

THE MIACIDAE (MAMMALIA,
CARNIVORA)

PART 1. THE SYSTEMATICS OF
ICTIDOPAPPUS AND *PROTICTIS*

GILES TERNAN MAC INTYRE

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 131 : ARTICLE 2 NEW YORK : 1966

THE MIACIDAE (MAMMALIA, CARNIVORA)



PART 1. THE SYSTEMATICS OF ICTIDOPAPPUS AND PROTICTIS

GILES TERNAN MAC INTYRE

*Instructor in Biology
Queens College, Flushing, New York*

SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY, IN THE
FACULTY OF PURE SCIENCE,
COLUMBIA UNIVERSITY

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 131 : ARTICLE 2 NEW YORK : 1966

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 131, article 2, pages 115–210, text figures 1–21,
plates 1–20, tables 1–12

Issued March 7, 1966

Price \$5.00 per copy

CONTENTS

INTRODUCTION	119
Scope and Purpose	119
History	120
Materials	120
Tooth Nomenclature	121
Statistics	125
Measurements	126
Illustrations	126
Abbreviations	126
Acknowledgments	126
STRATIGRAPHY AND GEOGRAPHY	129
The Meaning of the Word "Locality"	129
Nacimiento Formation	129
Some Topographic Features in the San Juan Basin	132
Lebo Formation	136
Shotgun Local Fauna	137
SYSTEMATICS	139
<i>Ictidopappus</i> Simpson, 1935	140
<i>Ictidopappus mustelinus</i> Simpson, 1935	140
?Cf. <i>Ictidopappus</i> , Unnamed New Species	146
<i>Protictis</i> Matthew, 1937, New Rank	148
<i>Protictis (Protictis)</i> Matthew, 1937	149
<i>Protictis (Protictis) haydenianus</i> (Cope, 1882).	149
<i>Protictis (Protictis)</i> sp..	166
<i>Protictis (Simpsonictis)</i> Mac Intyre, 1962, New Rank	168
<i>Protictis (Simpsonictis) tenuis</i> (Simpson, 1935)	168
<i>Protictis (Simpsonictis)</i> cf. <i>tenuis</i>	173
Cf. <i>Protictis (Simpsonictis)</i>	175
<i>Protictis (Bryanictis)</i> , New Subgenus	176
<i>Protictis (Bryanictis) microlestes</i> (Simpson, 1935)	177
<i>Protictis (Bryanictis)</i> cf. <i>microlestes</i>	189
<i>Protictis (Bryanictis) vanvaleni</i> , New Species	190
GENERAL DISCUSSION	195
Ecological Adaptations	195
Taxonomy.	196
Viverravine Relationships	197
Miacid Relationships	198
SUMMARY	206
REFERENCES	207

INTRODUCTION

MOST OF THE MAMMALS that lived near the end of the Mesozoic Era were evidently omnivorous or carnivorous, judged from their comparatively rare fossils. All the therian mammals of the late Cretaceous Period and most of those of the Paleocene Epoch show variations on the primitive tribosphenic dental pattern which had appeared in the early Cretaceous. By the time the placental mammals had become large and numerous enough to leave a good fossil record, they had also attained a uniform dental formula with the standard number of three molar teeth, four premolars, a canine, and three incisors on each side of the jaw.

By the beginning of the middle Paleocene, at least two kinds of small flesh-eaters had evolved—miacids and creodonts. The core families (Hyaenodontidae and Oxyaenidae) of the Creodonta are clearly related more closely to each other than they are to the Miacidae. The classic difference between these families lies in the emphasis on different pairs of opposing teeth as the main carnassials (the meat-cutting teeth). In primitive hyaenodontids, all three of the lower molars have some shear against their opposite numbers in the upper dentition; this is true of primitive mammals in general. In advanced hyaenodontids, there is an emphasis on M^2-M_3 ; in limnocyonids and oxyaenids, the carnassial pair is M^1-M_2 ; but, in miacids and all modern families of Carnivora, the carnassial pair is P^4-M_1 . There are other characters which serve to distinguish the Carnivora from the Creodonta (even isolated fragments of teeth may in some cases be distinguishable), but the above are sufficient to indicate that the living Carnivora were probably derived from the miacids and not from any of the creodont families.

The order Carnivora is now so diversified that it is impossible to frame a satisfactory, comprehensive diagnosis, but there is no serious disagreement over which of the living mammals belong in this order. Of the living carnivores, the Viverridae have probably retained most of the superficial features of the Miacidae. Most miacids were generally about the size and shape of a modern mon-

goose, although the smallest were about the size of a weasel, and the largest reached that of a wolf. The reconstructed jaw length of *Protictis* (*Protictis*) *haydenianus* is about 75 mm., which indicates an animal somewhat smaller than the living *Alopex* (Arctic fox; jaw length, about 80 mm.). The jaw of *P.* (*Bryanictis*) *microlestes* (estimated, 42 mm.) indicates a distinctly smaller animal but not one so small as the diminutive *P.* (*Simpsonictis*) *tenuis* (estimated, 28 mm.).

The two subfamilies of the Miacidae are most easily distinguished by the absence of M_3^3 from the Viverravinae and the presence of these teeth in the Miacinae. Otherwise, miacids have the dental formula of other primitive Eutheria. As the last molars were thus certainly present in their common ancestry, the miacines are more primitive than the viverravines in this respect. But the Miacinae are not known in the fossil record until the beginning of the Eocene, when they appear (already somewhat diversified) in both Europe and North America. The Viverravinae first appear abundantly in the middle Paleocene of North America, and one isolated tooth, apparently of a viverravine, now suggests that members of this subfamily were present here at the very beginning of the Paleocene (see text fig. 12).

As one might expect, the Paleocene viverravines are generally more primitive than the known Miacinae of the Eocene, and the typically Eocene Viverravinae (which appear first in the late Paleocene of North America) are clearly more advanced than their middle Paleocene ancestors. It is noteworthy that the earliest Eocene Miacinae have nothing about them that suggests direct descent from known Paleocene Viverravinae, although there are several features that suggest common ancestry.

SCOPE AND PURPOSE

The present paper is intended to set forth our current knowledge of the oldest miacids, as far as can be deduced from the fossils now available to me. Most of the forms discussed here have not been studied in detail for more than a quarter of a century. In this period

the number of available fossils has increased sharply, and new techniques of preparation have exposed some previously concealed features. Few really novel specimens have been found in the interim, but restudy of all the collections has led to some changes in the older classification and some new opinions about the beginnings of miacid evolution.

As the great radiation of the living Carnivora had its beginnings in the Miacidae, it would be best to begin with the common ancestors of the two miacid subfamilies. But these ancestors are still unknown.

If we assume that the ancestral miacids generally resembled the known Paleocene forms (except that the former had M_3^3), it is logical to begin with a close scrutiny of the primitive viverravines. Studies of the later viverravines and miacines have been partly completed and will be published later; the information now available on these is used here when needful.

HISTORY

Most of the forms discussed here were originally described by Cope, Matthew, and Simpson. It would be difficult to name a more illustrious trio of predecessors, and it has been correspondingly difficult to find reasons to justify a revision. As the particular history of each taxon is adequately covered in the discussions of genera and species below, it is necessary to mention here only the major papers which dealt with miacid classification in more general terms.

Cope (1882) described the first known Paleocene miacid, later summarizing his views on miacid (and other) classification in his monumental monograph of 1884 (Cope, 1884a). His original diagnosis of the Creodonta (Cope, 1875) included miacids, and he subsequently maintained this view.

Matthew (1909, 1915, 1937) provided a series of monographs on Paleocene and Eocene fossil mammals which adequately reviewed almost all the previous literature on miacids (among other groups) and supplied successively more succinct diagnoses of the family Miacidae. He consistently regarded the miacids as Creodonta, while recognizing (Matthew, 1929) their affinities with the later Carnivora.

Simpson (1937a, 1937b) added several pre-

viously undescribed forms and first studied miacids from a thoroughly modern viewpoint, using statistical methods for the first time in the study of this family. In his first major classification of the mammals (Simpson, 1931), he followed Cope and Matthew in assigning the miacids to the Creodonta; later (Simpson, 1945) he adopted the current opinion, first stated by Schlosser (1886), that they belong in the Carnivora.

Although a fuller discussion of the relationships between the miacids and the creodonts (*sensu stricto*) may be justified when all the miacids have been studied in detail, it now suffices to say that the close relationship between the miacids and the later fissipedes is unequivocal. On the other hand, the relationship of the creodonts to the miacids is at least debatable, so the major classification of Simpson (1945) is followed here.

The proposals of Wortman and Matthew (1899) and Wortman (1901) to include the miacines in the Canidae, and the more radical proposal of Gregory and Hellman (1939) to unite all the miacids with the Viverridae, have not been generally adopted. I agree in substance with Matthew (1909) in his implicit rejections of the proposals of Wortman and Matthew (1899), Matthew (1901), and Wortman (1901). I also agree with Simpson (1945) in his explicit rejection of the proposal of Gregory and Hellman (1939). Because these radical reclassifications are not particularly germane to the Paleocene miacids, further discussion is reserved for future papers on more directly related topics. The proposal of new names in bibliographic works such as those of Hay (1902, 1929–1930) will be mentioned in the synonymy of future papers where appropriate, but such derivative works have little bearing on the present discussion.

MATERIALS

Although more Paleocene miacid fossils are now available than ever before, they are still far from being as complete and plentiful as might be wished. About 120 individuals are represented in the species discussed here; the vast majority are represented by fragments of jaws and teeth, and only two include some scraps of postcranial skeleton.

A distinguished specialist in fossil reptiles has jocularly remarked that it often seems as

if the history of mammals consisted of sets of teeth mating and giving rise to other sets of teeth and so evolving more sets of teeth. Working with mammalian teeth does have some obvious limitations, but it also has some advantages which are obvious to the specialist but bear restatement from time to time.

Tooth enamel is the hardest substance in the body and in some cases the only part that survives in the fossil record. The teeth of primitive mammals are usually their most characteristic hard parts, often reflecting adaptations to particular kinds of food and hence providing an insight into their ecology by comparison with similar living forms. The crown pattern is predetermined by the genetic constitution of the individual and is fully formed (in brachydont teeth at least) by the enamel organ before the teeth are ever used. When they erupt, the enamel organ is ruptured, and thereafter the only possible changes are the destructive ones caused by wear, breakage, or decay. For the evolutionist, mammalian teeth are among the best materials for study, because changes in pattern must be caused by changes in the genetic constitution of the previous generation and normally cannot be affected by the age or personal history of individuals. Muscles, hence their bony attachments, become stronger under repeated stress and will weaken if not stressed. But once the teeth are fully erupted, no amount of exercise will increase the diameter of the crown, shift the relative positions of the cusps, or add a single wrinkle to the surface.

It is probably advisable to note in passing that the detailed (and often tedious) descriptions of most of the forms given here were written for slightly different reasons. The descriptions of *Ictidopappus mustelinus* and *Protictis* (*Simpsonictis*) *tenuis* are given because there are so few specimens, in order to facilitate future identification. In the case of *P. (Bryanictis) microlestes*, the object is to show the kinds and degree of variation within a single population sample. The details of *P. (Protictis) haydenianus* are discussed in full because the numerical data do not do justice to the range of morphology observed in the rather heterogeneous samples of this species; the reason here is to show what variants are present, so that, if and when future collections

from quarry sites are made, comparisons with all the surface collections can be undertaken in the search for constant differences among subsamples.

TOOTH NOMENCLATURE

It is clear that mammalian teeth are both commonly preserved as fossils and comparatively free from the effects of environmental (using this word in the broadest sense to include both internal and external environment) changes in the phenotype. In the present case, there is a final and compelling reason why the teeth are important: there is very little else known of these animals.

The specimens have been studied both qualitatively and quantitatively. The qualitative studies are summarized in detailed descriptions for all known forms. In these descriptions, the emphasis has been upon the variations in form and proportion which cannot be expressed simply in quantitative terms.

Text figure 1 summarizes the terminology used to describe tooth cusps in this paper. Virtually all the terms are standard, perhaps the only innovations being some modifications of the customary homologies implied by names given to the accessory cusps on the premolars. The reasons for these changes are explained in the discussion of *Protictis* (*Bryanictis*) *vanvaleni*.

Butler (1956) has pointed out that crests are not stable primary features but form along lines of tension between developing cusps in ontogeny. They may be "captured" if new cusps become more important than older ones. Some kinds of teeth have cusps that are conical or smoothly rounded, lacking many of the crests seen in primitive teeth. When present, crests are important functional parts of the crown pattern and must be considered when one is discussing occlusion in primitive dentitions. I do not believe it is necessary to add new terms when a slight modification of the familiar Cope-Osborn nomenclature will serve the same purpose.

I have accordingly referred to most crests and cingula by simple geographic terms or by appropriate modifications of the names of those cusps with which the crests are associated, *whether or not such cusps are actually distinguishable*.

For example, the crest from the paracone

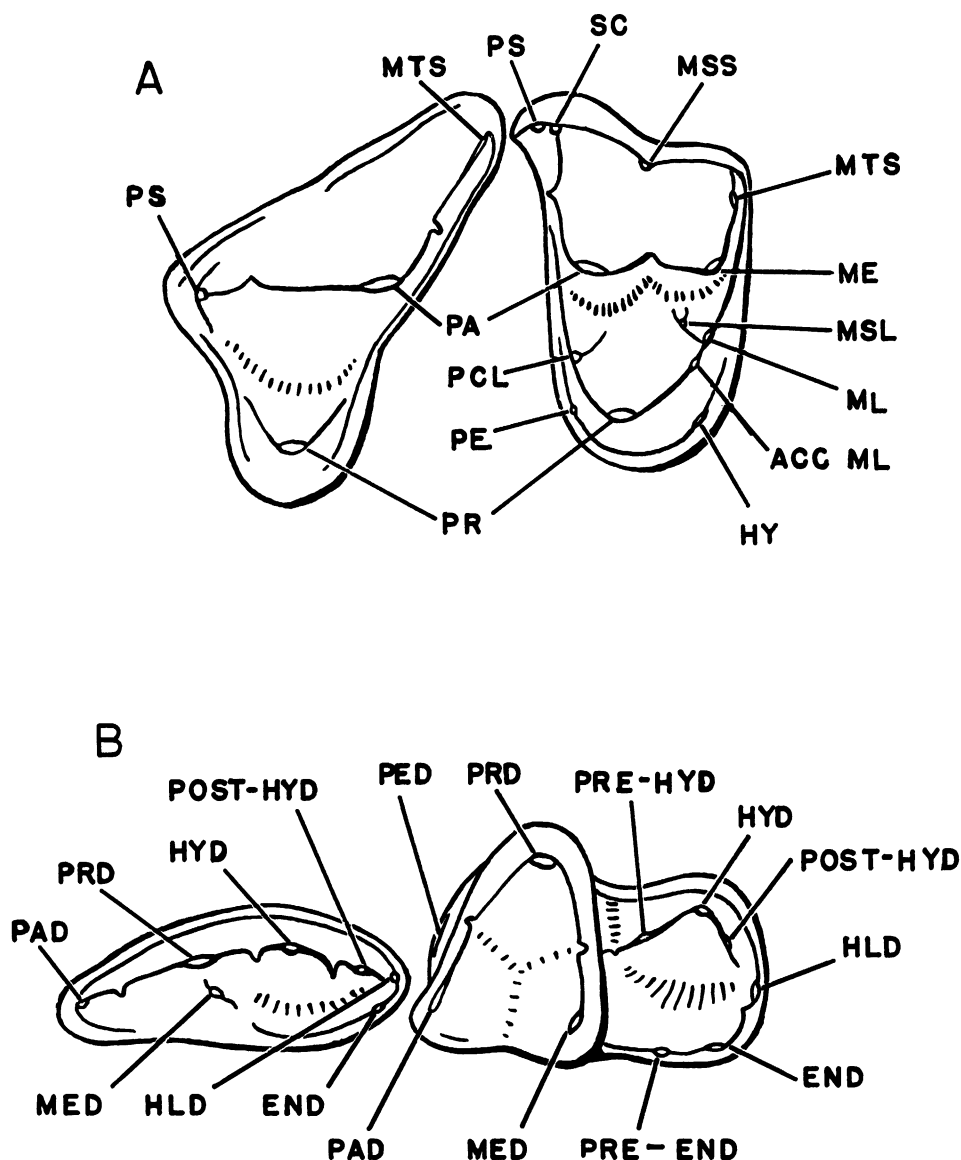


FIG. 1. Diagrammatic occlusal views of generalized miacid dentition, illustrating cusp terminology. A. Left upper teeth. B. Right lower teeth.

Abbreviations: ACC ML, accessory metaconule; END, entoconid; HLD, hypoconulid; HY, hypocone; HYD, hypoconid; ME, metacone; MED, metaconid; ML, metaconule; MSL, mesoconule; MSS, mesostyle; MTS, metastyle; PA, paracone; PAD, paraconid; PCL, paraconule; PE, pericon; PED, periconid; POST-HYD, post-hypoconid; PR, protocone; PRD, protoconid; PRE-END, pre-entoconid; PRE-HYD, pre-hypoconid; PS, parastyle; SC, stylocone.

to the stylocone (called simply the *paracone-stylocone* crest), which is a typical feature of Cretaceous therians, remains as a typical feature of the miacid M^1 , but the stylocone cusp *per se* is usually reduced to a mere crenulation and may be indistinguishable.

Text figure 2 explains the names applied to some crests, cingula, basins, and similar features found in primitive teeth. In general, miacid teeth preserve most or all of the primitive cusps and crests observable in Cretaceous therians (see Patterson, 1956), and all

but a few names will be obvious to anyone familiar with the standard nomenclature. A few terms which are new or peculiar to carnivores may be defined here.

CARNASSIAL NOTCH: The sharp excavation in the form of an inverted keyhole which occurs between the main shearing blades on meat-cutting teeth. In miacids, a carnassial notch occurs between paracone and metastyle on P^4 and between protoconid and paraconid on M_1 . In highly specialized carnivores, the carnassial notch may be elongated into a slitlike groove, called the *carnassial slit*; similarly shaped but less emphatic structures occur elsewhere in carnivore dentitions and may be called *carnassiform* notches.

PROTOCONE BASIN: The more or less excavated area labial to the protocone and lingual to the paracone-metacone crest. The corresponding flat or slightly depressed area on the labial side of the paracone-metacone crest is the familiar *stylar shelf*.

SULCUS OBLIQUUS: The groove (usually touched by the paracone of the opposing upper tooth) between the anterolabial base of the hypoconid and the posterolabial base of the protoconid. The sulcus obliquus is separated from the talonid basin by the *crista obliqua*, the usual crest from the hypoconid to the posterior face of the trigonid.

TRIGONID BASIN: The depression surrounded in part by the cusps of the trigonid, analogous to the familiar *talonid basin*.

The tall trigonid of the miacid lower carnassial is received by a cavity in the maxilla between the lingual roots of P^4 and M^1 ; the corresponding cavity between M^{1-2} is usually smaller (because the trigonid of M_2 is normally lower than that of M_1 in miacids) and may be imperceptible in some. Prominent *embrasure cavities* of this sort obviously correlate with the high trigonid of the lower molars—if the lower molar has a low trigonid, the reverse, obviously enough, will be observed.

This point is of some importance in the matching of unassociated lower and upper dentitions and is cited in the description of *Ictidopappus mustelinus* and will be cited in connection with some of the miacines to be discussed in a later paper.

At least two distinct sorts of wear surfaces are observable on the teeth of carnivores, and as far as possible I have tried to state

explicitly which kind of wear is meant in the descriptions. The first and perhaps most obvious variety of wear is the *shear facet*, caused by tooth-on-tooth action. This kind of wear in miacids is characteristically exemplified by the flattened facet on the posterior surface of the metastyle blade of P^4 and the anterior face of the M_1 trigonid. Shear facets are likely to be worn to oblique, flat surfaces, sometimes scored or scratched by the action of the opposing tooth. The edges of shear facets tend to become sharper as they are worn, although, as wear continues, these sharp edges may become chipped or splintered if they are honed down too rapidly.

The second type of wear occurs at the edges of crests or cusps (such as those of the anterior premolars) which do not actually touch the opposing teeth. This wear is caused by tooth-on-food abrasion and may be distinguished as *non-occlusal attrition*. Characteristically with age, such attrition surfaces show differential wear of exposed dentine and enamel, so that the edges of the resistant enamel stand up as ridges smoothly convex and distinct from the smoothly concave surface of the softer dentine. *Apical attrition* is often of this kind, resulting in the familiar *wear crater* at the tip of a cusp, resembling a volcano.

Carnivores are well known for their habit of gnawing bones. This chewing of hard substances may cause *equal* wear of enamel and dentine, so that, instead of a typical wear crater, the apices of cusps (anterior premolars may be cited again as an example) are worn smoothly flat, resulting in the appearance of a seamount or guyot top.

This peculiar variety of *horizontal attrition* may be distinguished from tooth-on-tooth shear by the fine chipping or rounding of the external enamel surface at the edges of the wear surface (*not* oblique as in tooth-on-tooth shear).

There is a third type of wear caused by the rubbing of adjacent teeth in the tooth row upon each other. This is notable in carnivore lower molars and premolars on the posterior surface of the talonid below the hypoconulid and on the anterior surface of the trigonid at the base of the paraconid. Such *vertical attrition* surfaces are also seen on the parastyle and metastyle corners of upper molars and posterior premolars. Al-

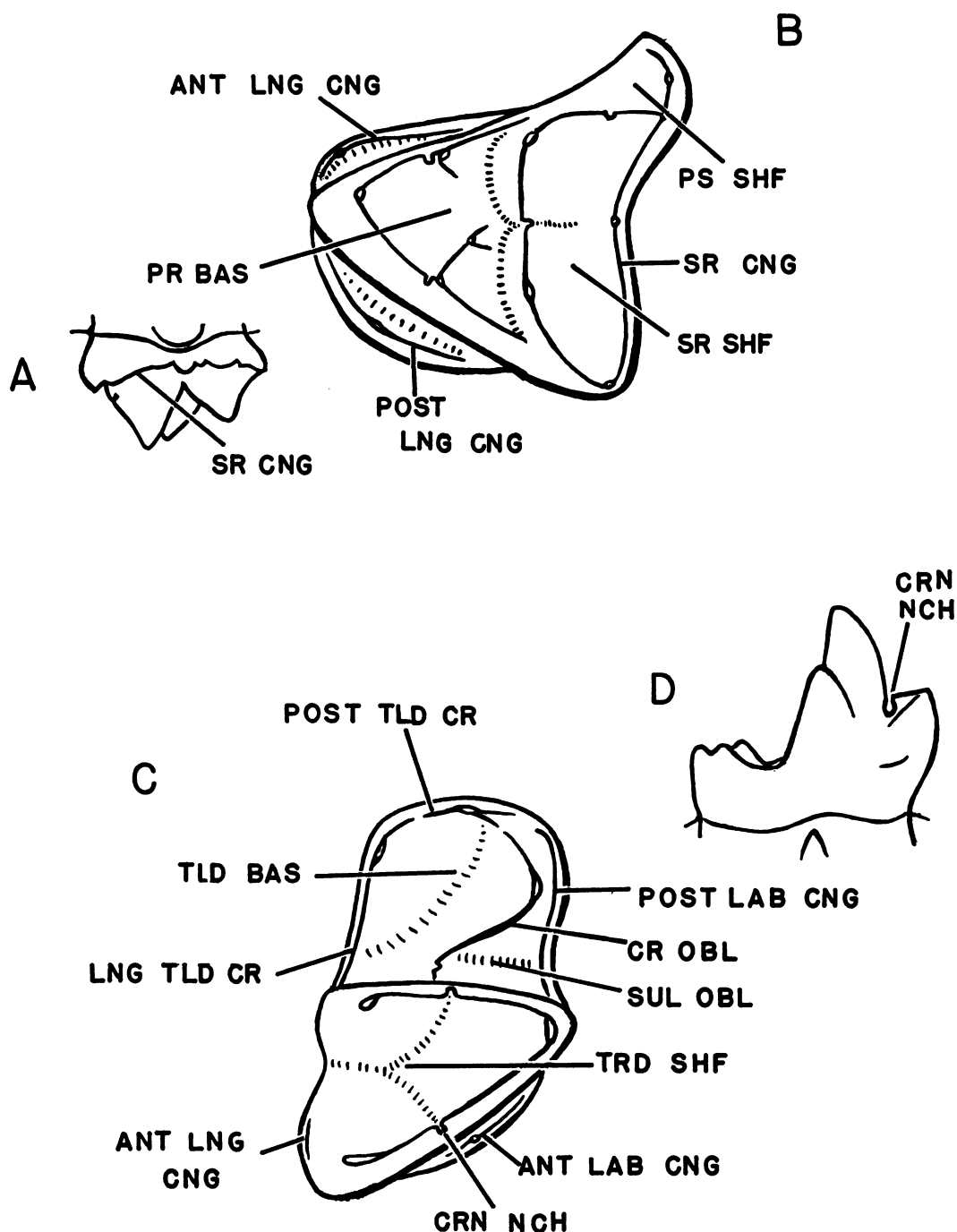


FIG. 2. Diagrams of generalized miacid molars, illustrating crest terminology. A. Labial view of upper molar. B. Occlusal view of upper molar. C. Occlusal view of lower molar. D. Lingual view of lower molar.

Abbreviations: ANT LAB CNG, anterior labial cingulum; ANT LNG CNG, anterior lingual cingulum; CRN NCH, carnassial notch; CR OBL, crista obliqua; LNG TLD CR, lingual talonid crest; POST LAB CNG, posterior labial cingulum; POST LNG CNG, posterior lingual cingulum; POST TLD CR, posterior talonid crest; PR BAS, protocone basin; PS SHF, parastyle shelf; SR CNG, stylar cingulum; SR SHF, stylar shelf; SUL OBL, sulcus obliquus; TLD BAS, talonid basin; TRD SHF, trigonid shelf.

though the absence of this sort of facet does not prove that adjacent teeth (in damaged specimens) were absent, the presence of such facets does prove the presence of adjacent teeth, if there are no other clues available.

STATISTICS

The quantitative side of the present study is not elaborate, but wherever possible the specimens have been carefully measured and, wherever the samples warranted, standard statistics (as presented in Simpson, Roe, and Lewontin, 1960) were calculated as part of the normal descriptive process. In all comparisons of samples, Student's *t*-tests were used for measurable dimensions, the results being expressed as values of *P*. The value $P < 0.01$ means that the chances are less than one in 100 that the two samples tested could have been accidentally drawn from populations having the same mean; such a result is taken here as valid evidence that there was in fact a significant difference between the two populations represented by the samples. If $P > 0.05$, the chances are greater than five in 100 that the two samples could have been drawn from the same population. Such differences are not assumed to be significant, although identity of the two samples is not necessarily assumed unless qualitative resemblances indicate that this is so. Intermediate values of *P* are not generally assumed to be significant, although they do indicate a degree of difference which may (or may not) be confirmed by qualitative observations. In this particular study, the nature of the samples made side-by-side comparison of specimens a frequent necessity.

Most samples from single localities are extremely small. Except for one quarry sample of 45 specimens, there are seldom more than half a dozen specimens from any one site, the usual quantity being one or two from each place (that is, if a particular locality has been recorded—the "locality" for many specimens is a laconic notation such as "Puerco-New Mexico").

Despite such limitations, the collection is reasonably extensive, and the parts that have survived are usually well preserved.

The relative reliability of the samples is also important. Samples drawn from a large field or a whole formation are of course not so

unified as those drawn from a single quarry. But this case is precisely wherein the statistical approach proves its value.

For example, in the description of *P. (Proctictis) haydenianus*, the assumption has been that all the known specimens found in the San Juan basin were members of the same species, although not necessarily members of a single local population or subspecies. There is, of course, some uncertainty in this assumption; a considerable time is represented by these sediments, and there is no assurance that some migration did not occur during that time or that some evolutionary change did not occur.

The facts that emerge from both quantitative and qualitative comparisons, however, do not show consistent, verifiable divisions among the different variants observed in the specimens drawn from this formation. It cannot be shown that more than one species is represented. Although the assumption that these specimens do represent one species is not rigidly proved by this procedure, it is the converse to this proposition that must be demonstrated if the differences between specimens are to be recognized formally in modern taxonomy.

The above reasoning applies with equal or greater force to the sample of *P. (Bryanictis) microlestes* from the Gidley quarry. Even without formal statistical comparisons, it is reasonable to assume that quarry samples made up of specimens that are very similar in typical ways were drawn from the same local populations (provided that the geological evidence indicates a quite depositional environment and little or no stream transport). Again, modern taxonomy requires proof that subsamples are really separable before we name new taxa based on these specimens. The statistical information provided about such a quarry sample is given primarily as an index of the variability observable in a sample drawn from a local population. Comparisons with other (usually smaller) samples may then be made on quantitative as well as qualitative bases.

It is clear from study of the Gidley quarry sample of *P. (B.) microlestes*, for instance, that rather high variability in minor cusps and crests should be assumed when one is comparing isolated specimens of Paleocene

miacids. Characteristic or diagnostic features become clear only when the reasonable limits of individual variation are revealed. Application of this criterion may result in concealing some real differences, but it is less likely to burden the literature with useless names. As collections continue to increase, it is almost inevitable that genuinely different taxa will become more clearly recognizable anyway.

MEASUREMENTS

All measurements were made with the same dial micrometer caliper graduated to one-tenth of a millimeter. Readings were taken to the nearest 0.05 millimeter, and all measurements were taken on the tooth enamel well above the root level. Approximate measurements on broken or distorted teeth were recorded on the original data sheets made up for each specimen, but none of these were used in the calculation of the statistics. The following is a list of measurements used, as illustrated by text figure 3 (numbers in brackets refer to points indicated in fig. 3).

PREMOLAR LENGTH (EXCEPT P⁴): Maximum anteroposterior diameter on major axis of tooth [13-15].

PREMOLAR WIDTH: Maximum diameter at right angles to major axis [14-16, 2-5].

LOWER MOLAR LENGTH: Maximum talonid-trigonid diameter [17-23].

LOWER MOLAR WIDTH (ANTERIOR): Maximum diameter, protoconid-metaconid [19-27].

LOWER MOLAR WIDTH (POSTERIOR): Maximum diameter, hypoconid-entoconid [21-25].

GRIND WIDTH (ANTERIOR): M₁ talonid, median, minimum across [20-26]; M¹ median, minimum inner edge to outer [8-11].

GRIND WIDTH (POSTERIOR): M₂ talonid, median, minimum across; M² median, minimum inner edge to outer.

LOWER MOLAR, LENGTH OF TRIGONID: Anterior end of crista obliqua to anterior end of trigonid at right angles to posterior face of trigonid [17-30].

LOWER MOLAR, LENGTH OF TALONID: M₁, most posterior edge of tooth to junction of crista obliqua with trigonid [23-30]; M₂, total length minus trigonid length.

M₁, LENGTH OF PARAONID: From notch to outer limit of cusp [18-28].

M₁, LENGTH OF METACONID: From notch to outer limit of cusp [27-29].

SHEAR LENGTH: Glenoid hinge to carnassial notch.

JAW DEPTH BELOW A TOOTH: Lingual ridge between roots or alveoli of tooth to bottom.

P⁴ LENGTH, LABIAL: Parastyle to metastyle corners [1-3].

P⁴ METASTYLE: Notch to outer limit of cusp [3-4].

P⁴ LENGTH, LINGUAL: Anterior edge of protocone to posterior edge of metastyle [3-6].

UPPER MOLAR LENGTH: Parastyle to metastyle corners [10-12].

UPPER MOLAR WIDTH (ANTERIOR): Diagonally from hypocone corner to parastyle corner [7-11].

UPPER MOLAR WIDTH (POSTERIOR): Diagonally from protocone to metastyle edge [9-11].

ANGLE γ : Formed by anterior and posterior shearing planes of M₁ trigonid or corresponding P⁴-M¹ embrasure, or both.

