinction in  $M^1$  between *Oxyaena* and the early hyaenodontids is the angle that the metacrista makes with a line joining the paracone and metacone, in occlusal view. This angle, which I call angle

Q, has a good but not perfect correlation with the degree of carnassial specialization of a single molar, although this degree of specialization of the entire tooth can, I think, be estimated only subjectively. A functionally analogous relationship holds for fissipeds (cf. Crusafont-Pairó and Truyols-Santonja, 1956). In the Proviverrini (except *Dissopsalis*) angle Q varies from 115 degrees to 130 degrees on  $M^1$ ; in *Prolimnocyon*, from 125 to 130 degrees; and in *Oxyaena*, from 135 to 150 degrees. In *Dipsalidictides* it is scarcely more than 120 degrees, and in *Palaeonictis*, despite the much-reduced metacrista, the angle is about 140 degrees. Angle Q in palaeoryctids is at least as sharp as in proviverrines, and the later members of each oxyaenoid lineage have more obtuse angles than the earlier ones.

In figure 14, angle Q is plotted against the labial length of the tooth for  $M^1$  of various oxyaenoids. All measurements were made from actual specimens. The trend seen in each group may in part be due to independent but concurrent evolution of a greater angle and larger size, but such is not true in all cases, and there may be a greater functional need for more efficient shear in larger animals than in smaller ones. It is not true for the proviverrines and most hyaenodontines that a single tooth with a high angle Q tends to predominate in the shearing and is enlarged, although such is more or less true for the other oxyaenoids.

The wear surfaces in *Oxyaena*, *Prolimnocyon*, and most Graybullian *Sinopa* show that both prevallum shear and postvallum shear were important, with a slight tendency for the latter kind to predominate. In addition, oxyaenids have a usually somewhat less-important shearing surface, which acts as the hypoconid and crista obliqua sweep by the centrocrista. This centrocrista shear is particularly well developed in *Palaeonictis*. The oxyaenids thus obtained a shortcut to the functionally advantageous, scissors-like, anteroposterior shear. *Sinopa* and *Prolimnocyon*, but not *Oxyaena*, also commonly show a truncation of the cusps of the trigon and trigonid caused by a retention of the grinding mode. The grinding mode is nearly absent from oxyaenids, or quite so, its place being taken by crushing from the protocone-

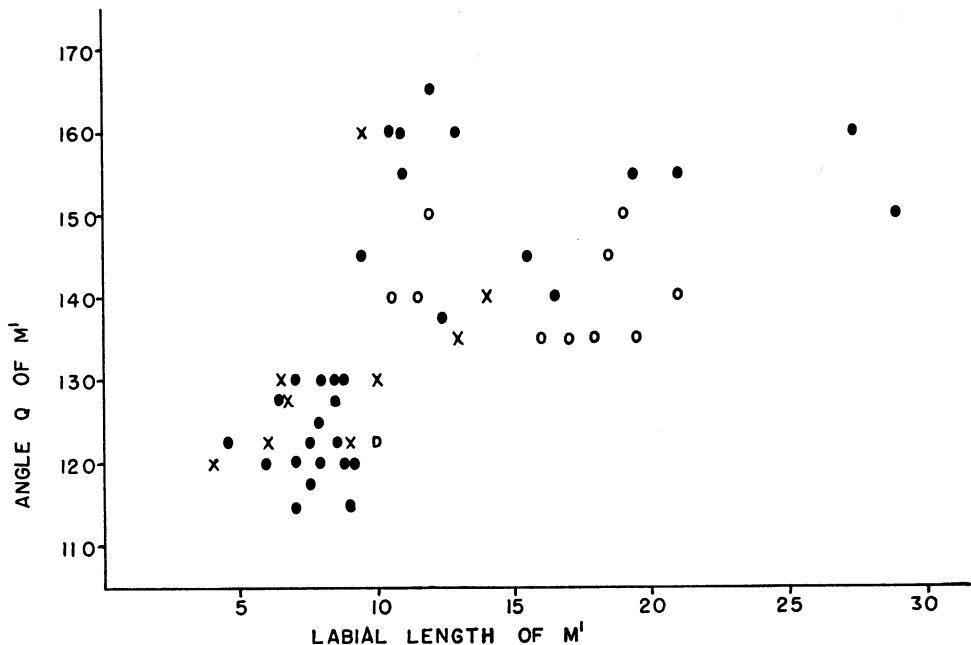


FIG. 14. Scatter diagram of angle Q (defined in text) and labial length (in millimeters) of  $M^1$  of various oxyaenoids except the Palaeonictinae. Each point represents one specimen. All specimens in the American Museum for which both measurements could be taken were used, and also *Dipsalidictides* from Princeton. Solid circles represent Hyaenodontinae; crosses represent Limnocyoninae; D represents *Dipsalidictides*; and open circles represent other Oxyaeninae.

postfossid and protofossa-hypoconid opposition in the shearing mode. The development of a preglenoid process in the Oxyaenidae permits much less propalinal movement of the mandible than in the Hyaenodontidae, from which a preglenoid process is absent, and this fact adequately accounts on the behavioral level for the difference in wear. For an excellent introduction to the mechanics of mammalian jaw movement, see Maynard Smith and Savage (1959).

These functional considerations provide an explanation for some of the differences between the Oxyaenidae and the other oxyaenoids. The relative height and connateness of the paracone and metacone are related both to their lingual shear in the oxyaenids and to their use in the grinding mode in the hyaenodontids. The relative reduction of the protocone in oxyaenids (and later members of the other groups) is related to the abandonment of the grinding mode, the protocone region serving mainly as a stop and to a slight degree as a part of the prevallum and post-

vallum. The higher metacrista and the greater angle between the metacrista and centrocrista in most oxyaenids are undoubtedly related to an evolutionary increase in the importance of postvallum shear, although this has not yet become greatly predominant. There is a good positive relation in carnivores, although not a perfect one, between the relative importance of postvallum shear as determined by wear facets and the degree to which the postvallum and prevallid of the carnassial teeth have become longitudinally placed. The hypoconid of  $P_4$  is high in oxyaenids presumably because of its shearing function. It is possible that the relative lowness of the hypoconid on the molars in this family is related to the fact that the protocone is lower on the occluding upper tooth and the entoconid must occlude on its lingual side to produce an efficient crushing.

The Oxyaeninae are the only group of oxyaenoids (except for the rare machaerodontines) that may have failed to reach Europe (but see *Argillotherium*). As noted by

Denison (1938), *Paroxyaena* is very probably a palaeonictine, and figures 17b and 17c of Teilhard (1927), labeled "Oxyénidé," are apparently premolars of *Palaeonictis*. *Sarkastodon*, however, shows that the Oxyaeninae did reach Asia in the late Eocene.

#### DIPSALIDICTIDES DENISON, 1938

In addition to the features mentioned in the comparison of *Oxyaena* with *Sinopa* and *Prolimnocyon*, there are other features of some importance in a determination of the affinities of *Dipsalidictides*. The angle between the anterior and posterior tooth borders of  $M^1$  is only 30 degrees, less than that in any other oxyaenid. The angle of inclination of  $P^4$  and  $M^1$  is similar to that of *Oxyaena gulo*. The lower jaw is even shorter than that of *O. platypus* and about as deep proportionally.  $P_1$  is two-rooted and pushed labially by the canine. The enamel is somewhat crinkled, but this feature is not well developed. There are deep notches in the maxilla above the embrasures, to receive the trigonids.

$P_4$  is quite similar to that of the type of *Sinopa mordax* and especially to A.M.N.H. No. 15747, the same or another species of *Sinopa*. The greatest difference is that in *Dipsalidictides* the anterior face of the protoconid is more vertical, as in early species of *Oxyaena*, especially *O. aequidens*. The tooth differs from that of *O. platypus* particularly in having a lower talonid (as in *Sinopa* and *Prolimnocyon*). It differs from  $P_4$  of *O. aequidens* in this feature and in having the paraconid a little more medial (as in *O. platypus*) and not marked off from the protoconid by a notch (a similarity to A.M.N.H. No. 15747), a much smaller anterolabial bulge of the protoconid (and of the talonid), the anterior face of the protoconid somewhat more vertical, and the cingula slightly less pronounced, and in being somewhat narrower.

$M_2$  is most similar to that of *Oxyaena aequidens*, but differs from it in that the paraconid is more anterior and a little smaller and at least the metaconid is relatively higher.

The prevalla are heavily worn on  $P^4$ ,  $M^1$ , and  $M^2$ . Except for the postvallum of  $M^1$  the postvalla are not worn so heavily. There is also considerable wear in the protofossa and

on the lingual side of the paracone and metacone; the apices of the cusps are not truncated. This is the typical oxyaenid wear pattern.

*Dipsalidictides* is nearly as distinct from *Oxyaena* as are the Palaeonictinae, but it should be kept in the primitive subfamily Oxyaeninae.

#### OXYAENA COPE, 1874

I can detect no structural difference between *Oxyaena gulo* and the type of *O. transiens*. The distinctions mentioned by Matthew (1915) that are observable appear to be due to breakage of the type of *O. transiens*. Since the types of these species come from different levels in the Gray Bull and differ in size more than is known to occur at any one level, *O. transiens* may be retained provisionally as a primitive subspecies of *O. gulo*.

A second specimen of *O. platypus* from the Clark Fork is available (A.M.N.H. No. 18667), consisting of a complete left  $P_4$  and some trigonids. The  $P_4$ , incomplete in the type, is generally similar to that of *O. gulo* but relatively a little taller and with a slightly shorter talonid. The paralophid and paraconid are also slightly more lingual, a presumably primitive character which is also found in the lineage of *O. aequidens* and *O. intermedia*. The specimen is a little larger than the type of *O. platypus*, in fact about as large as the type of *O. gulo transiens*, its length being 10.7 mm., but there is no reason to doubt its being conspecific with the type of *O. platypus*. I accept Denison's views (1938) on the interrelations of the species of *Oxyaena*.

The earliest known specimen of an oxyaenid consists of a left  $P^4$  and  $M^1$ , both incomplete, from the Tiffany just north of Mason Pocket, near Ignacio, Colorado. The specimen is A.M.N.H. No. 55499. It is about the size of, perhaps even a little larger than, the type of *Oxyaena gulo*, and is clearly a member of the genus *Oxyaena*.

The enamel is somewhat wrinkled vertically, although not nearly so much so as in the Eocene *O. gulo* and *O. intermedia* lineages. In other respects the specimen is very similar to *O. gulo* and *O. intermedia*, but a few differences from each exist. The meta-

TABLE 26  
MEASUREMENTS (IN MILLIMETERS) OF UPPER  
TEETH OF *Oxyaena simpsoni* AND  
Cf. *Oxyaena*, Sp. B

	<i>Oxyaena simpsoni</i> A.M.N.H. No. 48538		Cf. <i>Oxyaena</i> , Sp. B A.M.N.H. No. 48539
	P <sup>4</sup>	M <sup>1</sup>	M <sup>1</sup>
Anterior margin	—	—	6.85 ± 0.50
Posterior margin	—	—	8.40 ± 0.50
Labial margin	13.2	—	7.70 ± 0.10
Tooth width	8.3	11.1	—
Posterior height of metacone	—	—	4.75
Posterior height of protocone	—	—	3.30 ± 0.10

style and the protocone lobe of P<sup>4</sup> meet at a broadly obtuse angle as in *O. gulo*, not nearly or quite at a right angle as in *O. intermedia*. Also as in *O. gulo*, the base of the furrow on the labial face of P<sup>4</sup> between the paracone and the metastyle is more posterior than in *O. intermedia*. The protocone lobe of P<sup>4</sup> is smaller than in either Eocene species; the postprotocrista is smaller, as in *O. gulo*. The flatness of the lingual and labial faces of the metastyle of P<sup>4</sup>, and the relative largeness of the P<sup>4</sup> metastyle, are more suggestive of *O. intermedia*.

The M<sup>1</sup> of the Tiffanian specimen is similar to that of *O. intermedia* and different from that of *O. gulo* in having a relatively flat labial surface on the metastyle. The lingual cingulum is slightly smaller. No other differences from either species are detectable.

The differences of the Tiffanian specimen from *O. intermedia* are probably primitive features in *Oxyaena*; for this reason and because of its size the specimen may be considered as belonging to a species nearly or quite ancestral to *O. intermedia*. *Oxyaena aequidens*, from the Clark Fork, is probably directly ancestral to *O. intermedia* (Denison, 1938); it is probable that the Tiffanian specimen represents the previously unknown upper teeth of this species. The size of A.M.N.H. No. 55499 is appropriate for the upper dentition of *O. aequidens*.

### *Oxyaena simpsoni*, new species

Plate 8, figure 1; table 26

TYPE: A.M.N.H. No. 48538, left P<sup>4</sup>-M<sup>1</sup>.

KNOWN DISTRIBUTION: Early Eocene; "150 Quarry," San José Formation, near Lindrith, New Mexico, and Four Mile Fauna, Moffat County, Colorado.

ETYMOLOGY: After G. G. Simpson, who was in charge of the expedition that found the type specimen.

DIAGNOSIS AND DISCUSSION: *Oxyaena simpsoni* is about the size of a small specimen of *O. gulo*, but differs from the latter more than the latter differs from its contemporary *O. intermedia*. The parastyle on M<sup>1</sup> is smaller than in *O. gulo*, but on P<sup>4</sup> it is longer, more demarcated, and relatively taller, but less wide. The ectocingulum is also less well developed on M<sup>1</sup>; it is even discontinuous for a short distance. The metastylar area is narrower on P<sup>4</sup>. It is, however, the protocone region that is most different. On both P<sup>4</sup> and M<sup>1</sup>, but especially on P<sup>4</sup>, this lingual spur is markedly narrower transversely and somewhat shorter anteroposteriorly. The anterior and posterior walls are parallel on P<sup>4</sup>, perpendicular to the labial margin of the tooth and producing deep concavities in the anterior and posterior margins of the tooth, even more pronounced than in *O. intermedia*. M<sup>1</sup> differs from that of *O. gulo* in the same way but not so strikingly. There is no precingulum or postcingulum on either tooth, although a scarcely detectable bump is in the position of each on M<sup>1</sup>. The paracingulum and meta-cingulum are less developed on P<sup>4</sup> than in *O. gulo*; at least the metacingulum is absent from M<sup>1</sup>. The minute irregular vertical wrinkling of the enamel that is present on every other described oxyaenid species is virtually absent from *O. simpsoni*. A specimen from the Four Mile (U.C.M.P. No. 46698) is also referable to *O. simpsoni*. It consists of the posterolabial half of a left M<sup>1</sup> and shows that the metacrista curves somewhat labially. There are no known lower teeth referable to this species.

The relationships of *O. simpsoni* are obscure. It does not approach *Dipsalidictides*, and is apparently not ancestral to any later species despite its advanced character. It stands as the most divergent member of its genus.

Cf. *Oxyaena*, sp. B

Plate 8, figure 2; table 26

A second, undescribed species perhaps referable to *Oxyaena* is represented by a left M<sup>1</sup> (A.M.N.H. No. 48539), also from the San José. A fragment of an upper premolar accompanying the molar is not certainly the same species.

This tooth approaches that of the Proviverrini and of the Limnocyonini more than the M<sup>1</sup> of any other oxyaenid except that of *Dipsalidictides*, yet it is not similar to the latter and can be placed tentatively in the genus *Oxyaena*, although a new genus may be necessary for it when it is better known. It is the smallest oxyaenid known, being about the size of *Prolimnocyon atavus*. As do *O. simpsoni* and a majority of early hyaenodontids, it lacks any crinkling of the enamel. The parastyle projects anteriorly more than usual in oxyaenids, and it is nearly in front of the paracone, not more labial as is usual in *Oxyaena*. Both these characteristics are found with a greater or less frequency in *Prolimnocyon* and *Sinopa*. As in *O. simpsoni*, the cingula are reduced: the ectocingulum is not continuous, and there is no trace whatever of a precingulum or a postcingulum. However, the angle between the metacrista and centro-crista is even larger than in other oxyaenids, being about 155 degrees. The paracone and metacone are also completely connate to the height usual in *Oxyaena* and are slightly taller than in *Prolimnocyon*; the metacrista is little taller than the protocone. The lingual angle between the anterior and posterior borders of the tooth is about 65 degrees, markedly greater than the 40 degrees to 50 degrees found in other oxyaenids and even greater than is present in any of the smaller limnocyonines or proviverrines that I have measured. There is a possibility that this is a milk tooth, but I doubt that it is because of the well-developed and unseparated roots and the height of the crown. It is too small to be a DP<sup>4</sup> of any known Eocene oxyaenid. There is a slight possibility that it is a proviverrine or limnocyonine paralleling *Oxyaena* in certain respects, but in the absence of further material I prefer to regard it as an *Oxyaena* (sp. B) that retains a number of primitive features but has become divergently specialized in

some other respects. The wear pattern supports this view, for there is some shear on the lingual side of the paracone and metacone and no wear facet on the apex of the metacone (the apex of the paracone is broken off).

#### **PATRIOFELIS LEIDY, 1870**

The skull of *Patriofelis ulta* described by Gazin (1957) gives some information on the vascular system of the posterior region of the head. It is the only reported skull of an oxyaenid that retains the promontorium. A large medial entocarotid artery was present, as noted by Gazin and earlier writers. In addition, grooves on the promontorium indicate the presence of both a promontory artery and a stapedial artery. The promontory artery separated from the stapedial on the lateral side of the promontorium, about midway between the fenestra rotunda and the anterior border of the promontorium. It continued anterodorsally to the anterolateral corner of the promontorium, where the groove disappears and the artery presumably continued anteromedially through a broken area and dorsally into the braincase. The stapedial artery passed well in front of the fenestra rotunda, over the ventralmost surface of the promontorium, to the point where it gave rise to the promontory artery. It then made a 90-degree bend and continued posterodorsally toward the fenestra ovalis. A prominent foramen lateral to the fenestra ovalis, at the end of the deep groove for the chorda tympani, probably was the entrance to the skull of a ramus superior of the stapedial artery in addition to the chorda tympani, which was much too small to fill it. The facial nerve entered the skull just posterior to this foramen, so did not pass through it. A broad, shallow groove leading anteriorly from the tympanic fossa, medial to the Glaserian fissure, perhaps housed a ramus inferior of the stapedial artery. This groove is directed toward the posterior opening of the alisphenoid canal. Whether the internal maxillary artery was supplied by the external carotid, the stapedial, or both is therefore not known.

Gazin (1957) mentioned the large foramen and one smaller foramen or possibly two smaller foramina in the posterior region of the parietal. These provided access to the trans-

verse sinus for the veins draining the large temporal muscles. The transverse sinus presumably gave rise to the sigmoid sinus, which passed as usual through the jugular foramen, after joining the inferior petrosal sinus to become the internal jugular vein. A major anastomotic branch of the internal jugular vein, however, left it immediately after its emergence from the jugular foramen and passed into an enlarged hypoglossal canal. An endocast of this canal is present bilaterally. Upon reaching or nearing the braincase again, more posteriorly and medially, this vein merged with an equally large, more dorsal vein also coming from the region of the jugular foramen. This latter vein is presumably the condyloid vein, an additional branch of the sigmoid sinus. The occipital sinus formed by the merger of these two large veins was directed toward the foramen magnum, as shown by an endocast, and would soon become the longitudinal vertebral sinus. The temporal sinus emerged at least mainly through a large postglenoid foramen. A basically similar venous drainage has very recently been described for *Pterodon* by Guth (1962; see also Reinhard, Miller, and Evans, 1962).

#### DIPSALODON JEPSEN, 1930

Fragmentary upper teeth apparently belonging to *Dipsalodon matthewi* are included in A.M.N.H. No. 16068, a specimen from the Clark Fork beds north of Ralston, Wyoming. This specimen was mentioned by Denison (1938) but was inadequately described. The identifiable teeth represented are labial fragments and the roots of  $M^1$ , a complete but badly worn  $P^4$ , two fragmentary canines (jaw uncertain but the size of those of the type of *D. matthewi*), and also a fragment of  $P_2$  in a partial ramus. The root of a canine of *Pachyaena* (recognizable by size, thinness of root, concavity of posterior surface, and relatively great length of the closed root) is also included in the specimen.

$P^4$  of *Dipsalodon* is relatively somewhat wider than that of *Palaeonictis*; the lingual lobe is more transverse. The parastyle is apparently even shorter than in *Palaeonictis*. The paracone is tilted posteriorly more strongly than that of *Palaeonictis* and is not so convex labially. The ectocingulum is

higher on the tooth. The roots are stronger than in *Palaeonictis*, and there is less interradicular space. The enamel of the entire occlusal and lingual surfaces of the tooth is worn away except for a small amount on the lingual side of the protocone. Distinct grooves formed by the protoconid and hypoconid of  $P^4$  and the protoconid of  $M^1$  are visible, the groove from the hypoconid ending in a small pit excavated in the protofossa.

As in *Palaeonictis*,  $M^1$  is not so transverse as  $P^4$ ; apparently in *Dipsalodon*  $M^1$  as well as  $P^4$  had a more transverse lingual lobe than in *Palaeonictis*. The metacrista is stronger than in *Palaeonictis*, occupying most of the area occlusal to the posterolabial root, which is distinctly anteroposteriorly elongated instead of about equidimensional as in *Palaeonictis*. The metastyle lacks a labial cuspule that is present in *Palaeonictis*. The labial grooves anterior and posterior to the metacone are somewhat weaker than in *Palaeonictis*, and the ectocingulum is higher. As on  $P^4$  the enamel is worn off the occlusolingual surface, and there are clear grooves produced by the protoconid and hypoconid of  $M^1$  and the protoconid and even the paraconid of  $M_2$ .

#### ARGILLOTHERIUM DAVIES, 1884

*Argillotherium toliapicum*, from the early Eocene of the London clay, was named by Davies (1884) because the only specimen (B.M. No. 35688) was too imperfect to be referred to any known group. I have re-examined this specimen and find it not so extraordinary as described.

The specimen is virtually uncrushed and consists of parts of the following, none of which is complete: right and left maxillae, the right maxilla with several alveoli; right and left palatines; postnarial trough; and the parietals at the anterior end of the sagittal crest. In addition there are pieces of bone, possibly continuous with these but now covered with plaster, between the separated fragments.

The infraorbital foramen was over the middle of the third cheek tooth, and the orbit extended to a position over the fourth. The anterior part of the sagittal crest is moderately low; the postorbital ridges are of moderate height.

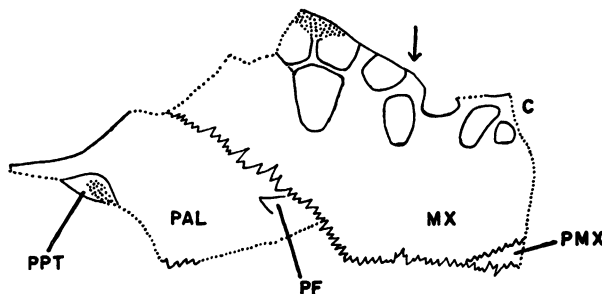


FIG. 15. Incomplete right half of palate of *Argillotherium toliapicum*, B.M. No. 35688. The arrow shows the position of the infraorbital foramen. Dotted lines and areas indicate broken edges and surfaces.  $\times 1$ .

Abbreviations: C, alveolus for (possibly deciduous) canine; MX, maxilla; PAL, palatine; PF, postpalatine foramen; PMX, surface of maxilla underlapped by premaxilla; PPT, broken lateral edge of postpalatine torus.

The most characteristic region of the specimen is shown in figure 15. There are possibly one or two more postpalatine foramina than the one figured, but they are much smaller and possibly due to disturbance at some time after death. Alveoli for five teeth are present. The alveolus of the canine would emerge immediately in front of the broken edge of the specimen. As shown by its more basal part, it is moderately large; it extends to a point about over the anterior root of the third cheek tooth, and considerably higher than the infraorbital foramen. The first two alveoli for cheek teeth probably represent different teeth, as shown by the sharpness of the ridge between them. The first is considerably smaller than the second. The next three alveoli belonged to one tooth, as shown by the low, rounded, and unsurfaced borders between them.

The homologies of the alveoli for the cheek teeth are somewhat questionable. Davies (1884) implied that the third cheek tooth was  $P^4$  and the fourth  $M^1$ , and also that the first two represented  $P^3$ . He failed to note the canine alveolus. I suspect, however, that the teeth represented by alveoli were all deciduous. The sutures show no tendency to fusion, the alveoli for single teeth are rather widely separated, and the tooth row is short. A considerable span is present between the most posterior alveoli and the closest reasonable approach of the posterior end of the palate, and I suspect that one or more molars were

about to erupt here. If an erupted tooth was actually present posterior to the fourth cheek tooth, it would not be at all similar to this fourth tooth but would be small and considerably posterior to it. The lingual edges of the alveoli for the third and fourth cheek teeth are raised somewhat, but the basins between them are shallow. A similar basin is present posterior to the fourth cheek tooth, with its posterior edge raised, but no alveolus is yet open behind it. If the fourth cheek tooth were  $M^1$ , then  $P^4$  (or  $DP^4$ ) would be remarkably close to the canine.

The features of the specimen suggest only carnivorous placentals, among early Eocene mammals, as Davies proposed. The short face, crowded premolars, and absence of diastemata suggest the Oxyaenidae. The lingual extension of the lingual root on the third cheek tooth suggests the Oxyaeninae rather than the Palaeonictinae; if so, this is the first European record of the Oxyaeninae, but the evidence is not conclusive. If correctly referable to the Oxyaenidae, *Argillotherium* is the first known oxyaenid with a one-rooted  $DP^2$  (and presumably also  $P^2$ ). It is otherwise not certainly distinct from *Oxyaena*, but should not be referred to this genus without further evidence.

The alveolar length of the third and fourth cheek teeth combined is  $24 \pm 1$  mm. (95% confidence interval), the distance between the posterior end of the canine alveolus and the posterior end of the alveoli of the fourth cheek

tooth is  $35 \pm 2$  mm., and the height of the infraorbital foramen is 8 mm.

#### FRAGMENTARY PALEOCENE SPECIMENS

A specimen from the Tiffanian of Bear Creek, Montana (A.M.N.H. No. 22220; pl. 8, figs. 4, 5), is probably referable to the *Deltatheridia*. It is an unworn left lower molar, probably  $M_1$ , from which the posterolingual edge of the talonid has been broken away. It is very similar to that of *Prolimnocyon atavus* but differs in several respects in addition to being a little smaller (tooth length, 3.40 mm.). It lacks the weak medial convexity of the protoconid, the paraconid is slightly lower and less developed posterolingually (there is even a weak concavity there), the hypoconid is a little higher, the crista obliqua is not quite so oblique, and the talonid is apparently slightly shorter. Its differences from *Sinopa* are similar to those from *Prolimnocyon atavus*, except that the relative hypoconid height may be equaled or exceeded in *Sinopa* (e.g., A.M.N.H. No. 15606, type of *S. vulpecula*, and A.M.N.H. No. 18670, species uncertain) and the shape of the lingual surface of the protoconid may be similar (A.M.N.H. No. 16155, species uncertain).

From *Protoproviverra palaeonictides* (= *Proviverra pomeli*) the Bear Creek specimen differs (in addition to being of somewhat smaller size) in that it lacks the weak medial convexity of the protoconid, the paraconid is slightly higher but has a weak posterolingual concavity, and the trigonid and hypoconid are a little higher.

All the differences from *Prolimnocyon atavus* can be matched in *Avunculus didelphodonti*. The specimen may be a didelphodontine related to *Avunculus* or *Didelphodus*, but I suspect it is at least as closely related to the ancestry of at least the hyaenodontids. It has well-developed roots, indicating that it is probably not a milk tooth. In addition to having a lower and somewhat more labial hypoconid, the tooth differs strikingly from that of *Avunculus* and all other palaeoryctids in the anterior position of the paraconid, produced by a shift of the prevallid to a more anteroposterior direction. This difference is the main one in the lower teeth of primitive hyaenodontids from those of the palaeoryc-

tids. It is perhaps of interest that *Cimolestes* apparently has a slightly more anterior paraconid on  $M_1$  than later didelphodontines; the paraconid of  $M_1$  of *Deltatheridium* is nearly as anterior as that of the Bear Creek tooth. The high hypoconid suggests that the Bear Creek specimen is closer to the hyaenodontids than to the oxyaenids.

The Bear Creek specimen differs from Paleocene viverravines as follows: it has a higher hypoconid, a lower entocristid, and a more separate and more squat paraconid; the shape of the lingual face of the protoconid is different; and the apex of the paraconid does not project forward in lingual view. Its differences from primitive miacines are generally similar, but the resemblance is even less.

The three following specimens from the Dragon are of interest in this connection:

U.S.N.M. No. 15763, a broken  $P_4$  apparently referable to a species of *Goniacodon*, has a talonid remarkably like that of the type of *Sinopa mordax* in occlusal view. The resemblance is less in other views, however, and is less marked when other specimens of *Sinopa* and *Prolimnocyon* are considered. If my identification of this tooth is correct it appears to preclude it from any relationship to the Hyaenodontidae, as other features of the Triisodontinae and of *Goniacodon* in particular do not support a relationship. Neither of the following teeth is at all similar to the corresponding ones of *Goniacodon*.

U.S.N.M. Field No. 5-39, a trigonid of a right  $M_1$  with the top of the protoconid broken away (trigonid width,  $3.0 \pm 0.2$  mm.), is identical with the sample of *Prolimnocyon atavus* with these small exceptions: the lingual part of the prefossid does not drop so steeply to the lingual margin of the tooth, and the paraconid is slightly lower and less developed lingually, with a slight concavity posterolingually. Everything else, including the wear facets and even size, is identical. Most of these differences are also present in *Protoproviverra palaeonictides*. As far as can be determined from a good cast, the only difference of the Dragon trigonid from that of *P. palaeonictides* is its slight posterolingual concavity of the paraconid. There is a vague possibility that this Dragon tooth is from a miacid, but both G. T. Mac Intyre and I doubt it.

This Dragon trigonid is similar to that of the Bear Creek specimen (A.M.N.H. No.

22220) but differs (in addition to being larger) as follows: the paraconid has a larger postero-lingual concavity, the lingual part of the prefossid does not drop so steeply to the lingual margin of the tooth, and a weak medial convexity of the protoconid is apparently present.

A third specimen from the Dragon (U.S.N.M. No. 15774; pl. 8, fig. 3) is an upper premolariform tooth, 4.45 mm. in labial length. The tops of all four cusps are broken off at about the same level, but it is clear that the paracone was much the tallest. A small metacone may have been present, but there is no evidence on this point. Immediately posterior to the paracone and partly connate to it is a metastyle of moderate size; these two cusps are joined by a sharp metacrista that extends up each. A parastyle a little smaller than the metastyle occupies the anterolabial corner of the tooth. It is concave on its entire posterolingual surface, which is bounded by two weak but distinct crests. The more labial of these crests (possibly the paracrista) reaches the paracone and does not extend up it. The more lingual crest soon fades out against the anterior base of the paracone. A moderately large protocone is present, a little wider than the paracone, with its apex two-fifths of the length of the tooth from the rear of the tooth. The apex is well on the labial side of the protocone. Its steep labial face is directed posterolabially, so that the preprotocrista meets (or at least nearly meets) the paracone. The postprotocrista extends to the metastyle. Small cingula are present sporadically around the tooth, but a precingulum and a postcingulum are scarcely detectable.

The tall and sharp preprotocrista, the anterolabial position of the protocone apex, and the expanded styler regions suggest that U.S.N.M. No. 15774 is a  $P^3$  or  $DP^3$  of *Acmeodon*. Cracks which may represent the borders of alveoli occur in A.M.N.H. No. 4063 in just the same positions on the site of  $P^3$  as the roots in the Dragon specimen.

## OTHER ORDERS

### FAMILY MESONYCHIDAE COPE, 1885

**APTERODON** FISCHER, 1880, AND  
**DASYURODON** ANDREAE, 1887

The genus *Apterodon* contains five species. Three of these, *A. macrognathus* (Andrews),

*A. altidens* Schlosser (1911), and *A. minutus* Schlosser (1911), are from the Fayum, Egypt. *Apterodon minutus* differs from at least *A. macrognathus*, in addition to being of smaller size, at least in having a more vertical anterior border of the coronoid process and less vertical postvallids of the lower molars. It may be referable to *Metasinopa*, but I do not now take this step. The type species of *Apterodon*, *A. gaudryi* Fischer (1880), which is from the French Phosphorites and which has never been figured or thoroughly described, is probably congeneric with the two larger Fayum species. *Apterodon flonheimensis* (Andreae, 1887), from the early middle Oligocene of Germany, is the type species of the genus *Dasyurodon*. *Dasyurodon* cannot be maintained as distinct from *Apterodon* on present knowledge, and the two larger Fayum species of *Apterodon* are surely congeneric with *Dasyurodon*. ?*Apterodon minutus* is similar to *A. flonheimensis* in the slope of its postvallids.

The relationships of *Apterodon* are questionable. It has some similarities to *Quercitherium* (for this genus, see Filhol, 1892; also Martin, 1906; and Piveteau, 1935), but the latter genus is both differently specialized and at least as old. Specifically, *Quercitherium* is differently specialized in the relatively enormous  $P^2$ , the enlargement of the metacone on the upper molars, the reduced  $M^3$ , the well-developed metaconids and small talonids on the lower molars, the bulbous nature of all the upper premolars, and the relatively anterior position of the infraorbital foramen. It therefore seems best to regard the similarities of these two genera as parallel or convergent, *Quercitherium* having evolved toward crushing teeth from slicing ones and *Apterodon* having evolved independently in one direction or the other, depending on its ancestry.

S. B. McDowell (in conversation) has suggested that *Apterodon* is a mesonychid. Cope at one time (1881, p. 1018) made *Apterodon* a synonym of *Mesonyx*, Winge (1923) included it in his Mesonychini (although as a primitive member and related to *Sinopa*), and Gromova (1952) thought it similar to mesonychids.

Similarities to at least some hyaenodontids but not to known mesonychids are the following: a relatively long basicranial region, the lack of an alisphenoid canal, the virtual loss of the protocone on  $P^4$ , and the vertical pro-

toconids and low or absent talonids of the lower premolars.

*Apterodon* has several similarities to at least some mesonychids but not to known hyaenodontids: there is a relatively short snout as compared with the skull length, there is relatively little divergence of the tooth rows, there is a well-developed preglenoid process, the palatine extends anteriorly only to the level of the junction of  $P^4$  and  $M^1$ , the jugular and carotid foramina are apparently joined, the masseteric fossa is shallow, the masseteric ridge does not continue below the top of the horizontal ramus, the distance from the posterior border of the lower canine to the posterior border of  $M_3$  is less than the length of the mandible posterior to  $M_3$ , and the talonids of the lower molars are both unbasined and relatively long. In one, or usually both, of the species of *Apterodon* in which upper teeth are known, there are constrictions in the anterior and posterior margins of the upper molars so that the protocone is a distinct lobe, the parastyle on the molars is relatively large, the height of the protocones of the molars is relatively great as compared with the paracones, the protocones of the molars are massive, the protocone lobes of the molars lack conules, and the posterior upper premolars are taller than the molars. The heavy wear of the molars, produced mainly by the grinding mode, is also much more characteristic of mesonychids than of hyaenodontids.

There does not seem to be a postglenoid foramen in *Apterodon*; a probable small foramen in this region is the right size and in the right place to carry the chorda tympani. A postglenoid foramen is present in hyaenodontids, in which it is lateral to the chorda tympani, and absent from most mesonychids (at least *Mesonyx*, *Harpagolestes*, *Synoplotherium*, and *Pachyaena*), but a minute one is present bilaterally in a specimen (A.M.N.H. No. 3359) of the middle Paleocene species *Dissacus navajovius*, and it is present in the Triisodontinae and other arctocyonids.

The following similarities of *Apterodon* to *Hyaenodon* also occur in mesonychids: the inflated junction of the basisphenoid and basioccipital, the high sagittal crest and flaring occiput, the posterior extension of the secondary palate by fusion and appression of

the pterygoid crests (in mesonychids approached only in *Harpagolestes*, and not to this extent), the fact that  $I^3$  is the largest upper incisor, the fact that the stylar shelf is absent from the upper molars, the absence of the metaconid from the lower molars, the fact that the paraconid is anterior on the lower molars, and many other characters. The metacrista on the upper molars is larger than in any mesonychid and smaller than in any hyaenodontid.

The weight of the foregoing evidence somewhat favors a mesonychid origin for *Apterodon*, but, as no known mesonychids approach it closely in structure, its reference to that family must be only tentative.

#### SUPERFAMILY ERINACEOIDEA

BONAPARTE, 1838

#### OPISTHOPSALIS, HYRACOLESTES, AND PRAOLESTES

As far as the single specimens known of *Opisthopsalis* and *Hyracolestes*, from the Gashato of Mongolia, are preserved, there are almost no generic distinctions between them. Matthew and Granger (1925c) misidentified the  $P_4$  of *Hyracolestes* as  $M_1$ . Matthew, Granger, and Simpson (1929) repeated this error, and made the same misidentification for *Praolestes*, the only specimen of which contains  $P_3$ ,  $P_4$ , and  $M_1$ . The entoconid is absent from  $P_4$  and  $M_1$  of *Hyracolestes* and present in *Opisthopsalis* (*Praolestes* is intermediate in this character but not in some others), and the posterior root of  $M_2$  is posteriorly directed in *Hyracolestes*, a fact that suggests that  $M_3$  is absent (it is enlarged, almost carnassial, in *Opisthopsalis*), but the specimens are too fragmentary, crushed, and distorted for much more to be determined.

The  $P_4$  of *Opisthopsalis* is submolariform.<sup>1</sup> It is generally similar to that of *Prodiacodon*, but differs especially in having a smaller talonid. The paraconids of the molars are larger (but cf. A.M.N.H. No. 35295), as is all of  $M_3$ . An even closer similarity is found,

<sup>1</sup> It is less worn than  $M_1$ , but this criterion, although valid in the present case, is not completely sound, as has been emphasized by Murphy (1959a, 1959b). It is not particularly uncommon in brachyodont mammals for  $M_2^2$  to be more worn than  $M_1^1$ , or  $M_3^3$  more than  $M_2^2$ , and in one specimen (*Oxycbaenus cuspidatus*, A.M.N.H. No. 16350)  $M^1$  is the least worn molar and  $M^3$  is the most worn.

however, to *Leptacodon* (*sensu stricto*; cf. McKenna, 1960a) and *Centetodon* (see Robinson, in McKenna, Robinson, and Taylor, 1962), and provisional reference of *Opisthopsalis*, *Hyracolestes*, and *Praolestes* to the Erinaceoidea is indicated. The similarities to *Prodiacodon* are probably indicative of the origin of erinaceoids from a leptictid-like ancestor (cf. also *Gypsonictops*). It is, nevertheless, possible that some or all of these Gashato genera are leptictids paralleling early erinaceoids in some respects. *Hyracolestes* is similar to A.M.N.H. No. 35288, from the middle Paleocene of Gidley Quarry, Montana, which is a *Centetodon*-like erinaceoid. The conclusions in this paragraph apply with equal force to *Xenacodon*, from the Tiffany of Colorado. The molar paraconids and  $P_4$  of this genus suggest that it was derived from *Gypsonictops* and is related but not ancestral to *Centetodon*. *Xenacodon* is probably ancestral to *Creotarsus*.

#### OTHER GENERA

#### CRYPTOPITHECUS, KOPIDODON, KOCHICTIS, AND DYSPTERNA

The history of the first two of these genera is complex. Schlosser (1887, pl. 4, figs. 55, 60, and 62) figured a mandible with  $M_1$  and  $M_2$ , from the probable late Eocene of the "Bohnerz von Heudorf" (= Frohnstetten), which he designated as "*Microchoerus*, *Heterohyus*?" In 1890 (p. 65) he made this specimen the type of a new genus and species, *Cryptopithecus sideroolithicus*, which he referred to the Primates, family Pseudolemuridae, near *Hyopsodus*. In 1902 he placed *Cryptopithecus* near *Pelycodus*. Also in 1902 Wittich described a species from the brown coal of Messel, near Darmstadt, and referred it to the same genus, *C. macrognathus*. The Messel coal is now dated as middle Eocene (Lutetian). In 1907 Schlosser said that *Cryptopithecus* (specifically *C. sideroolithicus*) was probably congeneric with *Pronycticebus*, and agreed with Wittich's generic reference of *C. macrognathus*. Stehlin (1916, p. 1423) gave reasons for separating *Cryptopithecus* and *Pronycticebus*, but was uncertain as to the true relationships of *Cryptopithecus sideroolithicus*. He saw most similarity to an undescribed specimen from Romainville which he tentatively referred to the Carnivora. As a

result of study of a cast of the type of *C. macrognathus* he believed this species had nothing to do with *C. sideroolithicus* but expressed no opinion as to its true affinities. Schlosser (1923), in his last opinion on the subject, tentatively synonymized *Cryptopithecus* with *Paroxylaenus* Teilhard, 1921, although *Cryptopithecus* was the older genus, and referred them to the Pantolestidae. Teilhard had referred *Paroxylaenus* questionably to the Oxycloenidae, apparently as much on similarities to *Promioclænus lemuroides* as to true arctocyonids, and he suggested affinities also with the Miacidae. Matthew (1937, written 1930 or earlier) accepted Teilhard's placement of *Paroxylaenus*.

Weitzel (1932) showed that *Cryptopithecus sideroolithicus* was not closely related to *C. macrognathus*, and referred the latter to the Creodonta on the basis of a new specimen and a cast of the type, which had been lost. Because of the position of the mental foramen under the anterior root of  $P_4$  he doubted that *C. sideroolithicus* was a pantolestid (but the mental foramen is in this position in *Coriphaeus montanus*). In 1933 Weitzel amplified these arguments, erected the genus *Kopidodon* for *Cryptopithecus macrognathus*, and placed *Kopidodon* together with *Paroxylaenus* in the new family Paroxylaenidae, which he referred to the Creodonta.

Russell and McKenna (1962) have shown that *Paroxylaenus* is a mioclænine hyopodontid, thus removing the basis for the family Paroxylaenidae of Weitzel (1933) and Kretzoi (1943), although subfamilial distinction may eventually prove necessary. The same affinities are true of *Kopidodon*; it is distinct from *Paroxylaenus* (in the characters described) only in its three-rooted  $P^2$  and two-rooted  $P^1$ , and its relatively smaller  $M^2$ . *Cryptopithecus* is probably a pantolestine, as discovered by M. C. McKenna. Such a probability may explain Schlosser's reference (1923) of *Paroxylaenus* to the Pantolestidae. *Cryptopithecus* specifically is similar to both *Bessoecetor* and the Sparnacian species *Palaeosinopa osborni*. These genera have vertical walls on the lower molars so that the cusps are not crowded, a more or less central paraconid that is somewhat reduced, a moderately tall trigonid, the protoconid slightly larger

than the metaconid,  $M_3$  about the size of  $M_2$ , and the entoconid high but not very well differentiated.

I have examined the type and only known specimen of *Cryptopithecus sideroolithicus* [B.S.P. No. A.S. (128)X1 1] and present the following additional information about it. A centroconid is present in the middle of the postfossid of  $M_1$  and  $M_2$  (the only teeth present), just lingual to the crista obliqua. The paraconid projects distinctly anteriorly, and there is a distinct concavity in side view between it and the anterior cingulum. The postfossid is shallow. Weak crenulations are present on the teeth, although not everywhere clear. They are usually nearly horizontal (an unusual condition) except near the base of the enamel, where they are vertical. The anterior roots of  $P_4$  and  $M_3$  are somewhat smaller than the posterior ones. A mental foramen is present under the middle of  $P_4$ . There is a deep masseteric fossa, but its ventral border is not sharply demarcated. The midlength of  $M_1$  is 2.1 mm.; of  $M_2$ , 2.0 mm. The trigonid width of  $M_1$  is 1.6 mm.; of  $M_2$ , 1.6 mm. The alveolar length of  $P_4$  is  $1.9 \pm 0.1$  mm. (approximate 95% confidence interval); of  $M_1$ , 2.0 mm.; of  $M_2$ , 1.8 mm.; and of  $M_3$ , 1.5 mm. The mandible depth below the protoconid of  $M_2$  is  $4.2 \pm 0.2$  mm.