ILLUSTRATIONS

The scales on all the plates (pls. 1-20) are divided into millimeters and are placed at the plane of focus.

Except for plate 1, figures 3, 4; plate 8, figures 6, 8-11, and plate 20, all photographs are by Mr. R. Van Frank. Text figures 1-3, 6, 7, 13, and 21 are by Miss E. Satzinger.

ABBREVIATIONS

The following abbreviations are used:

- A.M.N.H., the American Museum of Natural History
- C.N.H.M., Chicago Natural History Museum
- P.U.M., Princeton University Museum
- U.Cal.M.P., University of California Museum of Paleontology, Berkeley
- U.S.N.M., United States National Museum, Smithsonian Institution
- U.Wyo., University of Wyoming, Laramie
- N, sample size
- OR, observed range
- M, mean
- s, standard deviation
- V, coefficient of variation
- P, tabulated probability from Student's *t*-distribution

ACKNOWLEDGMENTS

If this study has any merit beyond that of previous investigations, it is very largely due to the present greatly increased accessibility of the fossils. It is likewise true that improved instruments and methods of study, mainly developed by others, have immeasurably enhanced the value of this work.

The entire collections of miacids at the American Museum of Natural History, the

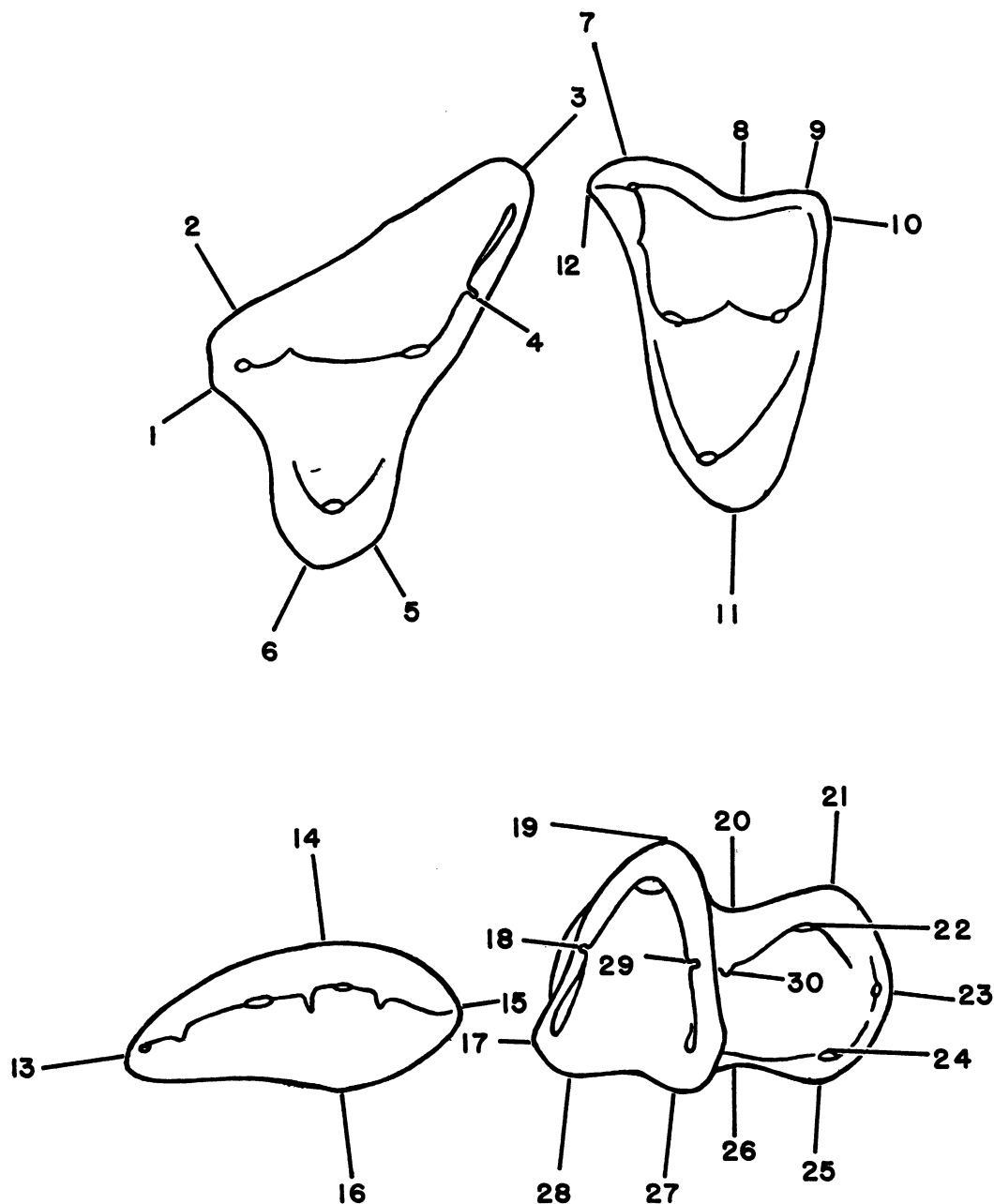


FIG. 3. Occlusal views of P_4^1 - M_1^1 , showing points between which tooth measurements were taken. For details, see page 126.

Yale Peabody Museum, the Museum of Comparative Zoölogy of Harvard University, the Carnegie Museum in Pittsburgh, the Academy of Natural Sciences of Philadelphia, the University of California Museum of Paleontology, and the University of Colorado Mu-

seum were lent for study. Parts of the collections at the Los Angeles County Museum, the United States National Museum of the Smithsonian Institution, the Amherst College Museum, and the Princeton University Museum were also lent, and the latter three

institutions were visited. Many specimens were thus made available for study which could not be borrowed; the collections of the Chicago Natural History Museum and the University of Michigan Museum of Paleontology are also included in the latter category.

Other collections of American Miacidae undoubtedly exist (Wilson, 1951, 1956, has mentioned some Torrejonian miacids in the University of Kansas collection, for example), but these are either under study by others or consist of small collections of species already adequately represented in the collections described here. It is believed that all institutions with collections that might include American Miacidae have been queried about possible loans of specimens.

A few European specimens identified as *Miacoides* were found in some of the above collections, and these will be discussed in a later paper. However, owing to the risk of loss in transit, no attempt has been made to borrow specimens from European institutions. In this connection, I am indebted to Dr. Donald Russell for information concerning European collections.

Proper expression of my deep and lasting gratitude to Dr. George Gaylord Simpson is difficult. He provided the original inspiration for this study, first opened the collections and facilities of the American Museum of Natural

History to me, and has continued to act as guide and critic during the entire project.

Dr. E. H. Colbert and the staff of the Department of Vertebrate Paleontology of the American Museum of Natural History continued to provide research facilities there after Dr. Simpson left, for which I am very grateful. It is a pleasure to acknowledge the benefits gained from many discussions of evolution and anatomy with Drs. Donald Baird, Theodosius Dobzhansky, Glenn L. Jepsen, Karl Koopman, Björn Kurtén, Bryan Patterson, Bobb Schaeffer, and Leigh Van Valen. I am indebted to Drs. C. Black, T. Downs, C. L. Gazin, G. L. Jepsen, P. O. McGrew, B. Patterson, H. Richards, P. Robinson, E. S. Simons, R. A. Stirton, and A. E. Wood for loans of specimens and other help.

Dr. Malcolm C. McKenna read the first draft, suggesting several useful revisions; he has been generous with his new collections and free with his advice and counsel. His help is much appreciated.

Mrs. Pamela Alexander Mac Intyre has been unfailingly helpful, not only with the chore of typing but with the interminable detail work associated with the whole project.

This investigation was carried out during the tenure of Predoctoral Fellowship GF12305 from the Division of General Medical Sciences, United States Public Health Service.

STRATIGRAPHY AND GEOGRAPHY

THE MEANING OF THE WORD "LOCALITY"

THE TERM "LOCALITY" has been used rather loosely in the literature and even on museum labels in the past. For some of the pioneers, "San Juan basin" or "Big Horn, Wyoming" were adequate descriptions of localities. Most modern students are more explicit and give the standard quarter section, township, and range designations or latitude and longitude at least. Some have taken great pains to be precise, giving "localities" almost down to the square foot (e.g., McKenna, 1960). In order to reflect the degree of precision in place designation used by different collectors, the following definitions are proposed:

FIELD: Exposures of fossiliferous rock within recognizable geographic boundaries, including at least one identifiable formation or part thereof.

AREA: A part of a field, with recognizably specific geographic position, yielding fossils from one formation.

LOCALITY: A part of an area, with stated geographic limits, usually about one-quarter or one-eighth of a square mile in size, yielding fossils from given beds within a formation.

SITE: An accurately designated part of a locality, usually about 100 feet square, yielding fossils from essentially the same level.

SPOT: An explicitly delimited small part of a site, usually about 10 or 20 feet square, yielding fossils which can reasonably be assumed to have been buried together.

QUARRY: A spot from which fossils have been obtained in place by digging into undisturbed original deposits.

These are provisionally used in this paper and are subject to future modification. It is hoped that they will serve to stimulate some discussion of what the word "locality" really means.

The above may be illustrated by the following imaginary example:

FIELD: Bighorn basin, Wyoming.

AREA: Head of Elk Creek, latitude 44° 18' N., longitude 108° 24' W. (approximately).

LOCALITY: NW. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 16, T. 50 N., R. 96 W., Big Horn County.

SITE: A.M.N.H. 62, flats below bluff to north of first branch of Elk Creek (see map).

SPOT: A.M.N.H. 62b, ant hill near north side of isolated hummock (see photograph).

QUARRY: A.M.N.H. 62c, in purple clay layer at base of low bluff on line from top of isolated hummock and ant hill A.M.N.H. 62b (see sketch) and about 50 feet from hummock.

Found by the American Museum of Natural History expedition, 1912; Granger, Olsen, and Stein.

Early Eocene (middle Wasatchian), Willwood Formation, Lysite beds, 380-foot level below top of Willwood Formation.

It has not been possible to pinpoint most of the "localities" discussed here so precisely, but text figure 4 indicates the general location of the major North American collecting fields important in the study of miacid evolution. Descriptions of most of these fields, their formations, and their stratigraphic relationships are available in Wood and his co-authors (1941). More detailed and recent information will be found in papers cited in the discussions of special problems below.

NACIMIENTO FORMATION

Protictis (*Protictis*) *haydenianus* is a well-known member of the Torrejon assemblage from the upper parts of this formation, and *P. (Bryanictis) vanvelani* is now added to the miacids in this assemblage. The Puerco assemblage from the lower parts of this formation is not separated from the Torrejon assemblage by any mappable disconformity, but it is generally conceded that the evolutionary differences between the two groups of fossils imply a greater change than one would expect to find within a single formation. The one tooth reported here as ?cf. *Ictidopappus* comes from the lowest level of the formation that has been known to yield fossil mammals. The specimen was one of many collected during an extensive washing operation conducted by the American Museum of Natural History in 1958. Sinclair and Granger (1914) remarked upon the absence of pebbles in the lowest fossil level of these beds, and the 1958 expedition confirmed the absence of pebbles in the tons of sediment that passed through their screens, convincing evidence that these clays were deposited by slowly moving water. The irregular occurrence of light-colored channel sandstones

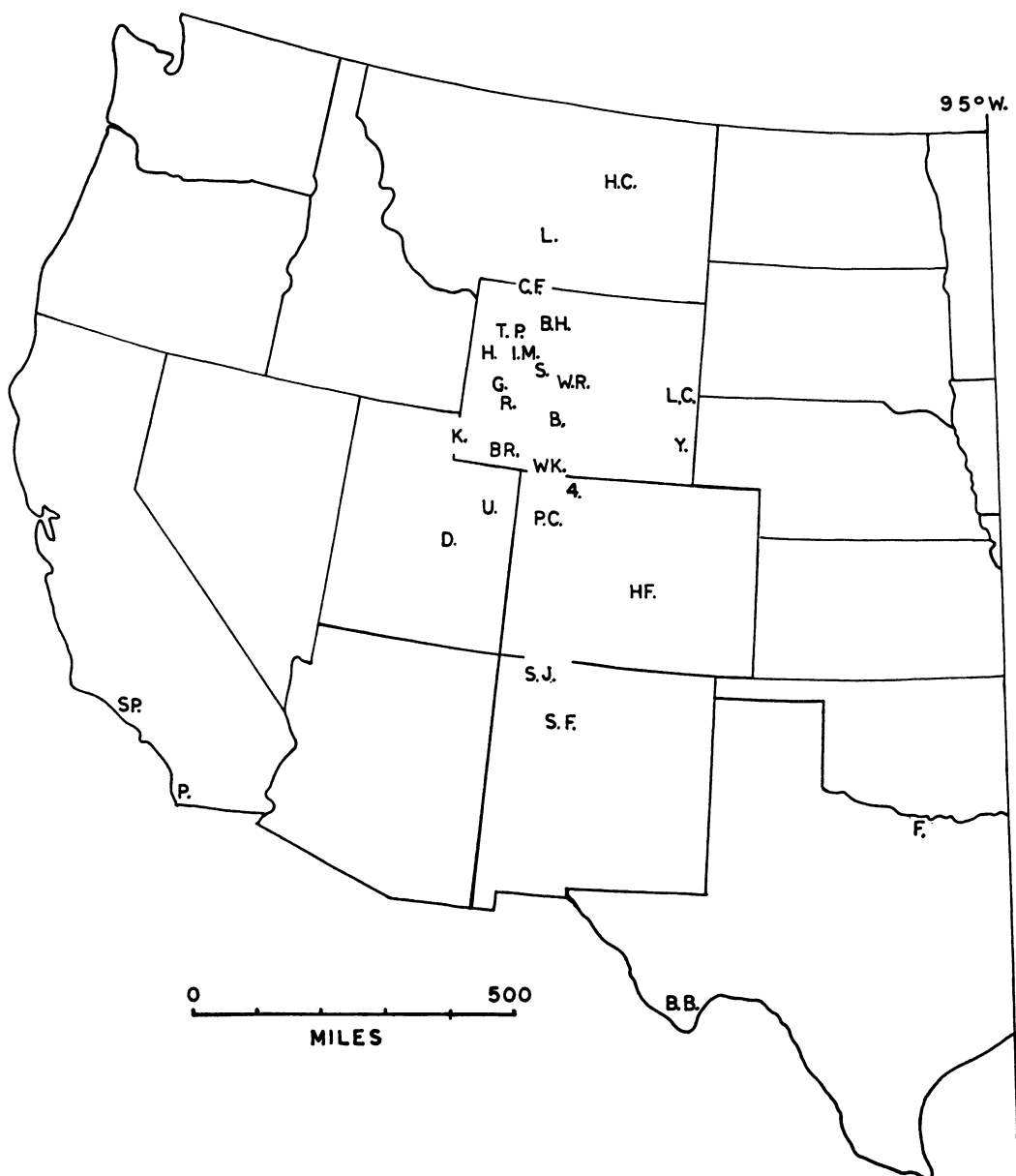


FIG. 4. Important Cretaceous, Paleocene, and Eocene collecting fields west of longitude 95° W. in the United States.

Abbreviations: B., Bison basin, Wyoming; B.B., Big Bend National Park, Texas; B.H., Big Horn basin, Wyoming; BR., Bridger basin, Wyoming; C.F., Clark Fork basin, Wyoming and Montana; D., Dragon Canyon, Utah; F., Forestburg, Texas; G.R., Green River basin, Wyoming; H., Hoback basin, Wyoming; H.C., Hell Creek, Montana; HF., Huerfano basin, Colorado; I.M., Indian Meadows, Wyoming; K., Knight Member, type Wasatch Formation, Wyoming; L., Lebo Formation, Crazy Mountain field, Montana; L.C., Lance Creek, Wyoming; P., Poway Formation, California; P.C., Piceance Creek basin, Colorado; S., Shotgun Member, Wyoming; S.F., Santa Fe field, New Mexico; S.J., San Juan basin, New Mexico; SP., Sespe Formation, California; T.P., Togwotee Pass, Wyoming; U., Uinta basin, Utah and Colorado; WK., Washakie basin, Wyoming and Colorado; W.R., Wind River basin, Wyoming; Y., Yoder Formation, Wyoming; 4., Four-mile Creek, Colorado.

among the clays and the variable nature of the level, rather thin successive beds of varicolored clay suggest meandering streams at or near base level, with occasional swampy lakes. Occasional pockets of silicified fossil wood in some places and the presence of small bits of carbonized plant remains scattered through the clays in other areas suggest that there were grassy or brush-covered areas as well as some trees. Numerous remains of large turtles, alligators, and garpikes reinforce the picture of a warm, humid swamp environment with enough good-sized bodies of water to accommodate these aquatic forms but enough solid ground and vegetation to support a fairly large population of herbivorous

and omnivorous terrestrial mammals. The presence of many large silicified logs in the underlying Ojo Alamo Sandstone indicates rather more heavily forested conditions, although the logs may have been transported from some distance away with the coarser sediments that make up the sandstone. The sediments of the Nacimiento Formation are not strikingly different between the levels that yield the Puercan mammalian faunan and those that yield the Torrejonian mammals, so that the same general type of environment may have persisted with some local changes throughout the time represented by these beds.

Sinclair and Granger (1914, p. 310) divided

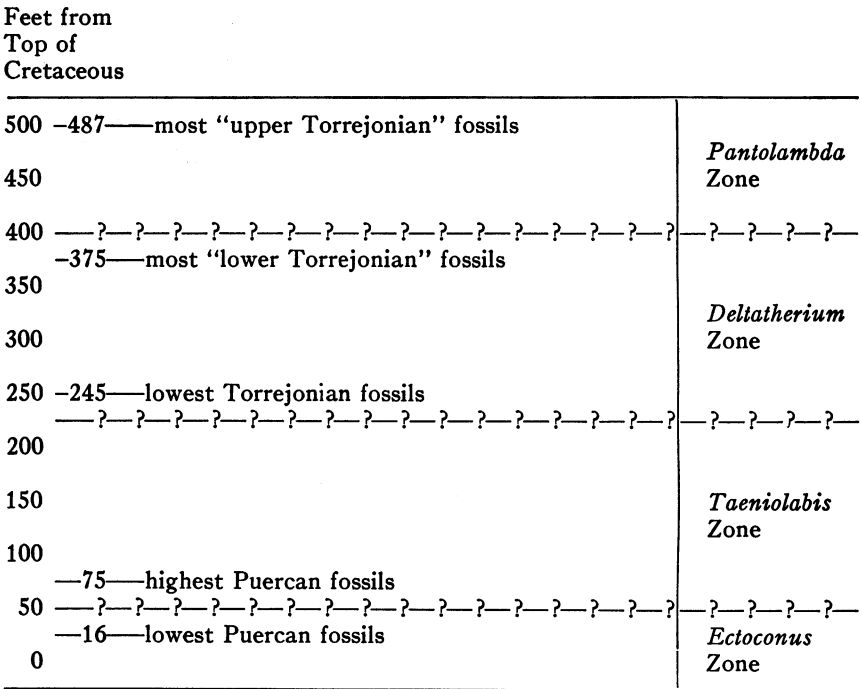


FIG. 5. Stratigraphic positions of miacid localities in the Nacimiento Formation, San Juan basin, New Mexico (modified after Sinclair and Granger, 1914; Granger, 1917; and Wilson, 1951, 1956). The "upper Torrejonian" localities include American Museum of Natural History localities 10 (west fork of Torrejon Arroyo), 11 (east fork of Torrejon Arroyo), and 13 (Alamito Arroyo) and United States National Museum locality 1936 (between east and west branches of Torrejon Arroyo). The "lower Torrejonian" localities include American Museum of Natural History localities 1 (Chico Spring, head of Gallegos Canyon), 8 (head of Kimbetoh Arroyo), 9 (Kimbetoh Arroyo, head of west fork), 11 ("Coots Canyon near Angels Peak"), and B (Bohannon Canyon), and University of Kansas locality 13 (Kutz Canyon near Angel Peak; same area as American Museum of Natural History locality 11). The lowest Puercan localities include American Museum of Natural History locality 7 (Tsosie Hill).

the Torrejon beds into upper and lower fossil levels (see fig. 5 of the present paper), said to be separated by 100 feet of sediment in the type section on the east and west forks of Torrejon Arroyo. The genus *Deltatherium* was said to be confined to the lower horizon, which occurs "in almost continuous outcrops from the East Fork of Arroyo Torrejon to the west branch of Kimbetoh Arroyo," and probably also westward and northward around Chico Spring at the head of Gallegos Canyon, in Kutz ("Coots" in Granger, 1917) Canyon near Angel Peak, and along the Animas River between the Colorado border and the San Juan River. Although none of the fossils collected before 1913 were definitely identified as to level, locality data make it reasonably sure that most of the fossils collected by David Baldwin in the 1880's [including the type of *Protictis* (*Protictis*) *haydenianus*] and by Jacob Wortman in 1892 came from the lower levels. Wortman's collections of 1896 and Granger's of 1912 were probably "from the upper horizon of Escavada, Torrejon and intervening arroyos." Sinclair and Granger (1914) also stated "that the upper horizon is rich in fossils to the eastward and almost barren in its western extent, while the lower horizon is highly fossiliferous in its westerly outcrops and only sparingly so to the eastward." In giving their locality data, they also noted that lower level fossils from localities 1 (Chico Springs) and 8 (head of Kimbetoh Arroyo) are concretion-covered, as are all but two (A.M.N.H. Nos. 3996c and 3371) of Baldwin's specimens in the American Museum of Natural History collection. Two of the others (A.M.N.H. Nos. 3374 and 3369a) were labeled by Baldwin "Cañon Gallego" and "Gallegos canon," which probably meant "Chico Springs" according to Sinclair and Granger (1914, footnote p. 310).

Expeditions from the University of Kansas have been active more recently in the Torrejonian of New Mexico. As reported by Wilson (1956), the presence of upper and lower fossil zones in the Torrejon beds is confirmed, with *Deltatherium*, *Triisodon*, and *Haploconus* being restricted to the lower zone; *Pantolambda* and *Claenodon* are characteristic of the upper zone. The *Deltatherium* zone, according to

Wilson, "possibly is largely flood plain in facies, but also partly arboreal and hence forest border in general aspect; the fauna of the *Pantolambda* zone . . . is more riparian."

It is clear from the foregoing that the various locations of collecting areas and some specific sites are probably important in understanding the stratigraphy of this field and the relative stratigraphic position of some specimens in the older collections. Unfortunately, there is some question as to the true position of some important localities because of the varied ideas of the names and correct relationships of some of the major landmarks and dry or intermittent stream beds. Short of a lengthy and detailed field investigation, which would be beyond the scope of the present paper, it is impossible to determine all the old localities with pinpoint accuracy. Some information has turned up in the course of study of the literature which appears to be worth recording at this time and may serve as a starting point for more work along these lines in the future.

The stratigraphic positions of the miacid localities in the Nacimiento Formation are summarized in text figure 5.

SOME TOPOGRAPHIC FEATURES IN THE SAN JUAN BASIN

At least two major topographic features are in question: Angel Peak and Escavada Arroyo.

Angel Peak is one of three distinctive buttes that rise over 7000 feet in the area southeast of Aztec and northeast of Chaco Canyon National Monuments, between New Mexico state highway 44 and the eastern corner of San Juan County, New Mexico.

The southernmost of the three peaks is "El Huerfano," or Huerfano mesa (of undisputed identity). About 8½ miles north-northeast of this, another prominent butte rises; this is known to local residents as "El Huerfanito," or Huerfanito mesa, and is so called on recent road maps of the Rand McNally Company and on sketch maps in Sinclair and Granger (1914), Matthew (1937), and Simpson (1948). But on the United States Geological Survey Aztec sheet (NJ 13-10) of the popular 1:250,000 series, this mesa (in the NW. ¼ of sect. 24, T. 27 N., R.

9 W., San Juan County, New Mexico) is called "Angel Peak"; a bench mark is at the summit.

The third of these buttes is about 5 miles north-northwest of the second. It has a bench mark at the major summit (in NW. $\frac{1}{4}$, sect. 5, T. 27 N., R. 9 W.), but it is unnamed on the United States Geological Survey 1:250,000 map. This is, however, the peak known as Angel Peak to the local residents and is so named on the road map and paleontologic maps above. (Oddly enough, Huerfano mesa is not shown on the Rand McNally map, although it is by far the most conspicuous of the three as seen from the main road.)

Angel Peak (or "Angels Peak" of Sinclair and Granger, 1914) is an important landmark mentioned by Granger (1917) and Wilson (1951) in descriptions of areas where vertebrate fossils were collected. In both cases, the peak to which they referred was the northernmost of the three discussed above and not "El Huerfanito," erroneously called "Angel Peak" by the United States Geological Survey.

The area under discussion has not yet been mapped in detail, and, if these errors are corrected as soon as possible, much future confusion can be avoided.

The second case of confused identity concerns a complex of intermittent streams emptying into the Rio Chaco (also intermittent) near Pueblo Bonito. About 4 miles northwest of Pueblo Bonito, a large arroyo enters the Rio Chaco from the north. Followed upstream, this large sand wash turns northwestward from the point where it meets the Rio Chaco and then westward for about 20 miles, passing "Escarbada" (on United States Geological Survey maps; Escavada in paleontologic literature) trading post, heading up 2 or 3 miles south of Lybrooks. This is labeled "Choukai Wash" on the United States Geological Survey map referred to above. Two other large sandy washes enter this watercourse; the first major tributary, "Kinebeto" (Kimbetoh) Wash, meets it about 4 miles from its mouth, and the second about a mile farther up.

Eight miles up Kimbetoh Wash, there is a trading post of the same name, and there does not seem to be any disagreement about

the name of either one, aside from variations in spelling. (In 1914, Sinclair and Granger called the trading post "Winter's store" and showed "Kimbetoh" south of the arroyo, as did Matthew in 1937, but this distinction is relatively unimportant now.)

The second large arroyo is a prominent sand wash lying between Kimbetoh Arroyo and the one called "Choukai" or "Escavada" above; this was described by Sinclair and Granger (1914) as a "nameless arroyo." Simpson (1959, p. 20) has discussed the various names applied to this arroyo (and other important paleontological collecting grounds) and settled on "Tsosie," which is "a simple and specific name in current use and understood locally." No township and range were supplied, however.

Unfortunately, the United States Geological Survey map (see above) has this important feature wrongly labeled "Escarbada Wash," despite the fact that it is more than 4 miles distant from "Escarbada" trading post, which is shown on "Choukai" Wash.

The confusion over the names of these features is compounded by the variation in drainage pattern shown by sketch maps in various older paleontologic papers. The drainage pattern shown by the United States Geological Survey 1:250,000 series map has been checked against aerial photographs of the area and appears to be correct. If the names of the various arroyos can be correctly assigned, the task of relocating the important fossil localities in this field will be greatly facilitated. The following spellings of place names are in accord with the prevailing usage of vertebrate paleontology.

KIMBETOH ARROYO: Site of Kimbetoh trading post, which is in sect. 31, T. 23 N., R. 9 W., San Juan County, New Mexico. The major part of this large sand wash extends from the region south of Nageezi, New Mexico (near the boundary between sects. 12 and 13, T. 23 N., R. 9 W.), southwestward to its mouth near the boundary of sects. 30 and 31, T. 22 N., R. 10 W.

ESCAVADA ARROYO: Site of Escavada trading post, which is on the line between sects. 14 and 23, T. 22 N., R. 8 W., San Juan County, New Mexico. The major part of this large sand wash extends from sect. 13, T. 22 N.,

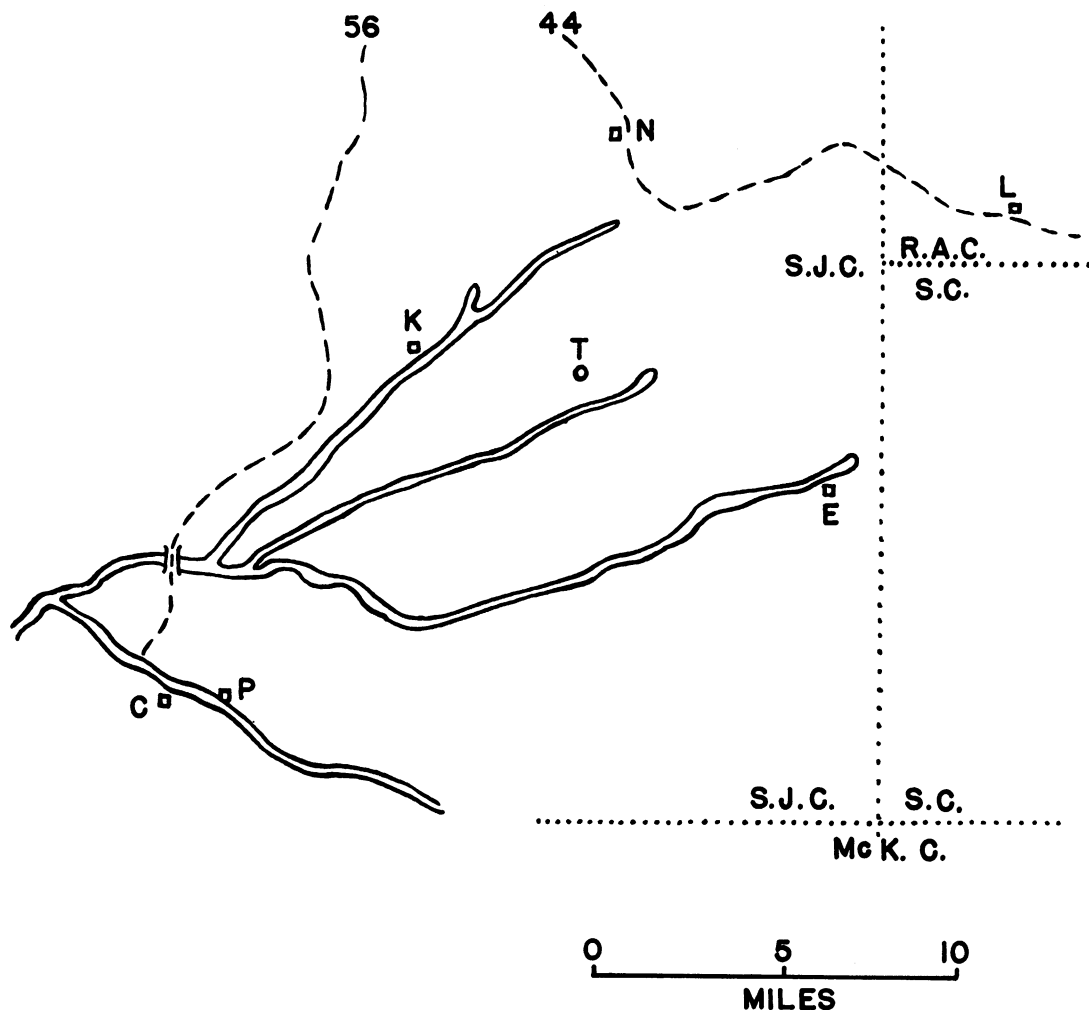


FIG. 6. Sketch map of portions of San Juan County (S.J.C.), Rio Arriba County (R.A.C.), Sandoval County (S.C.), and McKinley County (McK.C.) and parts of New Mexico state highways 56 (56) and 44 (44). The settlements of Chaco Canyon (C), Pueblo Bonito (P), Kimbetoh (K), Nageezi (N), Lybrooks (L), and Escavada (E) are marked with small squares. American Museum of Natural History locality 7 at Tsosie Hill (T) is marked with a circle. Only the major sand washes are shown.

R. 8 W., westward to sect. 32, T. 22 N., R. 10 W.

TSOSIE ARROYO: The large sand wash between Kimbetoh and Escavada arroyos, site of the important fossil locality 7 of Sinclair and Granger (1914, p. 315, pl. 26). The major part of this large sand wash extends from the SW. $\frac{1}{4}$ of sect. 31, T. 23 N., R. 8 W., to sect. 32, T. 22 N., R. 10 W., San Juan County, New Mexico.