*Kochictis* Kretzoi, 1943, from the middle Oligocene of Egerer, Hungary, was considered by its author to be a carnivore related to both *Paroxyclaenus* and the triisodontines, but he placed these all in separate families of his Caniformia (which included the Miacidae, Canidae, Viverridae, and others). *Kochictis* may be a hyopsodontid, probably a member of the Mioclaeninae, and is the latest known hyopsodontid. An additional post-Paleocene mioclaenine is "*Promioclaenus*" *gandaensis* Dehm and Oettingen-Spielberg (1958) from the middle Eocene of Pakistan, a species generically distinct from the American Paleocene ones. Reasons for this placement of *Kochictis* are the large, simple, bulbous, and posterior protocone on  $P_4$ , together with the central paracone and the lack of a sharp metacrista; the slight development of lingual cingula on  $M^1$ ; the simple, U-shaped curve of the protocristae of  $M^1$ ; the weak and lingual paraconids on the lower molars; the relatively short face; an upper canine apparently simi-

lar to that of *Paroxyclaenus*; and the emphasis on the grinding mode of occlusion despite trigonids of moderate height.

*Dyspterna woodi*, known from a fragmentary mandible with  $M_{2-3}$ , from the early Oligocene of the Isle of Wight, is most probably a pantolestid. It was described by Hopwood (1927) as an oxyclaenid creodont. Kretzoi (1943), as usual, created a separate family for it.

?*Dyspterna helbingi* Dal Piaz (1930) is based on a maxilla with  $P^3$  and alveoli for  $P^4$ - $M^3$ . Its affinities cannot be determined from the published description and figure.

#### EPAPHELISCUS, NEW GENUS

TYPE SPECIES: *Epapheliscus italicus*, new species.

TYPE OF *E. italicus*: M.G.P. No. 6834, fragment of maxilla with  $P^4$ - $M^3$ .

KNOWN DISTRIBUTION OF *E. italicus*: Probably from the early Oligocene of Monte Viale, Italy (see Dal Piaz, 1930).

ILLUSTRATIONS: Dal Piaz (1930, figs. 1-3).

DIAGNOSIS AND DISCUSSION: Apheliscine insectivore with  $M^1$  no wider (transversely) than long,  $M^3$  smaller than  $M^1$  but with its posterolabial area well developed, upper molars lacking a postcingulum and with only a weak ectocingulum, metacone larger than paracone on  $M^1$  and  $M^2$  and a distinct cusp on  $M^3$ , and protocrista of  $M^1$  and  $M^2$  more rounded than in *Apheliscus* and *Phenacodectes*. In addition the protocone of  $P^4$  is at least much reduced and is probably absent. Although it is just possible that this portion of  $P^4$  is broken off, there is no clear indication in the photographs that such is the case, and the possible area of breakage is relatively small. Dal Piaz (1930) noted the presence of a weak swelling on the posterior part of the lingual border of  $P^4$  and interpreted it as the vestige of a protocone. He made no mention of breakage in this region.

Dal Piaz (1930) tentatively referred the type of *E. italicus* to *Dyspterna woodi*, simply because both specimens were of the same age and were thought to be referable to the Procreodi. *Epapheliscus* is closely allied to, and probably descended from, *Apheliscus*, a probable pantolestid of the late Paleocene and early Eocene of North America (Gazin, 1959). Although I have not seen the only

known specimen of *Epapheliscus*, it is easily recognizable from the photographs given by Dal Piaz.

I do not believe the genera discussed above (p. 87) are apheliscines. In those with upper teeth preserved the paracone of P<sup>4</sup> lacks the backward tilt characteristic of apheliscines, and there are other differences. In those with lower teeth preserved the cusps are either more crowded or (*Cryptopithecus*) there is a well-developed protolophid, the paraconid is more anterior, and the teeth are wider.

#### PTOLEMAIA OSBORN, 1908

Osborn (1908) described a mandible from the Fayum of Egypt as *Ptolemaia lyonsi*, creating a new family for it and stating that it might be referable to a new order. Schlosser (1910, 1911) tentatively referred a mandible of a young individual to this species and placed *Ptolemaia* in the Hyaenodontidae, in part because he compared his specimen favorably with *Palaeosinopa*, which had been referred by Matthew (1901) to this family. Matthew (1918) correctly noted that Schlosser's specimen was not congeneric with *Ptolemaia lyonsi*, as is clear from the dental formula, the structure and relative size of the teeth, and the shape of the mandible, but he agreed with Schlosser's reference of the second specimen to the Hyaenodontidae despite his (Matthew, 1905, 1918) removal of *Palaeosinopa* to the Pantolestidae. In 1923 Schlosser questionably referred *Ptolemaia* to the Pantolestidae, and Matthes (1962) questionably put it in the Hyaenodontidae. Kretzoi (1945) created a family Ptolemayidae (a misspelled synonym of Osborn's family) and referred it to his order Creophaga. Hopwood and Hollyfield (1954) listed *Ptolemaia* as an "insectivore of uncertain position," following the order Chiroptera. Savage (1956) blindly followed this sequence and included *Ptolemaia* in the Chiroptera. McCutcheon and Wilson (1961) used the name *Ptolemaia* for a coral.

Neither specimen has any special similarity to the hyaenodontids, and both should be excluded from the Deltatheridia. I believe that Schlosser's specimen (still unnamed, although it is at least generically distinct from any other mammal known to me) is more probably a pantolestid than anything

else, that it is not congeneric with *Ptolemaia*, and that *Ptolemaia* is probably referable to the Insectivora (*sensu lato*). I provisionally follow the suggestion of Matthew (1918) that *Ptolemaia* is also related to pantolestids, but it is considerably different in detail from any known pantolestid.

*Ptolemaia* has a number of similarities to the Mongolian genus *Anagale*, of which the most important follow. Both have relatively high-crowned teeth with relatively thin enamel, high molar talonids, anteroposteriorly compressed molar trigonids with an unreduced and lingual paraconid, a high paraconid on the molars, and a high paraconid on P<sub>3</sub>. *Anagale* may be the closest known genus to *Ptolemaia*, but they are probably distinct at the subfamily level at least. Reference of *Anagale* to the Ptolemayidae would be premature at present. The condyle is high in *Anagale*, low in *Ptolemaia* and in the otherwise moderately similar genus *Onychodectes*, a taeniodont from the Puerco of New Mexico.

#### MISCELLANEOUS GENERA

The following genera, not discussed elsewhere in this paper, have been referred to the Creodonta (exclusive of explicit reference to the Arctocyonidae, Miacidae, or Mesonychiidae). In addition various groups such as the Borhyaenidae and Leptictidae have also been referred to the Creodonta, but these are discussed below.

*Aelurotherium* Adams (1896) is a synonym of *Patriofelis* (see Matthew, 1909).

*Amblyctonus* Cope (1880b) is a misspelling of *Ambloctonus*.

*Dipsalidictis* Matthew (1915) is a synonym of *Oxyaena* (see Denison, 1938).

*Hyainailouros* Biedermann (1863) [= *Hyainailurus* Rütimeyer, 1867; = *Hyaelurus* Stehlin, 1907] is a fissiped (see Helbing, 1925; Pilgrim, 1932).

*Hyaenodictis* Lemoine (see Lemoine, 1885, 1891) is a synonym of *Dissacus* (see Teilhard, 1921).

*Ischnognathus* Stovall (1948) is based on a toothless fragment of a mandible that is not identifiable even to order and should not have been named. Patterson (personal communication) says, however, that new material shows it to be a hyaenodontid, as originally

claimed; it must in this case belong to the Hyaenodontini.

*Limnofelis* Marsh (1872a) is a synonym of *Patriofelis* (see Wortman, 1894).

*Limnotherium* Marsh (1871a) is a synonym of *Notharctus* (see Cope, 1873).

*Lipodectes* Cope (1881e) is a synonym of *Deltatherium* (see Cope, 1882c).

*Neohyaenodon* Thorpe (1922) is a synonym of *Hyaenodon* (see Scott and Jepsen, 1936).

*Oreocyon* Marsh (1872b) is a synonym of *Patriofelis* (see Scott, 1892).

*Phiomia* Andrews and Beadnell (1902) is a proboscidian (see Andrews, 1906).

*Procyonictis* Lemoine (see Lemoine, 1885, 1891) was based on a  $P_3$  of the later-named genus *Arctocyonides* (see Teilhard, 1921; homology based on original observation).

*Prosinopa* Trouessart (1897) is a synonym of *Notharctus* (cf. Osborn, 1902).

*Protohyaenodon* Gromova (1952) is, as of the present time, invalid because its apparent type species is a *nomen nudum*.

*Pseudopterodon* Schlosser (1887) is a synonym of *Hyaenodon* (see Scott, in Matthew, 1903; Scott and Jepsen, 1936).

*Stypolophus* Cope (1872) is a synonym of *Sinopa* (see Scott, 1892).

*Taxotherium* Blainville (1841) is a synonym of *Hyaenodon* (see Schlosser, 1887).

*Telmalestes* Marsh (1872a) [= *Telmatolestes*, Marsh, 1872c] is a synonym of *Notharctus* (see Osborn, 1902).

*Telmatocyon* Marsh (1899; this paper is really Wortman's) is a synonym of *Limnocyon* (see Wortman, 1901–1902).

*Theriodictis* Mercerat (1891) is a canid (see Kraglievich, 1928).

*Thinolestes* Marsh (1872a) is a synonym of *Notharctus* (see Osborn, 1902).

*Thylacomorphus* Filhol (1877; he cites Gervais, 1876, *Zoologie et paléontologie générales*, vol. 2) is an artiodactyl, probably *Diplobune* (see Matthew, 1901).

*Tomitherium* Cope (1872) is a synonym of *Notharctus* (see Matthew, 1899; Granger and Gregory, 1917).

*Triacodon* Marsh (1871b) is probably either *Sinopa* or *Viverravus* (see Matthew, 1901; Wortman, 1901–1902; Thorpe, 1923). It was published 20 days before *Sinopa* and a year before *Viverravus*, and would be a *nomen oblitum* as well as virtually indeterminate except for its use by Hay (1930).

*Tricuspidodon* Lemoine (1885) is a condylarth descended from the arctocyonids or hyopsodontids.

*Tylodon* Gervais (1848) was based on a mistaken association of jaw fragments belonging to *Adapis* and *Hyaenodon* (see Zittel, 1893).

*Zipbacodon* Marsh (1872a) is indeterminate and probably not a carnivore (see Thorpe, 1923). The genus was last used as valid by Hay (1930).

#### SUBORDER ARCHAEOCETI FLOWER, 1883

Only two known families need be considered seriously as possibly ancestral to the archaeocetes and therefore to recent whales. These are the Mesonychidae and Hyaenodontidae (or just possibly some hyaenodontid-like palaeoryctid). No group that differentiated in the Eocene or later need be considered, since the earliest known archaeocete, *Protocetus atavus*, is from the early middle Eocene and is so specialized in the archaeocete direction that it is markedly dissimilar to any Eocene or earlier terrestrial mammal. It is also improbable that any strongly herbivorous taxon was ancestral to the highly predaceous archaeocetes. Furthermore, the oxyaenids are unlikely ancestors because of their short skull and the loss of  $M^3$ , and miacids are equally improbable because of their single well-developed carnassial tooth and the specialized pounding teeth posterior to this. Diverse and apparently equally valid objections exist for the various groups of Paleocene insectivores, one common to all being their small size. All marine mammals are large or rather large mammals.

Both the Hyaenodontidae and the Mesonychidae existed in the Paleocene, the latter known from fossils in both Europe and North America, the former not surely known in the Paleocene (see above) but occurring as a well-defined taxon in the earliest Eocene of Europe and North America.

*Protocetus* is known from a single skull from Egypt without the mandible and from fragmentary postcranial material, including a single vertebra from North America possibly referable to this genus. The skull, including the teeth, was well figured by Fraas (1904), and the basicranial region was figured by Kellogg (1936). Two partial mandibles of a related (not surely distinct) genus, *Pappo-*

*cetus*, from Nigeria, were figured by Andrews (1920). I have examined the specimens of *Pappocetus*; those of *Protocetus* were unavailable.

P<sup>4</sup>, M<sup>1</sup>, and M<sup>2</sup>, the least simplified upper cheek teeth (P<sup>3</sup> is the largest), consist of a poorly differentiated paracrista, a large paracone, and a moderately differentiated posterior cusp that is probably a metastyle but could be a metacone if the mesonychids were ancestral. A moderately pronounced lingual lobe is present, but this slopes smoothly to the palate and bears no trace of a protocone.

P<sup>3</sup> is remarkably similar to that of the middle Paleocene mesonychid *Dissacus navajovius*, and differs from that of hyaenodontids in the shape of the lingual lobe, the development of the metastyle, and the size relative to that of the other cheek teeth. P<sup>4</sup>, M<sup>1</sup>, and M<sup>2</sup> are similar to one another and generally premolariform in almost all mesonychids (including *D. navajovius*) and in *Protocetus*, but P<sup>4</sup> is rather different from the molars in hyaenodontids, although not sufficiently different to exclude a rapid spread of the appropriate growth fields to make them alike. Although both the Mesonychidae and early Hyaenodontidae have relatively large protocones, the protocone of the Mesonychidae (except *Microclaeodon*) is invariably somewhat larger and shows no evolutionary trend toward reduction such as is present in most late Eocene and later hyaenodontids (except on P<sup>4</sup> of *Apterodon*, if this genus is correctly referred to the Mesonychidae). However, in the mesonychids the protocone does not extend so far lingually as in the early hyaenodontids. Another similarity to mesonychids is the fact that the cusp in *Protocetus* tentatively interpreted as the metastyle is directly posterior to the paracone. Such is true in mesonychids but not in early hyaenodontids except to some extent on P<sup>4</sup>. In addition, the lingual lobes of P<sup>4</sup> through M<sup>2</sup> of *Protocetus* appear to be about central, and the paracone appears to be rather bulbous. These are both similarities to all known mesonychids and differences from hyaenodontids. M<sup>3</sup> is closest (except for the lack of a protocone) to that of the middle Eocene mesonychid *Ichthyolestes* (Dehm and Oettingen-Spielberg, 1958), but the fact may not be significant.

The talonid of DP<sub>4</sub> is smaller in *Pappocetus* than in either hyaenodontids or mesonychids,

but that of hyaenodontids is smaller than that of mesonychids. However, the relative height of the protoconid is less than that of hyaenodontids and closer to that of mesonychids. The lower molars are much more similar to those of mesonychids than to those of early hyaenodontids. This fact is particularly evident in respect to the talonid, which is much taller than in hyaenodontids (more than half of the height of the protoconid) and consists of a single moderately bulbous cusp with a longitudinal ridge on its top, as in mesonychids but unlike the condition in hyaenodontids. The trigonids of *Pappocetus* (B.M. No. 11414) are too broken for one to be certain of their entire structure, but they apparently consisted of little more than the protoconid, as in *Dissacus navajovius* and to some extent other mesonychids, but in marked contrast to all hyaenodontids. The paraconid has been lost, but the paralophid still extends lingually from the top of the protoconid. The metaconid is absent from at least M<sub>2</sub>. M<sub>3</sub> is unreduced (B.M. No. 11086). The separation of the anterior teeth is more characteristic of hyaenodontids than of mesonychids, but this is clearly a specialization for fish-catching and is foreshadowed in *Dissacus navajovius*, which, as an unimportant additional point, has a single-rooted P<sub>1</sub> as in *Pappocetus*. The symphysis of *Pappocetus* (B.M. No. 11086) is very long, extending to about the anterior end of P<sub>3</sub> (or DP<sub>3</sub>). This specimen has about 12 rather small mental foramina.

The wear of the teeth is identical to that of mesonychids and quite different from that of hyaenodontids. There is heavy wear on the apices of all cusps and on the paracrista and metastyle of the upper teeth. The only shear facet observed is on the middle of the labial surface of the talonid of M<sub>1</sub>, caused by the paracone of M<sup>1</sup>. This facet is heavy and is in the position characteristic of mesonychids and not that of hyaenodontids, which is farther anterior. There appears not to have been strong prevallum or postvallum shear, also unlike hyaenodontids, although this may have been still present but relatively weak as in mesonychids.

The lack of a preglenoid process is a difference from known mesonychids and a similarity to hyaenodontids, but this process is apparently weak in *Dissacus navajovius*, and a

preglenoid process is absent from its probable ancestor *Eoconodon*. A trend toward ventral fusion of the pterygoids to move the bony internal nares posteriorly is observed in middle Eocene and later hyaenodontids and *Harpagolestes* (also *Apterodon*), but is not present in earlier members of either family and is a common adaptation in predaceous tetrapods. The basicranium of *Protocetus* is specialized in many respects, but there appears to be a broad space between the petrosal and basioccipital bones as in mesonychids. A bony bulla is present in *Protocetus* and was evolved earlier in mesonychids than in hyaenodontids. The bulla in whales is wholly formed by the tympanic bone, as is probably that of mesonychids, while in *Hyaenodon* an entotympanic also contributes (van der Klaauw, 1931). The entepicondylar foramen of the humerus is lost in *Protocetus*, *Mesonyx*, and *Synoplotherium* but not in hyaenodontids or earlier mesonychids. The external auditory meatus in mesonychids and archaeocetes (especially *Protocetus*) is rather long and appressed closely against the base of the postglenoid process. The hyaenodontids (especially the earlier ones) differ in both these characters. The same statements can be made about a relatively gentle slope of the anterior border of the coronoid process of the mandible. A postglenoid foramen is absent from *Protocetus*, as also from Eocene and later mesonychids; this foramen is present in hyaenodontids. It is, however, present in *Eoconodon* and present, but small, in *Dissacus navajovius*. In both mesonychids and whales the venous drainage is mainly through an enlarged jugular foramen and the foramen lacerum medium. The posterior position of the glenoid fossa in *Protocetus* is characteristic of all mesonychids except the late genus *Apterodon* (if this is a mesonychid), and is not true of hyaenodontids, particularly the earlier ones. *Andrewsarchus* (Osborn, 1924), although it is a later genus, has a skull remarkably similar in shape to that of *Protocetus*, even to a largely longitudinal series of incisors (only inferred in *Protocetus*, by analogy with other archaeocetes, including *Pappocetus*). But many of the features of the skull of *Protocetus* are not similar to those of either the Hyaenodontidae or the Mesonychidae (or to any other terrestrial

mammal known to me) and probably represent to a considerable extent a reorganization of the skull, the chain of effects resulting from adaptation to hearing, feeding, locomotion, and other functions in an aquatic existence. The basicranial region might give more information if it were restudied on the original specimen. The total length of the skull in at least *Synoplotherium* (and, by comparison with individual bones, also in other mesonychids, including *Dissacus*) is about 15 per cent of the total length of the skeleton, but less than 10 per cent in early hyaenodontids. The skull is also large in early archaeocetes.

According to Slijper (1936), the stapedia artery is lost well before birth in recent whales, and the entire internal carotid becomes functionless later in life (but see Fraser and Purves, 1960, for an apparent exception). The medial entocarotid appears to be absent, the only branch remaining being the promontory (Boenninghaus, 1904). Kellogg (1936) interpreted a large groove in *Protocetus* extending anteromedially on the promontorium from just anterolateral to the fenestra rotunda as for the internal carotid. This interpretation seems more likely than not, and, if correct, it indicates that the promontory artery was probably functional in *Protocetus*. However, this provides little evidence on the origin of *Protocetus*, since there is a faint groove indicating the probable presence of a promontory artery in both mesonychids (*Mesonyx*, original observation) and hyaenodontids (*Tritemnodon*, Matthew, 1909; *Sinopa*, original observation; and their close relatives, the limnocyonines, in which it is conspicuous, Matthew, 1909) as well as in various other groups of mammals.

The mesonychids, including even *Dissacus*, had hooflike ungual phalanges; it is perhaps difficult to envision an ungulate becoming marine. But the ancestors of the Sirenia were ungulates, and the nature of the intermediate stage in this case is perhaps indicated (although not actually represented) by an unfigured Japanese skeleton of *Desmostylus* (Nagao, 1941; Reinhart, 1959). Perhaps, as a speculation that, however, is not contradicted by their anatomy, some of the mesonychids were mollusk eaters that caught an occasional fish, the broadened phalanges aiding them on damp surfaces (and cf. Matthew, 1915, p. 85).

To my knowledge the family Mesonychiidae is one of the relatively few groups of mammals (and even of reptiles) that has not been specifically suggested as ancestral to the whales, but in my opinion the preceding argument establishes them as at least the most likely candidate. There are no important and valid similarities of primitive archaeocetes to early hyaenodontids that are not also similarities to mesonychids, and the same statement can be made about other groups with which I or others have made comparisons but which are too clearly dissimilar to need discussion here. *Dissacus navajovius* is possibly directly ancestral, but little is known of the early history of the mesonychids, especially

outside North America. However, as the mesonychids are very probably descended from the Puercan genus *Eoconodon* (e.g., *E. gaudrianus*) or a very close relative, and archaeocetes are more similar to *Dissacus* than to *Eoconodon*, it appears probable that the whales did not take to the sea until middle or late Paleocene time.

The excellent serological arguments (Boydén and Gemeroy, 1950) and the questionable embryological ones (Mossman, 1937) for a special relationship between the Cetacea and the Artiodactyla are made somewhat more plausible by the evidence given above, although the relationship is probably not more than to other ungulates.