These three major intermittent stream beds meet in sects. 31 and 32, T. 22 N., R. 10 W., to form the large sand wash which is

crossed by a bridge carrying New Mexico state road 56. About 3 miles beyond the bridge, the arroyo meets the Rio Chaco. G. G. Simpson informs me (personal communication) that local people usually call this part Escavada Arroyo, considering that to be the main channel and Kimbetoh, Tsosie, and others as tributaries. The United States Geological Survey designation "Choukai" appears to be a variant of Chaco and is erroneous as applied. "Kinebeto" is an allowable variant, but "Escarbada" is wrongly spelled.

Were it not for the fact that the largest

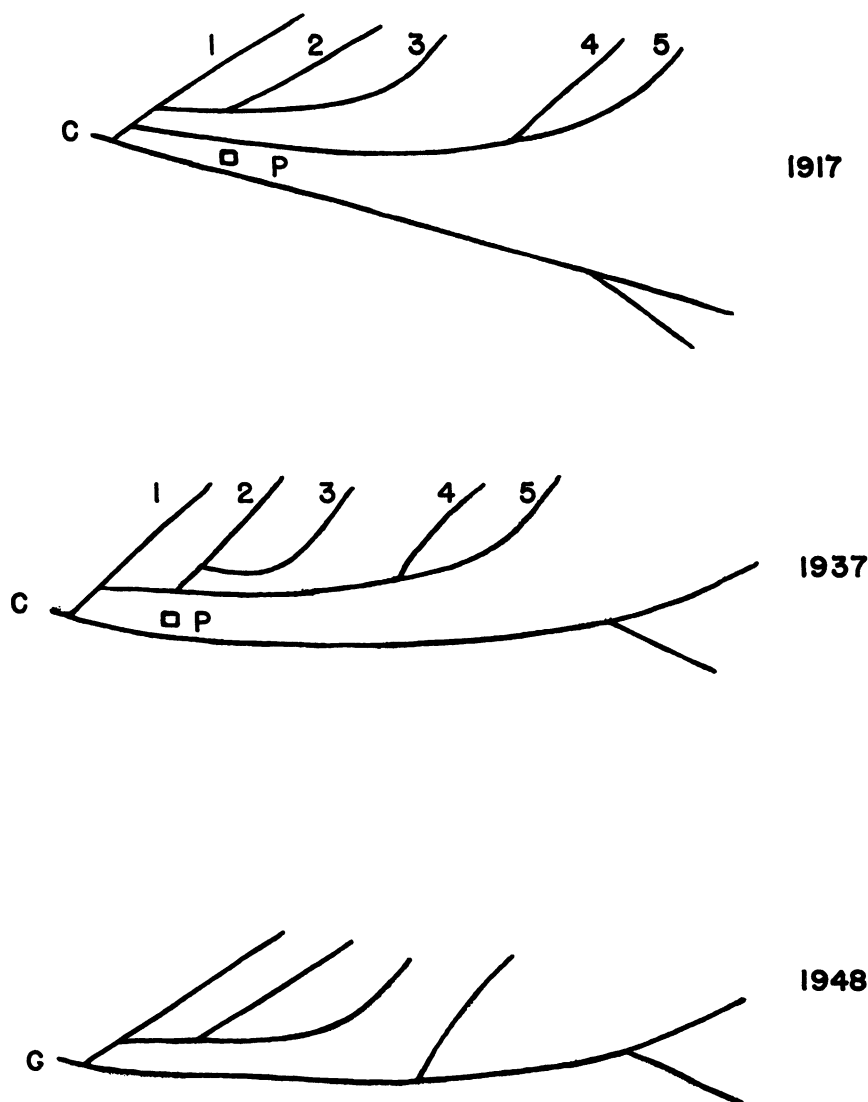


FIG. 7. Simplified diagrams of the three major patterns previously used to illustrate the arroyo complex near Pueblo Bonito in the San Juan basin of New Mexico. The Rio Chaco is shown receiving all the other arroyos in each case, but note that Sinclair and Granger (1914) have Alamo Arroyo joining Kimbetoh Arroyo separately, Matthew (1937) has all the tributaries joining Alamo before it joins Kimbetoh, and Simpson (1948) does not indicate exactly which arroyo is which. It is not clear from the published maps just which arroyo Sinclair and Granger's (1914) localities 12 and 13 were on, and there is no clear identification of just which branches of the Rio Chaco should now be called Alamo and Alamito arroyos.

Abbreviations: C, Rio Chaco; P, Pueblo Bonito; 1, Kimbetoh Arroyo; 2, Tsosie Arroyo; 3, Escavada Arroyo; 4, Alamito Arroyo; 5, Alamo Arroyo.

collections of fossils from the very beginning of the age of mammals have been in this part of the San Juan basin, these changes of names would be of small importance. It does not seem necessary to belabor the fact that retention of place names used in scientific literature for 30, 50, or 80 years has several obvious advantages and no visible disadvantages.

These are not the only cases in which confusion of geography has led to time-consuming detective work on the part of researchers, and the fault is not entirely the mapmakers'. The wide variations in stream pattern shown on different sketch maps have passed without comment in print by paleontologists, and persons who know the area best have not published the information known to them in full. Many other locations in this area (Alamo, Alamito, Barrel Spring, and Ojo Alamo arroyos, for example) are still not clearly identified in published literature or maps.

The few geographic designations supplied here are necessarily confined to the important miacid localities that I could identify. Full identification of all of the older localities would be beyond the scope of the present paper even if it were possible.

As paleontologists delve more deeply into microstratigraphy, paleo-ecology, and population studies, the importance of detailed locality data grows greater. For this reason, stability in geographic nomenclature will help future work on problems of evolution, correlation, and stratigraphy in the San Juan basin.

Text figure 6 indicates the relative positions of the major watercourses discussed above, and text figure 7 summarizes some previous interpretations of the stream pattern in the area north and east of the Pueblo Bonito ruins in Chaco Canyon.

LEBO FORMATION

The Paleocene of the Crazy Mountain field has been so well and thoroughly described by Simpson (1937a) that it is necessary here to outline only that material which particularly concerns the miacids. The only beds in this field that have yielded miacids are those of the upper Lebo (otherwise known as Fort Union number 2). *Protictis* (*Protictis*) occurs at every level where miacids have been found, but it is nowhere abundant in this field. *Protictis* (*Bryanictis*) is reported from locality

24, but no specimen number was mentioned by Simpson (1937a, p. 37), and I have not found any miacid in the American Museum of Natural History or United States National Museum collections marked with this locality. *Protictis* (*Bryanictis*) *microlestes* is otherwise reported only from the Silberling and Gidley quarries, where it is by far the most abundant miacid. *Protictis* (*Simpsonictis*) *tenuis* and *Ictidopappus mustelinus* are known only from the Gidley quarry, where both are comparatively rare.

The upper Lebo assemblage is equivalent to the Torrejonian in general composition, but no one has attempted to correlate the relative ages of the two in more precise terms. It is noteworthy that no one has yet applied the mass collecting method of washing and screening sediments to these rich middle Paleocene fields with a view to more detailed study of faunal composition and correlation than is possible at present.

As described by Simpson (1937a, pp. 63-64), the Gidley quarry appears to represent a sluggish body of fresh water surrounded by jungle. The scattered localities in the lower parts of the upper Lebo appear to represent deposits in the streams and ponds of a plains environment, more like that of the type Torrejonian (in the upper parts, at least).

The Silberling quarry is so close to the Gidley quarry, stratigraphically and otherwise, that the ecology and fauna of the two were evidently much the same. In both cases, the fossils were obtained from a comparatively thin bed, and there is no reason to doubt the essential unity of the samples of various species obtained from each quarry. There is in fact no evidence that suggests that these samples do not represent members of single interbreeding populations or demes.

The four miacids found in the Gidley quarry are all extremely primitive and archaic carnivores. But, unless the mesonychids (represented by only a few tooth fragments in this field) were truly predatory, the miacids were the only known mammals in this fauna that were really specialized for predation. *Ictidopappus* was the more specialized of the two genera; its great rarity in collections is perhaps due to a combination of real scarcity of individuals at the time represented by the

Feet Above
Basal Sandstone
Fort Union No. 1

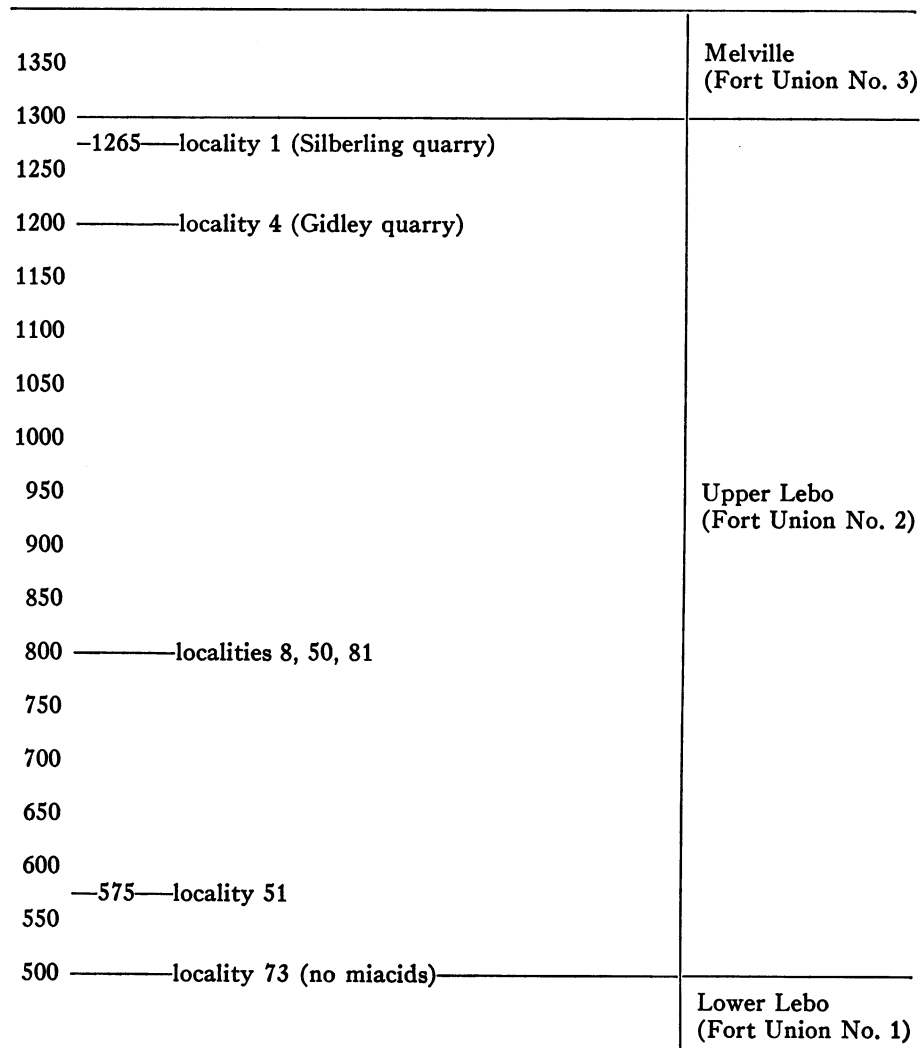


FIG. 8. Stratigraphic positions of miacid localities in the Crazy Mountain field middle Paleocene (modified after Simpson, 1937a).

Gidley and Silberling deposits and a normally upland habitat. The abundance of *Protictis* (*Bryanictis*) in the quarry samples and its scarcity in collections from the surface is undoubtedly a result of collecting hazards, as this form evidently was the most numerous miacid in the jungle habitat.

The stratigraphic positions of miacid localities in the upper Lebo formation of the Crazy Mountain field are summarized by text figure 8.

SHOTGUN LOCAL FAUNA

The Shotgun Member of the Fort Union Formation (the extension of this formation name from its type area near Buford, North Dakota, to remote areas in Montana and Wyoming may be debatable, but the usage seems general) was mapped by Troyer and Keefer (1955), and the same authors further investigated the stratigraphy (Keefer and Troyer, 1956). A fuller report by Keefer (1961) and short comments by Gazin (1961) have recently

been followed by proposal of the name "Shotgun local fauna" by Patterson and McGrew (1962), who also discussed some new mammals from the joint collection of Harvard University and the University of Wyoming (McGrew and Patterson, 1962). They assign an early Tiffanian age to this unit; Gazin (1961) had recognized such a possibility, although he then believed that there was some resemblance to the late Torrejonian Lebo assemblage. Keefer and Troyer (1964) have recently added a comprehensive study of the area.

The most fruitful collecting grounds in this unit have been centered around a locality in the NE. $\frac{1}{4}$ of SE. $\frac{1}{4}$, sect. 31, T. 6 N., R. 3 W., Fremont County, Wyoming. This locality is more than 8 miles east of Shotgun Butte itself, and it is more than $2\frac{1}{2}$ miles southwest of Jenkins Mountain. This last was the feature used by Gazin (1961, fig. 1) to identify the locality; Jenkins Mountain also gives its name to the 7.5-minute quadrangle map published by the United States Geological Survey in 1957, but it is surrounded by Paleozoic beds and seems inappropriate to signify a Paleocene locality. The nearest named topographic feature is a pair of hills called Twin Buttes. This name is inappropriate because of the risk of confusion with the better-known landmark of the late middle Eocene in the Bridger basin also called Twin Buttes. As McGrew and Patterson (1962) have already described their collecting ground as " $\frac{3}{4}$ mile SW of the more northerly of the Twin Buttes in the northern part of the Wind River basin," there is now no confusion with the Bridger basin Twin Buttes. But this will almost inevitably be shortened to "Twin Buttes" in usage, and that should be avoided.

Because none of the other names appear to be appropriate, I propose the name Keefer Hill for the more northerly of the Wind River

basin Twin Buttes and the name Troyer Hill for the more southerly of the same pair (which are separated by Trail Canyon). Keefer Hill is 6290 feet high at the summit in NW. $\frac{1}{4}$ of NE. $\frac{1}{4}$, sect. 32, T. 6 N., R. 3 E., and Troyer Hill rises to 6116 feet at the summit in SE. $\frac{1}{4}$ of SW. $\frac{1}{4}$, sect. 33, T. 6 N., R. 3 N., Wind River basin, Fremont County, Wyoming.

Because important collecting sites are more easily discussed and remembered if they are named (quarter-section, township, and range are convenient for precise designation but cumbersome in discussion), I also propose the name McGrew-Patterson Site 1 for the specific place where the Harvard-University of Wyoming collection of 1960 was made in NE. $\frac{1}{4}$ of SE. $\frac{1}{4}$, sect. 31, T. 6 N., R. 3 E., Fremont County, Wyoming.

Love, McGrew, and Thomas (1963) indicated that the fossils of the Shotgun Member were buried in the near shore facies of a fresh-water lake deposit, many of them evidently exhibiting the effects of passing through the digestive tract of crocodilians. The high proportion of small vertebrate remains and the fragmentary condition of larger fossils were cited as evidence of this process. The absence of *P. (Protictis)* may also be due to the same cause.

The miacids described from the McGrew-Patterson site by me are assumed to be of early Tiffanian age, following the current consensus. They tend to confirm this opinion, showing close ties with, but some differences from, related forms known to be of Torrejonian age. The available samples are as yet too small for unequivocal judgments, but the forms known from the Shotgun Member (and, more vaguely, the two fragments from the Bison basin Saddle locality) may represent slightly progressive stages of the better-known Torrejonian species.

SYSTEMATICS

THE VALIDITY of a classification, especially if it is to be based on the usually meager evidence available to a paleontologist, depends on the viewpoint of the student as much as on his observations. In modern taxonomic theory, the primary units, the species, must be classified with as much of the totality of systematics in mind as possible. The word "systematics" is to be understood in its broadest possible sense, and taxonomy here refers to the philosophy of classification, not merely to the arrangement of names.

It is, of course, true that what is actually classified is usually a small sample—a few organisms represented by the available specimens. What is or should be *named*, however, is the entire population of organisms—four-dimensional, never static, existing in all stages of ontogeny from zygote to fossilizing remains and in all stages of phylogeny from the separation of one particular gene pool complex from its nearest relatives to the change, division, or extinction of its descendants which marks the truly irreversible change from one species to one, two, or no others.

Giving a name to this dynamic, really unobservable entity is rather like trying to define the limits of a cloud of smoke pouring from a chimney. We may be sure that there is definitely and positively such an entity as species A. When it is alive, we can observe some parts of it and state with ever-increasing accuracy that it does not extend beyond this or that limit, that its individual particles usually can be recognized by this or that combination of characters, and that it is similar to, but separable from, related species B and C. There is no way of stating with precision that it is composed of exactly X individuals, all of which possess precisely this and that characteristic of size and shape or chemical composition. It is pointless to try defining species as chemical formulas are defined; species do not stand still to be counted and measured by the methods applicable to crystals.

As living species are only partly observable, so fossil species are only partly inferable. We must attempt to infer the biological reality

that once was from an even less complete sample than is available for living species. Moreover, the sample is inevitably biased (usually in several ways), and it is almost always entirely composed of hard parts of the anatomy. Even these are seldom complete and often may be subtly distorted by the processes of fossilization.

It is not my purpose here to rehash the various discussions of what constitutes a valid species, since this has been done elsewhere by others (a recent comprehensive discussion is available in Simpson, 1961, where many other references may be found). It does seem to be desirable to explain some of the methods and principles used to arrive at taxonomic decisions in this paper, not that any claim of originality is intended (the principles are implicit in much modern taxonomic work), but it seems proper to state explicitly what the basic assumptions have been. The fact that they were consciously made and not simply taken for granted also seems worth recording.

It should be clear that species are assumed to be real entities, although satisfactory definitions of species may be difficult to frame. It is also assumed that morphology provides a reasonably reliable guide to the genetic unity of taxa and to their normal range of variation. Within reasonable limits, the geologic information used here is assumed to be correct, and I will risk banality by stating that it is also assumed that miacids, like mammals generally, evolved by the usual, rather gradual mechanisms of change now generally understood to operate among sexually reproducing organisms. None of the facts that have emerged from my studies requires any unusual mechanism of saltation, orthogenesis, or the like for explanation.

Absolute objectivity and accuracy are seldom if ever possible in classification, but so far as possible all known relevant factors have been weighed; in debatable cases, the areas of uncertainty are stated as fully as possible, and the conclusions expressed here are, as usual, the nearest approximation to the truth attainable by this observer at this time.

Because of the limited nature of the present

part of this study, it would be premature to attempt a critical revision of the very full diagnoses provided by Matthew (1909, 1915), and the difficult problems of defining the higher categories of Carnivora (and Mammalia) may be left until the genera and species are more fully understood.

In this regard, the primary criterion for deciding upon the classification proposed here is simply the question, Is it impossible to believe that two samples showing this kind and degree of difference could belong to one taxon? The same question is asked at each taxonomic level. If credible, the taxa are left lumped; splitting is held to be permissible only if continued association is liable to obscure rather than clarify or simplify our understanding of evolution in this group.

ICTIDOPAPPUS SIMPSON, 1935

Ictidopappus SIMPSON, 1935, p. 237; 1937a, p. 213.

TYPE: *Ictidopappus mustelinus* Simpson, 1935.

DISTRIBUTION: Middle Paleocene of Montana (? and early Paleocene of New Mexico).

INCLUDED SPECIES: Type (? and unnamed new species represented by A.M.N.H. No. 58409).

DIAGNOSIS: "Differing from *Didymictis* [and *Protictis*] in the relatively smaller and much simpler P_{3-4} and relatively lower and longer trigonid of M_1 , from *Viverravus* in the wider and more triangular P_4 and more def-

initely basined talonids, and from other known miacids in the absence of M_3 ."

DISCUSSION: The above diagnosis is quoted from Simpson (1937a, p. 214) and is essentially the same as the original diagnosis. The words in brackets have been added to bring the diagnosis up to date.

A single tooth from the lower Puerco of New Mexico is tentatively associated with this genus. Although insufficient to warrant a new name, this specimen undoubtedly represents a new species. It is discussed below as ?cf. *Ictidopappus*.

Ictidopappus mustelinus Simpson, 1935

Plate 1; plate 2, figures 5-8; text figures 9-11

Ictidopappus mustelinus SIMPSON, 1935, p. 237; 1937a, p. 214, figs. 60-61.

TYPE: U.S.N.M. No. 9296, part of right dentary with P_3 - M_1 , anterior alveolus and talonid of M_2 , alveolus of C_1 , and part of P_4 alveolus. Figured by Simpson (1937a, fig. 60).

DISTRIBUTION: Middle Paleocene (Torrejonian), Lebo Formation, upper Lebo beds; Gidley quarry (locality 4), NW. $\frac{1}{4}$ of NE. $\frac{1}{4}$, sect. 25, T. 5 N., R. 15 E., Crazy Mountain field, Sweetgrass County, Montana.

HYPODIGM: Type and U.S.N.M. No. 9295, parts of right premaxilla and maxilla with P^1 , P^2 - M^2 , alveolus of C^1 , and anterior root of P^2 (figured by Simpson, 1937a, fig. 61).¹

¹ The remarkably complementary aspect of this specimen and the type leaves little doubt that they belong to the same species, and the similar state of wear even

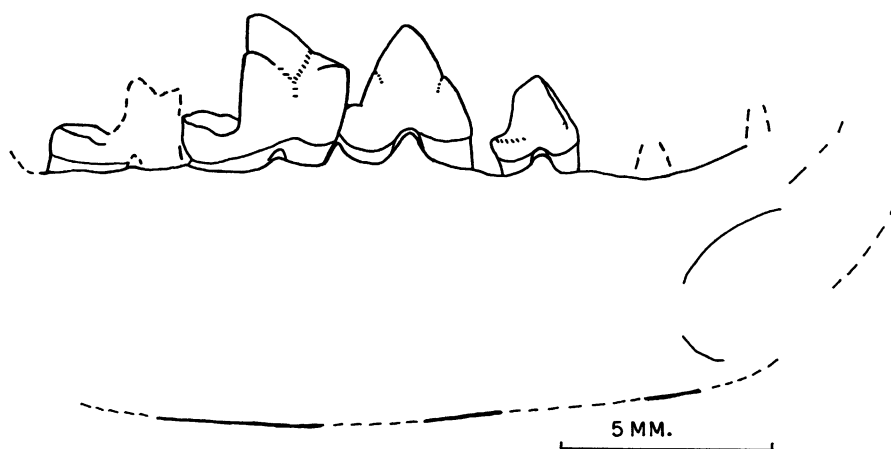


FIG. 9. *Ictidopappus mustelinus*. Reconstruction diagram of left lower dentition, based on the type but reversed for uniformity. Compare plate 1, figure 3.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF LOWER
DENTITION OF *Ictidopappus mustelinus*

P ₃	
Length	2.0
Width	1.2
P ₄	
Length	3.0
Width	2.0
Length/width	1.50
M ₁	
Length	4.1
Width (anterior)	2.3
Width (posterior)	1.9
Grind width (anterior)	1.9
Length of talonid	1.5
Length of trigonid	2.6
Length of paraconid	1.2
Length of metaconid	0.8
Length/width (anterior)	1.78
Width (posterior)/length of talonid	1.27
M ₂	
Width (posterior)	1.6
Grind width (posterior)	1.4
P ₄ length/P ₃ length	1.50
Depth below M ₁	6.2
Depth below M ₂	6.2

DIAGNOSIS: Only known species of genus. Fourth lower premolar with large decurved protoconid, small paraconid, no definite metaconid, no other cusps, and no cingula except for very short, wide talonid.¹

MEASUREMENTS: See tables 1 and 2.

DESCRIPTION: Dentition: The type shows all that is known of the lower teeth. There is no trace of the incisors or their alveoli. The lower canine is not present, but its single, large, procumbent root is indicated by a partial natural cast of the alveolus.

There was a diastema after the canine, but the region following this is damaged, and only the vague outlines of roots for P₁₋₂ can be seen. It seems possible that P₁ was small and one-rooted; P₂ was not large, but the root

raises the suspicion that they might represent the same individual.

¹ A diagnosis is a statement of characters wherein a taxon differs from known related peer taxa. As G. G. Simpson points out (personal communication), if there are no such, comparisons are impossible. I supply additional details wherever, as in this case, unnamed new peer taxa are known or suspected.

may have been partly subdivided. Both are now lost. (See pl. 2, figs. 5, 7.)

The third lower premolar is small and two-rooted, as are all the succeeding lower teeth. It has a single, trenchant, faintly recurved main cusp, a small anterobasal bulge without any cingula, and a weak, sloping heel without any distinct basin or cingula. There is a small posterior projection but no definite cusp on the heel. The usual anteroposterior crest begins lingual to the midline, curves slightly labiad, and rises almost straight to the apex of the protoconid, then falls nearly straight, but with a slight labial concavity, to the posterior end of the crown as seen in occlusal view. This tooth is smaller, relative to P₄, and simpler in structure than that in any other known Paleocene miacid. The tip of the protoconid is heavily worn, especially on the posterior side.

The fourth lower premolar is very distinctive in its large, triangular, decurved protoconid, in the short talonid, and in the strongly lingual position of the closely appressed, conical paraconid. There are no definite cingula, and the talonid is very short and broad, without clearly defined cusps. About halfway down the posterolingual edge of the proto-

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF UPPER
DENTITION OF *Ictidopappus mustelinus*

P ¹	
Length	1.5
Width	0.95
P ⁴	
Length, labial	5.0
Width	3.7
Metastyle	2.7
Length, lingual	5.1
Length, labial/width	1.35
Length, lingual/length, labial	1.02
M ¹	
Length	3.4
Width (anterior)	5.3
Width (posterior)	5.0
Grind width (anterior)	4.25
Width (anterior)/width (posterior)	1.06
M ²	
Length	2.6
Width (anterior)	3.75
Width (posterior)	2.7
Grind width (posterior)	2.7

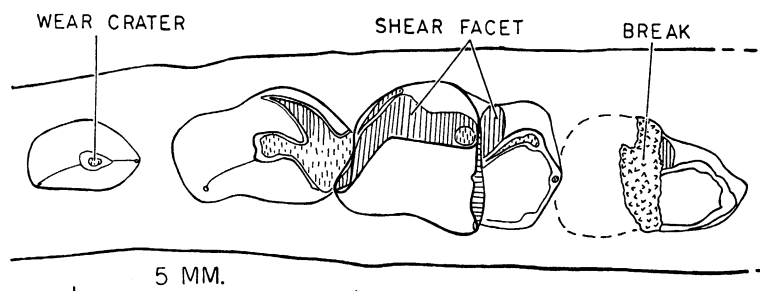


FIG. 10. *Ictidopappus mustelinus*. Diagram of right lower teeth, occlusal aspect, showing wear pattern. Compare plate 2, figure 5.

conid, a slight bulge suggests a rudimentary metaconid. (See pl. 1, fig. 3.)

The usual anteroposterior crest begins at the apex of the paraconid and drops slightly as it runs posterolabial, then turns posterior and rises straight to the apex of the protoconid. From that point, it falls in a curve which is convex lingual to the level of the talonid, where it turns labial toward the posterior corner of the tooth. The tip of the protoconid and the posterior crest are well worn. (See text fig. 10.)

The lower carnassial is heavily worn along the paraconid-protoconid shearing edge and at the tips of the cusps, but the major structures are plain. The trigonid is relatively longer and narrower and was apparently lower when unworn than that in *Protictis*; the paraconid is more extended and the metaconid relatively more retracted as well. The protoconid is as usual in miacids, the tallest trigonid cusp approximately tetrahedral and much worn at the apex. It has a vertical posterior face and a steep lingual face; the labial surface was curved sharply, but the anterior position has been flattened by wear.

The usual crests run from its summit down the labial edge to the metaconid and down the anterior edge to the paraconid. The posterior crest is essentially straight and interrupted by the usual carnassiform notch; the anterior crest turns sharply lingual at the anterior carnassial notch (which has been almost obliterated by wear) and proceeds anterolingual to the tip of the paraconid.

The talonid is broadly basined (relatively a little more so than in *Protictis*) and is surrounded by the usual raised rim which connects the base of the metaconid with the crista obliqua (not so very oblique here). The usual

three talonid cusps are present on this crest, but none is particularly prominent, and there are no cingula around their bases.

Between the bases of the protoconid and hypoconid, a deep groove has been worn in the sulcus obliquus by the M^1 paracone. If there was a cingulum here, it has now been obliterated.

Only the talonid of M_2 is preserved, and it is also rather broadly basined and has the usual cusps present but not well developed. The elongate oval shape of the talonid is typical of viverravines, and there is no doubt that M_3 was absent, although the jaw is broken off at this point. The missing trigonid of M_2 was probably elevated—a deduction based on the wear pattern seen in the upper teeth.

Much of the upper dentition is shown by the referred specimen. (See pls. 1 and 2.)

Except for an ambiguous structure which may represent part of the I^3 alveolar wall, nothing is known of the upper incisors.

The alveolus for the upper canine is matrix-filled but clearly indicates a large, stout, single root, oval in section. The labial wall of this alveolus is slightly crushed inward, but it now measures 1.9 mm. wide and 2.7 mm. long.

The upper canine is followed by a diastema of less than half of a millimeter, so that P^1 is very close behind. This small tooth is preserved with most of the apex worn away, but it shows an erect, faintly recurved crown, with sharp anterior and posterior crests. There is a small posterior projection at the end of the posterior crest which does not rise to form a true cuspule. There are no cingula and no other cusps. The root appears to be partly divided labially, but the division is

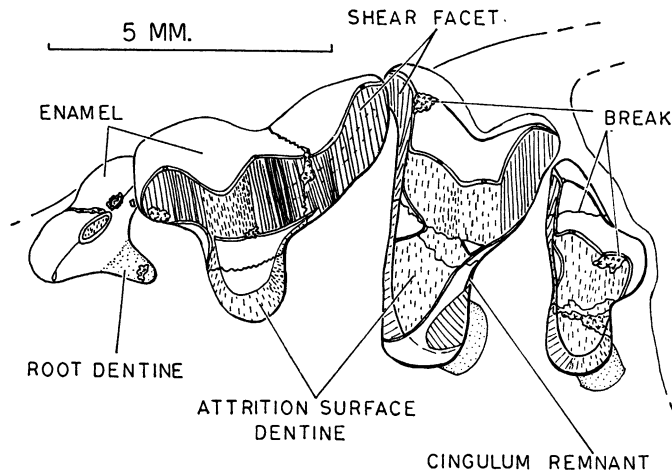


FIG. 11. *Ictidopappus mustelinus*. Diagram of left upper teeth, occlusal aspect, showing wear pattern. Compare plate 2, figure 6.

much fainter lingually; the root may be divided below the part now visible. All that remains of P^2 is the anterior root; this is implanted at a slight angle which implies a second root, but a portion of the maxilla has been lost here. The preserved root is 1.1 mm. wide at the flared-out upper end, so this tooth was evidently larger than P^1 .

The third premolar is fairly well preserved and quite complete except for minor damage. (See text fig. 11.) It is implanted at a sharp angle to P^4 , with the anterior end well lingual to the posterior end. It is worn only at the apex of the paracone, but this is what could be called "apical attrition," normal on premolars that do not occlude with other teeth and caused by the food material. This form of wear is decidedly different from the scored wear facets that result from tooth-on-tooth shearing action, and no sign of such wear is visible on P^3 . The paracone is the largest cusp and has the form of a narrow blade approximately parallel to the labial border of the tooth as seen in crown view. A very small parastyle is almost concealed by the sharp crest that connects it to the paracone without any intervening notch; the apex of the parastyle is thus a mere cuspule at the anterior end of this crest. A similar crest arises at a low rounded nodule at the metastyle corner of the tooth and passes to the apex of the paracone. The edge of this crest is chipped labially, exposing the dentine, but

there is no sign of any cuspules along its length. There are three roots: the usual pair along the outer margin of the palate and a third which diverges sharply and enters the palate obliquely directly anterior to the protocone root on P^4 . There is no protocone on P^3 , however, and no cingula can be seen anywhere on the premolars, even where they are quite unworn.