## RELATIONSHIPS AND SYNTHESIS

### DELTATHERIDIA

THE FIRST EXPLICIT SUGGESTION that the Oxyaenoidea arose from the Palaeoryctidae (in the present sense) was, I believe, made by Simpson (1928). He believed, however, that the arctocyonids and presumably the fissipeds were also derived from palaeoryctids. The only Cenozoic group other than the Palaeoryctidae that is at all similar to the Oxyaenoidea is the Miacidae. The miacids are considered explicitly below, but in general the similarities to oxyaenoids that exist are mainly explicable in detail on the grounds of adaptive similarity. Primitive retentions common to both are almost or quite without exception found also in the Palaeoryctidae (whenever the appropriate part of the anatomy is known in the Palaeoryctidae).

In the following comparisons the Oxyaenoidea are represented by their four most primitive known genera: *Sinopa*, *Prolimnocyon*, *Dipsalidictides*, and *Oxyaena*. All Wasatchian or earlier species of each genus were used. In the comparisons, the term "oxyaenoids" refers only to these four genera. Greatest emphasis among the Palaeoryctidae is placed on *Puercolestes* (with *Nyssodon* and *Cimolestes*), since this is the most primitive known palaeoryctid, but other genera (especially *Didelphodus*, *Deltatheridium*, and *Palaeoryctes*) are also considered.

The only respect in which the upper molars of *Sinopa* (and therefore of oxyaenoids considered as a group) differ from those of palaeoryctids is the greater specialization of postvallum shear on  $M^1$ . This can be expressed as, e.g., a greater ratio of the posterior tooth margin to the anterior tooth margin (Butler, 1946). Important similarities (all of which may be taken together as a diagnosis of the Deltatheridia, with allowance for occasional exceptions in the Didymoconidae and others) include the wide styler shelf (reduced in *Oxyaena*); the prominent parastylar and especially metastylar areas; the connate paracone and metacone; the incomplete metacingulum (permitting greater postvallum shear); the fact that the preprotocrista is higher than the postprotocrista; the anterior, tall, lingual, and steep-walled protocone; the

lack of a hypocone and a mesostyle; the absence or weakness of the precingulum and postcingulum; and the absence of interradicular crests.

The premolars are only slightly or not at all molariform, except in the sense that the molars are partly premolariform. The  $P^4$  of oxyaenoids differs consistently from that of palaeoryctids only in its more posteriorly slanting paracone and in being a little less transverse, although in most species a larger metastyle and a less anterior protocone are also present. The parastylar area is conspicuous, and usually a rather large parastyle is present anterior to the paracone. Only a weak ectocingulum is present. A moderately strong metacrista (shearing except in *Sinopa opisthotoma*) is also present. The paracone is fairly tall and is normally worn from its tip rather than from its entire posterior edge. The labial face of the protocone is usually almost flat, with a distinct although small preprotocrista and postprotocrista and a median ridge. The lingual face of the protocone is steep. Except in most species of *Oxyaena* there is no precingulum or postcingulum.

$P^3$  lacks a protocone in both groups (except a few species of *Oxyaena*), but a weak lingual lobe is present lingual or (usually) posterolingual to the paracone. A strong metastyle is present except in *Sinopa opisthotoma*, in which it is of moderate size. A parastyle is absent. In the few species in which  $P^1$  and  $P^2$  are known they are simple, having in addition to the paracone only a weak metastyle, if any.

The upper canines are moderately large, projecting well beyond the other teeth. The root is moderately short, not more than one and a half times the height of the crown. The root is largest a short distance below the surface of the bone and does not curve much posteriorly. The crown is only somewhat compressed transversely. It bears a posterior and an anterolingual ridge, but neither is pronounced.

The lower molars of *Sinopa* (and therefore of oxyaenoids as a whole) differ from those of palaeoryctids only in having a slightly more anterior paraconid, a part of their accentua-

tion of postvallum-prevallid shear on the molars. Notable similarities of the lower molars of oxyaenoids and palaeoryctids are the tall trigonids, the relatively great height of the protoconid (the protoconid is scarcely taller than the metaconid in *Protoproviverra palaeonictides*), the nearly equal height of the paraconid and metaconid (not in *Cimolestes* but true of all later didelphodontines), the lack of a metacristid, the almost or quite flat walls of the prefossid, the anterior projection of the base of the paraconid, the lack or weakness of lingual and labial cingula, the nearly but not quite lingual position of the paraconid, the sharpness of the paralophid, the common presence of a slit in the paralophid, the nearly vertical and transverse postvallid, the poorly differentiated talonid cusps, the fact that the talonid is narrower than the trigonid (the same width in  $M_1$  and  $M_2$  of some specimens of *Sinopa shoshoniensis*), the elongate nature of the entoconid and hypoconid, and the only moderately enlarged hypoconulid of  $M_3$ .

The structure of  $P_4$  and the more anterior premolars is also very similar in the two groups, although the  $P_4$  of the otherwise remote *Oxyclaenus cuspidatus* and *Bessoecetor* are almost identical to them. The combination of relative narrowness and relatively great height of  $P_4$  is, however, unique to the deltatheridians, although not present in all. The general simplicity of structure may be noted, together with (in most species) the about equally low paraconid and talonid, the slightly lingual but distinct paraconid, the slight to pronounced posterior leaning of the protoconid, and the single, central cusp of the talonid. The anterior premolars are crowded in palaeoryctids and oxyaenids but not in most hyaenodontids.

The lower canines are moderately large but not transversely compressed in either group and have an anterolingual and a posterior vertical crest. The root is scarcely or not at all concave on its posterior surface, is expanded below the surface of the bone, and is relatively short. The incisors are elongate labiolingually near the base, but semispatulate near the tip in at least *Didelphodus* and *Oxyaena* (cf. Denison, 1938).

The mandible is primitive and uncharacteristic in both the palaeoryctids and oxyaenoids

except for its deepening in oxyaenids, and the same is true for the rest of the skull. A few features nevertheless deserve specific mention because they are different from other more or less similar groups. All branches of the internal carotid artery are present, as are both a strong postglenoid and a weak entoglenoid process. An auditory bulla is present in at least some cases, but rests on and does not cover the medial side of the promontorium; there is no evidence for a posterior wall for the bulla. The basicranial region is not compressed anteroposteriorly. The mastoid has an appreciable lateral exposure. The stapedius muscle originates in a conspicuous pocket posterolateral to the fenestra rotunda. No processes of the petrosal or mastoid rise below the fenestra rotunda. An alisphenoid canal is present, in at least some and probably in all cases roofed with bone internally. Small and distinct paraoccipital and mastoid processes are present. A postorbital constriction of the cranium is present, as are a long jugal and a postpalatine torus. The jugal meets the facial expansion of the lacrimal. The palatine meets the lacrimal in oxyaenoids and probably in palaeoryctids. The infraorbital foramen is of moderate size and is situated above  $P^3$  or  $P^4$ . The lacrimal foramen is small; the postglenoid foramen is large to moderate. The mandibular condyle is on the same level as the teeth, and the masseteric fossa is rather deep.

The partial humerus of *Palaeoryctes* is unlike that of any other mammal, but *Palaeoryctes* itself is clearly not closely ancestral to the oxyaenoids. The ungual phalanx probably referable to *Didelphodus* is similar in its breadth and the presence of a fissure to that of the Oxyaenoidea. No other postcranial elements of the Palaeoryctidae are known.

The most important single character unifying the palaeoryctids and oxyaenoids and distinguishing them from other mammals is, in my opinion, the appression of the paracone and metacone. The only other mammals that I know of in which the paracone and metacone are not well separated are *Sarcophilus*, *Thylacinus*, most borhyaenids, and the mesonychids (except *Microclaenodon*), which are considerably different from all but a few of the latest oxyaenoids (see, e.g., the discussions above of *Apterodon* and the Archaeo-

ceti). These cusps are also rather close in *Geolabis*. The taxonomic distribution of this character, together with its association with a high paracone or metacone and its relation to the shearing faces of the tooth, suggests that the adaptive reason for its evolutionary appearance is related to the accentuation of shearing. By using P<sup>4</sup> as their only carnassial tooth, the miacids bypassed the need for such an adjustment of the molars, which remained largely primitive. Although the appression of paracone and metacone is in itself of only rather minor significance, it appears empirically to be a useful character. The virtual or complete absence of lingual cingula from the upper molars is an almost equally useful character.

Within the palaeoryctid-oxyaenoid assemblage there are evolutionary trends toward both a more connate paracone and metacone (*Palaeoryctes*, and perhaps continuing into the zalambdodonts; the Hyaenodontinae) and a greater separation of these cusps (*Didelphodus altidens*, *Micropternodus*, *Didymoconus*, and some Bridger specimens of *Sinopa*). That these trends went in the direction indicated is evident from the above discussion except for the last example given. *Sinopa grangeri*, a specimen probably conspecific with *S. grangeri* but referred to the earlier-named species *S. major* (A.M.N.H. No. 12080), and to some extent *S. rapax*,<sup>1</sup> have a moderately separate paracone and metacone, although connate at the base and not so separate as in, for example, the Arctocyoniidae. However, all Wasatchian specimens of *Sinopa* known to me have a more connate paracone and metacone, and the probable derivation of *Sinopa* from the Palaeoryctidae is an additional reason for believing the separation of paracone and metacone to be a reversal of an earlier evolutionary trend. The tooth from the early Eocene of Orsmael figured by Teilhard (1927, pl. 5, fig. 1) has the apices of the paracone and metacone moderately separate, but the figure suggests that the bases are connate. This tooth closely resembles DP<sup>4</sup> of *Prolimnocyon atavus*, and I suggest that it is the homologous tooth of this or a closely related species.

<sup>1</sup> But not *Sinopa minor*, despite the figure given by Wortman (1901-1902). The paracone and metacone of *Thinocyon velox* are also connate, despite Wortman's figure 77 (cited by Matthew, 1909, and McKenna, 1960a), as noted by Thorpe (1923).

Figure 6 of the same plate (Teilhard, 1927, pl. 5) may represent a right M<sup>2</sup> of the same species, but it is considerably more probable that this second tooth is a left molar of a proviverrine.

The oxyaenoids, palaeoryctids, and didymoconids form a phylogenetic unit (i.e., a sequence) that cannot be strictly defined (see the discussion of the Palaeoryctidae). Most have, and all are probably recently descended from genera that had, a more connate paracone and metacone than are present in almost any other mammal. The apex of the protocone is lingual, lingual cingula are usually minute or absent from the upper teeth, and postvallum shear is retained on at least one of the upper molars. The trigonids of the lower molars are always noticeably higher than the talonids, and there is no addition of cusps to either the upper or the lower molars except rarely a hypocone. Interradicular crests are absent. The lacrimal has a facial expansion, i.e., it is not completely confined within the orbit. A postpalatine torus is present (weak in *Didymoconus*). The feet are mesaxonic (the weight of the animal is most concentrated on the third digit, but see Denison, 1938; unknown in the Palaeoryctidae) and the ungual phalanges are fissured, insofar as known, except that the pes of *Tshelkaria* (and perhaps that of other didymoconids) does not show these characters (Gromova, 1960). The manus of *Tshelkaria* is, however, not abnormal. The medial entocarotid, the promontory artery, and the stapedia artery are all retained in every case in which the promontorium is known, although variously emphasized. A true postglenoid process is present.

I know of only three names that can reasonably be considered for this assemblage (Oxyaenoidea, Palaeoryctidae, and Didymoconidae). These are Creodonta (Cope, 1875), Creophaga (Kretzoi, 1945), and Pseudocreodi (Matthew, 1909). The name "Pseudocreodi" referred to the Oxyaenoidea alone and was explicitly made coordinate with the Acreodi, the Eucroedi, and (in 1915) the Procreodi. These names have been used or abandoned together since that time. Unless Matthew's other names are revived, I would prefer not to use "Pseudocreodi," although if an ordinal or subordinal taxon including only the Oxyaenoidea is proposed, "Pseudocreodi" would probably be its best name. The name "Creo-

phaga" is better in that it was used to include the Deltatheridioidea (now Palaeoryctoidea) as well as the Oxyaenoidea, but the Mesonychidae, Triisodontidae, "Ptolemayidae," and *Hyainailouros* were also included and *Disopsalis* was (perhaps inadvertently) excluded, as was *Didymoconus* explicitly. The name "Creophaga" has not been used in any other paper that I have seen, except one by Kretzoi (1957), and as it included extraneous elements as an essential part and was based on an incredible phylogeny of the mammalian carnivores, it seems best to let it decay in the room of abandoned names.

The name "Creodonta" has probably the best claim for use on the grounds of its familiarity. Originally (Cope, 1875, 1876) it included the genera then known of the Palaeonictinae, Oxyaeninae, Proviverrini, and Viverravinae, and also *Pterodon*. *Mesonyx* was explicitly excluded, and *Hyaenodon* was implicitly and later (Cope, 1877) explicitly excluded. The Mesonychidae were added to the Creodonta (by Cope, 1880b) before *Hyaenodon* was. At one time or another Cope added (often only temporarily) the genera, or species, then known of the Miacinae, Arctocyoniinae, Mesonychidea, Leptictidae, Oxyclaeninae, Triisodontinae, Periptychinae, Chrysochloridae, Didelphodontinae, Tenrecidae, Mioclaeninae, Taeniodonta, *Oxyacodon*, *Peratherium*, *Achaenodon*, *Cynodontomys*, *Pentacodon*, *Esthonyx*, *Apheliscus*, and *Hyaenodon*. Ameghino (e.g., 1889, 1891) added the Borhyaenidae, but this course was followed by only a few original workers (Tomes, 1906; Gaudry, 1908) and has been generally abandoned. Since 1900 the Creodonta have for the most part included only the Arctocyoniidae, Mesonychidae, Hyaenodontidae, Oxyaenidae, Miacidae, and of course families that have been split off from or later merged with these. McKenna (1960a; in McKenna, Robinson, and Taylor, 1962) tentatively added the deltatheridioids, and McDowell (1958) tentatively added *Apternodus*.

Each of these families has been excluded by one author or another, usually by several authors. To cite only the first instance known to me in each case, the Arctocyoniidae were excluded by Ameghino (1901; *Chriacus*, *Epichriacus*, *Tricentes*, and *Loxolophus* had been excluded by Osborn and Earle, 1895,

and Earle, 1898, and the pertinence of the Oxyclaeninae was doubted by Wortman, 1901–1902); the Mesonychidae, by Cope (1875); the Hyaenodontidae, by Kretzoi (1929; *Hyaenodon* but not *Pterodon* had been excluded by Cope, 1875); the Palaeonictinae, by Wortman (1901–1902); the Oxyaeninae, by Winge (1923); and the Miacidae, by Wortman (1886) and Schlosser (1886). The most consistent use has been to include the Mesonychidae, a family excluded from the original concept. Cope used the name "Creodonta" for a wide variety of groupings, but from 1880 he always included the Mesonychidae, as has every subsequent author (a statement that can be made about no other creodont group). If the name "Creodonta" were applied to the taxon consisting of the Oxyaenidae, Hyaenodontidae, Palaeoryctidae, Didymoconidae, and possibly the zalambdodonts, its meaning would be rather drastically altered, by both addition and subtraction of taxa, from the present usage and previous ones. The oxyaenoids are no more central than the mesonychids, both historically and conceptually, and are historically no more central than the arctocyoniids. To restrict the name "Creodonta" to the Oxyaenoidea and the Miacidae (in whole or, more strictly, in part), following the first usage of Cope, is legitimate only for a believer in types rather than common usage. *Hyaenodon* itself was originally excluded. I therefore believe that it is best to abandon the term "Creodonta" as a formal taxonomic name (cf. the usage of McKenna, 1960a) and let "creodont" lapse into the vernacular as a general name for either terrestrial carnivorous placentals other than the Fissipeda, or primitive carnivorous placentals regardless of affinity. To retain "creodont" in a formal sense would result in easily avoidable and serious ambiguity.

Mainly because of the inadequacies of the available names, but also to emphasize the separation of the group under consideration from the other placental carnivores, I propose the name Deltatheridia (suggested by M. C. McKenna) for this group. This name has the additional advantages of euphony, emphasizing the derivation of the oxyaenoids from the palaeoryctids (including *Deltatheridium*) and retaining at some level a name derived from the famous genus *Deltatheridium*.

# MIACIDAE

The origin of the miacids is hidden behind the curtain of the Dragon, and only a single tooth hints at the paths gone before. This tooth, a  $P_4$  from the Puerco, was described by G. T. Mac Intyre (1966). Some evidence, less direct and subject to contradiction by future discoveries, is nevertheless provided by comparisons with other groups. In the absence of intermediates, the most efficient way to determine the relationship of one taxon to each of two possibly ancestral taxa is to determine the differences between the members (especially the primitive members) of the two possible ancestors, and then use the characters thus extracted from the many less significant ones for comparison with primitive members of the third taxon. Extrapolation to an earlier time of trends of adaptation in all three taxa is also useful but more susceptible to the vagaries of the shifting adaptive zones available in the environment.

The two taxa that have in recent years been most often and with the most reason considered as ancestral or nearly ancestral to the Miacidae are the Deltatheridia and the Arctocyoniidae. As is discussed below, these two latter groups are probably among the most widely separated placentals in the Paleocene and earlier, and both are among the three or four groups of placentals now known from the late Cretaceous.<sup>1</sup> There are, however, considerable intergeneric differences in both groups, especially the deltatheridians, and for this reason it is difficult to find many characters that adequately separate them as groups. The following comparisons are based on all described pre-Bridgerian deltatheridi-

ans and all pre-Eocene arctocyoniids available before the summer of 1962. Emphasis in the deltatheridians is placed on the palaeoryctids, but early oxyaenoids are also included because their ancestors are not surely represented among known palaeoryctids. Specimens of the following species of miacids (chosen because they are more or less primitive) were used for all possible characters in the comparisons: *Simpsonictis tenuis* (see Mac Intyre, 1962), *Didymictis microlestes*, *Didymictis haydenianus*, *Oodectes proximus*, *Oodectes* sp. (A.M.N.H. Nos. 2681 and 56504), *Vulpavus australis*, *Vulpavus canavus*, *Miacis exiguus*, *Vassacyon promicrodon*, *Uintacyon massetericus massetericus*, *U. m. rudis*, *Uintacyon* sp. (Four Mile), and a possibly new genus of viverravines from the Torrejon (A.M.N.H. No. 16031), as well as the Puerco miacid  $P_4$  (A.M.N.H. No. 58409). Various other miacid species were also used for a few characters. In the following comparisons the terms "arctocyoniids," "deltatheridians," and "miacids" refer to only the forms mentioned above.

In the deltatheridians the paracone of  $P_4$  is somewhat narrower transversely than in that of the arctocyoniids. The miacids are intermediate but more similar to the arctocyoniids. When present in the deltatheridians, the commissure between the paracone and protocone of  $P_4$  is flatter than in the arctocyoniids. All miacids have this commissure; the miacines are generally more similar to the deltatheridians and the viverravines generally more similar to the arctocyoniids in respect to the shape of the commissure. Precingula and postcingula are absent from  $P_4$  in the deltatheridians and the miacines but present in the arctocyoniids and the viverravines. The parastyle of  $P_4$  is smaller in deltatheridians (except *Sinopa opisthotoma*) and miacines than in arctocyoniids; in the viverravines it is intermediate. Wherever the protocone of  $P_4$  is present in deltatheridians, it is shorter anteroposteriorly than it is in arctocyoniids (except for oxyaenids and some specimens of *Sinopa* and *Prolimnocyon*). A protocone is invariably present in miacids. The miacines are again generally similar to the deltatheridians and the viverravines generally similar to the

<sup>1</sup> Arctocyoniids of probably Cretaceous age are known from a small collection made in 1938 by Darwin Harbicht south of Fort Peck, Montana, and preserved in the American Museum. This faunule is nearly, or quite, equivalent to the Mantua. The arctocyoniids are distinctly more primitive than those of the Puerco. The differences between three pairs of similar species of arctocyoniids from the Montana and Puerco faunas are in general qualitatively similar to the differences between the samples of the three valid species of *Oxyclaenus* and *Loxolophus* from the lower and upper levels of the Puerco, but the former differences are considerably greater than the latter. A collection made in 1962 after the present report was written confirms the statements in this footnote, except that the age is probably slightly pre-Mantuan.

arctocyonids. From  $P^8$  the parastyle is absent or it is minute in deltatheridians and miacids, but of moderate size in arctocyonids. The height of  $P^8$  is greater than or equal to its length in deltatheridians (except some oxyaenids), less than or equal to its length in arctocyonids. The miacids vary in this respect but are closer to the arctocyonids.

In known deltatheridians the upper canine is less compressed transversely, and its posterior surface probably less concave, than in known arctocyonids and miacids.

In the upper molars of deltatheridians, the paracone and metacone are more connate and usually taller than in those of arctocyonids and miacids. The upper molars of deltatheridians (except most oxyaenids) are also more transverse than those of arctocyonids and miacids. In deltatheridians also the lingual cingula are less developed than in arctocyonids and most miacids, but they are poorly developed in *Oodectes* and less pronounced in the Cretaceous arctocyonids than the Puerco ones. With the base of the enamel used as a horizontal, the labial margin of the paracone and metacone is steeper than the lingual margin in deltatheridians (except the highly specialized *Palaeoryctes*), the same as or less steep in arctocyonids except *Chriacus* and *Eoconodon gadrianus*. This character is variable in miacids.

In deltatheridians the main talonid crest of  $P_3$  and  $P_4$  is on the labial half of the tooth (except *Palaeoryctes*, in which it is only slightly lingual of the midline), and lingual or, rarely, median in the arctocyonids. Miacids are similar to the deltatheridians in this character, except that the single known miacid tooth from the Puerco (A.M.N.H. No. 58409), a viverravine, has a distinctly lingual talonid crest. The labial height of  $P_4$  is greater than or equal to its length in deltatheridians (except some oxyaenids) and less than or rarely equal to its length in arctocyonids. The Miacinae are variable but more similar to the deltatheridians in this character, while the Viverravinae are uniformly similar to the arctocyonids.

In the lower molars of deltatheridians the trigonid is relatively higher than that of arctocyonids, and the talonid is usually lower relative to the length of the tooth.  $M_2$  and (when present)  $M_3$  of miacids resemble the

arctocyonids in this respect;  $M_1$  is of course specialized as a carnassial tooth in them. Lingual and labial cingula are absent from deltatheridians, at least labial cingula are present in arctocyonids, and the situation is variable in miacids.