As seen in crown view, P^3 has the general form of a slightly asymmetrical letter r, with the medial root forming the rather slender vertical bar and the labial cusps and crests forming the thicker horizontal limbs, the posterior limb being the longer.

In P^4 , this general form is even more asymmetrical, and the tooth assumes the shape of an irregular letter Y lying on its side (\succ). The longest branch is the posterolabial arm (bearing the metastyle blade), and the shorter branches are the parastyle and protocone corners, respectively. The lingual surfaces are heavily worn, with deeply scored shear facets severely modifying the original cusp pattern; the labial surfaces, on the other hand, are quite unworn. The smooth labial flanks of the paracone are marred by a few faint irregularities and a certain vague rugosity, but no definite cingula or cuspules comparable to those seen in *P. (Bryanictis) microlestes* are visible here.

The largest cusp on P^4 , as usual, is the paracone. In its present worn condition, this

cuspid is roughly pyramidal in form, the apex being blunted by the usual apical attrition.

The original edges of the crests on the lingual side of P^4 have been worn into a continuous single crest which begins at the anterior lingual base of the parastyle. This cusp is now distinguishable as a semicircular projection at the anterior labial corner of the tooth. The sinuous labial crest connects this cusp to the summit of the paracone (which is now visible as a similarly worn projection of the crest), with only a broad, shallow notch marking the separation of the cusp bases. The posterior limit of the paracone is similarly vaguely defined by a broader notch in the posterior part of the crest, which then reverses its curve at the summit of a low eminence near the metastyle corner of the tooth and passes directly posteriad to the posterior corner of the tooth. This crest defines the labial limit of an extensively worn area which is clearly divided into three zones. The anterior zone is a shear facet which has been gouged into the lingual surface of the parastyle by the protoconid of P_4 . The posterior zone is an elongated shear facet produced by the working of the lower carnassial protoconid and metaconid against the posterior lingual edge of the P^4 paracone-metastyle blade. Between these two shear facets, there is a low, rounded crest produced partly by the intersection of the shear facets and partly by the attrition of the food material. The distinction between these two types of wear surfaces can be made because in the case of the shear facets the exposed dentine is scored and gouged; the enamel and dentine are worn to an equal degree, so that it was necessary to use ultraviolet light to distinguish between enamel and dentine. Where there was no strong shearing of crest on crest, the resistant enamel stands out in the familiar pattern seen in ordinary attrition.

If there was a lingual cingulum on P^4 , it has been obliterated by the two deep wear facets; the usual position of the protocone is also occupied by a semicircular worn area, so that no distinct cusp can now be seen. Between this worn area at the protocone location and the paracone, there is an irregular remnant of unworn enamel which indicates that at least some sort of shelf or cingulum probably existed at the lingual base of the

paracone, but there is no sign of anterior or posterior extension of such a cingulum.

The first upper molar is relatively short and wide, approximately triangular, with a deep emargination in the labial border between the extended parastyle and metastyle corners of the tooth. The anterior border is nearly straight; the posterior border is sinuous, with slightly convex curves near the lingual and labial ends joining a concavity near the midline. A small patch of enamel remains on the lingual surface of the worn stump of the protocone; attached to this is a narrow band which separates the deep shear facet on the hypocone region from the triangular wear area labial to the protocone. The protocone was evidently close to the anterior border of the crown. The extreme labial end of the posterior lingual cingulum remains attached to this part of the enamel at the shortest part of the tooth near the midline. The rest of this structure was worn away, but it was evidently fairly well developed, although it did not extend so far as the lingual limit of the crown. If a hypocone was present, there is now nothing left of it.

There are no traces of conules, but these were not necessarily absent. The paracone and metacone have been heavily worn, but the outlines of their bases can be distinguished in the remaining enamel of the broad labial shelf. Two small enamel patches on the anterolingual base of the paracone and the posterolingual base of the metacone show that the adjacent grooves in the dentine mark reasonably accurate limits for these cusps and were not solely determined by wear.

Judged from the size and relationships of the parts preserved, the paracone was probably larger than the metacone and stood about one-third of the distance from the extreme labial margin of the tooth along the line from stylocone to protocone. The base of the metacone was evidently not so widely separated from the paracone as in *Protictis*.

A clearly marked crest passes from the anterior end of the paracone labiad to a triangular fracture area which is at the usual position of the stylocone. Although this crest may have been modified by the strongly worn shear facet on the parastyle shelf, it does not show any trace of a carnassiform notch.

This crest was probably connected to the stylar cingulum, which begins at the parastyle corner of M^1 and, curving linguad, runs into the fractured area representing the stylocone. The stylar cingulum continues, curving posteriad and less linguad in direction from the fracture surface so that it meets the emarginate labial border of the crown. It diverges again from the border of the crown as it proceeds posteriad and becomes rounded and indefinite beyond a small mesostyle.

There is a prominent oval shear facet on the posterior face of the crown which extends from the metastyle corner of the tooth to a point posterior to the metacone. This corresponds to the posterior shear facet on P^4 , and, if a metastyle cusp was present, it has been removed by wear.

The shear facet on the parastyle shelf of M^1 corresponds to a similar facet on M^2 ; both were caused by the trigonids of the corresponding lower molars, and these in turn correspond to the anterior shear facet on P^4 which was undoubtedly caused by wear against the protoconid of P_4 . Shear facets on the parastyle shelf of M^{1-2} are present in *Protictis (Bryanictis) microlestes*, but no such severe wear on the metastyle corner of M^1 was seen in that species as it was in *Ictidopappus mustelinus*.

From these facts it seems reasonable to deduce that the unknown trigonid of M_2 in *Ictidopappus mustelinus* was at least as high as in *P. (B.) microlestes* and may have been even more prominent.

The second upper molar is considerably smaller than M^1 , and it is undoubtedly the last tooth in the maxilla, since there are no traces of alveoli behind it. The over-all shape of M^2 resembles that of M^1 except that the metastyle corner of M^2 is reduced, as usual in the last upper molars of primitive mammals. The parastyle corner is similarly extended, however, and a labial crest extends from the extreme anterolabial corner of the crown to a small eminence (apparently slightly chipped) which corresponds to the stylocone. The stylar cingulum continues posteriolinguad until it meets the emarginated border of the crown; here it becomes rounded and indefinite and can be traced only vaguely to the middle of the labial base of the metacone and not beyond. There is

no posterior cingulum around the metacone.

Again (as in M^1) there is a crest from the small, broken stylocone to the labial base of the paracone. The paracone is not so heavily worn as in M^1 , and this fact, in combination with the relatively narrower stylar shelf, makes it appear to be relatively taller. Its lingual surface has been abraded into a steep, nearly flat facet by the M_2 hypoconid; this facet continues on the lingual surface of the metacone but at a slight angle.

The metacone is a little more clearly set off from the paracone labially than it is lingually. The enamel on the labial side of the two cusps is continuous from the paracone-stylocone crest around the posterior base of the metacone. (There is no trace of a posterior wear facet such as is seen on M^1 , because there was no M_3 .) The usual groove in this enamel marks the division between the two cusps. Because of the wear on the lingual side, a nearly continuous crest has been developed (as in M^1) which seems to unite the cusps. The trace of a definite notch between the cusps can still be seen, however, so they were not conjoined. The protocone is worn to a featureless stump; no cingula are now visible on this part of the notch, although such may have existed. No traces of conules are visible.

Skeleton: The type shows all that is known of the dentary, which appears to have been relatively short and deep, although its exact outlines are somewhat obscured by damage. A large mental foramen opens below P_3 (a deep blood vessel sulcus runs from it toward the anterior root of M_1); below P_{1-2} there is a smaller foramen facing anterodorsad. The symphysis is damaged and much of it lost, but the small remnant hints at rather more widely spread rami than usual among primitive carnivores.

A little of the palate and part of the snout are shown by the referred specimen. No definite sutures are visible.

At the extreme anterior end of this specimen, there is a segment of rounded bone which appears to be part of the posterolabial border of the incisive fenestra. Immediately labial to this remnant and separated from it by a ridge of bone, there is a shallow groove running dorsally which may be part of the I^3 alveolar wall. The bone curves sharply ven-

trad from the level of the palate in this region toward where the incisors were probably implanted.

There is a deep groove, as usual in primitive carnivores, immediately anterior to the upper canine for the reception of the tip of the lower canine. There is a distinct bulge in the maxilla marking the insertion of the canine root, and the margin of the palate swings sharply mediad before straightening out to follow the alignment of the succeeding premolars. There is a gap in the bone near P^2 where part of the maxilla was broken away.

The outer margin of the maxilla curves labiad in the area adjacent to P^3-4 . Although the bone is molded around the area of these teeth, the general outline of the palate becomes broader until the beginning of the zygomatic arch is reached above M^1 .

Part of the zygomatic process of the maxilla is preserved, projecting in the same general direction as the margin of the maxilla above P^4 . However, the alveolar margin turns linguad below M^1 and curves around behind M^2 until it is at right angles to the midline. There is a break near the posterior root of M^2 , and the remaining edges of bone are all broken.

There are definite hollows in the palate between P^4 and M^1 and between M^1 and M^2 ; these are for the reception of the trigonids of M_{1-2} . It is noteworthy that such cavities appear between P^4 and M^1 in all miacids; the cavity between M^1 and M^2 is usually the smaller (as it is here) and in some cases is not perceptible.

Some parts of these bones remain concealed by the plaster block which was left in place to protect the specimen. No other parts of the skull are known, and the postcranial skeleton is totally unknown.

DISCUSSION: The characters of P_4 would be sufficient to distinguish *I. mustelinus* from Puerco-Z if that specimen represents a second species of *Ictidopappus*.

The teeth and jaws of *I. mustelinus* are unexpectedly specialized for such an early form, the chief differences from the other viverravines lying in the more hypercarnassial¹ dentition and the short, powerful con-

struction of the jaws. The peculiar premolars, lacking the usual cingula and minor cusps, are very different in the shape and proportions of the cusps from those of any of the later miacids. It seems to me most unlikely that this species could have been ancestral to any known *Viverravus* species and quite impossible that any of the other later miacids could have been derived from it.

The molar structure is more obscured by wear, but the transversely elongate profile, the seemingly partly connate paracone and metacone of the uppers, and the strikingly trenchant trigonid of M^1 all contrast sharply with the more primitive conditions seen in the various forms of *Protictis*.

It is noteworthy that *I. mustelinus* has not been reported from collections made at middle Paleocene localities other than the Gidley quarry and that this species is still the rarest miacid from that quarry.

?Cf. *Ictidopappus*, unnamed new species

Plate 2, figures 1-4; text figure 12

DISTRIBUTION: Earliest Paleocene (early Puercan), Nacimiento Formation, lower Puerco beds; locality 7 of Sinclair and Granger (1914) on Tsosie Arroyo of Simpson (1959), SE. $\frac{1}{4}$ of SW. $\frac{1}{4}$, sect. 35, T. 23 N., R. 9 W., San Juan County, New Mexico.

HYPODIGM: A.M.N.H. No. 58409, an isolated right lower premolar (probably P_4).

MEASUREMENTS (IN MM.): Length as preserved, 3.2 minimum; width (anterior), 0.9; width (posterior), 1.3.

DESCRIPTION: As preserved, the specimen is intermediate in size between P_4 in *Protictis* (*Simpsonictis*) *tenuis* and that in *Protictis* (*Bryanictis*) *microlestes*. There were two roots, probably subequal, but the anterior root has been broken completely away, and the lower end of the posterior root is missing. The crown is relatively complete, but the apex of the protoconid is broken; part of the labial base of the paraconid has been lost, and some of the enamel around the posterior end of the tooth has flaked off. Since the edges of these broken parts are fresh and unworn, it is apparent that this damage was postmortem and may have occurred during the washing process; there is only slight evidence of weathering and very little wear.

Of particular interest is the prominent bulge on the lingual side of the protoconid.

¹ Term derived from hypercarnivore (see Crusafont-Pairó and Truyols-Santonja, 1956), referring to relatively well-specialized shearing teeth. Hypocarnassial is the antonym denoting relatively unspecialized shearing teeth.

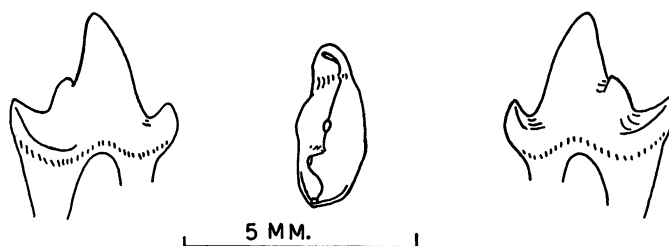


FIG. 12. ?Cf. *Ictidopappus* (Puerco-Z). Restored outlines of lower premolar. *Left*: Labial aspect. *Middle*: Occlusal aspect. *Right*: Lingual aspect. Compare plate 2, figures 1-4.

Although there is no distinct cusp, this bulge is reminiscent of the basal part of a metaconid.

The shape of the crown is illustrated in plate 2, figures 1-4, and a detailed description here seems unnecessary. The wear pattern requires closer study and provides some clues to occlusal relationships.

The apex of the paraconid shows very slight wear, but no typical wear crater has developed. The crest on this cusp shows a definitely delimited, but slightly developed, wear surface, which ends about one-quarter of the distance from the lower limit of this crest. The anterior crest on the protoconid shows only faint wear except for a small elongate area at about the level of the paraconid. The protocone of P^3 occludes with the tip of the P_4 paraconid in *P. (Bryanictis) microlestes*; a tall P^3 protocone might produce such a pair of wear facets on P_4 if it occluded between paraconid and protoconid. However, this deduction is uncertain, as neither of these two areas shows the typically striated surface of a shear facet.

The posterior crest of the protoconid appears unworn. The apex of the posterior accessory (hypoconid) cusp shows slight wear but no crater formed; a tiny but unmistakable shear facet has developed on the posterior crest of this cusp. Aside from a small triangular spot near the broken end of the labial posterior crest, this is the only wear visible on the posterior half of the crown. Both facets could have been caused by grazing contact with the apex of the P^4 protocone in centric occlusion or with the P^4 paracone during active occlusion.

There is no visible wear on the steep, slightly concave slope labial to the posterior flank of the protoconid and accessory cusps.

DISCUSSION: There is no doubt that this specimen is the lower premolar of a small

therian mammal, and there is very little likelihood that it is not the posterior premolar of a eutherian. Although this tooth undoubtedly represents a new taxon, it would be pointless and irresponsible to propose a formal name until enough additional specimens are collected to permit full description and to remove present doubts about its affinities. Pending this, I call it "Puerco-Z," a convenient informal term coined to avoid the cumbersome repetition of "A.M.N.H. No. 58409."¹

The precise relationships of Puerco-Z are uncertain (to say the least), but the high, rather sharp cusps and crests suggest a small predator, carnivorous, insectivorous, or both (although primitive omnivores sometimes have such premolars). The curving arrangement of the cusps and crests is peculiar, however, and suggestive of the miacids rather than of contemporary leptictids or other possible groups. The unusual sinuous curve of the median crest line is reminiscent of the P_4 in *Ictidopappus*, although that genus has a P_4 shorter and wider than this. The over-all outline of the Puerco-Z tooth, on the other hand, is more like that of P_4 in the much smaller *P. (Simpsonictis)*, although that subgenus shows a more orthodox single crest-curve (convex labially) and typically has the posterior accessory cusp (hypoconid) reduced or absent. Puerco-Z appears also to have a rudimentary metaconid, a structure that is more clearly developed but differently shaped

¹ It is to be hoped that this will escape the notice of a notorious author who is in the habit of attaching names to similar, deliberately nameless specimens described by qualified students. The natural annoyance of serious workers (who sometimes must cite that writer as the author of a taxon validated by the work of others) may be somewhat mitigated by the thought that citation of an author's name along with that of a taxon is not done to give credit but to assign responsibility.

in *P. (Bryanictis) vanvaleni* and absent from all other miacids except for *Ictidopappus mustelinus* (in which it is obscurely suggested by a similar bulge).

Because Puerco-Z resembles P_4 in *Ictidopappus* to a slightly greater degree than it resembles other miacid teeth, it may be tentatively assigned to that genus until its true affinities are clarified.

PROTICTIS MATTHEW, 1937, NEW RANK

TYPE: *Protictis (Protictis) haydenianus* (Cope, 1882).

DISTRIBUTION: Middle and late Paleocene of North America.

INCLUDED SUBGENERA: *Protictis (Protictis)* Matthew, 1937; *P. (Simpsonictis)* Mac Intyre, 1962, new rank; and *P. (Bryanictis)*, new subgenus.

DIAGNOSIS: Differs from *Ictidopappus* in having relatively higher and shorter M_1 trigonid; relatively larger and more complex P_{3-4} , with well-developed paraconids distinct from protoconids; and cingula on P^{3-4} and conules on M^{1-2} .

Differs from *Didymictis* in having relatively higher trigonids of M_{1-2} , bearing sharper cusps and crests, with sharply incised notch dividing crests between protoconid and metaconid of M_2 ; and shorter, narrower M_2 talonid.

Differs from *Viverravus* in having relatively more broadly basined molar talonids; relatively higher, shorter M_1 trigonid; and conules on M^{1-2} .

DISCUSSION: The first suggestion that the type species might be generically separable from *Didymictis* stems from Matthew (1937). He did not think the evidence was then sufficient for full generic separation, however, so named *Protictis* as a subgenus.

Simpson (1937a) discussed the position of the smaller species of *Protictis* (not known to Matthew, who died in 1930) and abandoned the subgeneric divisions. At that time, he thought that *P. (B.) microlestes* was closer to the ancestry of *Didymictis* than was *P. (P.) haydenianus*, and he suggested that *P. (S.) tenuis* probably could be separated generically if it were better known.

In 1962, I acted upon the latter suggestion, agreeing that this tiny form could hardly be left in the same genus as the much larger and

morphologically distinct allies of *Didymictis protenus*.

Since 1962, further study has shown that *Didymictis* is composed of species that are about as distinct from the Paleocene species formerly placed in that genus as are the species of *Viverravus*. These two genera represent diverging lines of specialization in the Eocene; both are derivable from rather similar Paleocene ancestry. As stated in the discussion of *Ictidopappus mustelinus*, it is impossible for *Didymictis* to have been derived from that species and unlikely that *Viverravus* had such a peculiarly specialized ancestry. The remaining species of Paleocene miacids have a number of points of resemblance with both of the typically Eocene genera, although the middle Eocene species of *Viverravus* diverged more markedly from the ancestral stock than did the species of *Didymictis* (which became extinct near the end of the early Eocene). Thus, a small cluster of Paleocene species appear to be related to both *Viverravus* and *Didymictis* but do not belong in either of these two genera. They are here placed in a separate genus, for which the name *Protictis* is the oldest name available under the Code.

There are now four definable species of *Protictis*. If only *P. (P.) haydenianus* and *P. (S.) tenuis* were known, they could undoubtedly be placed in different genera; the former is about two and one-half times the size of the latter, and there are clear-cut differences in morphology. It would be more difficult to justify generic separation of *P. (B.) microlestes* from the other two species on the basis of the limited evidence now known; there are some obvious morphologic differences, but this species shows much more resemblance to the other two than *Ictidopappus mustelinus* does to any of these. The size differential is not unduly large for species in a single genus: *P. (P.) haydenianus* is about one and one-half times the size of *P. (B.) microlestes*, which in turn is about one and one-half of the size of *P. (S.) tenuis*. The species are clearly different, but there now seems to be no reason why they cannot be united in one genus.

As to the fourth species, *P. (B.) vanvaleni*, it is clearly more closely related to *P. (B.) microlestes* than to either of the other two species. This special relationship seems to re-

quire some kind of grouping above the species level. If *P. (B.) microlestes* and *P. (B.) vanvaleni* are not to be split off as a separate genus (unjustified by present evidence), this grouping must be subgeneric. The new name, *P. (Bryanictis)*, is therefore proposed to unite these two species.

There is also now some evidence that indicates that there were more species of *Protictis* during the middle Paleocene than the four recognized here. Some specimens in collections not available for the purpose of this review may represent definable new species of the various subgenera of *Protictis*. The fossils now available to me, however, are inadequate to permit the application of new names. Because they appear to be more closely related to *P. (P.) haydenianus* than to any of the other species in this genus, a few specimens are described here as *P. (Protictis)* sp.

None of the evidence presented here requires the recognition of more than one species of *P. (Simpsonictis)*. The small sample of *P. (S.) tenuis* from the Gidley quarry and the specimens from other localities are adequate to show that this species cannot be placed in either *P. (Bryanictis)* or *P. (Protictis)*; the name *P. (Simpsonictis)* is available to include *P. (S.) tenuis*.

PROTICTIS (PROTICTIS) MATTHEW, 1937

Didymictis (Protictis) MATTHEW, 1937, p. 101.
Didymictis SIMPSON, 1937a, p. 209 (in part).

TYPE: *Protictis (Protictis) haydenianus* (Cope, 1882).

DISTRIBUTION: Middle Paleocene of North America.

INCLUDED SPECIES: Type only.

DIAGNOSIS: Differs from *P. (Bryanictis)* in having relatively shorter M_2 talonid; relatively lower, blunter paraconid and relatively smaller hypoconid but relatively larger posthypoconid on P_4 ; relatively higher M_1 trigonid and more rounded posterior end of M_1 talonid; and relatively shorter, wider upper molars bearing reduced lingual cingula.

Differs from *P. (Simpsonictis)* in having relatively lower M_2 trigonid and smaller talonid cusps on M_2 ; relatively lower trigonid cusps on M_1 , particularly the metaconid; and relatively larger posterior accessory cusps on P_4 .

DISCUSSION: The reasons for separating this subgenus are given under the discussion of the genus.

The type species was the first described Paleocene miacid and is the most numerous in collections. A few specimens, described below as *P. (Protictis)* sp., appear to belong in this subgenus but not in the type species. Because these specimens are so few and fragmentary, formal proposal of a new name should be avoided until better material is at hand.

There are, moreover, some additional specimens in collections not available for inclusion in this study which may represent even more new species of *P. (Protictis)*. For example, Wilson (1951, 1956) has specimens probably referable to this subgenus which may be separable from the type species. Further comment is necessarily reserved until a fuller report is published and the specimens become generally available. There are also some undescribed miacids from the Rock Bench quarry in the Princeton collection to which the above remarks may apply.

Protictis (Protictis) haydenianus (Cope, 1882)

Plates 3-7; plate 8, figures 2, 3, 5, 8, 10; plates 9, 11, 20; text figures 13-17

Didymictis haydenianus COPE, 1882, p. 464; 1884a, p. 306, pl. 23e, figs. 12-13. MATTHEW, 1897, p. 287; 1909, p. 361. SIMPSON, 1937a, p. 213, fig. 59a (in part). DORR, 1952, p. 86.

Didymictis primus COPE, 1884b, p. 309.

Viverravus haydenianus: MATTHEW, 1899, p. 29. WORTMAN, 1901, vol. 12, p. 145.

Didymictis (Protictis) haydenianus: MATTHEW, 1937, p. 102, pl. 15, figs. 3-5, pl. 16, figs. 2-3.

TYPE: A.M.N.H. No. 3368, left dentary with P_4 - M_2 , left maxilla with P^3 - M^2 . Figured by Cope (1884a, pl. 23e, figs. 12-13).

TYPE OF *Didymictis primus*: A.M.N.H. No. 3371, part of left dentary with M_{1-2} .

DISTRIBUTION: Middle Paleocene (Torrejonian), Nacimiento Formation, lower and upper Torrejon beds; San Juan basin, New Mexico.

Middle Paleocene (Torrejonian), Lebo Formation, upper Lebo beds, upper levels; Crazy Mountain field, Sweetgrass County, Montana.

Middle Paleocene (?pre-Torrejonian), North Horn Formation, Joe's Valley Member,

Dragon beds; Dragon Canyon, NW. $\frac{1}{4}$, sect. 9, T. 19 S., R. 6 E., Emory County, Utah. These deposits are currently believed to be approximately middle Paleocene, although they were placed between Puercan and Torrejonian in the correlation chart of Wood and his co-authors (1941).

HYPODGM: San Juan basin, probably lower Torrejon: A.M.N.H. Nos. 948, 17059, Bohannan Canyon, Animas River 3 miles north of Aztec; A.M.N.H. No. 1764, between Escavada and Torrejon arroyos; A.M.N.H. No. 1776, Chico Spring; A.M.N.H. Nos. 3369a, 3374, 3996c, Gallegos Canyon (probably Chico Spring); A.M.N.H. No. 16539, head of Kimbetoh Arroyo; A.M.N.H. No. 16540 (Matthew, 1937, pl. 15, fig. 5; pl. 16, fig. 3), east fork of Torrejon Arroyo; type and A.M.N.H. Nos. 3244a, 3372, 3453a, 3517, 4005, 4060, no data (?Chico Spring); U.S.N.M. No. 15345, divide between Kimbetoh and west Kimbetoh arroyos; U.S.N.M. No. 15346, east side of Kimbetoh Arroyo.

San Juan basin, probably upper Torrejon: A.M.N.H. Nos. 778, 1499, 2391, 2393, 15991, U.S.N.M. No. 5872, Torrejon Arroyo; A.M.N.H. No. 1765, between Escavada and Torrejon arroyos; A.M.N.H. Nos. 15992 (Matthew, 1937, pl. 15, fig. 3, pl. 16, fig. 2), 15994, 16536 (Matthew, 1937, pl. 15, fig. 4), east fork of Torrejon Arroyo; A.M.N.H. Nos. 15993, 15995, 16538, west fork of Torrejon Arroyo; A.M.N.H. No. 16537, Alamito Arroyo; U.S.N.M. Nos. 15347-15354, between east and west branches of Torrejon Arroyo.

San Juan basin, Torrejon: A.M.N.H. Nos. 3371, 12382.

Crazy Mountain field, upper levels of upper Lebo: A.M.N.H. Nos. 35389-35392, 35862, Gidley quarry (locality 4), NW. $\frac{1}{4}$ of NE. $\frac{1}{4}$, sect. 25, T. 5 N., R. 15 E.; U.S.N.M. No. 6145, Silberling quarry (locality 1), sect. 4, T. 5 N., R. 16 E.

Dragon Canyon: U.Cal.M.P. Nos. 47252, 51682.

DIAGNOSIS: Only valid species of the subgenus.

MEASUREMENTS AND STATISTICS: See tables 3-6.

DESCRIPTION: Dentition: The dentition of *P. (P.) haydenianus* is most fully illustrated

by A.M.N.H. No. 3374, which has at least one example of every tooth present, although some are partly concealed. The upper and lower teeth are in occlusion and firmly cemented together by matrix, so the task of separating the closely interlocked teeth has not been completed because of the risk of damage to this unique specimen. (See pl. 9, fig. 3.)

Because both upper and lower incisors and canines are preserved completely in this specimen only, they may be conveniently described together. All these teeth are illustrated in plate 3, figure 1.

The upper incisors are all preserved, I^1 being largest and I^3 smallest, exactly the reverse of the condition seen in the Eocene miacid specimens (and probably all later fissipedes). The lingual surfaces of these teeth are not fully exposed, but what can be seen shows that they are quite simple teeth, single-cusped, slightly recurved, convex labially, and less convex lingually, the two faces meeting at an acute angle. I^1 is more pointed than I^3 (I^2 , predictably, is intermediate), but all are more or less rounded rather than awl- or chisel-like.

The lower incisors now exposed labially are blunter and more spatulate than the uppers, and the crowns are markedly more expanded transversely. The sizes are in more usual order, I_3 being larger than the subequal I_{1-2} .

The canines in A.M.N.H. No. 3374 are quite complete except for the left C^1 . All are partly concealed lingually. U.S.N.M. No. 15346 shows the entire root and both sides of an incomplete right C^1 . The most striking feature of this tooth in both specimens is the peculiar series of shallow grooves which begin near the point of the crown and pass toward the root, becoming flattened into facets near the enamel line. These are five in number on the labial side, two more facets being discernible on the posterior lingual side. The tooth is rounded anterolingually, and no grooves or facets are present on the preserved part of this side of the crown; there is a sharp crest running along the posterior edge. Otherwise, the upper canine has the usual tall, slender, slightly procumbent, and recurved shape of that of many small carnivores. The root of

TABLE 3

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF LOWER DENTITION OF *Protictis (Protictis) haydenianus* FROM TORREJONIAN LOCALITIES IN NEW MEXICO

	N	OR	M	s	V
I ₁ width	1	1.0	—	—	—
I ₂ width	1	1.3	—	—	—
I ₃ width	1	1.2	—	—	—
P ₁ length	1	2.2	—	—	—
P ₂					
Length	4	3.95–4.1	4.06±0.04	0.075±0.026	1.85±0.65
Width	4	1.65–1.8	1.74±0.04	0.075±0.026	4.32±1.52
P ₃					
Length	5	5.0–5.8	5.37±0.15	0.326±0.103	6.08±1.61
Width	6	2.25–2.6	2.39±0.05	0.120±0.035	5.02±1.45
P ₄					
Length	11	6.4–7.4	6.95±0.09	0.308±0.066	4.43±0.94
Width	14	3.0–3.35	3.16±0.03	0.122±0.023	3.86±0.73
Length/width	9	2.12–2.30	2.17±0.02	0.065±0.015	2.98±0.70
M ₁					
Length	11	7.3–8.2	7.65±0.07	0.246±0.052	3.22±0.68
Width (anterior)	12	4.6–5.5	4.94±0.07	0.247±0.050	5.00±1.02
Width (posterior)	24	3.8–4.6	4.07±0.04	0.203±0.029	4.99±0.72
Grind width (anterior)	21	3.6–4.3	3.93±0.04	0.168±0.026	4.27±0.66
Length of talonid	19	2.9–3.7	3.26±0.05	0.217±0.035	6.67±1.08
Length of paraconid	11	2.2–2.7	2.45±0.04	0.143±0.030	5.83±1.24
Length of metaconid	12	1.9–2.3	2.03±0.03	0.108±0.022	5.32±1.09
Length/width (anterior)	10	1.49–1.71	1.56±0.02	0.066±0.015	4.25±0.95
Width (posterior)/length of talonid	17	1.11–1.50	1.25±0.02	0.090±0.016	7.23±1.24
M ₂					
Length	14	4.9–5.85	5.45±0.07	0.283±0.048	5.19±0.98
Width (anterior)	17	2.9–3.5	3.26±0.05	0.207±0.036	6.35±1.09
Width (posterior)	17	2.2–2.8	2.49±0.04	0.183±0.031	7.35±1.26
Grind width (posterior)	18	2.3–3.2	2.68±0.05	0.194±0.032	7.25±1.21
Length of trigonid	10	2.3–2.7	2.50±0.04	0.116±0.026	4.63±1.04
Length/width (anterior)	13	1.54–1.81	1.66±0.02	0.066±0.013	3.99±0.78
Length/grind width (posterior)	12	1.86–2.12	2.02±0.03	0.111±0.023	5.48±1.12
Length of talonid/trigonid	10	1.04–1.33	1.18±0.04	0.113±0.025	9.58±2.14
P ₁ –M ₂ total length	2	35.4–37.8	36.60	—	—
P ₁ –P ₄ total length	2	22.7–23.7	23.20	—	—
P ₄ length/P ₃ length	4	1.28–1.29	1.28±0.003	0.006±0.002	0.47±0.17
M ₁ length/M ₂ length	4	1.37–1.49	1.43±0.03	0.057±0.020	3.98±1.41
Depth below M ₁	15	10.0–13.3	11.02±0.25	0.951±0.173	8.63±1.57
Depth below M ₂	18	9.3–12.5	10.72±0.24	1.018±0.170	9.52±1.59

the upper canine is stouter, more laterally compressed, and straighter than the root of the lower canine. (See pl. 3, fig. 2.)

In addition to the two complete lower canines of A.M.N.H. No. 3374, there is a lower canine minus about half the crown but including most of the root in U.S.N.M. No. 15354. The latter shows the sharper curvature of the slender, more rounded root in this tooth

and illustrates a small anterolingual cingulum close to the enamel line. Two sharp crests, one directly lingual and the other (a stronger one) at the anterolingual corner of the tooth, arise from this cingulum, but the crown is broken off so that their extent is unknown. As on the upper canine, the lowers also have five longitudinal grooves which flatten into facets near the root.