I have been able to find no clearly diagnostic features whatever in the skull (other than the teeth) between the deltatheridians and the arctocyonids, partly because of the variability in both groups, but to a considerable extent also because both are groups of quite primitive placentals. It is possible that, when discovered, the skulls of pre-Eocene pantolestids, miacids, leptictids, and erinaceoids will also be almost or quite indistinguishable as groups. One or more diastemata are more or less developed in the region of the anterior premolars in all arctocyonids but are not developed in any palaeoryctid except the upper dentition (not the lower) of the late species *Didelphodus altidens*, and in *Hyotheridium*, which is very differently adapted from arctocyonids. Usually the anterior premolars of palaeoryctids are crowded, often crowded outside the usual tooth row. Diastemata develop in some hyaenodontids. Diastemata similar to those of arctocyonids are present in all miacids known to me.

Of postcranial features the most important difference between the deltatheridians and the arctocyonids is that the deltatheridians have a mesaxonic foot (but see Denison, 1938) and fissured ungual phalanges (the pes, but not the manus, of *Tshelkaria* is an exception to these two features), while the arctocyonids have a paraxonic foot and in some cases unfissured ungual phalanges. [The Arctocyoninae have at least usually fissured ungual phalanges (Donald E. Russell, 1964, and my own original observations), but A.M.N.H. No. 3157 (*Arctocyonides ferox*) has no indication of a fissure past the point where it begins in A.M.N.H. No. 16541, and *Chriacus gallinae* (A.M.N.H. Nos. 16223 and 48006) has a definitely unfissured ungual phalanx (cf. Matthew, 1915).] The miacids are similar to the arctocyonids in both these characters; their ungual phalanges are invariably unfissured. The deltoid crest of the humerus is high, usually ends abruptly, and has its most expanded part on the proximal half of the humerus in arctocyonids.

These characteristics are not particularly true of deltatheridians, although the deltoid crest of a young specimen of *Tshelkaria* is proximal. The Miacinae are similar to the arctocyionids in these characters. The Viverravinae are intermediate but more similar to the arctocyionids. The proximal third or fourth of the femur of deltatheridians is bent somewhat inward, a feature that is not found in arctocyionids or miacines. The viverravines are intermediate. The zygapophyses of the lumbar vertebrae are rather strongly curved in known deltatheridians, more so than in miacids. Most of these postcranial traits are unknown in palaeoryctids.

Although sections of arctocyionid teeth have to my knowledge never been prepared, the continuation of the tubes of the dentine into the enamel has been reported by Carter (1920) in *Hyaenodon*. This character is unknown in fissipeds, including miacids, but is of questionable significance.<sup>1</sup>

Since the above evidence (considered in the light of the evolving groups and not entirely as isolated characters; taxonomic judgment difficult to verbalize is also involved in a supplementary way, but it should be stated that my views on the ancestry of miacids have changed as a result of this investigation) indicates less phyletic similarity of the miacids to the deltatheridians than to the arctocyionids, further comparisons seem justified. Since the least-specialized members of Group M<sup>2</sup> are the early pantolestines, comparisons similar to those just described were made between *Bessoecetor thomsoni*, *B. diluculi*, and *Propalaeosinopa albertensis*, on the one hand, and *Oxyclaenus simplex*, *O. cuspidatus*, *Deltatherium fundaminis*, and pre-Puerco arctocyionids, on the other. *Deltatherium* was included because it is the only

arctocyionid reasonably likely not to have evolved from an ancestor very similar to *Oxyclaenus*. Nevertheless I suspect that even *Deltatherium* evolved from a similar source. The miacids compared with them are the same as those listed above. In the following comparisons the terms "arctocyionids," "pantolestines," and "miacids" refer only to the species used for the comparisons.

In the early pantolestines the postprotocrista of P<sup>4</sup> is larger than in arctocyionids and miacids, although A.M.N.H. No. 56504, a primitive species of *Oodectes*, has a postprotocrista larger than that of any arctocyionid. The ectocingulum is absent labial to the paracone in the pantolestines, present in the arctocyionids and miacids. The labial border of the tooth is convex in the pantolestines, concave in the arctocyionids and miacids (but it is occasionally convex in the miacids for a short distance just labial to the paracone). The paracone is relatively slightly narrower transversely in the pantolestines than in the arctocyionids and miacids, but in the miacids it is occasionally nearly as narrow as in *Bessoecetor*. On P<sup>3</sup> the protoconid is distinctly on the posterior half of the tooth in pantolestines and central in arctocyionids. Miocids vary in this character.

On the upper molars of pantolestines the paracone is taller relative to the anteroposterior length of the tooth than in arctocyionids and miacids, although some specimens of both subgenera of *Didymictis* are intermediate. The paracone and metacone are slightly closer to each other in the pantolestines and the tooth is relatively more transverse (the upper molars of *Deltatherium* are as transverse as these, but this feature is probably secondary) than in the arctocyionids and miacids.

The P<sub>3</sub> of pantolestines and miacids is relatively lower and narrower than that of arctocyionids. The talonid of the pantolestine P<sub>3</sub> is a little more developed lingually than that in the primitive arctocyionids, but not more than in other arctocyionids. Miocids are variable in this respect, but more similar to pantolestines. The P<sub>4</sub> of pantolestines is relatively lower than that of the primitive arctocyionids (but not lower than that of other arctocyionids). The Miacinae are variable but more similar to the Arctocyionidae in this character, while the Viverravinae are similar

<sup>1</sup> Contradictory observations by competent workers (e.g., Tomes, 1906; Carter, 1920) are not uncommon in the study of tooth sections, and considerable variation within related groups and convergence between unrelated groups have been reported or can be inferred in these papers and in those of Korvenkontio (1934), VanderHoof (1937), and Radinsky (1961), among others. Enamel tubes (more probably fibrous enamel: Carter, 1922; Moss and Applebaum, 1963) are known in fish (Mummery, 1917; Ockers, 1961), multituberculates, soricids, erinaceids, lemurids, *Tarsius*, macroscelidids, jerboas, and hyracoids as well as in marsupials and *Hyaenodon* (see Carter, 1922).

<sup>2</sup> See page 55, footnote 1.

to the Pantolestinae except that the  $P_4$  from the Puerco (A.M.N.H. No. 58409) is similar to that of the Arctocyoniidae. The  $P_4$  paraconid is slightly higher on the tooth in pantolestines than in arctocyoniids.<sup>1</sup> The Miacinae are similar to the arctocyoniids, and the Viverravinae are similar to the pantolestines in this respect. The central crest of the talonid of  $P_4$  is not directed lingually in pantolestines but is in primitive (not all) arctocyoniids. In this character the Miacinae are variable but more similar to the Arctocyoniidae, while the Viverravinae are similar to the Arctocyoniidae except that the Puerco  $P_4$  is similar to that in the pantolestines.

Labial and lingual cingula are absent from the lower molars of pantolestines, but at least the former cingulum is present in arctocyoniids. Miacids vary in this character. A meta-cristid is absent from pantolestines and miacids but present in arctocyoniids except the  $M_1$  of some specimens of *Deltatherium*. The entoconid is a strong cusp in pantolestines, and is at least as tall as the hypoconid on  $M_2$  and  $M_3$ . It is not quite so distinct in arctocyoniids, but is often as tall as the hypoconid. Miacids are similar to the arctocyoniids in this regard, except that the situation in *Didymictis microlestes* is closer to that of the pantolestines. The trigonid is relatively higher in pantolestines than in arctocyoniids. Except for the carnassial specialization of  $M_1$ , the miacids have low trigonids.

The mandible of pantolestines is somewhat shallower (at least relative to the height of the tooth) than in arctocyoniids and miacids, and the masseteric ridge in pantolestines is more vertical and narrower than in the other two families. The infraorbital foramen of pantolestines is dorsal to the anterior part of  $M^1$ , not dorsal to the anterior or middle part of  $P^3$  as in at least *Deltatherium*, *Tricentes*, *Protogonodon*, *Goniacodon*, *Arctocyon*, *Arctocyonides*, and probably *Loxolophus* and *Eoconodon*. The borders are more curved and less vertical in pantolestines also. Miacids are more similar to the arctocyoniids than to the pantolestines in these features, although some species are intermediate.

<sup>1</sup> It is relatively high in "*Claenodon*" *procyonoides*, a species approximately ancestral to the Tillodontia, which have an even higher paraconid (Van Valen, 1963c).

Arctocyoniids are invariably larger than the primitive pantolestines. Miacids are larger than primitive pantolestines except for *Simpsonictis*, which is of comparable size. The Puerco  $P_4$  (A.M.N.H. No. 58409) is larger, but not greatly larger, than the  $P_4$  of *Bessoecetor*.

It therefore appears that the Miacidae are in general phyletically somewhat more similar to the Arctocyoniidae than to either the Deltatheridia or Group M, although less different from Group M than from the Deltatheridia and possibly originating in or near Group M. If we mentally remove the carnassial specializations of primitive miacids, the result would probably qualify as a very primitive arctocyoniid.

Because of this phyletic divergence of the Deltatheridia and the Miacidae, it seems desirable to separate the Deltatheridia from the order Carnivora. The various similarities of members of these groups are presumably in every case either primitive retentions common to at least some other mammals, or homoplastic developments. The Deltatheridia are, in my opinion, sufficiently divergent phyletically and adaptively from all other mammals to warrant recognition of them as a new order. The alternative would be to include them in the order Insectivora (Wortman, 1886), but recent investigations are making this latter order appear in general phyletically more homogeneous (or at least the possible heterogeneity is more sharply defined) than was once thought. To include in it a large group of carnivores would be to destroy the relative homogeneity of adaptation which is its main unifying feature.

A suggestive bit of confirmatory evidence as to my view of the affinities of the placental carnivores is provided by carnassial function. The palaeoryctids, like the early oxyaenoids, have prevallum and postvallum shear about equally developed, in a functional relation to the use of more than one embrasure-trigonid pair as carnassials. On the other hand, the miacids tend even in the Paleocene to have prevallum shear of somewhat less importance than postvallum shear, and in them of course there is only one carnassial pair (except to a slight degree in *Simpsonictis* Mac Intyre, 1962, but even in this genus the specialization is marked). Since the presence of multiple carnassials relatively unspecialized for post-

vallum-prevallid shear is demonstrably primitive in all three groups of oxyaenoids, it seems improbable that (as proposed by Loris S. Russell, 1954) the oxyaenoids were derived from a group that much earlier was already more specialized in these important functional aspects and that has increased these specializations (or others even more divergent) to the present. This argument, however, does not in itself preclude the possibility that the miacids arose from palaeoryctids.

There was apparently an early evolution in the miacids away from the grinding mode (note that this term is positional), although they retained their arctocydonid-like broad and flat molars used in pounding and some grinding in both modes. The grinding mode was, of course, later accentuated in some lineages.

Possibly the two subfamilies of the Miacidae differentiated independently, conceivably even from different families. There is at present little evidence on this point except the necessarily inconclusive similarities and dissimilarities of the two subfamilies to each other. Single teeth which are more or less specialized as carnassials, ranging in the upper jaw from  $P^3$  to  $M^2$ , have been evolved independently in the Limnocyoninae, Hyaeodontinae, Oxyaenidae, Miacidae, Talpidae, *Opisthopsalis*, *Oligoryctes*, and probably elsewhere. It could have, but may well not have, happened twice independently to the  $P^4$ - $M_1$  pair.

A specimen of *Metachriacus* cf. *M. punitor* (A.M.N.H. No. 35353) from the Torrejonian of Gidley Quarry, Montana, is somewhat convergent to the miacids in having a more posteriorly tilted paracone on  $P^4$ , but the protocone is no farther forward than in *Oxyclaenus cuspidatus* (a miacid-like labial rota-

tion of the metastylar area, carrying the whole tooth with it, makes the protocone even more posterior), the metacrista is scarcely larger than in other arctocydonids, and postvallum shear is not accentuated on  $P^4$ . This specimen may nevertheless represent a sterile parallel of the origin of the miacid  $P^4$ .

The isolated trigonid from the Campanian figured by Loris S. Russell (1962) and referred tentatively to the Miacidae is probably a marsupial. It is similar to Type 5 of Simpson (1929a), and could well be from an  $M_1$  of the same genus as A.M.N.H. No. 58767, from the Lance, which cannot be distinguished from the Didelphidae. This specimen is also of about the same size as Russell's.

The  $P_4$  of A.M.N.H. No. 16031, an undescribed viverravine from the Torrejon, has a distinct metaconid lingual to the protoconid, a feature unique in miacids. It is uncertain whether the presence of a metaconid on  $P_4$  is to be regarded as primitive for miacids; if it is, then the simple premolars of other miacids cannot legitimately be used as evidence for a relationship to other groups with simple premolars.

There is, in any event, no good evidence for associating the Miacidae and the Oxyaenoidea in the same order, and much evidence against such a course. Whatever the actual origin of the Miacidae, their carnivorous specializations were developed quite independently of those of the Oxyaenoidea and of the Mesonychidae. The great distinction of the Carnivora (Fissipeda and seals) from other placentals is this very set of carnivorous specializations. By the criteria outlined elsewhere (Van Valen, 1963c), the Fissipeda and the Oxyaenoidea should therefore be referred to separate orders.

## ARCTOCYONIDAE

The Arctocyonidae will be discussed at length in another paper, but a brief discussion of them seems pertinent here because of their possible relationship to the miacids. As has been particularly well demonstrated by Loris S. Russell (1954), the arctocydonids are more or less specialized for a herbivorous diet, and there is no indication that they were directly ancestral to any carnivorous mammal except

the Mesonychidae (see below). However, there is evidence (Gazin, 1941; Simpson, 1936b, 1953), which I believe is strong enough to be considered proof, of the descent of the Phenacodontidae from the Arctocyonidae. Primitive arctocydonids are very similar to both primitive hyopsodontids and anisonchines and very probably gave rise to at least the latter. The didelodontids are clearly

descendants of the arctocyonids, either directly or through an early phenacodont (cf. Simpson, 1948a).

It therefore appears that the latest common ancestor of the phenacodonts and at least some other condylarths lies in the Arctocyonidae. The order Condylarthra (Cope, 1881c) was based on *Phenacodus*. Other genera (including *Mioclaenus*, which included some species at present put in the Arctocyonidae) were referred to the order tentatively. Therefore if the order Condylarthra is to be monophyletic at the family level it must include the Arctocyonidae; in fact the latter family is the most central one of the order. This conclusion is supported, and not refuted, by consideration of the adaptive evolution of the arctocyonids. Ameghino (1901) and Kretzoi (1943) also referred the arctocyonids to the Condylarthra on more or less adequate grounds. It should be noted that the rebuttal of Ameghino by Matthew (1909) was made when Paleocene condylarths were relatively poorly known.

Very probably, as can be determined from a comparison of *Microclaenodon* and *Dissacus navajovius*, on the one hand, with *Goniacodon* and *Eoconodon gaudrianus*, on the other, the Mesonychidae arose from early members of the Triisodontinae. Therefore the Mesonychidae cannot be retained in the order Carnivora if the latter is not to be polyphyletic at the subfamily (or perhaps higher) level. I propose to transfer them to the Condylarthra, despite their great adaptive dissimilarity to the usual members of this order (but compare *Ailuropoda*, *Proteles*, and *Felis*), although they did evolve hoofs and a rather artiodactyl-like astragalus. It may eventually prove desirable to remove them to a separate

order. They may at present be regarded as subordinally distinct from the other condylarths, and the name "Mesonychoidea," although in the form more usual for a superfamily, is available for this suborder. The other condylarths (Arctocyonidae, Hyopodontidae, Didolodontidae, Phenacodontidae, Periptychidae, Meniscotheriidae,<sup>1</sup> and Tricuspidodontidae) may be considered as a suborder Arctocyonoidea. I should state that at least some of these taxonomic conclusions were reached independently by Bryan Patterson and Malcolm C. McKenna.

The removal of the Arctocyonidae, Mesonychidae, Oxyaenidae, and Hyaenodontidae from the order Carnivora to two other orders destroys the suborder Creodonta. The probably diphyletic origin of the Pinnipedia (McLaren, 1960) removes the basis for this suborder, so at present there are no valid suborders of the Carnivora (cf. Leone and Wiens, 1956, and Pauly and Wolfe, 1957).

The cohort Ferungulata of Simpson (1945) may be phyletically valid (with the addition of the Tillodontia and Cetacea), but its use is not so compelling as it once seemed, and it is probably best to make the highest-level taxonomic division of the Eutheria between the condylarths and their descendants, on the one hand, and all other eutherians (including the Carnivora; see fig. 16), on the other hand. The names "Ungulata" and "Unguiculata" would not have their meanings inordinately transformed if they were used for these groups. If, however, the primates diverged from the ancestors of arctocyonids much later than the miacids, as is possible, then the validity of the proposed cohort separation would be doubtful.

## INSECTIVORA

The term "Insectivora" was first used by Bowdich in 1821 (Cuvier, 1817, had proposed such a grouping and this term in the vernacular) as a result of grouping forms presently known as the Soricidae, Talpidae, Erinaceidae, Chrysochloridae, and Tenrecidae. The Tupaiidae and Macroscelididae, as well as other families, were discovered later and referred to the Insectivora. These latter two families were separated by Haeckel in 1866

(p. clx) as the Menotyphla, while he applied the name "Lipotyphla" to the families known by Bowdich in 1821. There are therefore two usages of the name "Insectivora" that are consistent with the original concept of Cuvier and Bowdich. One is to restrict it to the families they knew and included, and the other is to include in addition all or some

<sup>1</sup> *Meniscotherium* and especially *Orthaspidothierium* should be compared closely with *Protoselene*.

families later discovered and believed to be more or less closely related to the five original ones. Unless the first (and indefensible) alternative is chosen, "Insectivora" is not a senior synonym of "Lipotyphla," but of course the former name could be restricted to this group if it were thought desirable on other grounds. A grouping of the Erinaceidae with the Chrysochloridae in 1817 surely was based not on anything that can readily be transformed into a phylogenetic argument, but rather on general morphological and adaptive facies and what we would call primitive retentions. I believe that these reasons are still valid (phylogeny does not contradict them) and apply to at least the first seven groups discussed in the following paragraph.

About seven probably natural groups of Insectivora are now recognizable, although not all are of equal rank. One, Group M (p. 55, footnote 1), contains the Pantolestidae (probably including the Apheliscidae), Mixodectidae, Leptictidae, Zalambdalestidae (not certainly distinct from the Leptictidae on the family level), and probably the Apatemyidae and *Endotherium*, and is more or less closely related to condylarths and primates as well as to other insectivores. A second group, the Tupaiidae, may well be subordinally related to the first, or may be better placed in the Primates. The third group, the Macroscelididae, is of uncertain origin. The fourth group contains most of the dilambdodont Lipotyphla, including the Erinaceidae, Soricidae, Talpidae, Dimylidae, Amphilemuridae, and Nyctitheriidae. The fifth group, the zalambdodont Lipotyphla (a possibly diphyletic group), includes the Tenrecidae (including the Potamogalidae), Apternodontidae (not certainly distinct from the Tenrecidae on the family level), Solenodontidae, and Chrysochloridae. The sixth group contains only *Nesophontes*. *Ptolemaia*, the only member of the seventh group, is of uncertain affinities but is possibly related to Group M. The Palaeoryctidae and Didymoconidae would form an eighth group if placed in the Insectivora. The Picrodontidae are also distinct and may be bats or, more probably, primates. If the Dermoptera are not separated ordinally, they are clearly distinct from all other insectivores subordinally. The middle Cretaceous Forestburg specimens are probably referable

to the Insectivora (see below), and would form another group.

Most of the difficulty in the major classification of the Insectivora now involves the origin of the zalambdodonts. The two serious possibilities for ancestral groups are the Palaeoryctidae and the dilambdodont Lipotyphla (specifically early Erinaceoidea). Origin from either group would necessitate the secondariness of the zalambdodonty, brought about by a loss of the metacone. No zalambdodont therians are known earlier than the middle Eocene (McKenna, *in* McKenna, Robinson, and Taylor, 1962). If they had been derived directly from pantotheres or even therapsids independently of other therians (Matthew, 1909; Gregory, 1934; Butler, 1939, 1941, but not 1956; probably Hough, 1956), some earlier record should be available (although not necessarily so, and Butler seems to consider *Palaeoryctes* and *Deltatheridium* zalambdodonts). Furthermore, as discussed in part by McDowell (1958) for *Solenodon* and the Tenrecidae, by McKenna (MS) for the Apternodontidae, and by earlier writers cited in these two papers, there are numerous resemblances to other placentals, of such a degree that a separate origin from pantotheres is to me inconceivable (cf. Patterson, 1956). Even on the teeth a protocone is usually present.

The adaptive significance of such a reversion to pantothere-like teeth is, however, unclear in detail, although presumably related in part to an increased efficiency of slicing. The protoconid surface moves somewhat lingually relative to the paracone when the jaw is closed, so food caught in the prefossid and the styler shelf (inside the stylocone, which functions as a brace) is trapped and readily sliced. Despite the claim of Patterson (1956), it seems improbable that the grinding mode is present in zalambdodonts, at least in young individuals. The steep labial faces of the metaconid and paraconid are normally nearly or quite as heavily worn as the lingual face of the protoconid; there is no corresponding facet on the upper molars, which would be required if the protoconid facet were produced by crest-on-crest action. The abandonment of the grinding mode appears to be almost necessary for zalambdodonty. It is therefore tempting to think that the evolu-

tion of therian molars from pantotherian ones was related to the incipient development of a grinding mode, but the evidence on this point is unclear.

In *Solenodon* as well as in other zalambdodonts the paracone occludes labial to the hypoconid (as shown by wear facets and the structure of  $M_3$ ), the normal situation and one not supporting the reinterpretation of cusp homologies proposed by McDowell (1958) partly on the basis of paracone occlusion.