TABLE 4

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF UPPER DENTITION OF *Protictis*
(*Protictis*) *haydenianus* FROM TORREJONIAN LOCALITIES IN NEW MEXICO

	N	OR	M	s	V
I ¹					
Length	1	1.4	—	—	—
Width	1	1.4	—	—	—
I ²					
Length	1	1.1	—	—	—
Width	1	1.15	—	—	—
I ³					
Length	1	0.9	—	—	—
Width	1	1.0	—	—	—
P ¹ length	1	2.25	—	—	—
P ²					
Length	2	4.1 – 4.25	4.18	—	—
Width	1	2.2	—	—	—
P ³					
Length	5	4.9 – 6.1	5.45 ± 0.18	0.433 ± 0.137	7.97 ± 2.52
Width	2	3.2	3.20	—	—
P ⁴					
Length, labial	5	7.5 – 8.2	7.77 ± 0.12	0.259 ± 0.082	3.34 ± 1.06
Width	5	5.4 – 6.4	5.85 ± 0.19	0.430 ± 0.136	7.34 ± 2.32
Metastyle	4	2.4 – 2.8	2.70 ± 0.10	0.200 ± 0.071	7.40 ± 2.62
Length, lingual	4	9.0 – 9.4	9.22 ± 0.09	0.171 ± 0.060	1.85 ± 0.65
Length, labial/width	4	1.24– 1.52	1.36 ± 0.06	0.116 ± 0.041	8.52 ± 3.02
Length, lingual/length, labial	4	1.12– 1.22	1.19 ± 0.02	0.046 ± 0.016	3.84 ± 1.36
M ¹					
Length	7	5.5 – 6.5	6.15 ± 0.14	0.384 ± 0.103	6.23 ± 1.67
Width (anterior)	6	8.3 – 9.4	8.93 ± 0.17	0.411 ± 0.119	4.60 ± 1.33
Width (posterior)	6	6.3 – 7.65	7.34 ± 0.23	0.555 ± 0.160	7.57 ± 2.19
Grind width (anterior)	6	6.4 – 7.6	7.20 ± 0.18	0.442 ± 0.128	6.13 ± 1.85
Width (anterior)/width (posterior)	5	1.19– 1.31	1.23 ± 0.02	0.047 ± 0.015	3.86 ± 1.22
M ²					
Length	5	2.9 – 3.6	3.26 ± 0.12	0.270 ± 0.086	8.28 ± 2.62
Width (anterior)	5	5.1 – 6.8	5.68 ± 0.30	0.676 ± 0.214	11.9 ± 3.76
Width (posterior)	5	3.7 – 4.8	4.13 ± 0.19	0.432 ± 0.137	10.5 ± 3.32
Grind width (posterior)	5	4.0 – 5.1	4.51 ± 0.18	0.404 ± 0.128	8.98 ± 2.84
P ¹ –M ² total length	1	31.6	—	—	—
P ¹ –P ⁴ total length	2	22.5 – 24.0	23.25	—	—
I ¹ –M ² total length	1	50.5	—	—	—

The first lower premolar is known only in A.M.N.H. No. 3374, where it is visible on the left side. It is separated from the canine by a long diastema and from P₂ by a considerably shorter one. It is a small tooth, single-rooted, and slightly procumbent. The crown shows the primitive form frequently seen in carnivore first premolars: moderately high, essentially conical, slightly recurved, with a slight bulge on the posterior end but no distinct heel, and no trace of cingulum or acces-

sory cusps. Except for size, this tooth is very like P₁ in *P. (B.) microlestes*.

The second lower premolar is present in A.M.N.H. Nos. 3374, 12382, 16540, and 16537 and U.S.N.M. No. 15350 from the Torrejon and in A.M.N.H. No. 35389 from the Lebo Gidley quarry. All these specimens are essentially alike: two-rooted, erect, rather primitive premolars with a single, moderately high, slightly recurved main cusp. A small, variably distinct node which does not form

TABLE 5

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF *Protictis (Protictis) haydenianus* FROM THE UPPER LEVELS OF THE UPPER LEBO FORMATION, CRAZY MOUNTAIN FIELD, MONTANA

	N	OR	M	s	V
P ₂					
Length	1	4.4	—	—	—
Width	1	1.85	—	—	—
P ₄					
Length	1	7.4	—	—	—
Width	1	3.2	—	—	—
Length/width	1	2.31	—	—	—
M ₁					
Length	2	7.2–7.65	7.43	—	—
Width (anterior)	3	5.0–5.2	5.07±0.07	0.116±0.047	2.28±0.93
Width (posterior)	2	3.9–4.2	4.05	—	—
Grind width (anterior)	2	3.8–3.9	3.85	—	—
Length of talonid	3	2.9–3.0	2.93±0.03	0.058±0.024	1.98±0.81
Length of trigonid	2	4.2	4.20	—	—
Length of paraconid	3	2.4–2.5	2.43±0.03	0.058±0.024	2.38±0.97
Length of metaconid	2	2.1	—	—	—
Length/width (anterior)	2	1.44–1.47	1.46	—	—
Width (posterior)/length of talonid	2	1.35–1.40	1.38	—	—
M ₂					
Length	2	5.2–5.75	5.48	—	—
Width (anterior)	2	3.2–3.4	3.30	—	—
Width (posterior)	2	2.4–2.75	2.58	—	—
Grind width (posterior)	2	2.4–2.8	2.60	—	—
Length of trigonid	2	2.2–2.25	2.22	—	—
Length/width (anterior)	2	1.63–1.69	1.66	—	—
Length/grind width (posterior)	2	2.05–2.16	2.10	—	—
Length of talonid/trigonid	2	1.36–1.56	1.46	—	—
Shear length	1	37.0	—	—	—
M ₁ length/M ₂ length	2	1.33–1.38	1.36	—	—
Depth below M ₁	1	12.0	—	—	—
Depth below M ₂	1	11.5	—	—	—
P ₃					
Length	1	4.9	—	—	—
Width	1	2.3	—	—	—
P ₃ width	1	3.4	—	—	—
P ₄					
Length, labial	1	8.0	—	—	—
Width	1	6.55	—	—	—
Metastyle	1	2.8	—	—	—
Length, lingual	1	9.5	—	—	—
Length, labial/width	1	1.22	—	—	—
Length, lingual/length, labial	1	1.19	—	—	—

a distinct cusp is at the anterobasal end of a low crest on the anterior edge of the tooth. This crest rises in a convex curve (marred by a few minute crenulations in some specimens) to the posterior corner of the tooth, terminating in a minute, variably expressed nodule. There is an indistinct posterior cingulum

which outlines a variably developed concavity on the heel in some specimens, but this is nowhere a distinct talonid.

The third lower premolar is complete in A.M.N.H. Nos. 3374 and 16540 and U.S.N.M. Nos. 15350 and 15354; six other specimens show parts of this tooth more or less damaged.

TABLE 6
MEASUREMENTS (IN MILLIMETERS) OF *Protictis*
(*Protictis*) *haydenianus* FROM
DRAGON CANYON, UTAH

P ⁴ length, lingual	10.4
M ¹	
Width (posterior)	8.7
Grind width (anterior)	8.7
M ²	
Length	2.85
Width (anterior)	5.2
Width (posterior)	4.0
Grind width (posterior)	4.1

Compared to that in P₂, variability in P₃ is more obvious, probably because the features of P₃ are more pronounced.

The two most unlike specimens were collected from the area near the head of Torrejon Arroyo but from the lower (A.M.N.H. No. 16540) and upper (U.S.N.M. No. 15354) levels of the Torrejon, as designated by Sinclair and Granger (1914). The "lower-level" specimen has a P₃ more like P₂ than like P₄. The anterobasal node is slightly larger than that in P₂ but does not form a cusp; the posterior crest is more crenulate. Small lingual and labial cingula are definitely present on the posterior third of the tooth, and the hypoconulid (posterior cingulum cuspule) is clearer than in P₂. This is the specimen figured by Matthew (1937, pl. 15, fig. 5; pl. 16, fig. 3). The "upper-level" specimen shows stronger development of the posterior labial and lingual cingula. There is also a small but definite anterior labial cingulum with a small paraconid (anterobasal cuspule) clearly set off from the main cusp. This cuspule is placed somewhat lower on the tooth than the corresponding node on the lower-level specimen just described. The cusps are more nearly in a straight line, and the heel is somewhat broader. These characters are shared by U.S.N.M. No. 15350 but are less pronounced in that more worn specimen, and A.M.N.H. No. 3374 is intermediate in character between U.S.N.M. No. 15350 and A.M.N.H. No. 16540. The remaining specimens indicate a range of variation such that the extremes appear as the ends of a cline rather than as sharply separable forms.

Thirteen specimens from the Torrejon have

the fourth lower premolar more or less well preserved. The type and two others show parts of the heel only. A.M.N.H. No. 3374 has P₄ well preserved but partly concealed by hard matrix.

The P₄ of *Protictis* is easily distinguishable from that tooth in *Didymictis* by the presence of a prominent extra posterior accessory cusp (post-hypoconid) in the former. The first posterior accessory cusp (hypoconid) is close to the main cusp (usually called the protoconid) and separated from it by a narrow carnassiform notch; the cleft posterior to it is deeper and in some specimens wider. The second posterior accessory cusp is always somewhat shorter and usually blunter. A small posterior cingulum cusp (probably corresponding to the hypoconulid) is present, but this is variable in height. In some specimens, a bladelike crest connects the cingulum cusp (hypoconulid) to the second accessory cusp (post-hypoconid); this ridge may be faintly notched, indicating the presence of an incipient third accessory cuspule.

There is always an anterior basal cusp (paraconid), but this varies from a more or less pointed shape to a bladelike shape set off from the main cusp by a distinct carnassial notch. Although the cusps on P₄ are arranged in an anteroposterior row, they form a curve concave lingually, the main cusp being most labial. The curving alignment is somewhat straighter in some specimens than others, but it is never quite straight.

Most specimens have a pronounced labial cingulum running from the anterobasal cusp to the posterior cingulum cusp. This continues along the lingual side to the base of the main cusp but never passes the midpoint of the tooth. About half of the specimens have no lingual cingulum anteriorly; a small one is present on the rest.

These variations in the details of premolar cuspidation are not correlated in any regular way, so that the available specimens cannot be divided into definable groups on the basis of premolar characters.

The lower carnassial, M₁, is preserved intact in A.M.N.H. Nos. 16536 and 16539 and U.S.N.M. No. 15353 from the Torrejon, as well as in A.M.N.H. No. 35389 from the Gidley quarry of the Lebo Formation. Fourteen more specimens, including the type,

have most of this tooth preserved but more or less broken or obscured by matrix, and another 15 specimens show only the talonid. (See pls. 6, 7, and 11.)

The trigonid cusps are high and sharply pointed, particularly the protoconid. The metaconid is subequal to or higher than the paraconid and more pointed, because the shearing blade of the metaconid is at an angle to the nearly horizontal paraconid blade. Both these cusps are markedly lower and less pointed than the protoconid. There are well-marked carnassial notches at the junctures of the sharp crests from the protoconid to the other two cusps. Wear facets indicate that there was some shear on the posterior face of the trigonid, but this was less important than the shear on the anterior face, as indicated by greater wear there.

A sharply defined anterobasal cingulum is invariably present, bearing variable crenulations but no clearly defined cusps, although in most specimens this cingulum is highest at a point lingual to the position of the anterior carnassial notch.

In 10 out of 12 Torrejon specimens, a small cingulum variously expressed is present at the lingual base of the paraconid; this is not present in the type or in two of the three Lebo specimens and is very faint in the third specimen. All the trigonids are tall and show a small angle γ . The three Lebo specimens appear to have a slightly larger angle γ than the Torrejon sample.

The talonid of M_1 is preserved in more specimens than is the trigonid, which is to be expected where the trigonid is relatively tall and slender. Twenty-seven specimens show this part of the tooth sufficiently well preserved for analysis. A striking peculiarity which is immediately observed is the presence of an extra cuspule between the hypoconid and the hypoconulid of 13 specimens, all from the Torrejon. This is, however, merely another of the variable characters within this species. Another 13 specimens do not have this cuspule well developed, and several of this number lack it. The type is too worn and broken to be useful here, but it does show the basined talonid, short labial cingulum, and typically primitive ridges running from the base of the metaconid to the entoconid (the lingual talonid crest) and thence to the hypo-

conulid and hypoconid. The hypoconid is a prominent cusp connected to the base of the trigonid. At the posterior base of the trigonid and directly below the posterior carnassial notch, a sharp crista obliqua begins and runs posteriad and laterad to the summit of the hypoconid. This crest divides the talonid basin from the steep sulcus obliquus which lies between the hypoconid and the posterior base of the protoconid. In normal occlusion, the tall paracone of M^1 bites down into this groove so that the tip of this cusp just grazes the posterior labial cingulum which marks the ventral limit of the sulcus obliquus. This cingulum is short and does not pass around the base of the hypoconid to meet the posterior talonid crest. The latter slants sharply upward and ends at or near the hypoconulid. The posterior talonid crest may be faint or absent. When both these cingula are well developed, they are often also variably crenulated.

The last lower molar, M_2 , is well preserved in 12 specimens from the Torrejon and in two from the Lebo; 11 more specimens from the Torrejon and one from the Lebo show this tooth partly obscured or damaged. The type is among those with the M_2 damaged, but it is well enough preserved to show the general characteristics found in most of the other specimens. The outline of the tooth is approximately fusiform in crown view; the trigonid is relatively much lower than in M_1 but definitely higher than the M_2 talonid, which is relatively longer and narrower than in M_1 and is basined more narrowly. The trigonid cusps are all clearly separated, and there are small carnassiform notches dividing the crests between the protoconid and the other two cusps. The paraconid is slightly smaller than the metaconid (damaged in the type), which is smaller than the protoconid (very worn in the type). All three cusps are relatively low and blunt in unworn specimens.

The type M_2 shows a large hypoconid, but the prominent hypoconulid and variable entoconid visible on unworn specimens are broken away. In unworn specimens, the hypoconulid is generally prominent and may be higher than the hypoconid. On the other hand, the entoconid is prominent in some specimens and reduced almost to the vanishing point in others (the three specimens from

the Lebo Gidley quarry show that both extremes occurred in a single population). Several intergrades are also known.

An anterior labial cingulum is invariably present. This does not extend onto the lingual surface of the crown, nor does it connect with the short posterior labial cingulum present in most specimens between the labial bases of the hypoconid and protoconid. The latter cingulum is not present in A.M.N.H. Nos. 35390 and 35389 from the Lebo but is found in all specimens from the Torrejon; in A.M.N.H. No. 16539 it nearly connects to a cingulum running from the base of the hypoconid to the hypoconulid.

It should be noted that the higher trigonid of M_2 is nevertheless functionally an extension of the M_1 talonid because the smaller second tooth never grows to such a size that its lower talonid is on a level with the talonid of M_1 . In occlusion, the tall paracone of M_2 bites down into the lingual groove between the bases of the protoconid and hypoconid of M_2 , just as in the M_1 pair.

The first upper premolar was described by Cope (1884b)¹ as single-rooted. Further preparation and microscopic examination of A.M.N.H. Nos. 3374 and 3244a clearly demonstrate two roots on the right and left P^1 of the former and two alveoli in the latter (also seen in U.S.N.M. No. 15354, but less clearly). Unfortunately, the crowns of these teeth in A.M.N.H. No. 3374 were somewhat cracked (as were nearly all the others) by the same crushing process that fragmented the rest of this fossil, but enough remains to show that this tooth is a rather typical carnivore anterior premolar, comparatively smaller and simpler than P^2 but basically of the same pattern reduced to essentials. The tooth is slightly procumbent, and the main cusp is approximately triangular in outline but faintly recurved. There is a small posterobasal node but no definite cuspule here and no sign of a cingulum or anterobasal cuspule. The lingual side is not exposed.

The second upper premolar is preserved in A.M.N.H. Nos. 3374 and 948 from the Torrejon and A.M.N.H. No. 35862 from the Gidley quarry. The specimens from the Tor-

rejon agree well in the preserved parts with each other and with the slightly more robust Gidley quarry specimen. All have two roots and are erect, moderately sharp, and elongate oval in section. There is a small posterior cuspule behind the slightly recurved paracone, and there is a poorly defined anterobasal node which does not form a definite cuspule.

There is no posterolabial cingulum on P^2 (see pl. 3, figs. 5, 6). There is a small anterolabial cingulum on this tooth in A.M.N.H. No. 35862 but only a faint trace of this in A.M.N.H. No. 3374. None of the other specimens show this part of the tooth. The lingual cingulum is shown in the former specimen, in which it is more sharply defined than in A.M.N.H. No. 948, but in neither does it extend more than three-quarters of the length of the tooth, being obsolete posteriorly. The posterobasal cuspule (metastyle) is clearly defined in the three specimens mentioned above, and in the largest (A.M.N.H. No. 35862) the crest which runs from its summit to the opposing crest on the paracone is set off by a minute carnassiform notch between the two. This specimen also shows a definite crest on the anterior face of the paracone. This crest is less emphatically developed in the other two specimens.

The paracone is nearly the shape of an equilateral triangle in side view, although the posterior edge is faintly concave. In crown view, the tooth is flat labially and convex lingually at the base of the crown, but no definite protocone can be seen, although this is barely hinted by a small node on the internal cingulum of A.M.N.H. No. 35862. The differences of this specimen from the others are merely in degree of development and are probably due only to its slightly greater size and robustness.

The third upper premolar is preserved in five specimens from the Torrejon, including the type, and in A.M.N.H. No. 35862 from the Gidley quarry. The important features of P^3 can be briefly summarized as accentuated development of the same features seen in P^2 . A slightly longer anterolabial cingulum, the development of a posterolabial cingulum in some but not all specimens (e.g., not in the Gidley quarry specimen), a posterior extension and broadening of the lingual cingulum, the addition of a third root (alveoli seen

¹ Cope also noted here the unusual size gradient of the upper incisors and the "facets" of the canines.

in U.S.N.M. No. 15354 and A.M.N.H. No. 3244a, roots in others) midway under this cingulum, and the variable development of a protocone (weakest in A.M.N.H. No. 948 and strongest in the Gidley quarry specimen) go along with the extension and expansion of the posterior basal cuspule into a small (metastyle) shearing blade (weakest and strongest, respectively, in the two specimens just mentioned) and a more triangular outline in crown view. This last point is of some interest, for P^3 in the type, although damaged, shows clearly that this specimen illustrates the forward shift of the protocone seen in P^4 , and the form of P^3 in the type is exceeded only by P^3 in the Gidley quarry specimen in its approach to the shape of P^4 . At the opposite extreme is A.M.N.H. No. 948, which shows only a rudimentary protocone cuspule slightly posterior to the midline of the tooth and not nearly so lingually extended, although a definite third root is present. The other specimens intergrade between the two extremes represented by A.M.N.H. Nos. 948 and 35862, so these premolar differences cannot now be shown to be taxonomically significant (see pl. 3, figs. 5–11).

None of the known specimens of the upper fourth premolar are quite complete and unbroken, although four fairly complete specimens of this tooth are known. These are A.M.N.H. Nos. 15995 and 17059 from the Torrejon, U.S.N.M. No. 6145 from the Lebo, and U.Cal.M.P. No. 47252 from the Dragon. Seven more specimens from the Torrejon (including the type) are in the American Museum of Natural History collection, but these are less useful because of damage or matrix encrustation. These specimens were used for comparison as far as possible, and the exposed portions agree well with one another and with the better-preserved specimens listed above (see pls. 4 and 8).

This tooth has the shape of a plump Y, with a nearly straight posterolingual margin but distinct median concavities in the labial and lingual margins. The anterior emargination is deeper than the labial one; the latter varies from a slight sinuosity to a sharp curve in different specimens.

The paracone is the largest cusp and is situated near the center of the tooth. It is approximately triangular in section, with

crests running down the posterior and anterolabial angles toward the carnassial notch and parastyle, respectively; the anteromedial face is rounded. This cusp appears to lean backward sharply because of its nearly vertical posterior edge. The protocone is situated at the extreme anterolingual corner of the tooth. It is larger than the parastyle and has the form of a blunt cone, slightly bulging at the external parts of the base. The parastyle is at the extreme anterolabial corner of the tooth and is more nearly pyramidal in shape, owing to a slight flattening of the labial and anterolingual faces. There is a definite crest running on the internal side of this cusp toward the opposing crest on the paracone. These crests are separated by a small notch near the base of the parastyle. In most specimens, there is no corresponding crest on the protocone. A few have variously positioned short ridges on the internal face of the protocone, but these do not extend very far and are not associated with any corresponding crest on the paracone. Such ridges are found variously near the lingual or labial sides of the protocone and may be anywhere in between.

All specimens of P^4 have a sharply defined cingulum on the posterolingual base of the crown. Beginning at the posterior corner of the metastyle blade, this cingulum runs diagonally from the occlusal edge of this corner toward the midpoint of the posterior root, then levels off and passes along the base of the paracone to the base of the protocone, where it may end abruptly (five specimens) or turn sharply toward the summit of this cusp (two specimens). In the latter event, the cingulum becomes obsolete before it reaches the tip of the protocone. A short anterior cingulum connects the base of the protocone with the base of the parastyle. In no case does this connect to the posterolingual cingulum or to the styler cingulum. The styler cingulum begins near the labial side of the summit of the parastyle, runs in a steep curve to the posterior base of this cusp, and follows the outer margin of the tooth posteriad, becoming more crenulated and narrower as it approaches the narrowest part of the tooth opposite the deep carnassial notch between the paracone and metastyle blade. This cingulum may merge into the rugose

flank of the metastyle blade at this point, or it may continue to the posterior end of the metastyle blade; most specimens show intergrades between these two possibilities. In two specimens that are nearly unworn, a faint second cingulum may be seen between the main one and the edge of the blade. The area between these two cingula is rugose, but the enamel is quite smooth above and below.

The metastyle blade is high and sharp. Nearly flat lingually, it is convex labially. The undamaged specimens show no separation of metacone and metastyle. The specimen from the Dragon (U.Cal.M.P. No. 47252) appears to have a shallow notch behind the highest point (immediately posterior to the carnassial notch) which suggests a former separation between these two cusps, but the specimen is slightly damaged, and this may be illusory. There is no way to decide, therefore, whether the metastyle blade in this species represents that cuspule alone or a fusion with the metacone.

In this connection, the use of the term "metastyle blade" does not imply any prejudice but is merely a descriptive convenience.

The first upper molar is well preserved in A.M.N.H. Nos. 948 and 15991 from the Torrejon; A.M.N.H. No. 12382 and U.Cal.M.P. No. 47252, from the Torrejon and Dragon, respectively, are little worn but partly missing; A.M.N.H. No. 3369a from the Torrejon and U.S.N.M. No. 17059 from the Lebo are worn but essentially complete. Six other specimens, including the type and A.M.N.H. No. 3374, show various degrees of fracture and concealment in flinty matrix.

The description given here is taken largely from the first two specimens mentioned above; the remarks on variability are based on comparison of these with other specimens. As nearly as can be ascertained from the worn, shattered, and partly obscured M^1 of the type, these two specimens resemble it and A.M.N.H. Nos. 3374 and 12382 most closely. The other specimens appear to differ in varying degrees (see pls. 3, 4, and 8).

There is a definite parastyle cuspule on the stylar cingulum at the anterolabial corner of the tooth; this is usually simple (e.g., in A.M.N.H. No. 948) but may be connected to the stylocone by a short crest (e.g., in A.M.N.H. No. 15991). The stylocone is re-

duced to a barely distinguishable swelling on or near the stylar cingulum at the end of the stylocone-paracone crest, which is separated from the paracone by a carnassial notch. The crest continues to the summit of the paracone, curving around from the labial to the anterior edge of that cusp, and then passes to the base on the posterior side. A similar crest, separated by a small carnassiform notch from the foregoing, follows the anterior edge of the smaller, lower metaconid to its summit, then, curving linguad, passes to the stylar cingulum. On unworn A.M.N.H. Nos. 948 and 15991, two small cuspules may be seen on this crest near the base of the metacone; one of these may represent a metastyle remnant.

The stylar shelf is wide and more or less rugose; U.Cal.M.P. No. 47252 from the Dragon is markedly so where this part is preserved. It also possesses a well-defined, single metastyle cuspule at the base of the metacone, and the stylar cingulum is continuous around the base of this cuspule, not separated by a decided gap as in topotypic *P. (P.) haydenianus*.

The paracone is a sharply pointed cusp, twice as high as the metacone. The protocone is sharp and between the paracone and metacone in height; it is connected to the parastyle by a long crest (nearly straight in crown view) upon which the well-developed paraconule is situated midway between paracone and protocone. A shorter, more curved crest runs from the protocone toward the metastyle area; there appear to be two metaconules on this crest. The first is indistinct, low, and crenulated on unworn teeth and after some wear appears as an oval wear crater barely separated from the more definite second cuspule which lies closer to the metacone. This second (probably definitive) metaconule marks the point where the protocone-metastyle crest gives off a short branch which connects the metaconule with a small cuspule (mesoconule) near the lingual base of the metacone. The main part of the crest continues in a curved path toward the metastyle, but it is interrupted by a small gap before it reaches the metastyle corner. This gap is pronounced in A.M.N.H. No. 15991 but small in A.M.N.H. No. 948; in U.Cal.M.P. No. 47252, there is no gap, and the cingulum is

complete around the base of the metastyle. The M^1 from the Dragon has the cingula generally more strongly developed and crenulated than does that of the specimens from the Torrejon. Its stylar area is somewhat wider; the paracone is a larger cusp and closer to the protocone. The metacone area is damaged, but this cuspule was probably larger. There is a more pronounced "hypocone," but this is more of a high point on the posterior lingual cingulum than a definite cusp. The posterior lingual cingulum approaches the anterior lingual cingulum more closely, and a row of faint irregular crenulations hints at an incipient (or regressing?) connection.

There is a definite metastyle cuspule at the base of the metacone and well separated from the stylar cingulum on the Dragon specimen.

The parastyle corner of M^1 is extended, the stylar cingulum being convex to a point approximately opposite the cleft between paracone and metacone. The cingulum then runs approximately parallel to the paracone-metacone crest and forms almost a right angle with the posterior border of the crown. The posterior border is slightly convex around the base of the metacone and concave at the "waist" of the tooth near the metacone. The anterior border is concave from the parastyle corner to a point just anterior to the paracone, then runs almost straight to the end of the anterior lingual cingulum, which is faintly convex for its whole length. The base of the protocone is semicircular and slightly bulbous between the lingual ends of the two cingula.

The tip of the protocone is closer to the anterior border of the crown than it is to the posterior border. Its anterior face is hence steeper than its posterior face. The paracone similarly appears to lean anterolabially.

The development of the lingual cingula is various. In none of the Torrejon specimens do the posterior lingual and anterior lingual cingula meet to form a continuous lingual cingulum. The anterior lingual cingulum is slightly longer and less sharply curved than the posterior lingual cingulum. In A.M.N.H. No. 948, the posterior lingual cingulum is shorter and narrower than in A.M.N.H. No. 15991. The specimen from the Dragon has

the widest, longest posterior lingual cingulum of the three; at the most posterior corner, the largest of the several crenulations on this cingulum might be called a hypocone, and a small but definite cuspule is situated at the most lingual end of the anterior lingual cingulum. These cuspules are merely suggested by corresponding crenulations in the two specimens from the Torrejon mentioned above and in A.M.N.H. No. 12382, a specimen that is closest to the Dragon specimen in the slightly more emphatic development of cuspules and crenulations on the cingula. In this regard, the specimens discussed above form a graded series, U.Cal.M.P. No. 47252 (cf. pl. 8, fig. 5, and pl. 4, fig. 7) showing the most pronounced development of all features with A.M.N.H. Nos. 12382, 15991, and 948 illustrating progressive diminution of these features.

Compared with conditions seen in the upper premolars, the intergradation in the M^1 characters of these specimens shows that they also could all have belonged to a single species.

The last upper molar, M^2 , is well preserved in A.M.N.H. No. 3374 from the Torrejon and in U.Cal.M.P. No. 51682 from the Dragon. Three more Torrejon specimens (including the type) and one from the Lebo have this tooth present but more or less damaged or partly obscured. All these differ slightly in detail, apparently owing to normal variability, and much larger samples would be needed to show whether the differences are taxonomically significant or not.

In crown view, the tooth is approximately the shape of a scalene triangle, with a distinct metacone at the obtuse angle formed by the labial and posterior borders. The stylocone and protocone are near the more acute anterior and lingual corners, respectively. The posterior and lingual corners are rounded, with the bases of the metacone and protocone forming smooth curves there.

The stylar cingulum begins at the metacone and runs forward along the labial edge of the crown but does not extend onto the posterior border. There is no distinct metastyle; small irregularities may represent this.

The metacone is a relatively low, conical cusp. It has only one crest. This runs from the apex to the base on the anterior side and

is divided from the corresponding crest on the posterior edge of the paracone by a distinct carnassial notch.

The paracone is directly anterior to the metacone and about equidistant from the anterior and labial borders of the crown. This is the tallest, sharpest cusp on M^2 , but it is neither relatively nor absolutely so tall and sharp as the corresponding cusp on M^1 , which is true of all features of M^2 compared with M^1 .

The anterior crest of the paracone curves labially and is interrupted by another carnassial notch near the base of the cusp. The crest continuing labial to this notch is sharp and almost as high as the stylocone, which is visible as a small swelling on, or just lingual to, the styler cingulum.

Just anterior to the stylocone and directly on the anterior end of the styler cingulum, a small cusplule may represent the parastyle in U.Cal.M.P. No. 51682 and A.M.N.H. No. 948. If this was present on the other specimens, it is not now visible and may have been worn off.

There is a good-sized paraconule and some smaller crenulations on the anterior protocone-stylocone crest. The posterior protocone-metacone crest has two subequal cusplules, the more labial of which is more distinct and hence may be called the metaconule. There is a small, gently crenulate posterior lingual cingulum which is widely separate

from the corresponding anterior lingual cingulum; the latter is larger than the former.

Skeleton: No complete lower jaws of *P. (P.) haydenianus* are known, and only one (A.M.N.H. No. 35390 from the Gidley quarry) illustrates the posterior end, including the angle, condyle, and the base of the coronoid process (see pl. 7, figs. 3, 4).

The horizontal ramus or body of the dentary is essentially complete in A.M.N.H. No. 3374, and six other specimens from the Torreon are sufficiently well preserved to show the morphology of this part of the jaw (see pl. 9, fig. 3). In section, this bone may be shallow and rounded anteriorly in gracile specimens or deeper and more oval in robust ones.

The symphyseal region is sloping, with only a faint break in the line of the ventral edge to mark the end of the chin region below P_1 . The body becomes progressively deeper until a point under M_1 is reached. From here on, the ventral border of the jaw rises until a point under the dental foramen is reached, then it gently curves downward toward the end of the angle.

The dorsal border of the jaw slopes gently upward along the line of the incisor alveoli to a point near the posterior edge of the canine. It then becomes slightly concave back to the alveoli of P_2 and is nearly straight from there to the posterior end of M_1 . Parallel to the rise in the ventral border, the dorsal border also rises in the area occupied by M_2 and immediately behind this, then it turns steeply upward along the anterior face of the coronoid process.

This process is mostly missing, but the remainder shows it to be straight in profile and distinctly concave in section near the base. The crista coronoidea,¹ a strong ridge that runs up the anterior border of the coronoid process on the lateral side, begins below and behind M_2 . In some more robust specimens, the beginning of this ridge is more anterior and ventral. The coronoid process measures 20 mm. long at the base but only 0.5 mm. at the thinnest diameter along the same line. This delicate sheet of bone has not been preserved above the baseline at the level of the condyle.

¹ This and similar terms are from Ellenberger and Baum (1891).