*Palaeoryctes puercensis* is nearly as close to complete zalambdodonty as it is possible to be without achieving it; in fact the cusps are even higher than in any zalambdodont I know. But if some or all zalambdodonts originated from the Palaeoryctidae, as the semizalambdodonty, elimination of the grinding mode, and reduction of the medial entocarotid artery of *Palaeoryctes*, the rather central position of the paracone, the structure of  $P^4$ , and other features seem to indicate, many or probably all of the osteological characters mentioned by McDowell (1958) as distinguishing the Lipotyphla (and particularly his Soricomorpha) from the Menotyphla would have been evolved independently in the zalambdodont and dilambdodont lipotyphlans. This conclusion is necessary because these characters do not occur in palaeoryctids. The occurrence of *Gypsonictops* in the Cretaceous makes it unlikely that the dilambdodont Lipotyphla arose from palaeoryctids. The presence of a pyriform fenestra in palaeoryctids is a similarity to *Solenodon* and the Apternodontidae but not to most tenrecoids. It also occurs in shrews and some bats and therefore has evolved a minimum of two times. The first person to relate zalambdodonts to deltatheridians (*Hyaenodon* and *Pterodon*) was apparently Huxley (1880).

McKenna (in McKenna, Robinson, and Taylor, 1962) tentatively referred the Apternodontidae to the Palaeoryctidae as a subfamily of the latter. In my opinion, if the apternodontids prove to be descended from the palaeoryctids, the point of acquisition of complete zalambdodonty would be an excellent place to draw a subordinal boundary. If the metacone of *Potamogale* is secondary, this classification should be unexceptionable, since, even though *Palaeoryctes* could easily

be included in the Zalambdodonta, its close relative *Pararyctes* tends in a quite different direction. *Micropternodus* and *Didymoconus* would not fit easily in the Zalambdodonta. If, on the other hand, it can at some time be shown that the metacone was never lost in the ancestors of *Potamogale*, an extension of the Zalambdodonta downward would probably be warranted. Until such a demonstration is made, it does not seem desirable so to extend the Zalambdodonta.

The existence at some time of *Nesophontes* appears indisputable, a fact that causes additional difficulties for the derivation of all zalambdodonts from the Palaeoryctidae. McDowell (1958) has presented an impressive amount of evidence, enough to convince me at present, that *Solenodon* is at least as closely related to *Nesophontes* as to the Tenrecoidea. But *Nesophontes* has dilambdodont teeth and has a number of special resemblances to the Soricidae. Possibly *Nesophontes* is secondarily dilambdodont, as the  $M^2$  of *Micropternodus* probably is; if not, it is unlikely that *Solenodon* arose from the Palaeoryctidae.

It is of interest in this connection that interradicular crests, characteristic of the dilambdodont Lipotyphla (including *Nesophontes*), also occur in *Solenodon* but not in the Tenrecidae or Chrysochloridae, as shown by specimens in the American Museum. In some species of chrysochlorids the interradicular region of the tooth extends below the surface of the palate or mandible in a groove. The entire interradicular region, however, and not, as in the dilambdodonts, *Solenodon*, and various other mammals, a crest within this region, does so.

The two investigations that would probably shed most light on the origin or origins of the zalambdodonts are a detailed study of the relations of the Apternodontidae to the Palaeoryctidae and to all recent zalambdodonts, and a thorough study of the early history of the dilambdodont Lipotyphla (and *Nesophontes*).

The suggestion of Loris S. Russell (1959) that the lagomorphs are zalambdodont and related to the zalambdodont insectivores seems to me unsound. Although his observation (and that of various other authors) that there is one central cusp on the upper molars

is approximately correct, at least in the Leporidae (I have confirmed this fact on specimens of *Palaeolagus*, *Lepus*, *Sylvilagus*, and *Brachylagus*), the high-cusped, shearing, and piercing teeth of the zalambdodonts, with small and peculiar talonids on the lower molars, are notably different from those of lagomorphs. The rest of the animal is no more similar. In addition, P<sup>3</sup> of *Mytonolagus*, the earliest lagomorph with a nearly unworn tooth, has a cusp that could well be a metacone (Wood, 1949). The fate of the metacone in lagomorphs is unknown at present, and even the identification of the central cusp as the paracone is uncertain (Wood, 1940, 1957a).

The various groups of insectivores are placed in the same order mainly because they have not evolved sufficiently divergent overall specializations from the ancestral placentals to warrant our creating separate orders for them, even though most living insectivores are highly specialized in individual characters. On this basis the Palaeoryctidae are insectivores (but so are early taeniodonts, arctocyonids, and primates). Most placentals are assigned to other orders because they or their near descendants (or rarely only their close relatives or ancestors: perhaps some mice) occupy highly different adaptive zones from those of the ancestral placentals. This

point has been discussed at greater length elsewhere (Van Valen, 1963c) in connection with the Tillodontia. The Lipotyphla (even if a monophyletic group) are not broadly distinct adaptively, as a group, from Group M, and these taxa should not be separated at the ordinal level. All insectivores are, as a conspicuous point, "insectivorous," i.e., they feed mainly on small animals, especially invertebrates. The whole pattern of radiation of insectivores seems to me generally similar, in both adaptive and structural scope, to that of other large mammalian orders (cf. pigs and cows, tapirs and horses, pandas and cats).

The fact that the Oxyaenoidea arose from the Palaeoryctidae, and the probability that no other carnivores did so, necessitate the erection of a new order, if the order Insectivora is to be even moderately homogeneous adaptively. The Palaeoryctidae should be included in this order, if only because it is doubtful that the Hyaenodontidae and Oxyaenidae arose from the same palaeoryctid. If it is shown that some or all zalambdodonts also were derived from the Palaeoryctidae, they, too, should be included in the Deltatheridia. This order would in this case be less homogeneous adaptively, but would still contain a major group difficult to include in the Insectivora (the order of the stem placentals).

## THE EARLY HISTORY OF THE PLACENTAL MAMMALS

The light from our narrow phyletic windows does not yet illuminate much of the Cretaceous; the beams blur and merge but do not indicate how or when except for the relative placement of the windows in the wall and passing breaks in the fog. It is in the Cretaceous that the common ancestors of at least the condylarths, erinaceoids, taeniodonts, Group M (p. 55, footnote 1), miacids, and deltatheridians must be sought. The bats, primates, and just possibly the edentates and lagomorphs may also extend separately so far, but it is probable that the other placental orders were derived from some of these groups in the Paleocene or even later.

The earliest known possible placental is *Endotherium* Shikama (1947), from the early or middle Cretaceous (Patterson, 1956) of Manchuria. It is known from three lower

molars, a jaw fragment, a scapula, and a humerus. Only the teeth have been described and figured, and the figures are mutually inconsistent in some respects. Further knowledge of all elements and of any wear surfaces on the teeth would be of assistance. *Endotherium* is probably a placental, as Shikama suggested. Saban (1954, 1958) has compared it favorably with the Pantolestidae and actually placed it in that family. This step seems premature, although the known features seem rather close to those of pantolestids. Chow (1953) believed *Endotherium* to be close to *Zalambdalestes*, and such a relationship also seems plausible.

The only other known pre-Maestrichtian possible placentals are those described by Patterson (1956) from the middle Cretaceous of Forestburg, Texas. The apparent presence

of four lower premolars and the central or more labial hypoconulid on the molars suggest a greater similarity of them to known placentals than to known marsupials. This is not to say that they probably had a placenta, although other evidence suggests that they probably did (cf. Hill, 1895, and Sharman, 1961), but simply that among known placentals there are forms that are closer to the Forestburg specimens than are any known marsupials. The marsupials may or may not have been derived from such nominal placentals. The presence of four lower incisors in a Forestburg specimen is probably not distinctive of marsupials, for *Deltatheridium* had four upper incisors and this number or more is probably primitive in both infra-classes. A moderately large stylocone and a wide stylar shelf are also present in early members of both infra-classes.

I suggest that the Palaeoryctidae are, in their total known anatomy, closer to the earliest placentals than is any other Cenozoic group. This is not to say that they should serve as a base for deriving all other placentals, since in the appression of the paracone and metacone they are somewhat specialized, and individual genera are specialized in their individual ways. It is nevertheless of interest that in the Forestburg upper molars the paracone and metacone are closer in two out of three cases (excluding the last molars) than is usual in mammals.

The lower molars of many early mammals, including the deltatheridians, are not particularly distinctive and resemble those found at Forestburg, although the narrow talonid and relatively high trigonid are characteristic of both deltatheridians and the Forestburg teeth. Only one premolar was found there, more probably than not  $P^4$ , as indicated by the strong metacrista. If correctly identified, it is more similar to the corresponding tooth of *Deltatheridium* than to that of any other placental that I know. The Forestburg fragment of jaw is not particularly suggestive of any other, although it is of interest that, as in deltatheridians, the canine root (as indicated by the alveolus) was short. It is the upper molars that are particularly characteristic of both the deltatheridians and the Forestburg therians. In both the Paleocene palaeoryctids and the Forestburg teeth the

upper molars are transverse, anteroposteriorly compressed, with rather long (anteroposteriorly) embrasures between them. The surface of the crown is relatively high above the palate (lower in the Forestburg specimens). Lingual cingula are absent or are faint bulges. There is a wide stylar area, and the stylocone is prominent (more so on the Forestburg specimens). The paracone and metacone are more or less connate in the palaeoryctids, close in a majority of the Forestburg teeth. There is a strong metacrista on at least  $P^4$ , and probably on  $M^1$  and  $M^2$ , of all the forms under consideration; the metacrista shows evidence of a shearing action. The anterior protocrista is higher than the posterior protocrista. The palaeoryctids differ from the Forestburg therians particularly in having higher teeth, a larger protocone and conules, a smaller stylocone, a closer paracone and metacone, usually more crowded anterior premolars, a longer mandibular symphysis, and a second mental foramen under a posterior premolar.

The few known Maestrichtian placentals (an erinaceoid, *Gypsonictops*; one or more palaeoryctids [*Nyssodon*, and possibly the Shabarakh Usu general]; three species of arctocyonids; and possibly a leptictoid, *Zalambdalestes*; six additional species, including a leptictid, were discovered in 1962) are not sufficiently different from their Paleocene relatives to warrant separate discussion here, and the main features of the early Cenozoic radiations are sufficiently well known not to require comment. I present, however, an informal phylogeny (fig. 16) of most groups. I wish to stress that certain aspects of it are merely speculative, but no other published phylogeny is available that is based on recent knowledge.

In *Palaeosinopa* the height of the trigonids increases regularly from  $M_1$  to  $M_3$ , as it does, but to a lesser extent, in its ancestor *Bessoecetor*. This feature is also well marked in *Deltatheridium*, *Opisthopsalis*, and, of course, the proviverrines, is suggested in *Prodiacodon* and an undescribed genus of middle Paleocene leptictids (A.M.N.H. No. 35295), and may be primitive in the Deltatheridia and perhaps Group M. It may equally well be a secondary adaptation.

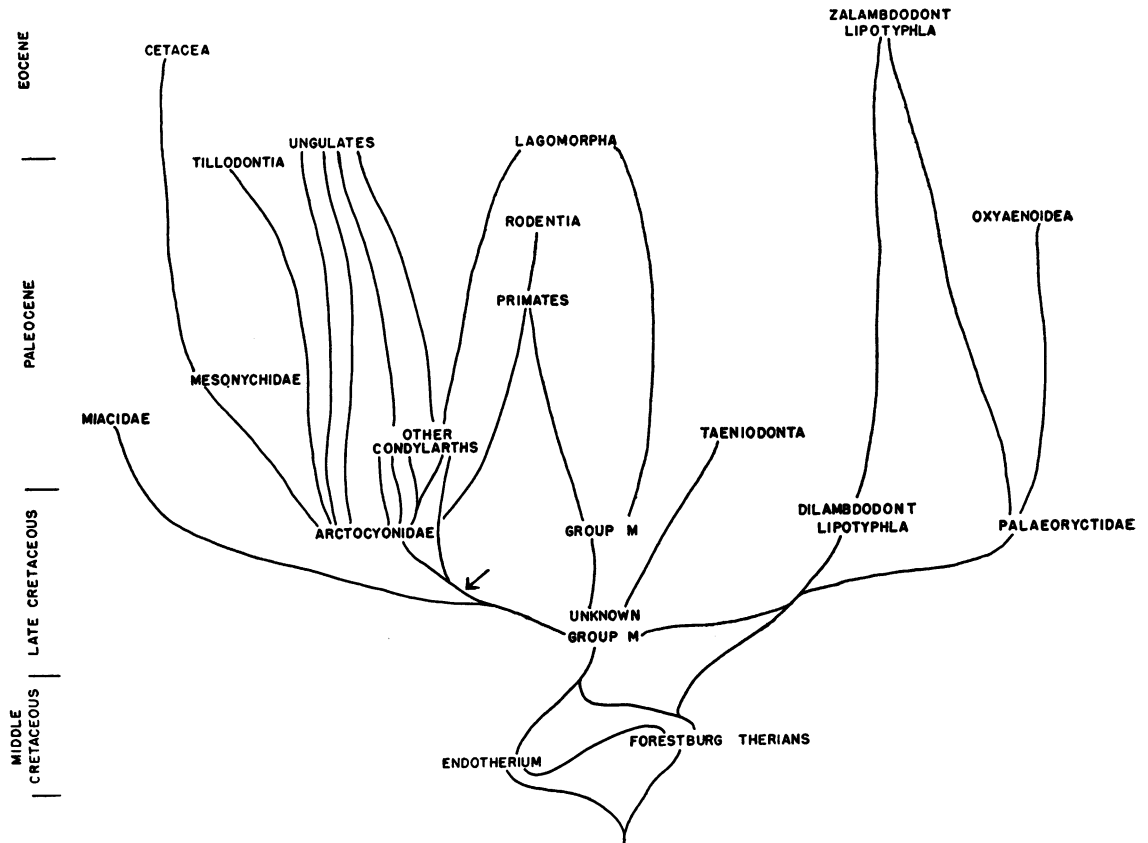


FIG. 16. Informal and speculative phylogeny of some early placentals. Double derivation of a unified group signifies much uncertainty and not diphyly. The time scale is not uniform. The arrow points to the proposed point of division between the Ungulata and the Unguiculata. The relative age of *Endotherium* and the Forestburg therians is not well established. The possibility that rodents arose from hyopsodonts does not seem to be completely excluded yet.

### CLASSIFICATION OF THE DELTATHERIDIA

The phyletic unity of the families grouped in the Oxyaenoidea is open to question, but there is now no good reason to abandon this convenient group. Within this superfamily there are three major lineages, which were recognized by Gazin (1946, 1952, 1962) as families: the *Limnocyonidae*, the *Hyaenodontidae*, and the *Oxyaenidae*. This course was followed by McKenna (1960a). But these groups are not all coordinate, as was shown by Denison (1938) and as is discussed in the present paper. In phylogeny, structure, and detailed function the *Oxyaenidae* are divergent from the others. I believe it is best, and roughly consonant with groupings elsewhere

in the Mammalia, to follow Denison (1938) in recognizing only two families of oxyaenoids: the *Hyaenodontidae* and the *Oxyaenidae*. Since it is nevertheless desirable to have taxonomic terms that refer to the two divisions of the *Hyaenodontidae*, I suggest with some hesitation that the subfamilies used by Denison (1938) and Simpson (1945) be reduced to tribes. They are structurally perhaps a little broader than is usual for mammalian tribes, but the difference, if present, is not great, and I believe that convenience justifies the change.

Although Article 36 of the International Code of Zoological Nomenclature requires

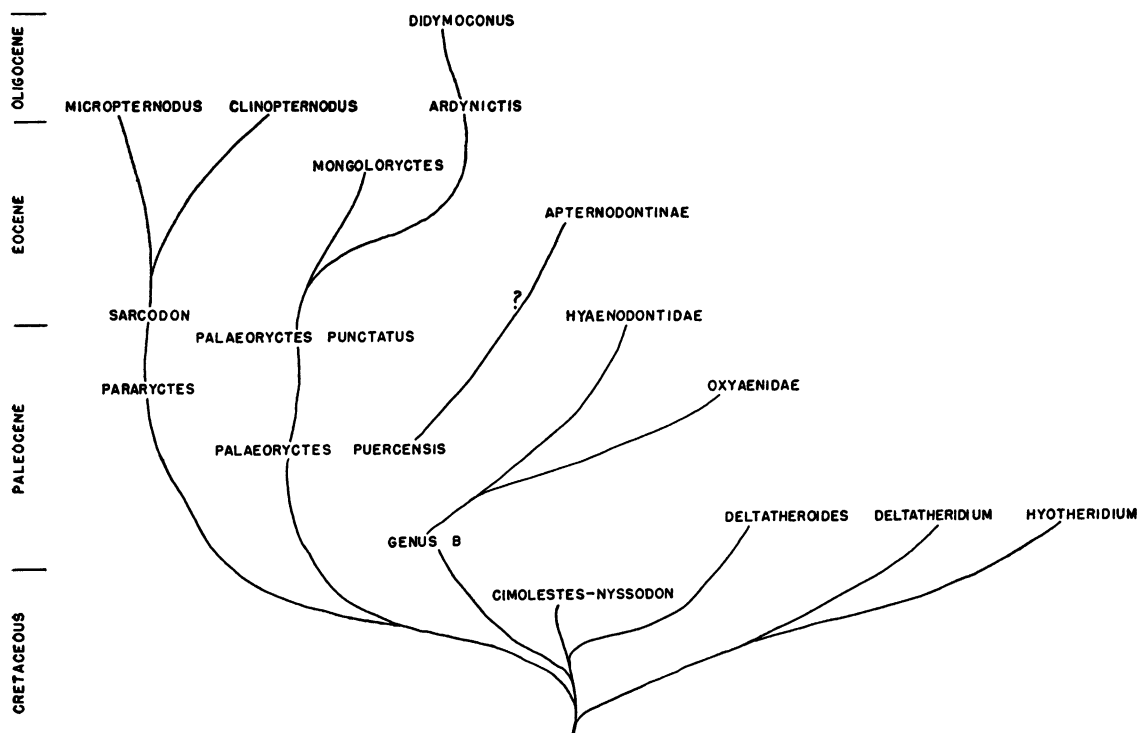


FIG. 17. Suggested phylogeny of the Palaeoryctidae and their descendants. A derivation of one genus from another indicates merely that this relationship is possible on the basis of known palaeoryctids.

the substitution of Palaeonictinae by Ambloctoninae, Oxyaenoidea by Hyaeodontoida, and Deltatheridoidea by Palaeoryctoidea, I have requested the International Commission on Zoological Nomenclature to suppress the first two of these changes, and by Article 80 of the Code the changes need not be made until a decision has been made. I am grateful to Ernst Mayr for pointing out that I do not need to make these changes, contrary to my former belief (Van Valen, 1963b).

A classification and suggested phylogeny (fig. 17) of the Deltatheridia follow. The author of a name in its present form is given without parentheses; the author by Article 36 of the Code is given in parentheses when different. A question mark before a genus signifies doubt as to the validity of the genus. The classification is provisional only. For each questionable taxon, the likelihood that the arrangement given is correct is discussed above. It is also probable that the zalambdodont insectivores belong in the Deltatheridia, but they are outside the scope of the present

paper.<sup>1</sup>

<sup>1</sup> An important paper by Vandebroek (1961) was received too late for inclusion in the present study. Good photographs of teeth of *Deltatheridium*, *Didelphodus*, and *Palaeoryctes* are presented. The erection of an order Zalambdodonta, including the recent zalambdodonts, the Apternodontinae, and the Palaeoryctidae, corresponds to the present order Deltatheridia except for the important exclusion of the Oxyaenoidea, *Micropternodus*, and the Didymoconidae. The complete zalambdodonts are believed to have come from the Palaeoryctidae. Despite Vandebroek's arguments, I do not believe that *Didelphodus* is more zalambdodont than, for example, *Pedimys* (which he excludes from the Marsupialia because it does not fit his theory!) or the Forestburg therians. To consider the Docodonta as the ancestors of the therians, mainly because they have a lingual cusp on the upper molars (any incipient lingual cusp on a premolar is almost necessarily rather similar to any other), which by Vandebroek's argument necessitates the presence of a well-developed precingulum and postcingulum with crests to the protocone being primitive in therians, is in my opinion to misinterpret the evidence of the known Cretaceous therians. None of these are at all similar to the Docodonta, and some do approach the Dryolestoida. The unfortunate resurrection of the premolar analogy theory, which identifies developmental homology with historical homology, need not be refuted here.