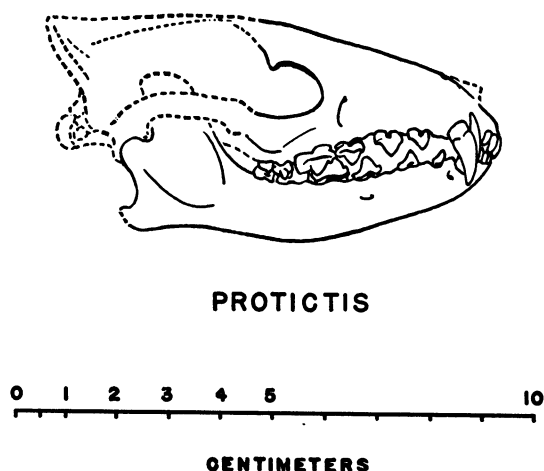


FIG. 13. *Protictis (Protictis) haydenianus*. Restored outlines of skull and jaws, right lateral aspect. Compare plate 3, figure 1; plate 7, figure 4; and plate 9, figure 3.

The only condyle known is present on A.M.N.H. No. 35390. It is a little over 10 mm. broad (a small part of the mesial end has been lost) and a little under 0.5 mm. thick at the maximum diameter of the articular surface. This condyle of *Protictis* is hence slightly smaller than the corresponding part in *Alopex* and has approximately the same shape as in the latter and other canids, differing from these recent forms in the convex dorsal profile and more pointed lateral end. This condyle of *Protictis* also appears to project more posteriorly than in *Alopex* or in the viverrid *Nandinia*, because the excavation of the posterior end of the jaw is deeper here than in most recent carnivores.

The angular process is directed posteriad more than ventrad. Its lateral surface is nearly flat, but the internal surface shows ridges presumably marking the insertion of the internal pterygoid muscle. The tip of the angle has been lost, but the preserved parts hint that it was slightly hooked, as in *Didymictis protenus*.

Posteriorly, the lateral side of the jaw shows a low crest, the crista condyloidea, curving ventrad and antieriad from the end of the articular process and becoming indistinct as it approaches the crista coronoidea. Below this crest the bone is thickened and has a rather flat surface which accommodated part of the masseter insertion.

Above the crista condyloidea, there is a distinct concavity, the masseteric fossa. This marks the ventral limit of the temporalis muscle, which inserted on the lateral surface of the coronoid process. There is no distinct anteroventral border to this fossa. Instead, it becomes shallower and blends smoothly with the lateral surface of the jaw below the crista coronoidea. In more robust specimens (A.M.N.H. No. 2391 and U.S.N.M. No. 15353), the crista condyloidea is distinct almost as far as the crista coronoidea, and a second crest can be seen ventrally, the linea masseterica. The latter is not clearly defined in the other specimens where this region is preserved (A.M.N.H. No. 35390 and U.S.N.M. No. 15351), but it evidently marks the insertion of the masseter.

Anteriorly, the lateral side of the jaw is marked by a small mental foramen under the posterior root of P_3 and a larger one under

P_1 . A third mental foramen faces directly antieriad under the incisor roots.

The medial surface of the jaw shows that the long, slanted oval of the symphysis ends under P_2 . The surface of this articulation is pitted and covered with rounded irregularities, but no strongly interlocked suture is indicated. A rounded ridge extends from the posteroventral end of the symphysis posteriorly; this becomes obsolete under P_4 . The surface of this ridge is roughened slightly as for muscle attachment; evidently the mylohyoid and (chiefly) geniohyoid muscles were inserted here.

Just below the juncture of the coronoid process with the body of the jaw on the medial side, there is a small curved tubercle which marks the anteroventral limit of the temporal muscle insertion. Two faint crests, one following the anteromedial border of the coronoid process vertically and one running horizontally to the dorsal limit of the dental foramen, hence define the anterior and ventral limits of the insertion of this muscle.

The distance from the condyle to the posterior edge of M_1 in A.M.N.H. No. 35390 is 31 mm.; in A.M.N.H. No. 3374, the distance from the posterior edge of M_1 to the anterior edge of I_1 is approximately 44 mm. When these two specimens are matched side by side, the total length is about 75 mm., and this is probably close to the total length of the lower jaw in *P. (P.) haydenianus*.

The most nearly complete skull of *P. (P.) haydenianus* is preserved in A.M.N.H. No. 3374. This specimen consists of the forepart of the skull and jaws broken off behind the postorbital process and at or near the rear ends of the last molars. What was then visible was accurately described by Cope (1884a), and his description is quoted by Matthew (1937, p. 102), who slightly revised Cope's description of the species. (See pl. 20.)

By the use of an Airdent, a machine only recently invented (see Stucker, 1961), the specimen has been freed of the flinty matrix that partly obscured the right side and wholly concealed the left. A number of specimens not available to Cope or Matthew permit some comparisons not possible when they wrote, and a modern binocular microscope reveals a few details of the dentition not apparent to them. Unfortunately, the fossil

is crushed laterally, and the bones have separated into a mosaic of small fragments, cemented together by matrix. Thus, although the superficial topography of the skull is fairly clear, the suture pattern is obscured to the point that a description would be based almost as much upon imagination as upon observation. (See pl. 9.)

In brief, there is nothing visible here to show that the skull of this species differs radically in structure from the corresponding bones in *Didymictis protenus* or *D. altidens*, although there is a considerable difference in size. The snout is moderately long and slender and rather foxlike in general form. A comparatively minor feature is the presence of a well-developed postorbital process in this specimen (also visible but broken in U.S.N.M. No. 15354). In the two comparable specimens of Eocene *Didymictis* (A.M.N.H. No. 17030 and P.U.M. No. 14917), there is no distinct projection in this region of the skull. (See text fig. 13.)

A broken postorbital process can be detected in U.S.N.M. No. 15354 and A.M.N.H. No. 3244a, and these two specimens (the former crushed dorsoventrally and the latter crushed laterally) tend to confirm the more or less elongate shape of the snout seen in A.M.N.H. No. 3374. A few other specimens (A.M.N.H. Nos. 3368, 3369, 3372, 3517, 4005, and 4006) have parts of the skull present, but these are either buried in flinty nodules or so checked and distorted as to be useless.

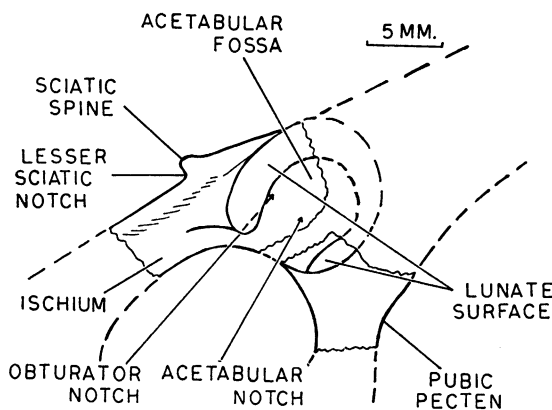


FIG. 14. *Protictis (Protictis) haydenianus*. A.M.N.H. No. 948. Reconstruction diagram of acetabular region of right side of pelvis, ventrolateral aspect. Compare plate 9, figs. 1, 2.

The infraorbital canal is illustrated by A.M.N.H. Nos. 3374 and 3244a; it opens above P^3 as it does in *Didymictis*. The usual groove between I^3 and C^1 for the reception of the tip of C_1 is seen in A.M.N.H. No. 3374; this is also seen in *Didymictis* (and primitive mammals generally).

The only identifiable parts of the postcranial skeleton are fragments of a right innominate bone and femur (A.M.N.H. No. 948) and dubiously associated calcaneum and astragalus fragments (A.M.N.H. No. 12382). Both these specimens include well-preserved teeth.

The fragments of innominate bone (see text fig. 14) show parts of the right ischium and pubis, including the posterior ends of the lunate articular surface which encloses the acetabular fossa. A well-developed sciatic spine (origin of the gemelli muscles) is sharply defined by the lesser sciatic notch immediately behind and below it. A deep obturator notch, overhung by a strong ridge on the ischium, is also apparent on the lateral surface. The dorsal surface shows a clearly defined muscle scar just anterior to the sciatic spine for tail muscles, probably corresponding to the lateral coccygeal. The acetabulum appears relatively shallow, possibly owing to slight lateral crushing of the specimen. Aside from this apparently shallow acetabulum and the relatively well-developed sciatic spine, the specimen generally resembles equivalent parts in *Genetta* and *Herpestes* among recent carnivores of comparable size. But *Sciurus* and *Lepus* also have these parts of the pelvic girdle similarly developed, so no special relationship is implied by this resemblance. The much larger *Didymictis protenus* (A.M.N.H. No. 3276) and all other miacids for which pelvic parts are known are likewise similar in this area. The miacid closest to *Protictis* in size is *Miacis parvivorius* (A.M.N.H. No. 11495), and, except that the preserved scrap of ischium is a little more slender in *Protictis*, there are no appreciable differences in the parts preserved. Both *Miacis* and *Protictis* have rather primitive pelves, without any outstanding peculiarities that can be determined from the available material. Until more complete *Protictis* material is at hand, more extended comparisons are likely to produce more speculation than information.

The fragment of right femur associated with the above pelvic fragment shows most major structures of the proximal end, which is nearly complete but somewhat crushed anteroposteriorly. (see text fig. 15.) The head is well set off from the shaft and evidently was of the usual hemispherical form (about 7.5 mm. in diameter as preserved), with a shallow fovea (fossa for the ligamentum teres) on the posteromedial face a little dorsal of the midline. The neck is relatively a little longer and more slender than in the femur of *Miacis* (A.M.N.H. No. 11494). In *Protictis*, the lesser trochanter is partly damaged but was clearly present just distal to the neck. It appears to have been further from the neck than the lesser trochanter is in *Miacis*. On the lateral edge, distal to the level of the lesser trochanter, there is, in *Protictis*, a small but distinct third trochanter. This lies at the end of a crest which passes proximally to the great trochanter. The latter process is well developed and set off from the shaft posteriorly by a narrow trochanteric (digital) fossa.

Because the femur of A.M.N.H. No. 948 is crushed, it is impossible to compare it exactly with those of other miacids. As preserved, it is similar in size to the femur of *Miacis* (A.M.N.H. No. 11495) and differs only in the slightly more distal position of the damaged lesser trochanter and the slightly less robust development of the intertrochanteric crest running ventrad from the posterior side of the greater trochanter. Both of these conditions may, however, be illusory.

Comparison with the femur of Eocene *Didymictis*, a much more robust form, shows only minor differences. The lesser trochanter of *Didymictis* is posteromedial. In *Protictis*, this feature appears to be more nearly medial, but the process is broken, and the position may also be illusory because of crushing of A.M.N.H. No. 948. None of the available *Didymictis* femora is undamaged, and several are partly obscured by very hard matrix. Until better material becomes available, it seems useless to carry comparisons too far. In any case, the few remains of *Protictis* postcranial skeletons do not alter the taxonomic picture that is the main concern of the present paper.

If *Protictis* may be assumed to have had an arrangement of muscles more or less similar

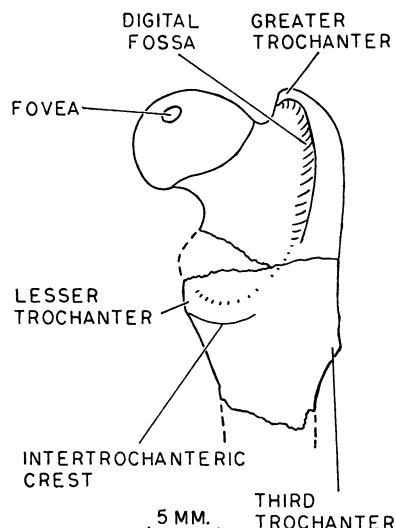


FIG. 15. *Protictis* (*Protictis*) *haydenianus*. A.M.N.H. No. 948. Diagram of proximal end of right femur, posteroventral aspect. Compare plate 8, figure 3.

to conditions seen in modern dogs and cats, some information on leg muscles may be appropriately inserted here.

The lesser trochanter is the insertion point of the iliopsoas, quadratus lumborum, and psoas major muscles. These adductor muscles act generally to pull the leg forward in running. The third trochanter is the insertion point of the superficial gluteal muscle, which has its origin in the sacral region and acts to abduct the hip joint and move the leg backward. The dorsal end of the greater trochanter is the insertion point for the gluteus medius, which abducts the femur. The gluteus profundus is an abductor which inserts a little below the gluteus medius on the anterior face of the femur and pulls the femur forward. There are no clear signs of separate insertion for these muscles, but the greater trochanter is as well developed as in *Miacis* (A.M.N.H. No. 11496), the third trochanter is clear but slightly less prominent and somewhat lower on the shaft than in *Miacis*, and the lesser trochanter is present but damaged.

To sum up the available evidence, it is fair to say that *Protictis* evidently had a primitive acetabulum-femur complex and that the known postcranial remains indicate that the hip-joint region was perhaps a little more primitive than the corresponding parts of

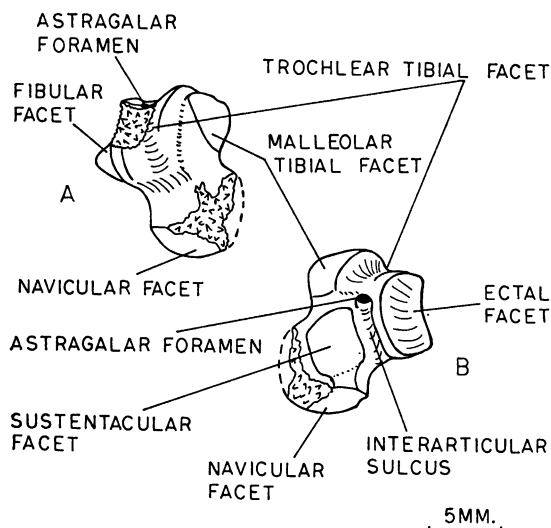


FIG. 16. *Protictis (Protictis) haydenianus*. A.M.N.H. No. 12382. Diagram of dubiously associated right astragalus. A. Anterodorsal aspect. B. Plantar aspect. Compare plate 9, figures 4, 6, 8, 10. See plate 10 for equivalent views of undoubted *Didymictis protenus* astragali.

Didymictis but not very different in essence. Comparison with equivalent parts of miacines shows greatest affinity in size and morphology with *Miacis* and increasing divergence through the series *Oodectes*, *Vulpavus*, and *Palaeoarctonyx*.

Tentatively associated¹ with A.M.N.H. No. 12382 are a slightly damaged right astragalus and broken left calcaneum. (See text figs. 16 and 17.)

The astragalus, when compared with corresponding bones of Eocene *Didymictis protenus* (A.M.N.H. Nos. 2855, 55417, and 15637) and *D. altidens* (A.M.N.H. No. 14781), shows general similarity of structure but some difference in detail (see pls. 9 and 10). The dorsal surface of the Torrejonian specimen has a groove for the tibial trochlea which is relatively deeper proximally and appears shallower distally. (The specimen is damaged distally, and it is difficult to be sure of this last point.) Such is the condition seen in *Vulpavus* (A.M.N.H. Nos. 11497, 11478, and

12626) and *Miacis* (A.M.N.H. No. 11509). The facet for the malleolar part of the tibia is slightly more sharply delineated and faces a little more dorsad in A.M.N.H. No. 12382 and the miacines than in *Didymictis*. The fibular facet is wider and directed more anterodorsad in A.M.N.H. No. 12382 than in any of the Eocene specimens. The navicular facet appears more convex, but the medial part of the head and neck are damaged, so the appearance may be illusory. The astragal foramen is closer to the medial edge of the trochlear facet.

The distal edge of the astragalus in A.M.N.H. No. 12382 shows a cuboid facet less sharply defined than in any of the Eocene specimens compared. On the ventral side, the sustentacular facet also had an anteromedial extension which has been lost anteriorly in this specimen but is not present in any of the Eocene specimens. This implies an anterior astragal facet on the calcaneum. The ectal facet is relatively longer and narrower in A.M.N.H. No. 12382 than in A.M.N.H. No. 11497 (*Vulpavus*) and A.M.N.H. No. 11509 (*Miacis*).

Unfortunately, the calcaneum fragment doubtfully associated with A.M.N.H. No. 12382 lacks most of the distal part and part

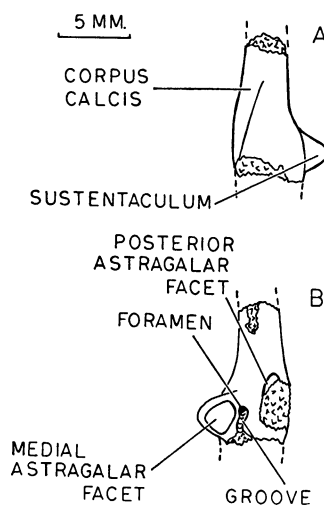


FIG. 17. *Protictis (Protictis) haydenianus*. A.M.N.H. No. 12382. Diagram of dubiously associated left calcaneum fragment. A. Plantar aspect. B. Anterodorsal aspect. Compare plate 9, figures 5, 7, 9, 11. See plate 10 for equivalent views of undoubted *Didymictis protenus* calcanea.

¹ The original museum label (Brown, expedition of 1904) states "lower jaws and astrag. ass.?" The locality is given as "20 m. E. Putnam San Juan Basin, N.M.," a designation too vague to be useful even if "Putnam" could be found now.

of the posterior end; it hence shows only the middle part of the body. The remaining parts differ little from the corresponding parts of the early Wasatchian *Didymictis* mentioned above (A.M.N.H. No. 2855 and others) and Bridger *Vulpavus* and *Miacis*. The Paleocene specimen shows a broadly triangular sustentaculum, which projects directly mediad. This process bears the middle astragalar facet on its dorsal face and in the Eocene early Wasatchian *Didymictis* quite fills the visible surface, which is not the case in the Paleocene specimen or in late Wasatchian *Didymictis* (A.M.N.H. No. 14781) and Bridger *Vulpavus*, in which the facet is clearly smaller than the process and a depressed rim is left around the anteromedial margin. This facet is sharply delimited laterally by a sulcus which ends posteriorly at a conspicuous (?nutrient) foramen absent from the Eocene forms.

On the lateral side of this sulcus is the facet astragali posterius, which faces mediad more than dorsad in Eocene miacids. Most of this facet has been broken away, but the small portion preserved near the posterior end indicates that the Paleocene specimen did not differ from available Eocene counterparts.

It must be emphasized that these damaged tarsal specimens are not certainly associated with the *Protictis* (A.M.N.H. No. 12382) teeth found with them, nor can they be said to be associated with one another, as they are not from the same side of the body, do not fit together, and appear to be of different sizes. Both appear to be primitive enough to be *Protictis* bones, but it is perfectly possible that they pertain to a small condylarth or similar primitive mammal.

Because of the fragmentary nature of the specimens and their uncertain locality and associations, speculation upon the tarsal structure of *Protictis* might be misleading. This description is provided chiefly in the hope that, if more complete and definitely associated material is found, these specimens may be compared in detail and their real affinities decided.

DISCUSSION: More than 60 specimens referable to *P. (P.) haydenianus* are known. Some 40 of these are fragments of lower jaws with teeth; about 20 partial upper dentitions

are known. A few parts of the skull are available, but no basicranial material is known, and very few identifiable postcranial bones have been found. The majority (more than 40 specimens) have been collected in the Torrejon beds of the San Juan basin in New Mexico.

Unfortunately, no adequate samples are recorded from any one locality or clearly established stratigraphic horizon in this field, and many of the specimens lack specific information as to locality and level. The San Juan basin is certainly not too large for occupation by a single subspecies of carnivore, but we have no assurance that the time during which the Torrejon beds were being deposited was so short as to preclude the replacement of one population by another—quite the opposite. Wilson (1951, 1956) has confirmed the presence of more than one faunal level in these beds, as originally reported by Sinclair and Granger (see section on Stratigraphy and Geography above). This introduces some uncertainty into the assumption that all these specimens represent one species.

The over-all question of the validity of samples was examined in the Introduction of this paper, but some information relating directly to this species can be presented here.

If the combined American Museum of Natural History and United States National Museum collections are measured and the standard statistics calculated, the broad sample drawn from the whole formation does not exceed the reasonable limits of variation found in a single species (see tables 3 and 4). An attempt was made to divide the combined collections into two groups derived from the "upper" and "lower" levels, and the standard statistics were recalculated on that basis. Student's *t*-tests showed that the two subsamples differed only in the size of the M_1 paraconid, and this difference was not decisive ($0.01 < P < 0.02$). Some minor changes in coefficients of variation occurred but not in any regular fashion. There is a possibility that reasonably large samples, drawn from more precisely identified localities and levels, might show clear, consistent differences between "upper" and "lower" assemblages, and the species might then be divided into subspecies. But there is now no way to demonstrate that more than one spe-

cies is represented by these fossils, nor does the present evidence give any clear indication of subspecific divisions.

Qualitative observations of variation in tooth characters not subject to quantitative treatment (relative development of cingula and minor cuspules, for example) tend to confirm the conclusions based on the statistical results. Although an effort was made to find such, no character or complex of characters was found that showed consistently correlated deviation in any one direction, and most specimens showed intermediate conditions between the extremes.

Such striking characters as the unusual size gradient of the incisors (I^1 largest, I^3 smallest) and the peculiarly grooved and faceted canines are now useless as diagnostic features because of the great rarity of these teeth among Paleocene miacids. As collections continue to grow, however (particularly by washing and screening sparsely fossiliferous deposits), these peculiarities of *P. (P.) haydenianus* will undoubtedly become more important, so are worth more than passing mention.

The type specimen requires some special consideration because it is damaged and rather deceptive in appearance (see pl. 11). To begin with, it was probably a rather small individual and the teeth were well worn. Post-mortem damage has produced the illusion of still smaller size and some alteration of the apparent morphology. Microscopic comparison shows that the type is morphologically close, in comparable parts, to A.M.N.H. No. 16540 (from the lower level Torrejon) and A.M.N.H. Nos. 3374 and 3369a (from Gallegos Canyon). The last two are also invested with the same sort of flinty matrix as the type and were also collected by Baldwin in the early 1880's.

Given these admittedly slender clues and the information outlined in the section on Stratigraphy and Geography above, it seems reasonable to assume that the type locality was probably in the lower level exposures—very possibly near Chico Spring.

If the sample from the Torrejon beds of New Mexico may be considered to represent the species as a whole, there is some basis for comparison with small samples from other fields. Two specimens from Dragon Canyon, Utah, and nine specimens from the Crazy

Mountain field, Montana, were available to me for inclusion in this study.

The two specimens from Dragon Canyon are isolated tooth crowns, so it is not possible to be absolutely certain about their relationships to the Torrejon assemblage, but they are not now separable from *P. (P.) haydenianus* and are described above as part of that species. One individual (represented by U.Cal.M.P. No. 51682, an isolated M^2 ; see pl. 3, fig. 4) is somewhat smaller than the mean for the New Mexico sample; the other (represented by U.Cal.M.P. No. 47252, isolated P^4-M^2) is somewhat larger than the mean size; but both are within the range of variation observed in the New Mexico assemblage. Minor differences in some cuspules appear to be within the limits of individual variation, although comparisons have been strictly limited by the small number of undamaged specimens available for comparison.

Six of the specimens from the Crazy Mountain field were collected in the Gidley and Silberling quarries, which are in the uppermost levels of the Lebo formation (about 1200 feet above the base). They evidently represent a population that is probably, but not certainly, distinguishable from the New Mexico assemblage. Student's *t*-tests show that the specimens from the uppermost Lebo differ from the New Mexico assemblage in having a shorter M_1 trigonid ($0.01 < P < 0.02$), shorter M_2 trigonid ($0.01 < 0.02$), and greater talonid length/trigonid length ratio of M_2 ($0.01 < P < 0.02$). As the level of significance is nearly, but not quite, decisive, and none of the morphological differences is sufficiently clear-cut to require taxonomic recognition, these specimens are described above as part of *P. (P.) haydenianus*.

There remain three specimens from scattered localities at or below the 800-foot level of the Lebo Formation; these are discussed separately below as *P. (Protictis) sp.*

Protictis (Protictis) sp.

Plate 8, figures 1, 4, 6, 7, 9, 11

Didymictis haydenianus: SIMPSON, 1937a, p. 213, fig. 59b (in part).

DISTRIBUTION: Middle Paleocene (Torrejonian), Lebo Formation, upper Lebo beds, lower levels; Crazy Mountain field, Sweetgrass County, Montana.

HYPODIGM: U.S.N.M. No. 9930, locality 51, SW. $\frac{1}{4}$, sect. 24, T. 4 N., R. 15 E.; A.M.N.H. No. 35422, locality 81, near middle of S. $\frac{1}{2}$, sect. 23, T. 6 N., R. 15 E.; U.S.N.M. No. 6143, locality ?50, near middle of S. $\frac{1}{2}$, sect. 9, T. 3 N., R. 15 E.¹

MEASUREMENTS (IN MM.): U.S.N.M. No. 9930: P_4 width, 3.85. A.M.N.H. No. 35422: M^1 width (posterior), 8.7; P^4 width, 7.7. U.S.N.M. No. 6143: P^4 length, lingual, 11.8; P^4 metastyle, 3.6.

DESCRIPTION: There is only one lower tooth represented, the posterior half of a P_4 from the 575-foot level. The specimen has been broken off between the protoconid and hypoconid, but the remaining part shows the characteristically subequal hypoconid and post-hypoconid cusps, the latter being somewhat lower than the former. There is a small hypoconulid on the posterior edge of the crown. This cuspule is on a crest that passes from the base of the protoconid posteriad as a posterolabial cingulum and continues around the posterior edge of the crown, finally becoming the lingual rim of a small tal-

onid basin. There are clearly marked carinasiform notches separating the surviving median cusps. The basic form of this fragment is very close to that of A.M.N.H. Nos. 2391 and 15992 in the corresponding parts. The Lebo specimen is nevertheless significantly larger (width, $P < 0.01$) and clearly represents a more robust form than any other comparable specimen (see pl. 8, figs. 6, 9, and 11).

There are two specimens with upper teeth from the 800-foot level; both have parts of P^4 - M^1 preserved, but none is quite complete. Both examples of P^4 are generally similar to the comparable parts of New Mexico specimens, although there is one significant difference (lingual length, $P < 0.01$) in the measurable dimensions and two that approach significance (width, $0.01 < P < 0.02$; metastyle, $0.02 < P < 0.05$). It is noteworthy that the one specimen from New Mexico (A.M.N.H. No. 15995) that appears to be close to these specimens in size is damaged, and its measurements had to be discarded. The damage was not evident, however, until a thick coating of flinty matrix had been removed, revealing a number of matrix-filled cracks.

The two fragments of M^1 from the 800-foot level differ from comparable New Mexico specimens in more robust appearance and stronger lingual cingula. In U.S.N.M. No. 6143 the lingual cingulum is complete, and in A.M.N.H. No. 35422 it is barely interrupted. Such conditions are not seen in the comparable specimens from New Mexico; the nearest approach is seen in the otherwise different specimen (U.Cal.M.P. No. 47252) from Dragon Canyon, Utah. There is only one measurable dimension available for comparison; this shows no significant difference from the New Mexico sample.

DISCUSSION: Of the two groups of *P. (Protictis)* from the upper Lebo Formation (no miacids are known from the lower Lebo or "Fort Union No. 1," a unit occupying the first 500 feet of the formation; the upper Lebo extends from the 500-foot level to the 1300-foot level), the specimens discussed here from the "lower" localities are visibly more robust than those from the Gidley and Silberling quarries. In and of themselves, these two groups would not be separable on the basis of such small samples. When each is compared with the large New Mexico sample, however,

¹ Simpson (1937a, p. 37) mentioned a "partial upper jaw" of *P. (Protictis)* from locality 8, without mention of a specimen number. This locality is near locality 81 and at the same level, but no such specimen has been found in the United States National Museum or American Museum of Natural History collections. A damaged P^4 (U.S.N.M. No. 6143) was figured by Simpson (1937a, fig. 59b), but no locality was given, and the locality data found in the box with this specimen are confusing. There is a slip of paper, evidently a field note, stating "locality 50," "field no. 80," and "lot no. 137." There is also an old, handwritten museum label giving 137 as the "original number," but no locality. Finally, there is a newer, typed museum label, giving "locality 1" (Silberling quarry). If the specimen really came from locality 50, there is no mention of it in Simpson's (1937a, p. 38) faunal list for that locality. If it came from the Silberling quarry, this would be a second specimen, whereas Simpson (1937a, table 1) showed only one "*Didymictis haydenianus*" from that locality (undoubtedly U.S.N.M. No. 6145). If it is from locality 8, one wonders why none of the records now with the specimen show locality 8. After almost 30 years, it is too much to expect that Simpson himself could settle the questions of which specimen came from locality 8 and from which locality U.S.N.M. No. 6143 was collected. I follow the information (apparently authentic) found on the field slip with the specimen and assume that it was from locality 50. If it did come from locality 8, it was still from the 800-foot level, so it belongs with the "lower" locality assemblage discussed here, not with the "upper" Silberling quarry assemblage (see text fig. 8).

some significant and some nearly significant quantitative differences appear. The qualitative differences between these "lower" specimens and the New Mexico sample are clear and tend to confirm the quantitative data. As stated above in the discussion of the type species, such is not true of the "upper" specimens from the Lebo. In short, the "upper" specimens from the Lebo fit with the New Mexico assemblage, but the "lower" specimens do not.

There is little doubt that this "lower" group of robust specimens represents a new taxon, but a new name for this taxon would not really be useful until more complete fossils are described. It is now more practical to postpone proposal of a new name until some really diagnostic material is at hand.

**PROTICTIS (SIMPSONICTIS) MAC INTYRE, 1962,
NEW RANK**

Didymictis: SIMPSON, 1937a, p. 209 (in part).
Simpsonictis MAC INTYRE, 1962, p. 1.

TYPE: *Protictis* (*Simpsonictis*) *tenuis* (Simpson, 1935).

DISTRIBUTION: Middle and ?late Paleocene of North America.

INCLUDED SPECIES: Type only.

DIAGNOSIS: Differs from *P.* (*Protictis*) in having relatively higher trigonid and larger talonid cusps on M_2 ; relatively higher metaconid and trigonid on M_1 ; relatively smaller, single, posterior accessory cusp (hypoconid) on P_4 ; and in the absence of such a cusp on P_3 .

Differs from *P.* (*Bryanictis*) in having relatively higher molar trigonids; weaker paraconid and much smaller, single hypoconid on P_4 ; reduction or absence of hypoconid or metaconid on P_{3-4} ; and relatively higher metaconids on M_{1-2} .

Differs from all other miacids by the characters of the genus.

DISCUSSION: The reduction of this taxon to subgeneric rank is necessitated by a reappraisal of the basic nature of these animals and their relationship to the other Paleocene miacids. The reasons are given in the discussion of *Protictis*.

***Protictis* (*Simpsonictis*) *tenuis*
(Simpson, 1935)**

Plate 12; plate 17, figures 2, 4, 7; text figure 18

Didymictis tenuis SIMPSON, 1935, p. 238; 1937a, p. 22, fig. 58.

Simpsonictis tenuis: MAC INTYRE, 1962, p. 1, figs. 1-3.

TYPE: U.S.N.M. No. 9297, fragment of left dentary with M_1 and part of P_4 . Figured by Simpson (1937a, fig. 58).

DISTRIBUTION: Middle Paleocene (Torrejonian), Lebo Formation, upper Lebo beds; Gidley quarry (locality 4), NW. $\frac{1}{4}$ of NE. $\frac{1}{4}$, sect. 25, T. 5 N., R. 15 E., Crazy Mountain field, Sweetgrass County, Montana.

HYPODIGM: Type and A.M.N.H. Nos. 35347-35350. A.M.N.H. No. 35348 figured by Mac Intyre (1962, figs. 1-2); A.M.N.H. No. 35350 figured by Mac Intyre (1962, figs. 1, 3).