- Order Deltatheridia, new. Late Cretaceous-middle Oligocene, North America; early Eocene-middle Oligocene, Europe; ?early Paleocene-early Pliocene, Asia; early Oligocene-Miocene, Africa
- Superfamily Palaeoryctoidea (Winge, 1917, p. 161), new rank [= Deltatheridioidea (Gregory and Simpson, 1926, p. 6) Simpson, 1931, p. 268]. Late Cretaceous-early Oligocene, North America; ?early Paleocene-late Oligocene, Asia
- Family Palaeoryctidae (Winge, 1917, p. 161) Simpson, 1931, p. 268 [= Deltatheridiidae Gregory and Simpson, 1926, p. 6; = Cimolestidae Marsh, 1889, p. 89]. Late Cretaceous-early Oligocene, North America; ?early Paleocene-late Paleocene, Asia
- Subfamily Didelphodontinae Matthew, 1918, p. 571. Late Cretaceous-middle Eocene, North America; ?early Paleocene, Asia; middle-late Paleocene, Europe
- Cimolestes* Marsh, 1889. Late Cretaceous, North America
- ?*Nyssodon* Simpson, 1927. Late Cretaceous, North America
- ?*Puercolestes* Reynolds, 1936. Early Paleocene, North America
- Genus B, described above. Early Paleocene, North America
- Deltatheroides* Gregory and Simpson, 1926. ?Early Paleocene, Asia
- Acmeodon* Matthew and Granger, 1921. Middle Paleocene, North America
- Abolylestes* Russell, 1964. Middle-late Paleocene, Europe
- Gelastops* Simpson, 1935 [= *Emperodon* Simpson, 1935]. Middle Paleocene, North America
- Avunculus*, new. Middle Paleocene, North America
- Didelphodus* Cope, 1882 [= *Didelphyodus* Winge, 1923; including *Phenacops* Matthew, 1909]. Early-middle Eocene, North America
- Subfamily Deltatheridiinae (Gregory and Simpson, 1926, p. 6) Simpson, 1945, p. 48. ?Early Paleocene, Asia
- Deltatheridium* Gregory and Simpson, 1926. ?Early Paleocene, Asia
- Hyotheridium* Gregory and Simpson, 1926. ?Early Paleocene, Asia
- Subfamily Palaeoryctinae (Winge, 1917, p. 161), new rank. Middle-late Paleocene, North America
- Palaeoryctes* Matthew, 1913. Middle-late Paleocene, North America
- Pararyctes*, new. Late Paleocene, North America
- Subfamily Micropternodontinae Stirton and Rensberger, 1964. ?Late Paleocene, Asia; early Oligocene, North America
- Sarcodon* Matthew and Granger, 1925. ?Late Paleocene, Asia
- Micropternodus* Matthew, 1903 [= *Kentrogomphios* White, 1954]. Early Oligocene, North America
- Clinopternodus* Clark, 1937 [= *Clinodon* Clark, 1936, not Regan, 1920]. Early Oligocene, North America
- Family Didymoconidae Kretzoi, 1943, p. 194 [= Tshelkariidae Gromova, 1960, p. 42]. Late Eocene-late Oligocene, Asia
- Mongoloryctes*, new. Late Eocene, Asia
- Ardynictis* Matthew and Granger, 1925. Early Oligocene, Asia
- Didymoconus* Matthew and Granger, 1924. Late Oligocene, Asia
- ?*Tshelkaria* Gromova, 1960. Late Oligocene, Asia
- Superfamily Oxyaenoidea (Cope, 1877, p. 89) Osborn, 1910, p. 527 [= Hyaenodontoidea (Leidy, 1869, p. 38) Trouessart, 1885, p. 8; = Pseudocreodi Matthew, 1909, p. 327]. Late Paleocene-middle Oligocene, North America; early Eocene-middle Oligocene, Europe; late Eocene-early Pliocene, Asia; early Oligocene-Miocene, Africa
- Family Oxyaenidae Cope, 1877, p. 89. Late Paleocene-middle Eocene, North America; early-late Eocene, Europe; late Eocene, Asia
- Subfamily Oxyaeninae (Cope, 1877, p. 89) Trouessart, 1885, p. 15. Late Paleocene-middle Eocene, North America; early Eocene, ?Europe; late Eocene, Asia
- Oxyaena* Cope, 1874 [including *Dipsalidictis* Matthew, 1915]. Late Paleocene-early Eocene, North America
- ?*Argillotherium* Davies, 1884. Early Eocene, Europe
- Dipsalidictides* Denison, 1938. Early Eocene, North America
- Protopsalis* Cope, 1880. Early Eocene, North America
- Patriofelis* Leidy, 1870 [including *Limnofelis* Marsh, 1872; *Oreocyon* Marsh, 1872; *Aelurotherium* Adams, 1896]. Middle Eocene, North America
- Sarkastodon* Granger, 1938. Late Eocene, Asia
- Subfamily Palaeonictinae (Osborn, 1892, p. 104) Denison, 1938, p. 174 [= Ambloctonidae Cope,

1880, p. 84; = *Amblyctonidae* Cope, 1880, p. 78]. Late Paleocene-early Eocene, North America; early-late Eocene, Europe

*Dipsalodon* Jepsen, 1930a. Late Paleocene, North America

*Palaeonictis* Blainville, 1842. Early Eocene, North America, Europe

*Ambloctonus* Cope, 1875 [= *Amblyctonus* Cope, 1880]. Early Eocene, North America

*Paroxyaena* Martin, 1906. Late Eocene, Europe

Family Hyaenodontidae Leidy, 1869, p. 38. Early Eocene-middle Oligocene, North America; early Eocene-middle Oligocene, Europe; late Eocene-early Pliocene, Asia; early Oligocene-Miocene, Africa

Subfamily Hyaenodontinae Leidy, 1869, p. 38. (Distribution as for Hyaenodontidae)

Tribe Proviverrini (Schlosser, 1886, p. 293), new rank [= *Stypolophinae* Trouessart, 1885, p. 11]. Early-middle Eocene, North America; early-late Eocene, Europe; late Eocene-early Pliocene, Asia

?*Sinopa* Leidy, 1871 [including *Stypolophus* Cope, 1872]. Early-middle Eocene, North America

?*Protoproviverra* Lemoine, 1891 (May) [not *Protoproviverra* Ameghino, 1891 (August)]. Early Eocene, Europe

?*Prototomus* Cope, 1874. Early Eocene, North America

*Proviverra* Rüttimeyer, 1862. Middle Eocene, Europe

?*Tritemnodon* Matthew, 1906. Early-middle Eocene, North America

*Cynohyaenodon* Filhol, 1873. Late Eocene, Europe

?*Pseudosinopa* Depéret, 1917. Middle Eocene, Europe

*Imperatoria* Matthes, 1952 [= *Prodissopsalis* Matthes, 1952]. Middle Eocene, Europe

?*Geiselotherium* Matthes, 1952. Middle Eocene, Europe

?*Prorhyaena* Rüttimeyer, 1891. Middle Eocene, Europe

?*Galethylax* Gervais, 1850. Late Eocene, Europe

*Quercitherium* Filhol, 1882. Late Eocene, Europe

*Paracynohyaenodon* Martin, 1906. Late Eocene, Europe, Asia

?*Metasinopa* Osborn, 1909. Early Oligocene, Africa

*Dissopsalis* Pilgrim, 1910. Early Pliocene, Asia

Tribe Hyaenodontini (Leidy, 1869, p. 38), new rank. Late Eocene-middle Oligocene, North America, Europe; early Oligocene-Miocene, Africa; late Eocene-late Oligocene, Asia

*Propterodon* Martin, 1906. ?Middle Eocene, ?Europe; late Eocene, Asia; ?early Oligocene, ?North America

*Pterodon* Blainville, 1839. ?Middle Eocene, late Eocene-early Oligocene, Europe; late Eocene, North America, Asia; early Oligocene, Africa.

*Ischnognathus* Stovall, 1948. Early Oligocene, North America

*Hemipsalodon* Cope, 1885. Early Oligocene, North America

*Hyaenodon* Laizer and Parieu, 1838 [including *Pseudopterodon* Schlosser, 1887; *Taxotherium* Blainville, 1841; *Neohyaenodon* Thorpe, 1922; *Protohyaenodon* Stock, 1933]. ?Middle Eocene, late Eocene-late Oligocene, Europe; late Eocene-middle Oligocene, North America, Asia; early Oligocene, Africa

*Metapterodon* Stromer, 1926. Miocene, Africa

Subfamily Limnocyoninae Wortman, 1902, p. 117. Early-late Eocene, North America; ?early-late Eocene, Europe

Tribe Limnocyonini (Wortman, 1902, p. 117), new rank. Early-late Eocene, North America; ?early-late Eocene, Europe

*Prolimnocyon* Matthew, 1915. Early Eocene, North America, ?Europe

*Thinocyon* Marsh, 1872 [including *Entomodon* Marsh, 1872]. Middle Eocene, North America

*Limnocyon* Marsh, 1872 [= *Telmatocyon* Marsh, 1899]. Middle-late Eocene, North America

*Oxyaenodon* Wortman, 1899. Late Eocene, North America

*Thereutherium* Filhol, 1877. Late Eocene, Europe

Tribe Machaeroidini (Matthew, 1909, p. 330), new rank. Middle-late Eocene, North America

*Machaeroides* Matthew, 1909. Middle Eocene, North America

*Apataelurus* Scott, 1937. Late Eocene, North America

## SUMMARY

A RECONSIDERATION OF THE PHYLOGENY of some early placental mammals, especially the creodonts, has resulted in the removal of all creodonts except the Miacidae from the Carnivora. The Arctocyonidae and their descendants, the Mesonychidae, are placed in the Condylarthra, and a new order, the Deltatheridia, is created for the Oxyaenoidea, the Palaeoryctidae, the Didymoconidae, and *Micropternodus*. The zalambdodont insectivores may or may not also be referable to the Deltatheridia. A survey of taxonomically significant characters indicates that the Miacidae are apparently closer to the Arctocyonidae than to the Pantolestinae or to the Deltatheridia. The whales were probably derived from mesonychids in the Paleocene.

A detailed consideration of the morphology, systematics, and evolution of the Didelphodontinae is presented, and observations are made on many other mammalian genera, mainly, but not exclusively, of the Deltatheridia. Greatest emphasis is placed on the evolution of dental structure and occlusion, and cranial circulation. A detailed

terminology is proposed for the structures of primitive therian teeth. Teeth of possible Tiffanian and Puercan oxyaenoid ancestors are described. *Apterodon* is tentatively referred to the Mesonychidae; *Micropternodus*, *Nyssodon*, and *Sarcodon* are referred to the Palaeoryctidae; *Kochictis* and *Kopidodon*, to the Mioclaeninae; *Argillotherium* is referred to the Oxyaeninae; and *Praolestes*, *Opisthopsalis*, *Hyracolestes*, and *Xenacodon* are referred to the Erinaceoidea. New genera are *Avunculus* in the Didelphodontinae, *Pararyctes* in the Palaeoryctinae, *Mongoloryctes* in the Didymoconidae, and *Epapheliscus* in the Apheliscinae. A new species of *Palaeoryctes* is described from the late Paleocene; one of *Oxyaena*, from the early Eocene; and one of *Oxyaenodon*, from the late Eocene.

A possible case of geographic speciation in *Didelphodus* is presented, and comments are made on determining the relative adaptiveness of different characters, conditions of competitive exclusion, criteria of taxonomic definitions, and other theoretical matters.

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**PLATES 1-8**

# PLATE 1

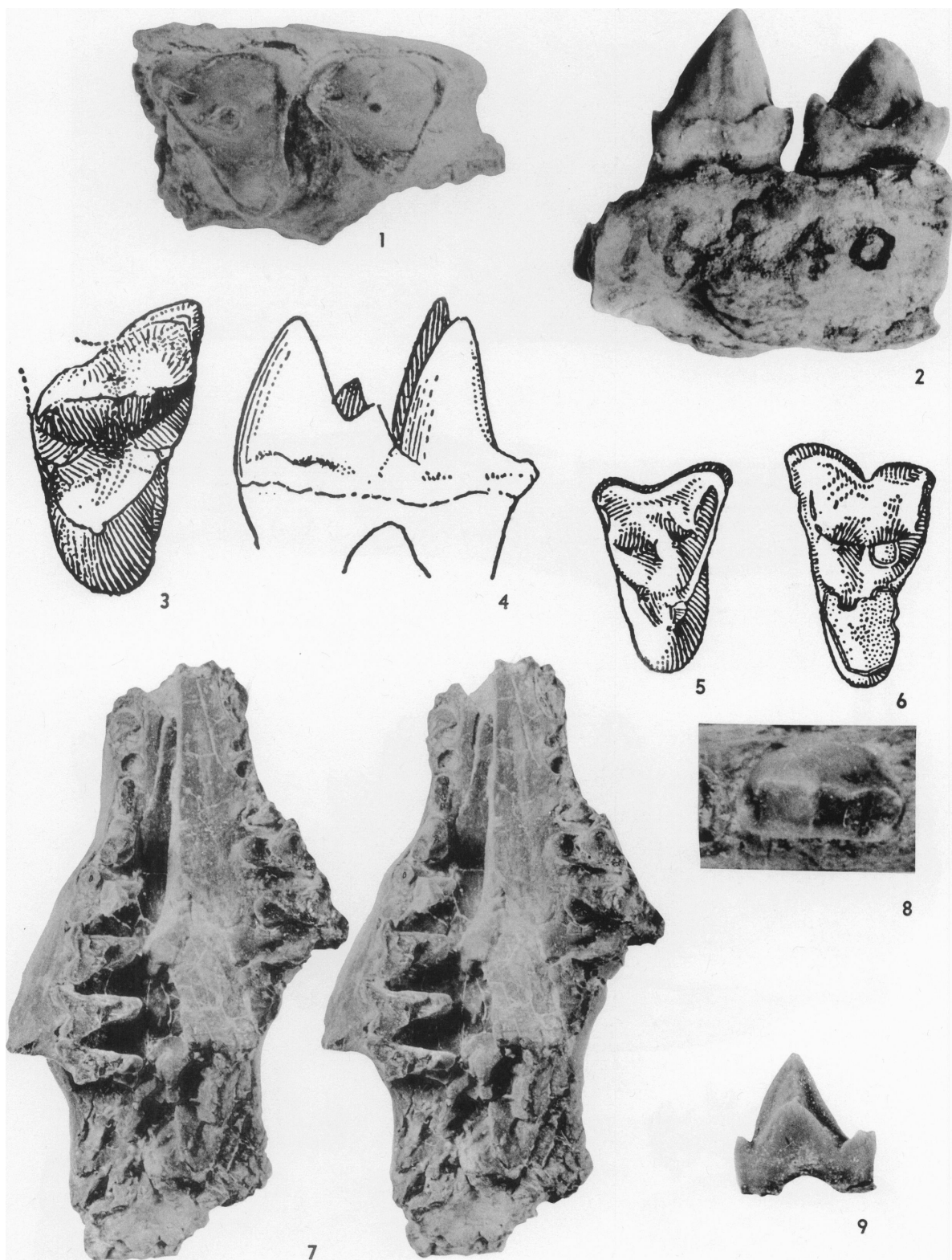
1, 2. Unretouched photographs of right  $P^3-4$ , *Didelphodus absarokae* (Cope), A.M.N.H. No. 16240; Almagre. 1. Occlusal view. 2. Labial view. Both  $\times 7.4$ .

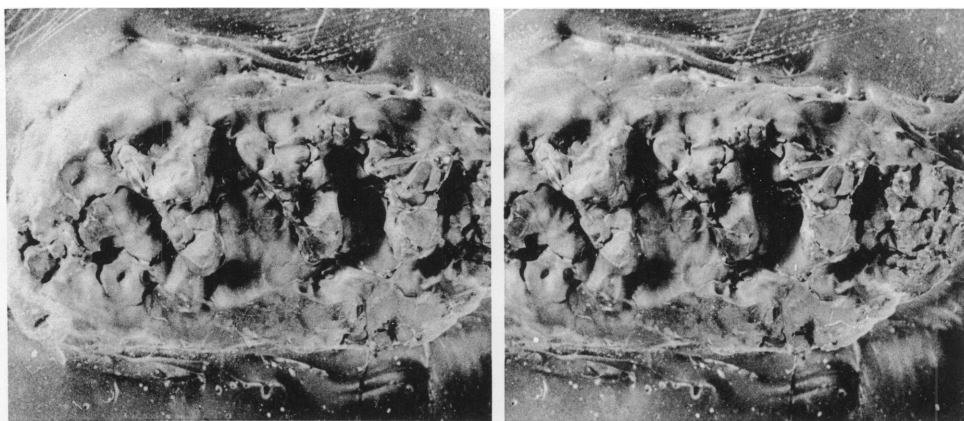
3, 4. *Nyssodon punctidens* Simpson. Left upper molar, type specimen, Y.P.M. No. 13654; Lance Creek. 3. Occlusal view. 4. Posterior view. Parastylar and part of metastylar areas broken away. Reproduced from Simpson (1929). Both  $\times 12$ .

5, 6. Two specimens of *Didelphodus absarokae* (Cope), occlusal view; Four Mile. 5. U.C.M.P. No. 44027B, right  $M^3$ . 6. U.C.M.P. No. 44027A, left  $M^3$ , with protocone and tip of metacone broken off. Reproduced from McKenna (1960a). Both  $\times 6$ .

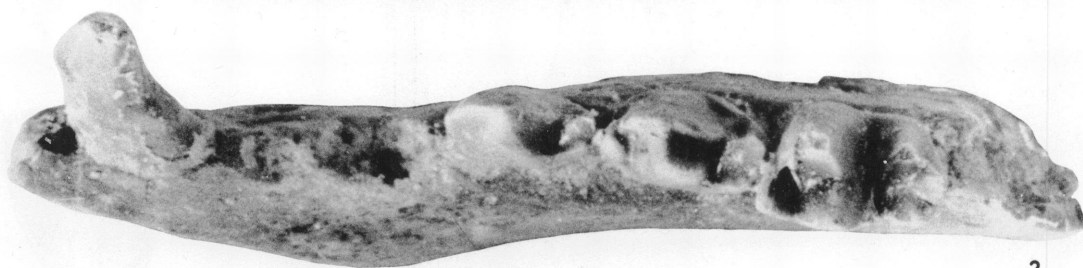
7. Unretouched stereophotographs of palate of *Puercolestes simpsoni* Reynolds, type specimen, U.C.M.P. No. 36658; lower fossil level of Puerco. The teeth are broken in various ways.  $\times 3$ .

8, 9. Unretouched photographs of right  $P_4$ , *Didelphodus absarokae* (Cope), A.M.N.H. No. 4228, type specimen; Gray Bull. 8. Occlusal view.  $\times 7.4$ . 9. Lingual view.  $\times 6.4$ .

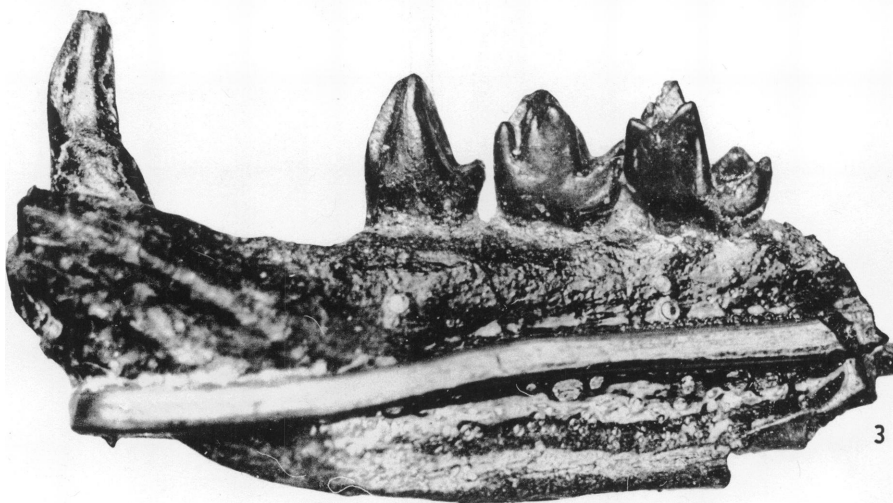




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## PLATE 2

1. Unretouched stereophotographs of *Acmeodon secans* Matthew and Granger, A.M.N.H. No. 4063, right P<sup>4</sup>-M<sup>2</sup>; Torrejon. Occlusal view. There is much breakage but almost no distortion.  $\times 3.4$ .

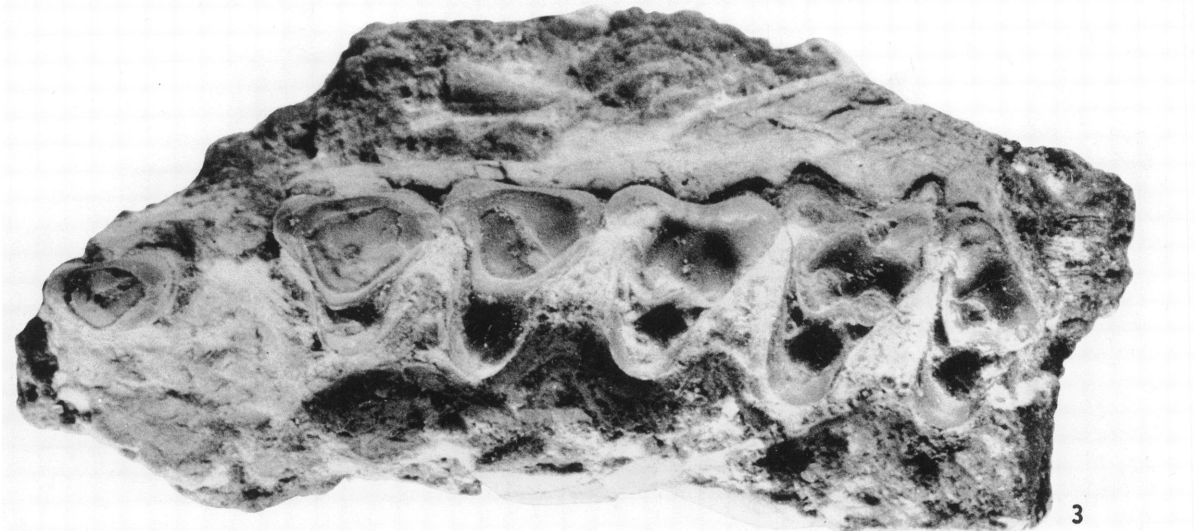
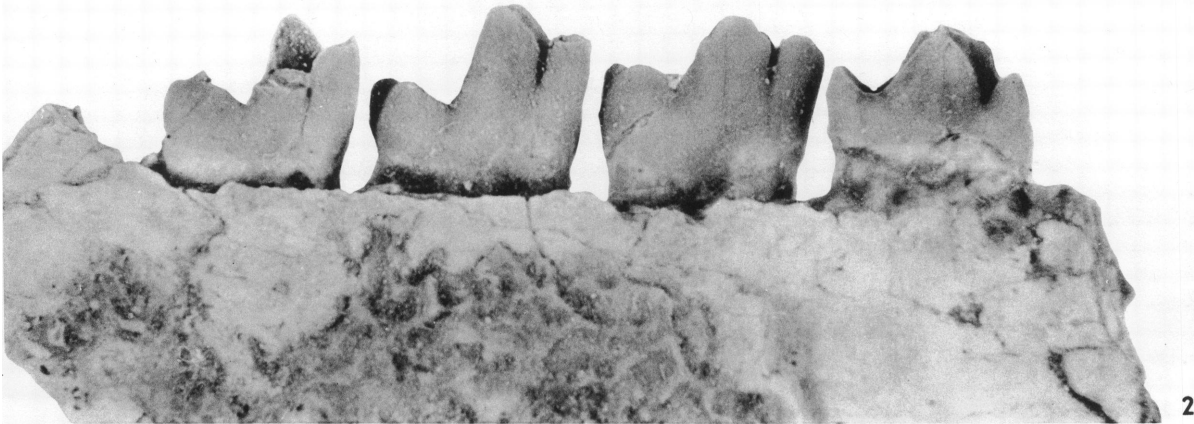
2-5. Unretouched photographs of *Gelastops parvus* Simpson; Gidley Quarry. 2. Occlusal view of right mandible with C and P<sub>3</sub>-M<sub>1</sub>, A.M.N.H. No. 35226.  $\times 7.5$ . 3. Lingual view of right mandible with C and P<sub>3</sub>-M<sub>1</sub>, A.M.N.H. No. 35226.  $\times 5.8$ . 4. Occlusal view of left M<sup>2</sup>, U.S.N.M. No. 9554.  $\times 6$ . 5. Posterior view of left M<sup>2</sup>, U.S.N.M. No. 9554.  $\times 6$ .