DIAGNOSIS: Characters of the subgenus, with P_4 having the posterior accessory cuspule (hypoconid) reduced to a trace on the posterior edge of the main cusp or absent entirely. The molar talonids are broadly basined, not trenchant, with the "hypoconid and entoconid about equally high and distinct" (Simpson, 1935); these two cuspules are larger on M_1 than on M_2 .

MEASUREMENTS AND STATISTICS: See table 7.

DESCRIPTION: Dentition: No trace of the incisors or their alveoli remain.

The remaining part of the canine alveolus shows only that this tooth was not unduly reduced in proportion to the size of the jaw and that it was probably single-rooted.

The alveolus for P_1 is separated from the canine by a 1.5-mm. diastema and indicates that this tooth was single-rooted and slightly procumbent. The alveolus measures about 1.3 mm. in length and 0.8 mm. in width. (See pl. 17, figs. 2, 4.)

After a very short diastema (0.4 mm.), the alveoli for P_2 begin; both contain root fragments, and the limits of the alveoli indicate a tooth about 1.9 mm. long. From here backward, the teeth form a continuous series with no diastemata, and P_2 - M_2 are two-rooted (see pl. 12).

The only known P_3 of this species is the one preserved in A.M.N.H. No. 35348. It is a rather simple tooth, with the moderately high main cusp (protoconid) broken near the summit and somewhat worn thereafter. It has a small, conical paraconid cuspule (also

TABLE 7
MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF *Protictis (Simpsonictis)*
tenuis FROM THE GIDLEY QUARRY, CRAZY MOUNTAIN FIELD, MONTANA

	N	OR	M	s	V
P ₃					
Length	1	1.9	—	—	—
Width	1	0.75	—	—	—
P ₄					
Length	3	2.35–2.6	2.48 ± 0.07	0.126 ± 0.051	5.07 ± 2.07
Width	3	1.1–1.15	1.12 ± 0.02	0.029 ± 0.012	2.59 ± 1.16
Length/width	3	2.14–2.36	2.23 ± 0.07	0.117 ± 0.048	5.27 ± 2.15
M ₁					
Length	2	2.6–3.1	2.85	—	—
Width (anterior)	3	1.8–1.9	1.85 ± 0.03	0.050 ± 0.021	2.72 ± 1.11
Width (posterior)	4	1.4–1.6	1.49 ± 0.04	0.085 ± 0.030	5.73 ± 2.03
Grind width (anterior)	4	1.4–1.5	1.45 ± 0.03	0.058 ± 0.020	3.90 ± 1.38
Length of talonid	3	1.0–1.1	1.03 ± 0.03	0.058 ± 0.025	5.60 ± 2.28
Length of trigonid	3	1.4–1.8	1.57 ± 0.12	0.208 ± 0.085	13.25 ± 5.38
Length of paraconid	2	0.75	—	—	—
Length of metaconid	2	0.7–0.8	0.75	—	—
Length/width (anterior)	2	1.37–1.67	1.52	—	—
Width (posterior)/length of talonid	3	1.36–1.45	1.40 ± 0.03	0.045 ± 0.018	3.24 ± 1.32
M ₂					
Length	4	2.4–2.8	2.56 ± 0.08	0.168 ± 0.060	6.57 ± 2.32
Width (anterior)	4	1.4–1.5	1.42 ± 0.02	0.050 ± 0.018	3.51 ± 1.24
Width (posterior)	4	1.1	1.10	—	—
Grind width (posterior)	4	1.2	1.20	—	—
Length of trigonid	4	1.2–1.3	1.26 ± 0.02	0.048 ± 0.017	3.81 ± 1.35
Length/width (anterior)	4	1.71–1.87	1.80 ± 0.03	0.068 ± 0.024	3.76 ± 1.33
Length/grind width (posterior)	4	2.00–2.33	2.14 ± 0.06	0.128 ± 0.045	5.98 ± 2.11
Length of talonid/trigonid	4	0.85–1.15	1.03 ± 0.07	0.136 ± 0.048	13.2 ± 4.67
P ₁ –M ₂ total length	1	13.2	—	—	—
P ₁ –P ₄ total length	1	8.4	—	—	—
P ₄ length/P ₃ length	1	1.32	—	—	—
M ₁ length/M ₂ length	1	1.08	—	—	—
Depth below M ₁	4	3.8–4.4	4.00 ± 0.14	0.283 ± 0.100	7.07 ± 2.50
Depth below M ₂	5	3.5–4.0	3.68 ± 0.09	0.192 ± 0.064	5.23 ± 1.66

broken), which was well separated from the protoconid, and a long heel posteriorly which terminates in a larger, pointed, posterior cingulum cusp (hypoconulid). A low crest runs antieriad from the hypoconulid toward the labial side of the base of the protoconid, broadens as it reaches its lowest point, then turns slightly linguad and runs up the posterior edge of the protoconid. This crest is slightly damaged, but it gives the impression of having been (originally) somewhat crenulated. On the anterior edge of the protoconid, a small but definite crest runs from the base to near the summit; this crest is not connected to the paraconid. There are no definite

cingula, but a pair of low, dull crests delimit the posterior heel region rather vaguely on the lingual and labial sides of the median crest.

The fourth premolar is preserved in three specimens (A.M.N.H. Nos. 35347, 35348, and 35350) and is partly preserved in the type (U.S.N.M. No. 9297). Of these, the best-preserved tooth is in A.M.N.H. No. 35347. The protoconid is tall and conical, with anterior and posterior crests arranged as in the P₃ described above, but slightly more accentuated and placed more definitely on the labial side of the midline of the tooth. The posterior crest bears a conspicuous swelling about halfway down the edge of the main

cuspid; this is worn, but it does not appear to have formed a distinct accessory cusp (hypoconid). A similar swelling appears in the same position in A.M.N.H. No. 35350, but this is slightly broken as well as worn. A trace of this feature is also visible in A.M.N.H. No. 35348, but no distinct signs are obvious in the P_4 of the type (see Simpson, 1937a, fig. 58).¹ As might be expected, there is normal variability here, but nowhere does more than a trace of a hypoconid or any such accessory cuspule appear in this species.

The posterior cingulum cuspule (hypoconulid) is conical and sharply pointed; a short cingulum evidently ran from the summit of this cusp to the labial base of the main cusp in A.M.N.H. Nos. 35347 and 35348. A trace of a labial cingulum was also present low on the flank of the paraconid in these specimens. However, these are mere traces on A.M.N.H. No. 35350, and the posterior cingulum has been largely obliterated by a deep wear facet (caused by the P^4 paracone) on all these specimens, so that its full extent posteriorly is obscure.

There is no cingulum anteriorly on the lingual side of P_4 , but there is a series of blunt crenulations along the lingual side of the posterior heel, which is definitely basined in A.M.N.H. No. 35348 and rather obscurely so in the remaining specimens. The heel is divided by a more or less median crest, as in P_3 described above.

The first lower molar is the largest tooth in the series and shows the typically primitive form of the early miacid lower carnassial. This tooth is most complete in A.M.N.H. No. 35348 and is present (more or less damaged) in the other specimens except for A.M.N.H. No. 35350, from which it was lost.

The body of the trigonid is much elevated above the talonid and is surmounted by the usual three cusps. The protoconid is tallest, but the metaconid is nearly as tall; both of these are sharply pointed. The paraconid is much lower than the metaconid and is not nearly so pointed. There is a distinctly blade-like crest running from the apex of each of these cusps to the anterior and posterior

carnassiform notches which divide the bases of these cusps from the base of the protoconid. Similar crests rise from these notches to the summit of the protoconid, but these are much steeper than the corresponding crest on the metaconid, which is in turn much steeper than the crest on the paraconid. The latter becomes even lower in worn specimens, but it can be observed unworn on A.M.N.H. No. 35349.

Distinct wear facets are observable on the edge of the paraconid blade and on the anterior face of the trigonid. These indicate normal fissipede occlusion with a carnassial P^4 shearing past the M_1 talonid anteriorly. A distinct wear facet can be seen down the posterior edge of the metaconid. There are also a marked worn area on the edge of the metaconid blade and a wear facet on the posterior face of the protoconid—all clear signs of normal occlusion with M^1 .

The talonid of M_1 is clearly basined, but the basin is relatively a little narrower and deeper than in *P. (Protictis)* or *P. (Bryanictis) microlestes*. In unworn specimens, the three talonid cuspules are sharp and distinct and of about equal height. In worn specimens, the hypoconulid is obscure, and the entoconid appears smaller than the hypoconid but remains distinguishable. The surface of the talonid is worn by the protocone on M^1 , and a strong wear facet appears in the sulcus obliquus, almost obliterating the cingulum which runs from the base of the protoconid around the base of the hypoconid to the labial face of the hypoconulid—obvious evidence of a tall paracone on M^1 . The presence of a well-developed metacone on M^1 is similarly indicated by a wear facet on the posterior face of the hypoconid, which nearly obliterates this part of the cingulum in worn specimens.

The last molar, M_2 , is preserved in all four American Museum of Natural History specimens but is absent from the United States National Museum type. It is most complete in A.M.N.H. No. 35347, whereas A.M.N.H. No. 35349 shows this tooth nearly unworn but slightly damaged (see pl. 17, fig. 7).

The trigonid is markedly higher than the talonid but not nearly so high as in M_1 . The M_2 trigonid projects well above the talonid of the preceding tooth, so that it must have

¹ Simpson (1937a, p. 213) remarked that this tooth might not belong to this specimen, but there is now hardly any doubt that it does, although it is damaged.

occluded in the M^{1-2} interdental embrasure. However, the slight development of wear facets on the anterior edges of the M_2 protoconid and metaconid indicates that no strong shearing took place between M^1 and M_2 . The posterior face of the M_2 trigonid, on the other hand, shows that this part of the tooth sheared past the anterior edge of M^2 , and the well-worn M_2 talonid basins of some specimens bear witness to the normal occlusion with the M^2 protocone. As in M_1 , wear facets anterior and posterior to the labial side of the hypoconid indicate that the paracone and metacone on M^2 were relatively tall.

The protoconid is the tallest trigonid cusp, but it is not so tall relative to the metaconid as the corresponding cusp on M_1 . As in the preceding tooth, these two cusps are separated by a carnassiform notch which divides the two bladeliike crests on the lingual and labial sides of the protoconid and metaconid, respectively. On the protoconid, this crest rises at a steeper angle than the opposing crest on the metaconid.

A similar crest runs down the anterior edge of the protoconid, then turns labiad at the lowest point and follows the anterior edge of the paraconid (without the interruption of a carnassiform notch) to the low summit of that cusp.

The paraconid is relatively lower than the corresponding cusp on M_1 , and the bladeliike anterior crest is nearly horizontal in A.M.N.H. Nos. 35349 and 35347 but somewhat more angular in the remaining specimens. There is a definite anterobasal cingulum which extends diagonally upward from the labial base of the protoconid to the base of the paraconid on the midline of the anterior edge. When the teeth are in their normal relationship, the lingual end of this cingulum is hence immediately behind the hypoconulid of the preceding tooth. This cusplule fits into the small concavity between the paraconid and the cingulum on M_2 , so that a mortise-tenon effect is attained, and lateral shifting of the individual teeth is restrained. A similar mechanism locks the posterior end of P_4 into the anterior face of M_1 .

The talonid of M_2 is narrower than the trigonid and bears the usual three cusplules around the basin. The hypoconid and entoconid are of about the same height, and both

are markedly lower than the prominent conical hypoconulid. This cusp rises at the posterior corner of the tooth almost as high as the paraconid does at the anterior end.

There are no wear facets on the exterior faces of hypoconulid or entoconid, but both cusplules share the general wear on the internal slopes of the talonid basin.

Since the dentine is exposed in the talonid basin after some wear, the harder enamel rim continues to appear cusplulate as the curves at the bases of the cusplules are worn unequally. Thus it may appear that there are differences in talonid cusp height, but these are really due to the state of wear.

Skeleton: The most complete single specimen known of this species is A.M.N.H. No. 35348, a left dentary with P_3 - M_2 and alveoli for C_1 - P_2 , as shown in plate 12. The teeth are small for the sample, fully erupted, and show moderate wear; the individual was therefore a mature adult. Another specimen, A.M.N.H. No. 35350, shows more of the posterior part of the dentary, including an unbroken portion of the vertical edge between the condylar process and the angle. The distance from this edge to the posterior edge of the P_2 alveoli is 19 mm. The distance from the corresponding point in A.M.N.H. No. 35348 to the rear edge of the C_1 alveolus is 5 mm. If about 1 mm. be allowed for the missing condyle and 1 to 2 mm. for the missing anterior end of the jaw, a reasonable estimate of total length would be between 27 and 28 mm. Such a measurement is greater than the length of the jaw of the smallest living carnivore¹ but distinctly smaller than that of any of the other known miacid jaws.

The preserved portions of the dentary indicate a relatively shallow, slender ramus, with a deep masseteric fossa on the labial side and a relatively slight crest marking a shallow fossa on the lingual side. This crest terminates anteriorly in a distinct tubercle at the base of the coronoid process, and the ventral limit of the temporalis muscle is thereby marked.

¹ *Mustela rixosa* (A.M.N.H. No. 129276 was examined), the least weasel, has a jaw about 17 to 18 mm. in length. A related form, *M. frenata* (see A.M.N.H. No. 174252), has jaws about 27 to 28 mm. in length. However, the jaws in these mustelids are short relative to skull length, a proportion probably not true of *P.* (*Simpsonictis*).

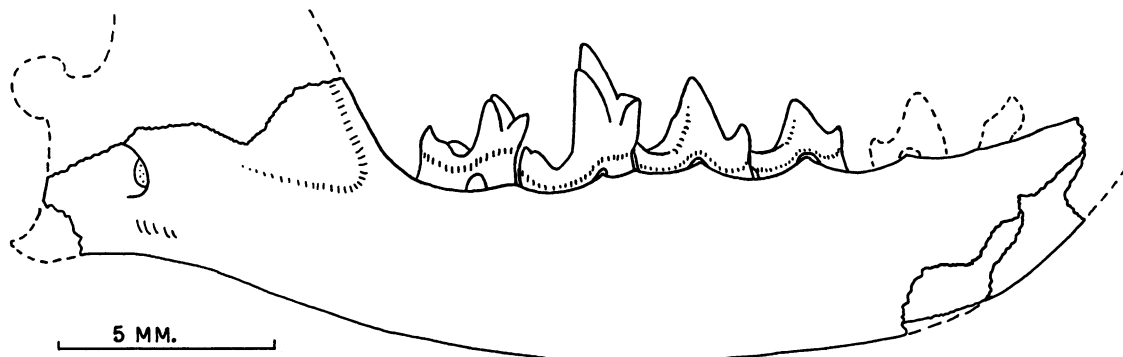


FIG. 18. *Protictis* (*Simpsonictis*) *tenuis*. Reconstruction diagram of left lower dentition and jaw. Compare plate 12.

The ventral edge of the symphyseal end shows a sloping chin marked off from the remainder of the ventral edge of the jaw by a definite change in contour. From this point onward, the ventral border of the jaw is a smooth convex curve which gradually becomes concave below the middle of the coronoid process, then turns slightly downward toward the broken end of the angle.

The dorsal border of the jaw is slightly concave from the posterior border of the canine alveolus to P_2 and is essentially straight from that point to the beginning of the coronoid process behind M_2 . Only the basal parts of the coronoid process have been preserved, and its posterior limits are unknown.

The labial side of the jaw is convex in section. The lingual side is nearly flat, but a shallow, broad concavity follows the approximate path of the dental canal inside the bone. However, this concavity may be due to slight crushing after burial.

A conspicuous mental foramen, facing dorsad and a little anteriad, issues from the labial side of the jaw about 2 mm. below the posterior edge of the canine alveolus. A slightly smaller, oval mental foramen is situated below P_3 , and the dental foramen is visible on the lingual side of the jaw, about 2.5 mm. from the posterior edge described above and about 1.5 mm. from the ventral edge. A small pit at the rearmost edge of the symphysis may have led to a small foramen, but this has been left filled with matrix.

Nothing is known of the skull or postcranial skeleton.

DISCUSSION: The original description of

this species by Simpson was limited by the single specimen then available. The four additional specimens from the Gidley quarry made it obvious that this species did not belong in *Didymictis*, and, since it could not be associated with any of the other genera in the family, it was named the type of a new genus. It is now clear that none of the miacids in the Gidley quarry really belonged in the genus *Didymictis*.

The process of measurement and detailed description of all the specimens in this species led, by a chain of partly fortuitous events, to a slight but significant change in my original opinions about their true nature. A heavy coating of protective lacquer, previously inconspicuous, was noticed while the specimens were being measured. As this was being removed with solvent, a vertical crack in the jaw of A.M.N.H. No. 35348 that passed between the paraconid and protoconid of P_4 was opened, and the specimen was removed from the supporting wire. When the excess glue, lacquer, and remnants of matrix were finally removed and the specimen was reconstructed, the over-all outline was shown somewhat more clearly. When all four American Museum of Natural History specimens were cleaned carefully, the wear facets on the teeth were revealed. Comparison of these with the wear facets in other species (also visible only after cleaning) allowed some reasonable inferences about the unknown upper dentition of *P. (Simpsonictis) tenuis*. Minor variations in the details of the teeth were also revealed, giving a clearer understanding of the way in which even this small sample reflected the

variability of the species. With this came a heightened awareness of the basic similarity of this species to the others in the genus *Protictis*.

It is now clear, for example, that *P. (S.) tenuis* had the basic carnivore adaptation of the P^4 - M_1 carnassial system (although not so specialized as in some of its close relatives). Presumably, when the upper dentition of this species is described, it will show a recognizably miacid-like upper dentition, with a shearing P^4 rather than the unspecialized P^4 which might have been expected from the rather insectivore-like lower M_1 . So much can be deduced from the strong shear facet on the anterior face of the M_1 trigonid.

On the other hand, some insectivore-like features are still clearly visible in the known teeth. The dentition as a whole presents a series of pointed, awl-like cusps, in marked contrast to that of the contemporary *P. (B.) microlestes*, in which there is a predominance of bladelike crests. The tall, pointed cusps on the teeth of *P. (S.) tenuis* suggest a primary adaptation for piercing rather than for shearing. The last molar is strikingly different from this tooth in its contemporary relatives. In these related species, M_2 is functionally an extension of the talonid on M_1 ; in *P. (S.) tenuis*, M_2 obviously is a tooth with a functional role of its own.

The grooves worn into the labial surface of the P_4 and molar talonids are convincing indications of tall cusps (specifically tall paracones and metacones) on P^4 and the upper molars. This deduction adds to the impression of insectivore-like adaptations in this species but does not contrast too sharply with the nature of the other species in the genus *Protictis*.

It remains true that *P. (S.) tenuis* is the most primitive known species of the genus and hence the most primitive of the subfamily. Were it not for the absence of M_3 (and, undoubtedly, M^3 also), it would be the most primitive known miacid.

Protictis (Simpsonictis) cf. tenuis

Plate 19, figures 6, 7

Didymictis, near *D. tenuis*: GAZIN, 1956, p. 35.

DISTRIBUTION: Late Paleocene (early Tiffanian); Saddle locality, E. $\frac{1}{2}$, sect. 28, T. 27

N., R. 95 W., south rim of the Bison basin, Fremont County, Wyoming. As reported by Gazin (1956), Saddle locality is the lowest stratigraphically among the four localities of early Tiffanian age in the Bison basin area.

HYPODIGM: U.Wyo. No. 1063 and an uncatalogued lower jaw, bearing M_2 and part of M_1 , in 1961 Harvard-University of Wyoming collection.

MEASUREMENTS AND STATISTICS: See table 8.

DESCRIPTION AND DISCUSSION: The first specimen of *P. (Simpsonictis)* reported from anywhere outside the Crazy Mountain field was described by Gazin (1956) as "*Didymictis*, near *D. tenuis*." I am indebted to Dr. P. O. McGrew for the loan of this specimen and

TABLE 8
MEASUREMENTS (IN MILLIMETERS) AND
STATISTICS OF *Protictis (Simpsonictis)*
CF. *tenuis* FROM THE SADDLE LOCALITY,
BISON BASIN, WYOMING

	N	OR	M
M_1			
Length	1	3.1	—
Width (anterior)	1	2.1	—
Width (posterior)	2	1.5–1.75	1.68
Grind width			
(anterior)	2	1.4–1.65	1.52
Length of talonid	2	0.95–1.1	1.02
Length of triconid	1	1.65	—
Length of paraconid	1	1.0	—
Length/width			
(anterior)	1	1.48	—
Width (posterior)/			
length of talonid	2	1.58–1.59	1.58
M_2			
Length	2	2.5–2.85	2.68
Width (anterior)	2	1.35–1.5	1.48
Width (posterior)	2	1.15–1.3	1.22
Grind width			
(posterior)	2	1.2–1.25	1.22
Length of trigonid	2	1.15–1.3	1.22
Length/width			
(anterior)	2	1.85–1.9	1.88
Length/grind width			
(posterior)	2	2.08–2.28	2.18
Length of talonid/			
triconid	2	1.17–1.19	1.18
M_1 length/ M_2 length	1	1.09	—
Depth below M_1	1	3.4	—
Depth below M_2	2	3.1–3.4	3.25

to him and Prof. Bryan Patterson for the loan of another specimen collected by them in 1961.

The first specimen (U.Wyo. No. 1063) is a fragment of the left dentary bearing M_2 and the talonid of M_1 . The preserved parts indicate that the specimen was somewhat damaged by postmortem weathering, but the undamaged cusps and crests show very little wear, although M_2 is fully erupted. It appears to have been a young adult, about the same size as A.M.N.H. No. 35350 from the Gidley quarry.

The anterior root and the trigonid of M_1 have been lost, but the posterior wall of the alveolus here shows that this was a relatively strong, stout root and evidently supported a typically high trigonid.

The trigonid of M_1 has been broken away, and the enamel has been lost from the tip of the entoconid and nearly the entire labial surface of the talonid, including the tip of the hypoconid. Only the hypoconulid is well preserved, and this cuspule differs from the corresponding parts in the Gidley quarry *P. (S.) tenuis* sample only in the slightly more posteriad direction of the apex.

The protoconid of M_2 has been lost. The sharply pointed underlying dentine in the low paraconid and tall metaconid is revealed by the loss of the enamel from the tips of these cusps. There appears to be a small carnassiform notch at the junction of the crest from the paraconid to the protoconid, but the enamel is lost from the opposing crest on the protoconid so that this point is somewhat uncertain. The basic form of the rest of the trigonid, however, does not differ from that of the Gidley quarry sample.

Most of the hypoconulid has been broken off, and the tips of the other two talonid cusps have been denuded as were the trigonid cusps. Although the labial face of this tooth has also lost most of its enamel, the dentine clearly shows a labial cingulum running from the posterior base of the protoconid to the hypoconulid. There is a small worn cuspule just anterior to the entoconid.

The preserved parts of the dentary bone show that there was a deep masseteric fossa on the lateral side and a small bony protuberance at the anterior edge of the crest on the

medial side marking the limit of the temporal muscle.

The lateral surface of the ramus is weathered, but the bone is quite uncrushed, and the medial surface is smooth and essentially flat, without any sign of the lengthwise "channeling" observed in some Gidley quarry specimens. It seems that this "channeling" was an artifact caused by slight crushing along the line of the mandibular canal.

The second specimen (collected in 1961) is much better preserved than the foregoing. It is part of a right dentary, with M_2 and most of M_1 . Other than the bleaching of the surface of the bone and some spots on the teeth, there are no signs of weathering, and the specimen is otherwise dark in color. The specimen is uncrushed, but the jaw is broken off in front of M_1 , part of the ventral edge is missing below M_1 , and posteriorly the articular process, the tip of the angle, and most of the coronoid process are absent. The remaining part of the dentary is essentially similar to the corresponding parts preserved in the Gidley quarry specimens, but the ridges and processes for muscle attachment are more pronounced and the whole specimen appears slightly more robust (see pl. 19, figs. 6, 7).

Most of the posterior part of the M_1 trigonid has been broken away, but the remaining parts of that tooth and all of M_2 are preserved without notable breakage and with little wear. The sharp edges of all fracture surfaces indicate that the specimen was probably fossilized before the breakage occurred; it is certain that the damage was postmortem.

This individual is perceptibly larger than U.Wyo. No. 1063, although the comparable parts of each agree very well in shape.

The trigonid of M_1 is relatively high, as in the Gidley quarry sample, but this tooth is visibly more robust than in any of the latter. The paraconid bears a typically bladelike crest which is nearly horizontal and shows a shear facet along the edge. This facet has a labial extension down the face of the protoconid and is convincing evidence of normal carnivore P^4 - M_1 occlusion. The carnassial notch separating the base of the protoconid from the paraconid is clearly marked. There is an anterobasal cingulum extending diagonally downward from the middle of the base

of the paraconid to low on the flank of the protoconid but not so far as the labial side of this cusp. The protoconid and metaconid have been lost, but enough remains of their bases to show that they were not very different in form from the corresponding cusps in the Gidley quarry specimens.

The talonid is much lower than the trigonid and has a comparatively deep basin. The hypoconid was apparently slightly larger than the entoconid but is a little more worn, so that the difference is less apparent. The hypoconulid is essentially similar to the corresponding cusp in the Gidley quarry specimens, but, being less worn, it is more clearly set off from its neighbors. This cusp does not show so much posterior extension as that in U.Wyo. No. 1063, but it does fit into the anterior groove on M_2 as before.¹

The entoconid is a distinctive conical cuspule, nearly unworn and in the usual position opposite the hypoconid. There is a minute cuspule between it and the base of the metaconid which, if originally present on the Gidley quarry specimens, is not now observable on any of them.

The labial cingulum is fainter on this specimen and is not continuous, being represented by a few minute crenulations on the labial face of the hypoconid. Two small wear facets can be seen, as before, where the paracone and metacone of M^1 occluded on each side of the hypoconid.

The last molar, M_2 , is also essentially similar to the corresponding teeth described in the Gidley quarry sample. It differs from these in the slight accentuation of the antero-basal cingulum, in the presence of a faint carnassial notch between paraconid and protoconid, in the relatively fainter development of the labial cingulum, and in the presence of a small crenulation immediately anterior to the entoconid. None of these differences is greater than what one would expect as normal individual variation. The small additional cuspule just anterior to the entoconid is present in both M_1 and M_2 of both speci-

mens from the Bison basin locality and cannot be detected in any of the Gidley quarry specimens.

The better-preserved second specimen from the Saddle locality does appear to be larger and more robust, with cusps and crests accentuated more than in the Gidley quarry sample, but the other specimen from the Saddle locality falls within the size range of the Gidley quarry specimens, and the two samples cannot be separated on a strict statistical basis. It can be said that these two allochronous and allopatric samples probably represent a slight change in the nature of the species, *P. (S.) tenuis*, but the present material does not permit a statement as to whether or not the change was great enough to require taxonomic recognition.

Cf. *Protictis* (Simpsonictis)

Plate 19, figures 2, 3, 9, 10

DISTRIBUTION: Late Paleocene (early Tiffanian), Fort Union Formation, Shotgun Member; NE. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 31, T. 6 N., R. 3 E., Wind River basin, Fremont County, Wyoming.

HYPODGM: Uncatalogued P^{23} and P^4 in 1960 Harvard-University of Wyoming collection.

MEASUREMENTS (IN MM.): P^{23} : length, 3.2; width, 1.6. P^4 : length, labial, 3.8; width, 2.6; metastyle, 1.4; length, lingual, 4.2; length, labial/width, 1.46; length, lingual/length, labial, 1.10.

DESCRIPTION: The crown of the P^4 is beautifully preserved and very little worn; only the scars of the three roots remain. The outline of the crown in occlusal view is the usual dented-triangle shape, with a large paracone, a strong parastyle at the labial corner, a prominent protocone at the lingual corner, and a shearing metastyle blade at the posterior corner. A clearly defined lingual cingulum connects the base of the protocone with the base of the metastyle corner, and a somewhat weaker styler cingulum extends from the parastyle posteriad. There is a short anterior cingulum also, but none of these cingula completely encircles the base of any of the corner cuspules. The paracone is tall and sharply pointed. A sharp crest runs from the apex

¹ Similar structures are present in the Forestburg Cretaceous therians and other primitive mammals. See Patterson (1951; 1956, figs. 5, 7, 8a, and 9a) for a discussion of a similar adaptation in triconodonts. This functional resemblance is clearly convergent.

almost to the base of the anterolabial edge, then ends suddenly without reaching the limit of the groove separating this cusp from the parastyle.

A similar crest follows the nearly vertical posterior edge of the paracone into a deeply incised carnassial notch, followed by the usual high, sharp metastyle blade. No clear separation of metacone and metastyle is visible in this blade, which has a wear facet along the lingual side. This wear facet is also visible on the other side of the carnassial notch; the posterior edge of the paracone is worn far enough to expose the dentine deeply. The edge of the metastyle blade shows less wear but some irregular chipping along the edge (possibly not postmortem damage). The protocone and parastyle are simple conical cusps without any definite crests on their slopes. The protocone comes to a blunt peak, but it is sharper than the blunt, peglike parastyle.

The second specimen in this collection is obviously a two-rooted upper premolar. The crown is only very slightly damaged and scarcely worn. There is a tall, long, erect, slightly recurved paracone, with two very keen crests fore and aft. The parastyle is a low, sharp, hook-shaped cusp at the extreme anterolabial corner of the tooth; the metacone, now broken, was a larger cusp at the posterior end. There is a distinct, sharp, conical protocone at the lingual extremity of the narrowly triangular crown, but this was well posterior to the midpoint and differs from *P. (Bryanictis)* P^3 in this respect. There is more resemblance in general (and in this last point in particular) to the much larger P^3 in *P. (Protictis)*, but the emphasis of the sharp cusps and crests in this tiny tooth is quite distinctive.

DISCUSSION: The generally primitive aspect of the P^4 and its small size are entirely consonant with the subgeneric assignment assumed here, but the rounded corner cusps provide further clues to its identity. The corresponding basal cuspules on the lower premolars known for *P. (Simpsonictis)* are similarly rounded and well separated from the base of the main cusp. Complete certainty of identity must await the discovery of associated upper and lower dentitions, but the present interpretation is believed to be correct.

The identification of the P^{23} is more dubi-

ous, as this tooth cannot certainly be identified as that of a miacid. There is a certain resemblance to P^3 in *P. (Protictis)* and slightly less resemblance to P^3 as known from the Gidley quarry sample of *P. (Bryanictis) microlestes*, so the assignment to *Protictis* is probably justified. There remain the possibilities that it could be the unknown P^2 of *P. (Bryanictis)* or the premolar of some non-miacid genus, but the best possibility is *P. (Simpsonictis)*.

If subsequent discoveries do not contradict these identifications, these teeth indicate the presence of *P. (Simpsonictis)* in the Shotgun local fauna. The geographic range of this subgenus during the early Tiffanian would thus be slightly extended.

PROTICTIS (BRYANICTIS),¹ NEW SUBGENUS

Didymictis: SIMPSON, 1937a, p. 209 (in part).

TYPE: *Protictis (Bryanictis) microlestes* (Simpson, 1935).

DISTRIBUTION: Middle and ?late Paleocene of North America.

INCLUDED SPECIES: *Protictis (B.) microlestes* (Simpson, 1935) and *P. (B.) vanvaleni*, new species.

DIAGNOSIS: Differs from *P. (Protictis)* in having relatively larger P_3 , bearing paraconid and in some cases hypoconid; relatively larger, bladelike paraconid and single large hypoconid on P_4 ; relatively broader posterior end of P_4-M_1 ; lower, longer trigonid of M_1 ; and relatively longer, narrower upper molars, bearing cingula.

Differs from *P. (Simpsonictis)* in having relatively lower molar trigonids; stronger paraconid and much stronger hypoconid of P_4 ; and relatively lower metaconid of M_{1-2} .

Differs from both of these in having relatively stronger cuspules on M_2 talonid.

DISCUSSION: The reasons for separating *P. (Bryanictis)* from the other two subgenera are given in the discussion of the genus.