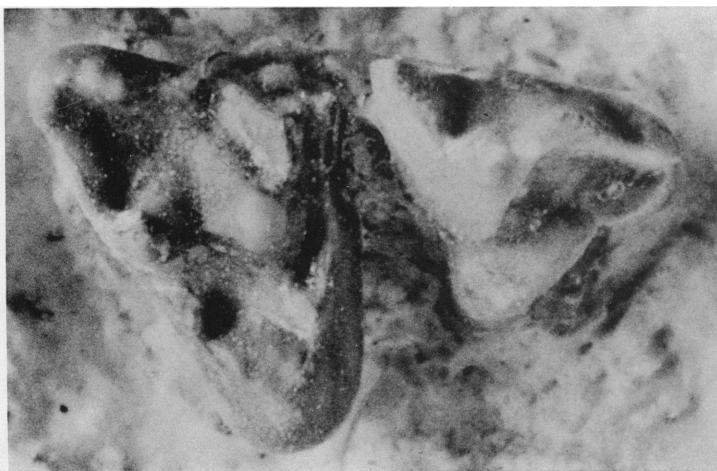
6. Unretouched photograph of *Avunculus didelphodonti*, new genus, new species. Lingual view of A.M.N.H. No. 35297, left P<sub>3</sub>-M<sub>1</sub>, type specimen; Gidley Quarry.

### PLATE 3

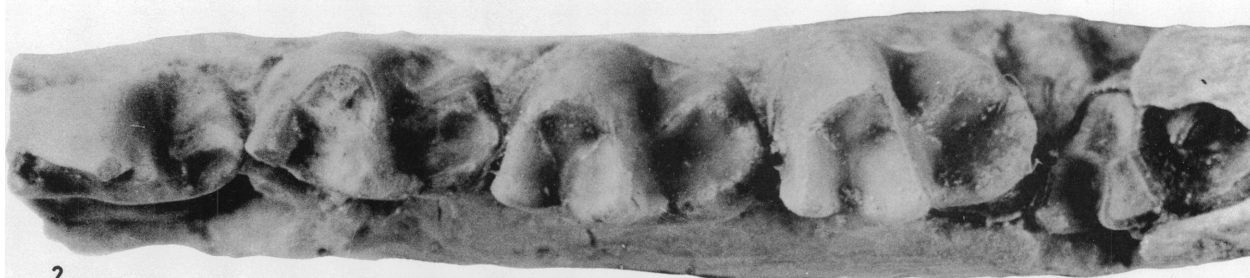
1, 2. Unretouched photographs of left  $P_4$ - $M_3$ , A.M.N.H. No. 16825, type of *Didelphodus absarokae secundus* Matthew; Gray Bull. The metaconid of  $M_3$  and part of the protoconid of  $P_4$  are broken away. 1. Occlusal view. 2. Lingual view. Both  $\times 7.6$ .

3. Unretouched photograph of occlusal view of left  $P^2$ - $M^3$ , *Didelphodus altidens* (Marsh), U.S.N.M. No. 18369; Lost Cabin. The paracones of  $P^{2-4}$ , the protocone of  $P^3$ , the paracone and metacone of  $M^{2-3}$ , and the parastylar and metastylar areas of  $M^2$  are partially broken away.  $\times 7$ .

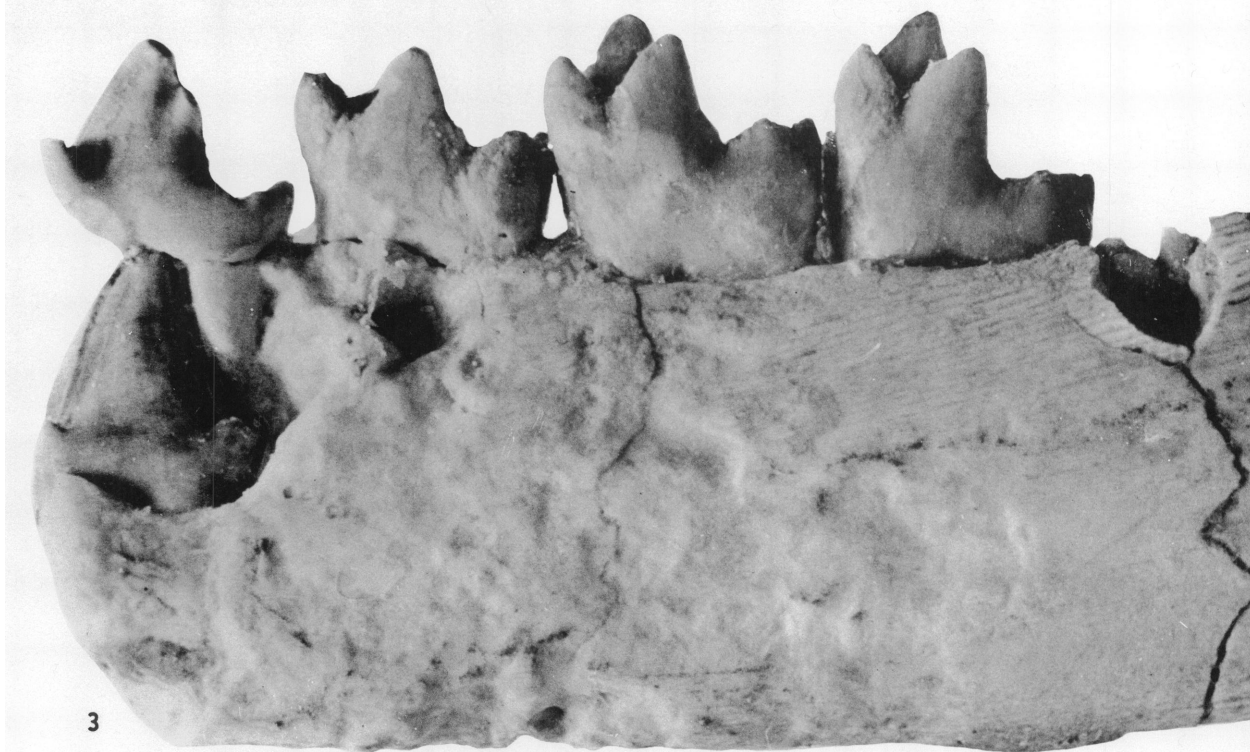




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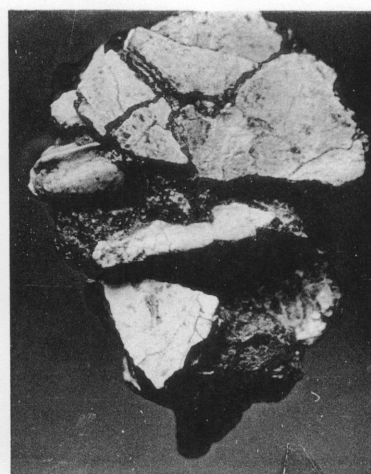
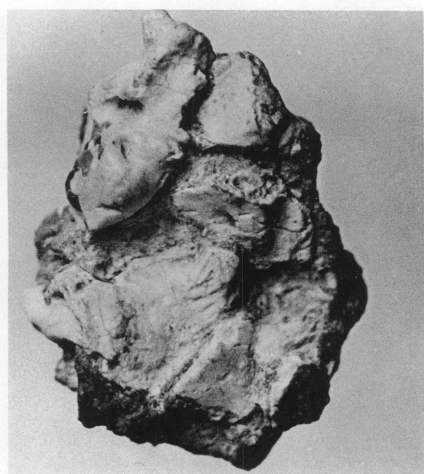
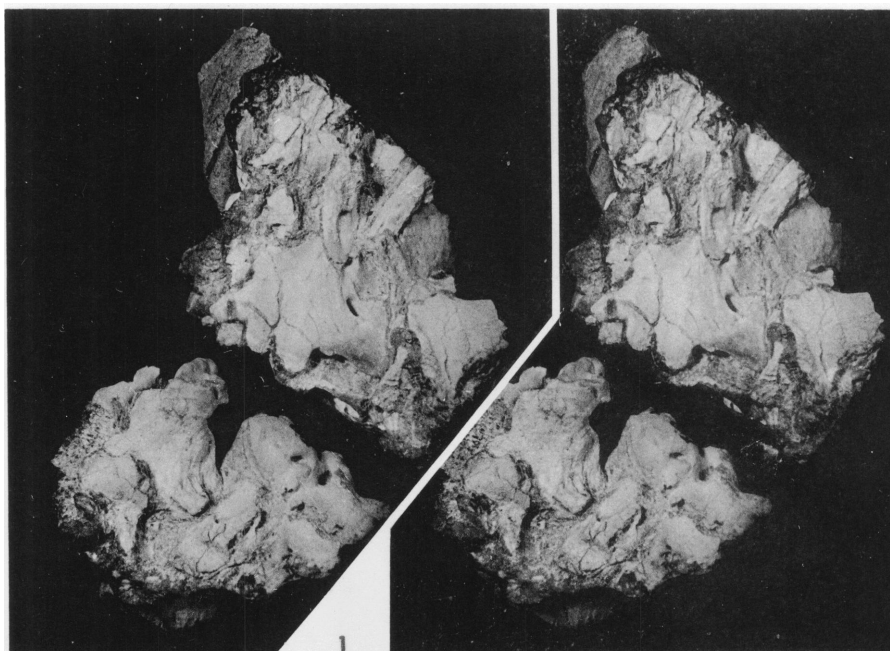
3

PLATE 4

1-3. Unretouched photographs of *Didelphodus altidens* Marsh, M.C.Z. No. 3461; Lost Cabin. The protoconid and part of the metaconid of  $M_3$ , the protoconid of  $DP_4$ , the anterior root of  $DP_3$ , and part of the parastylar area of  $M^1$  are broken away. Part of bone removed to expose unerupted  $M_3$ . 1. Occlusal view of right  $DP^4-M^1$  (possibly  $DP^3-4$ ).  $\times 12$ . 2. Occlusal view of right  $DP_3-M_3$ .  $\times 10.7$ .

#### PLATE 5

1-3. Unretouched photographs of broken and distorted basicranium of *Didelphodus altidens* (Marsh), U.S.N.M. No. 18369; Lost Cabin. See text figure 7 for interpretation. 1. Stereophotographs of ventral view. The lateral face of the right mastoid is conspicuous to the left of the left promontorium; the internal auditory meatus is partly visible on the now anterior surface of the right petrosal.  $\times 2.8$ . 2. Posterior region, ventral view.  $\times 3.7$ . 3. Internal side of right promontorium projecting through dorsal surface of skull. The carotid groove is conspicuous.  $\times 3.7$ .



2

3

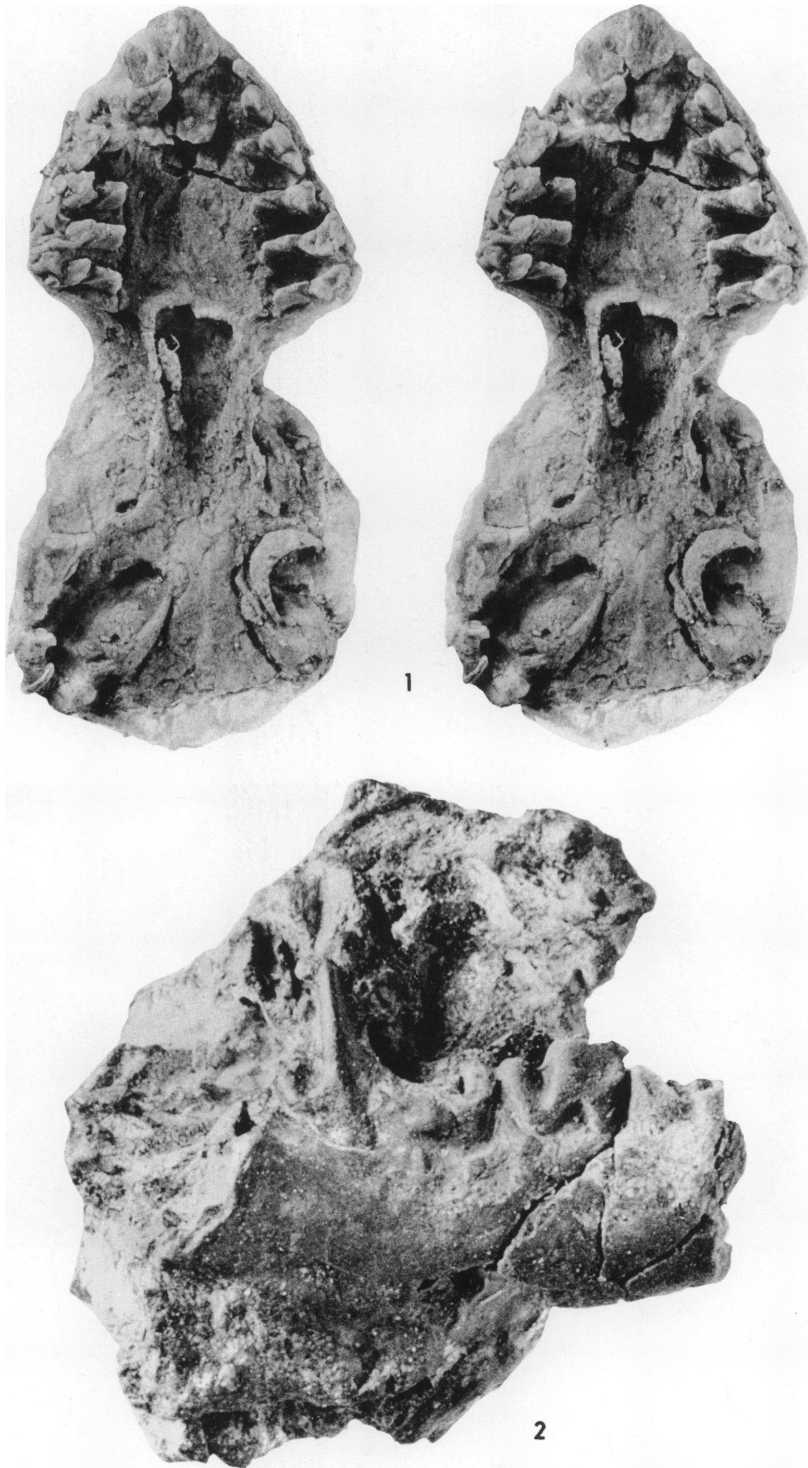


PLATE 6

1. Unretouched stereophotographs of type skull of *Palaeoryctes puercensis* Matthew, A.M.N.H. No. 15923; Torrejon. The teeth are partly broken in various ways. See text figure 11 for interpretation of basicranium.  $\times 4.3$ .

2. Unretouched photograph of labial view of right mandible with  $P_4$ - $M_3$  of *Palaeoryctes punctatus*, new species, A.M.N.H. No. 15850, type specimen; Clark Fork. The trigonids of  $P_4$ - $M_2$  are broken off.  $\times 8.4$ .

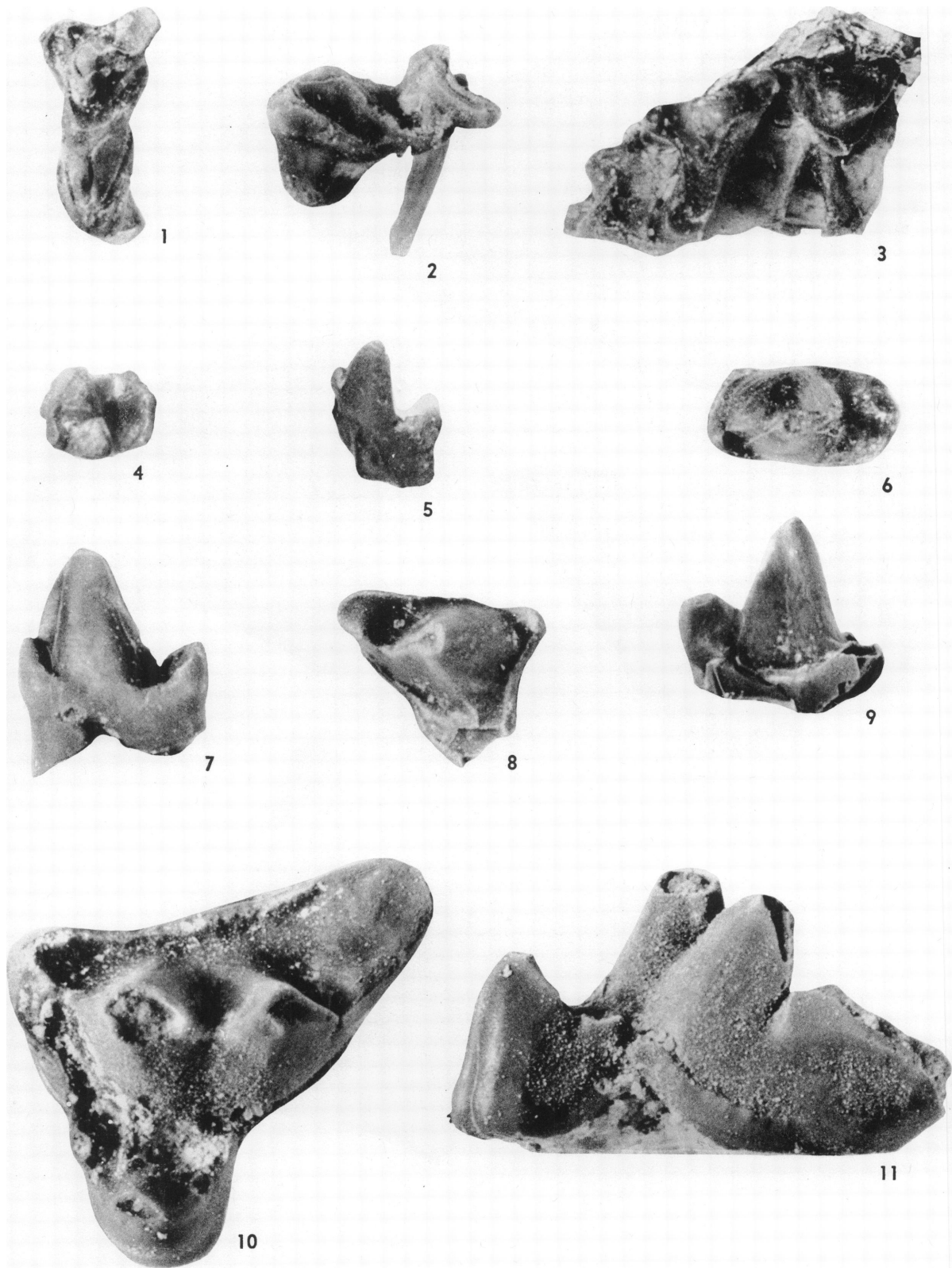
## PLATE 7

1-5. Unretouched photographs of *Pararyctes pattersoni*, new genus, new species; Bison Basin. 1. Occlusal view of U.W. No. 2002, left M<sup>1</sup>, type specimen. 2. Posterior view of U.W. No. 2002, left M<sup>1</sup>, type specimen. 3. Occlusal view of U.W., No. 2005, left P<sup>4</sup> and labial half of M<sup>1</sup>. 4. Occlusal view of U.W. No. 2003, right M<sub>1</sub> with apices of metaconid and protoconid broken away. 5. Lingual view of U.W. No. 2003, right M<sub>1</sub> with anterior root and apices of metaconid and protoconid broken away. Note steep anterior rise of base of enamel. All  $\times 11.8$ .

6, 7. Unretouched photographs of right P<sub>4</sub> of Genus B, A.M.N.H. No. 59910; lower fossil level of Puerco. 6. Occlusal view. 7. Lingual view. Both  $\times 12.7$ .

8, 9. Unretouched photographs of right P<sup>4</sup> of Genus B, A.M.N.H. No. 59896; lower fossil level of Puerco. Protocone broken away. 8. Occlusal view. 9. Labial view. Both  $\times 12.7$ .

10, 11. Unretouched photographs of left ?DP<sup>4</sup>, cf. *Prolimnocyon atavus*, U.C.M.P. No. 44772A; Four Mile. 10. Occlusal view. 11. Posterior view. Both  $\times 12$ .





# PLATE 8

1. Unretouched photograph of occlusal view of right P<sup>4</sup>-M<sup>1</sup> of *Oxyaena simpsoni*, new species, A.M.N.H. No. 48538, type specimen; San José. The paracones of P<sup>4</sup> and M<sup>1</sup> and the metacone and metastyle of M<sup>1</sup> are broken away. ×4.4.
2. Unretouched photograph of occlusal view of left M<sup>1</sup> of A.M.N.H. No. 48539, cf. *Oxyaena*, sp. B; San José. Apices of paracone and parastyle broken away. ×8.
3. Unretouched photograph of occlusal view of right premolariform tooth, possibly P<sup>3</sup> of *Acmeodon*. U.S.N.M. No. 15774; Dragon. Apices of all cusps broken away. ×12.5.
- 4, 5. Unretouched photographs of left lower molar of deltatheridian, A.M.N.H. No. 22220; Bear Creek. Posterolingual edge of talonid broken away. 4. Occlusal view. The trigonid is distinctly broader than the talonid; the material labial to the latter is matrix. 5. Lingual view. Both ×12.6.