The type species is well represented in collections from the Crazy Mountain field of Montana. A new species from the Torrejon local fauna of New Mexico is now known from a single specimen. Additional specimens referable to the subgenus and not now sepa-

¹ Named for Prof. Bryan Patterson of Harvard University.

rable from the type species are described here from the earliest Tiffanian of Wyoming. Some specimens possibly representing additional taxa within this subgenus are known in collections not available for the purposes of this study.

Protictis (Bryanictis) microlestes
(Simpson, 1935)

Plates 13–15; plate 16, figures 1–5, 7;
plate 17, figures 1, 3, 6, 9; plate 18,
figures 2–5; text figure 19

Didymictis microlestes SIMPSON, 1935, p. 238;
1937a, p. 210, figs. 56–57.

TYPE: U.S.N.M. No. 9301, left dentary with P_4 – M_2 . Figured by Simpson (1937a, fig. 56).

DISTRIBUTION: Middle Paleocene (Torrejonian), Fort Union Formation, upper Lebo beds; Crazy Mountain field, Sweetgrass County, Montana.

HYPODIGM: Type and U.S.N.M. Nos. 8631, 9298–9308, 9310, 9581, 9855, 10049, A.M.N.H. Nos. 35360–35388 (a total of 45 specimens), Gidley quarry (locality 4), NW. $\frac{1}{4}$ of NE. $\frac{1}{4}$, sect. 25, T. 5 N., R. 15 E.; U.S.N.M. Nos. 6146, 6147, 9875, Silberling quarry (locality 1), NE. $\frac{1}{4}$, SW. $\frac{1}{4}$, sect. 4, T. 5 N., R. 16 E.; U.S.N.M. Nos. 12151, 16870, unspecified localities in the Crazy Mountain field.

DIAGNOSIS: Differs from *P. (B.) vanvaleni* in absence of metaconid lingual to protoconid and narrower talonid lacking entoconid on P_4 and in having M_1 with relatively higher metaconid and larger, more anteriorly directed paraconid.

MEASUREMENTS AND STATISTICS: See tables 9–11.

DESCRIPTION: Dentition: The variation of dentitions in the Gidley quarry sample is described first.

No lower incisors are known, and only dubious traces of incisor alveoli are preserved in A.M.N.H. Nos. 35376 and 35378. From these traces, it appears probable that the incisors were as usual in most carnivores—small and not particularly specialized.

No canines are preserved, but a lower canine alveolus is present in A.M.N.H. No. 35378 which shows that this tooth was single-rooted, comparatively large, and nearly round in section at the base but perhaps slightly flattened medially. The root was procumbent,

extending back under P_2 , but the crown probably curved upward and may have been essentially erect as usual in carnivores (see pls. 13, 14, and 17).

A complete P_1 is present in A.M.N.H. No. 35373, and a root is visible in A.M.N.H. No. 35387; three other specimens show alveoli. The crown of this small, simple tooth has a single, slightly recurved, pointed protoconid which bears a dull, convex anterior crest and a sharper, concave posterior crest which terminates near the base of the crown. Here there is a small posterior projection which cannot properly be called a posterior cingulum cuspule since there is no cingulum, only a pair of indistinct, rounded crests which blend into the flanks of the crown as they curve forward and rise toward the summit of the main cusp. In the best-preserved specimen, the tooth appears unusually erect (perhaps unnaturally), but the other specimens show a procumbent root which is more usual in primitive mammals.

The second lower premolar is preserved in U.S.N.M. No. 9308 and A.M.N.H. Nos. 35378 and 35387, a fragment of the crown remains in A.M.N.H. No. 35388, and roots or alveoli are present in four other specimens. This tooth is two-rooted, as are all that follow, and has a tall, pointed, slightly recurved protoconid and a small, conical, posterior basal cuspule. This cuspule is connected to the summit of the protoconid by a sharp ridge. A shorter lingual crest is variably developed and in U.S.N.M. No. 9308 and A.M.N.H. No. 35387 defines a small, shallow basin which is not clearly delimited in the other two specimens. There is a low, rounded, poorly defined crest on the labial side of the crown on the opposite side of the median crest, but no basining is seen here.

The anterior edge of the protoconid is formed by a curved crest which is convex labially and terminates in a small basal swelling or node. There is no anterior basal cingulum or cuspule, however, and no other sign of accessory cusps.

Extreme apical wear, probably caused by the attrition of resistant food, has produced near elimination of the main cusp in A.M.N.H. No. 35387; the top of this cusp is worn nearly flat here on P_2 .

The third lower premolar is preserved in

TABLE 9

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF LOWER DENTITION OF *Protictis (Bryanictis) microlestes* FROM THE GIDLEY QUARRY, CRAZY MOUNTAIN FIELD, MONTANA

	N	OR	M	s	V
P ₁					
Length	1	1.35	—	—	—
Width	1	0.8	—	—	—
P ₂					
Length	3	2.5 - 2.6	2.53±0.03	0.058±0.024	2.29±0.94
Width	4	1.0 - 1.15	1.09±0.03	0.063±0.022	5.78±2.04
P ₃					
Length	4	3.5 - 3.85	3.71±0.08	0.156±0.055	4.20±1.48
Width	5	1.4 - 1.65	1.54±0.04	0.093±0.030	6.07±1.92
P ₄					
Length	18	3.8 - 4.9	4.31±0.06	0.260±0.043	6.02±1.00
Width	16	1.9 - 2.25	2.03±0.04	0.145±0.026	7.18±2.58
Length/width	14	2.00- 2.22	2.11±0.02	0.073±0.014	3.44±0.65
M ₁					
Length	15	4.3 - 4.8	4.60±0.04	0.162±0.030	3.54±0.64
Width (anterior)	18	2.6 - 3.05	2.87±0.03	0.126±0.021	4.40±0.73
Width (posterior)	16	2.4 - 2.8	2.60±0.03	0.120±0.021	4.60±0.81
Grind width (anterior)	17	2.25- 2.6	2.41±0.03	0.113±0.019	4.69±0.81
Length of talonid	16	1.5 - 2.1	1.86±0.04	0.156±0.028	8.40±1.48
Length of trigonid	17	2.5 - 2.9	2.74±0.03	0.122±0.021	4.47±0.76
Length of paraconid	18	1.4 - 1.7	1.54±0.02	0.084±0.014	5.46±0.91
Length of metaconid	17	1.1 - 1.3	1.23±0.02	0.071±0.012	5.76±0.99
Length/width (anterior)	14	1.46- 1.72	1.60±0.02	0.079±0.015	4.95±0.94
Width (posterior)/length of talonid	14	1.24- 1.60	1.40±0.03	0.098±0.018	6.98±1.32
M ₂					
Length	9	3.4 - 3.8	3.61±0.04	0.118±0.028	3.26±0.77
Width (anterior)	10	2.0 - 2.3	2.18±0.03	0.082±0.018	3.77±0.84
Width (posterior)	8	1.8 - 1.95	1.90±0.02	0.050±0.013	2.65±0.66
Grind width (posterior)	10	1.75- 1.95	1.87±0.02	0.062±0.014	3.30±0.74
Length/width (anterior)	9	1.54- 1.85	1.65±0.03	0.091±0.021	5.52±1.30
Length/grind width (posterior)	9	1.84- 2.00	1.93±0.02	0.058±0.014	3.02±0.71
P ₁ -M ₂ total length	1	21.5	—	—	—
P ₁ -P ₄ total length	3	12.7 -14.6	13.77±0.56	0.971±0.397	7.05±2.88
P ₄ length/P ₃ length	3	1.10- 1.20	1.16±0.03	0.053±0.022	4.56±1.86
M ₁ length/M ₂ length	5	1.21- 1.30	1.25±0.02	0.035±0.011	2.80±0.89
Depth below M ₁	11	5.3 - 6.3	6.03±0.09	0.290±0.063	4.82±1.03
Depth below M ₂	9	5.3 - 5.7	5.47±0.04	0.122±0.029	2.24±0.53

seven specimens from the Gidley quarry. As usual, the premolars increase in size and complexity from P₁ to P₄, so that P₃ is intermediate in size and morphology between P₂ and P₄. The protoconid is more definitely recurved in shape than that in P₂ but bears similar crests on the anterior and posterior edges. There is a strongly developed paraconid (broken in most specimens) which is sharply pointed and in some cases bladelike. The blade ranges from sharp and high (as in

A.M.N.H. No. 35373) to comparatively dull and low (as in U.S.N.M. No. 9308). There is also a distinct hypoconid which varies from clearly separate and strong (U.S.N.M. No. 9308) to indistinct and weak (A.M.N.H. No. 35373) and which may be largely removed by wear.

The posterior cingulum cusplule is prominent; a median crest connects it with the base of the posterior accessory cusp. Sharp labial and lingual cingula are connected to it

around the rim of a definite talonid concavity which may be relatively shallow or quite deep, as in A.M.N.H. No. 35373. A small anterolingual cingulum may be present; this may be reduced to a trace or be absent entirely, as in A.M.N.H. No. 35372. In worn specimens, there is heavy attrition on the tip of the protoconid and on the posterior vertical crest. No sure evidence of tooth-on-tooth wear or shearing facets on the first three premolars can, however, be seen. It thus appears that these teeth functioned as grasping or crunching teeth, holding, piercing, and (simultaneously) crushing food but not acting as any part of the shearing mechanism.

Twenty specimens of the fourth lower premolar from the Gidley quarry are preserved. All show similar essential characters: a tall, pointed, slightly recurved protoconid is the main cusp; there is a bladelike anterior basal paraconid, a large posterior accessory cusp (hypoconid), and a small posterior cingulum cuspule (now identifiable as the hypoconulid) with a definitely basined talonid. The broader posterior end of this tooth (noted by Simpson, 1935, p. 238) may be contrasted with the more pointed or rounded outlines of the other premolars when seen in occlusal view; the anterior end of P_4 comes to a narrow, rounded point.

Although interrupted by carnassiform notches at the bases of the cusps, a curved, sharp line of crests, convex labially, passes from the paraconid to the hypoconulid. The paraconid has this crest developed into a sharp blade, as noted by Simpson (1937a, p. 211), and this, in crown view, is angled sharply toward the labial side of the tooth, where it meets the base of the protoconid. The angle of this crest relative to the midline of the tooth varies. It may be relatively small, but in most specimens it is clear, and in these the whole crest appears to be shifted toward the labial side of the paraconid. This feature is recalled in the discussion of *P. (B.) vanvaleni* below.

The protoconid is tall, sharp, and slightly recurved and, except for larger size, resembles the same feature in P_3 . There is a prominent hypoconid in all well-preserved specimens (five are damaged or heavily worn posteriorly), and a crest posterior to this connects to the base of the small hypoconulid.

The latter lies closer to the lingual border of the crown than does the hypoconid. The median crest just mentioned is sharply concave lingually, and, in eight of 14 specimens, bears a minute post-hypoconid cuspule which is hardly more than a crenulation in some specimens.

The posterior cingulum is continuous around the basin of the talonid and extends onto the lingual and labial borders of the crown. In only four specimens, however, is there a continuation of the cingulum past the base of the protoconid. In the remainder, the cingulum becomes obsolete labially and lingually turns into a low crest which curves up toward the summit of the protoconid and disappears halfway up. In no case does this lingual crest show any sign of becoming cuspidate.

There is invariably an anterior labial cingulum, but this does not extend around the anterior end of the tooth. In A.M.N.H. Nos. 35380 and 35388, there is an anterolingual cingulum. These are also the only specimens with a clear posterolingual cingulum which continues anteriorly past the base of the main cusp, although a few other specimens show faint traces of such a cingulum.

There are 14 specimens from the Gidley quarry which have the first lower molar well preserved and five more with this tooth more or less damaged. The trigonid is high, but not so elevated above the talonid as in *P. (Simpsonictis)*. The protoconid is the tallest cusp, nearly triangular in cross section, with the labial corner rounded and the anterior and posterior lingual corners sharp. The lingual face is not quite flat but slightly convex, and there is a low, rounded vertical swelling near the lingual base of the cusp which separates the slight concavities formed by the bladelike crests to the paraconid and metaconid. These two crests end in distinct carnassiform notches, the anterior one of which is the definitive carnassial notch where the paraconid blade terminates.

The metaconid is much lower than the protoconid but higher than the paraconid. Both of these cusps bear sharp, bladelike crests, but the crest on the metaconid is steeper and that on the paraconid is slightly longer transversely.

There is a well-developed anterolabial cin-

TABLE 10

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF UPPER DENTITION OF *Protictis* (*Bryanictis*) *microlestes* FROM THE GIDLEY QUARRY, CRAZY MOUNTAIN FIELD, MONTANA

	N	OR	M	s	V
P ³					
Length	6	3.35-4.1	3.84±0.09	0.228±0.066	5.94±1.72
Width	5	1.75-2.35	2.16±0.10	0.236±0.075	10.91±3.45
P ⁴					
Length, labial	8	4.7-5.3	4.86±0.07	0.195±0.049	4.02±1.00
Width	10	3.5-4.1	3.72±0.05	0.172±0.038	4.60±1.03
Metastyle	8	1.6-2.05	1.73±0.06	0.156±0.039	9.02±2.26
Length, lingual	8	5.7-6.75	5.98±0.13	0.379±0.095	6.33±1.58
Length, labial/width	7	1.26-1.42	1.31±0.02	0.053±0.014	4.03±1.08
Length, lingual/length, labial	7	1.16-1.44	1.24±0.03	0.092±0.025	7.46±2.00
M ¹					
Length	6	3.7-4.6	4.18±0.11	0.280±0.081	6.70±1.94
Width (anterior)	7	4.85-6.05	5.40±0.15	0.406±0.108	7.52±2.01
Width (posterior)	8	4.45-5.0	4.73±0.06	0.178±0.045	3.76±0.94
Grind width (anterior)	9	4.25-4.7	4.48±0.06	0.170±0.040	3.80±0.90
Width (anterior)/width (posterior)	5	1.05-1.21	1.13±0.03	0.064±0.020	5.67±1.79
M ²					
Length	5	2.6-2.9	2.74±0.06	0.137±0.044	5.02±1.59
Width (anterior)	5	3.8-4.25	4.02±0.07	0.158±0.050	3.93±1.24
Width (posterior)	5	2.85-3.45	3.20±0.11	0.244±0.077	7.61±2.41
Grind width (posterior)	5	3.0-3.4	3.26±0.07	0.167±0.053	5.12±1.62

gulum at the base of the protoconid. In U.S.N.M. No. 8631 and A.M.N.H. Nos. 35372, 35384, and 35388, there is also a short, variable anterolabial cingulum on the base of the paraconid. This feature appears in some specimens and not in others. It is also seen in other miacids as a variant and even occurred in the Forestburg therians (see Patterson, 1956, figs. 7-9).

There is a labial cingulum between the bases of the hypoconid and protoconid. Traces of a continuation of this cingulum with the posterior cingulum on the hypoconid are visible in a few specimens, but in most these are separate. The posterior cingulum is a narrow shelf which begins at the posterior base of the hypoconid and rises diagonally to the hypoconulid. The crest linking the hypoconulid with the entoconid continues to the base of the metaconid, then rises toward the summit of that cusp, becoming rounded and indefinite as it proceeds, until it disappears near the summit.

The usual crista obliqua from the hypoconulid to the hypoconid runs from the posterior cingulum to the hypoconid, then turns and

angles across the talonid until it reaches the midpoint of the posterior face of the trigonid. It may extend part way up this part of the trigonid, just below the posterior carnassiform notch.

The crests just described form a rim for the broadly basined talonid, and the three cusps mentioned are nearly equidistant from one another. The hypoconulid in M₁ is much smaller than the other two talonid cusps and is at the midpoint of the posterior edge of the crown. The other two cusps are considerably higher, and, although the entoconid is slightly taller than the hypoconid, the latter appears bulkier because its internal face slopes more gradually toward the central basin. The talonid is nearly as wide as the trigonid, and the posterior corners are more sharply rounded than in *P. (Protictis)* or *Didymictis*, so that the posterior edge of the talonid is flattened.

There are 10 specimens of the second lower molar preserved from the Gidley quarry. This is a smaller tooth than the foregoing, and it has a much lower trigonid and relatively longer talonid. Other striking differences from M₁ are the relatively larger hypoconulid and

smaller protoconid (which is smaller than the metaconid and hardly larger than the paraconid). Between the crest from protoconid to paraconid in U.S.N.M. No. 9309 and A.M.-N.H. No. 35377, there is a carnassial notch, but this is poorly developed in these two and absent from the remaining specimens. A definite carnassiform notch does persist between the protoconid and metaconid in most specimens; however, this is obscured by wear or breakage in many. Below this point, on the posterior face of the trigonid, the crista obliqua to the hypoconid begins. This crest defines the labial rim of the talonid. It passes diagonally posteriad and labiad across the talonid to the hypoconid, then turns linguad and runs to the base of the hypoconulid. The edge of the crista obliqua is invariably worn, so that the underlying dentine is exposed for most of its length as a trough between two ridges of enamel, and the posterior part of the crest is usually more heavily worn (between hypoconid and hypoconulid) than the anterior part.

The hypoconulid is the tallest and most posterior cusp on the talonid, being subequal in size to the paraconid. It stands just lingual to the midline of the tooth and is shaped like a half-cone, convex posteriorly and flat or slightly concave anteriorly. A short labial cingulum begins abruptly at the base and slants steeply downward to the posterior base of the hypoconid.

The entoconid is lower than the hypoconulid and of similar form; it is taller but less bulky than the hypoconid. A sharp lingual crest, which defines the border of the talonid basin, runs linguad and anteriad from the summit of the hypoconulid to the lingual base of that cusp, rises to the summit of the entoconid, turns anteriad, and then falls in a curving line toward the posterior base of the metacone, becoming obsolete as it rises again toward the summit of the trigonid cusp.

In three specimens, there is a short labial cingulum between the base of the hypoconid and the base of the protoconid as in M_1 , but this is never complete around the base of the hypoconid, and it is ill defined in or absent from most specimens.

Where it is present in worn specimens, this cingulum clearly shows the small wear facet caused by the M^2 paracone, just as in M_1 the

similar wear facet caused by the M^1 paracone can be seen. A small wear facet on the posterior cingulum provides similar evidence that the metacones of M^{1-2} occluded behind the hypoconids of M_{1-2} . The heavy wear on the hypoconid crests has already been noted. The entoconid shows a little wear near the summit, but the lingual crest associated with this cusp shows virtually no wear at all, and no signs of wear are visible in the talonid basins—strong evidence that the protocones of the upper molars did not fit snugly into these basins but rather occluded with the crests and cusps around the margins. Study of the upper molars shows that wear caused by the talonids of the lower molars occurred at the peaks of all cusps, then extended progressively to the crests between the major cusps and eventually involved most of the area between the protocone and the paracone-metacone crest. It appears, then, that the action of these parts was a true grinding rather than simple crushing, even though there was some limitation of the ectal movement because of the interlocking cusps. Part of the cheek-tooth action was, to be sure, a shearing action of crest on crest. The anterior and posterior borders of the upper molars show clearly that the trigonid cusps sheared past these crested edges, and the trigonids of the lower molars show definite wear on their posterior and anterolabial faces. (In passing, we may note that the M_2 metaconid is in some cases sharp and nearly unworn on the same tooth where the paraconid and protoconid show heavy attrition at the tips and shear facets along the crests.)

Also, as might be expected, the carnassial shearing system shows shear facets on the anterior faces of the M_1 protoconid and paraconid and on the posterior edge of the P^4 paracone and along the lingual side of the metastyle blade.

That some shear occasionally occurred between the posterior edge of the M_2 trigonid and the anterior edge of M^2 is also evident from the wear on these parts in some individuals. This was not so in all specimens, however, and some show little or no wear on these parts, although the grinding area of the talonid crests and protocone may be heavily worn on the same specimens.

No traces of the upper incisors or canines

are known, and nothing is known of the first upper premolar. The second upper premolar is represented by alveoli only, which indicate that P^2 was double-rooted and slightly smaller than P^3 . Behind P^2 is a diastema measuring 0.8, 0.6, and 0.5 mm. in the three specimens available (U.S.N.M. No. 9300, A.M.N.H. Nos. 35360 and 35361), all of which were broken off through the anterior alveolus of P^2 . Obviously a weak spot was present here in the maxilla.

The third upper premolar is preserved in six specimens, five of which have not been described before. These are A.M.N.H. Nos. 35360, 35361, 35364, 35365, and 35366; U.S.N.M. No. 9299 was described and figured by Simpson (1937a, fig. 57). There are two main roots. On specimens with a prominent protocone, a third root may be present but cannot be surely distinguished from the large posterior root (see pls. 15 and 16).

The outline of the crown is triangular in occlusal view. The paracone is in the center of the tooth, and there is a prominent conical parastyle. A metastyle is present on all specimens, but it varies from a distinct shearing blade in some specimens to a small conical cuspule which is not at all bladelike in others. In intermediate specimens, a distinct metacone can be observed as a low cusp sharply separated from the paracone by a deep carnassiform notch but less clearly separated from the metastyle posterior to it.

A stylar cingulum extends from the metastyle of P^3 anteriorly toward the parastyle but fails to reach that cuspule in all specimens, except for A.M.N.H. No. 35365, which also lacks a protocone and shows the poorest development of the metastyle blade of all specimens in the sample. Were it not for the high degree of variability in such details which is exhibited by this sample, one might be tempted to separate this specimen from the others, but A.M.N.H. No. 30360 shows nearly as much reduction of the protocone and metastyle blade. Since intermediates do exist, A.M.N.H. No. 35365 must be interpreted as merely an extreme within the population represented by this sample.

The protocone of P^3 is present in most specimens in the sample, but it is a well-developed independent cuspule on some, a barely distinguishable crenulation on others,

and absent from at least A.M.N.H. No. 35365. Although all have a similar lingual cingulum extending from the parastyle around the base of the paracone toward the metastyle corner of the tooth, this is variable in extent and completeness, as is the crest extending from the base to the summit on the anterior edge of the paracone. The anterior cingulum is complete on most but interrupted on some specimens.

The upper carnassial, P^4 , is preserved completely or partly in all the specimens listed above as having P^3 . P^4 is also present in U.S.N.M. Nos. 9855 and 9300 and A.M.N.H. Nos. 35362, 35363, 35367, 35369, and 35370 from the Gidley quarry. In general, this tooth shows the typical form of the miacid P^4 . The crown is triangular in section and is dominated by the large central paracone, with a strong metastyle blade forming the narrow posterolabial wing, a well-developed paracone in the anterolingual position, and a distinct parastyle at the anterolabial corner.

The paracone is sharply pointed and appears almost recumbent because the knife-edged posterior side is vertical, whereas the anterior side is raked sharply backward from base to summit. There is usually a sharp crest arising near the base of the anterior side of this cusp, but this is variable in length and bulk. A corresponding crest on the posterior face of the parastyle occurs in most specimens and is correspondingly variable. Both of these crests are reduced in A.M.N.H. No. 35360 and absent from A.M.N.H. No. 35365.

The parastyle is a small, sharp, approximately pyramidal to conical cuspule, one corner usually being formed by the crest described above and the labial and lingual corners less clearly defined by extensions of the labial and anterior cingula. The anterior "corner" is more or less rounded off, and the anterior and stylar cingula are variably disposed around the base of the cuspule but in no instance form a complete cingulum. In most specimens, the anterior cingulum runs from the middle of the anterior edge of the tooth to near the summit of the parastyle, and the stylar cingulum does not extend much past the base of that cuspule. In a few it does reach the summit, as in A.M.N.H. No. 35365, which is exceptional in other ways (see above).

The stylar cingulum is usually complete (a few specimens show short gaps) from the anterior base of the paracone back to the metastyle corner, where it rises toward the posterior end of the metastyle blade. It does not connect to the long lingual cingulum which runs from this corner of the tooth to the protocone. The lingual cingulum generally runs part of the way around the base of the protocone and stops abruptly; in A.M.N.H. No. 35370 it continues, joining with the anterior cingulum on the base of this cusp.

The protocone is a low, generally conical cusp, larger than the parastyle but much smaller than the paracone. There is usually a sharp crest connecting its summit to the parastyle, and a lower, duller, more variably developed (in some cases absent) crest on the midline of the concavity between the base of the paracone and the base of the protocone. On the lingual face of this cusp in U.S.N.M. No. 9855 there is a third crest. In most other specimens from the Gidley quarry the P^4 protocone is smoothly rounded lingually above the basal cingulum, but a few specimens show faint traces of the third vertical crest.

The metastyle blade is highest immediately posterior to the carnassial notch which divides it from the paracone. In the description of P^3 , it was noted that a definite division between metacone and metastyle may be observed; this is not true of P^4 . Although there appears to be a bulge in some specimens which might be a rudimentary metacone in the bladelike shearing crest, I see no definite signs of a second cuspule.

In addition to the predictable wear facet along the lingual side of the metastyle blade and paracone and the usual wear of the lingual cingulum on the upper carnassial, all caused by the shearing action of the trigonid on M_1 , there is also a wear facet on the anterolabial face of the protocone caused by the main cusp of P_4 . The tips of the protocone and parastyle are worn into the usual crater-like shape resulting from differential wear of the softer dentine at the center and the ring of enamel around it. Such attrition is caused directly by the food and can be distinguished from the wear facets produced by teeth on one another. In well-worn specimens, a trough

is worn down the lingual side of the parastyle by contact with the tip of the main cusp of P_4 as it closes in the initial phase of a bite. As the teeth come into full occlusion, the P_4 main cusp is shifted linguad, until its posterior edge comes into contact with the anterior face of the P^4 protocone. The action of the lower carnassial upon the upper similarly begins with initial contact of the M_1 protoconid with the metastyle blade and the M_1 paraconid with the P^4 paracone and continues with a linguad shift of the lower tooth. Thus, at the fully closed position, the M_1 protoconid is lingual to the P^4 paracone, and the paraconid of M_1 falls just behind the P^4 protocone. These statements and others about occlusal relationships are based on actual manipulation of upper and lower dentitions.

The first upper molar is preserved in U.S.N.M. Nos. 9581, 9299, and 9300 and A.M.N.H. Nos. 35360–35364 and 35368 from the Gidley quarry. This tooth is approximately oblong in outline, the primitive triangular shape being obscured by the expansion of the lingual cingula (which are united to form a complete shelf in some specimens) and the stoutness (strictly speaking, length) of the protocone area. Most specimens have a definite hypocone, and the posterior lingual cingulum is larger than the ectocone cingulum. These and the stylar cingulum tend to be crenulated. Some of the crenulations on the stylar cingulum are large enough to be called cuspules, and these usually form at the conventional locations of the stylocone, metastyle, and mesostyle.

The tallest cusp on M^1 is the erect, sharply pointed, conical paracone. This cusp is relatively closer to the labial border of the tooth than in *P. (Protictis)* and *Didymictis* but lies about as close to the anterior border as in *P. (Protictis)* and *Didymictis*. There are two sharp crests on this cusp, running from the base to near the apex. The anterior crest turns sharply labiad near the base and is continuous with the stylocone crest which is short and ends before it reaches the labial cingulum. The stylocone is a very small cuspule (variably developed) on the stylar cingulum and is smaller than the parastyle, which is just anterior to it on the same cingulum.

The posterior crest on the paracone is equally sharp and usually about as steep as

the anterior crest. In unworn specimens, it is barely separated from a corresponding crest on the anterior face of the metacone by a very small carnassiform notch at the bases of these two cusps.

The metacone is considerably lower than the paracone, although it is by no means inconspicuous. It is sharp, conical, and slightly recumbent to erect in various specimens and is immediately posterior to and a little more lingual than the paracone. In addition to the straight, sharp, anterior crest that is mentioned above, there is a sharp posterior crest running from the apex to the base. This crest curves toward the metastyle corner of the tooth. It reaches the posterior edge of the crown and turns sharply toward the metastyle, which is a small cuspule, variably developed, at the extreme posterior end of the stylar cingulum.

The protocone is a stout but sharply pointed cusp, intermediate in height between the paracone and metacone, and situated near the lingual side of the tooth.

The two crests usually present on the protocone in primitive mammals extend toward the paraconule and metaconule, respectively, in this species. The anterior crest begins at the apex of the protocone, curves sharply labiad, and ends at the base of the paraconule, being separated from the corresponding crest on the lingual side of that cusp by a small notch. The paraconule is a sharp cuspule with three crests, two of which continue, in a nearly straight line, the anterior crest on the protocone. The third crest extends toward the lingual base of the paracone, but this crest is variable in direction and extent.

The crest which extends from protocone to paraconule to parastyle continues to the apex of the parastyle in A.M.N.H. No. 35368, which is virtually unworn. In the other specimens, the connection with the apex of the parastyle was evidently obliterated rather quickly, since it has been removed from some that show only slight wear elsewhere. In the absence of associated lower and upper dentitions, it is difficult to be sure, but it seems likely that the apex of the M_1 protoconid is responsible for the wear facet observed at the lingual side of the parastyle of M^1 .

There is, of course, a longer wear facet which develops all along the anterior face of

M^1 . This facet is worn by the crest-on-crest shearing of the posterior edge of the lower carnassial trigonid as it comes more fully into occlusion.

To return to the morphology of M^1 , the posterior crest on the protocone curves more than the anterior crest just described, so that it is much more concave labially before it reaches the metaconule. The metaconule is a smaller cuspule than the paraconule but shows a similar pattern of crests reversed as in a mirror image. The posterior crest continues around the base of the metacone as a cingulum which meets the crest on the posterior slope of the metacone. The single crest thus formed joins the stylar cingulum, as described above.

The second upper molar is well preserved in five specimens and partly present in a sixth. These are U.S.N.M. Nos. 9299, 9300, and 9581 and A.M.N.H. Nos. 35360, 35364, and 35362. In occlusal view, the outline of the crown is that of an obliquely truncated oval, with the flatter end on the labial side. The anterior side is longest because of the more extended parastyle corner (judged from the condition in M^1 , the cusp here identified as the parastyle is probably that and not the stylocone), and, compared with M^1 , the tooth is generally similar in pattern but smaller and simpler. The stylar cingulum is less well developed and relatively much narrower around the base of the metacone. This cingulum is separate from the posterior lingual cingulum in four out of five specimens, and none shows the posterior crest on the metacone described in M^1 ; this corner of the tooth is distinctly reduced and more rounded than in M^1 . The lingual cingula are also reduced, and none of the six available specimens has a complete lingual cingulum. In all of these, the posterior lingual cingulum is visibly smaller than the ectocone cingulum, and in U.S.N.M. No. 9300 the posterior lingual cingulum is a barely perceptible swelling, although the ectocone cingulum is clear but small.

Compared with the conditions seen in M^1 , the paracone is relatively lower on M^2 and the protocone relatively higher, so that these two cusps are here subequal. The metacone is relatively about the same size in M^2 as in M^1 although, of course, of considerably smaller absolute size. The absolute size of all

TABLE 11

MEASUREMENTS (IN MILLIMETERS) OF *Protictis (Bryanictis) microlestes* FROM THE SILBERLING QUARRY AND UNSPECIFIED LOCALITIES IN THE CRAZY MOUNTAIN FIELD, MONTANA

	U.S.N.M. No. 6146	U.S.N.M. No. 12151	U.S.N.M. No. 6147	U.S.N.M. No. 16870	U.S.N.M. No. 9875
P_3					
Length	4.0	—	—	—	—
Width	1.8	—	—	—	—
P_4					
Length	4.7	—	—	—	—
Width	2.35	—	—	—	—
Length/width	2.00	—	—	—	—
M_1					
Length	—	4.75	—	—	—
Length of talonid	—	1.8	—	—	—
Length of trigonid	—	2.8	—	—	—
Length of paraconid	—	1.5	—	—	—
Length of metaconid	—	1.3	—	—	—
P^4					
Length, labial	—	—	5.15	5.4	—
Width	—	—	3.8	4.15	—
Metastyle	—	—	1.65	2.0	—
Length, lingual	—	—	5.9	6.4	—
Length, labial/width	—	—	1.36	1.30	—
Length, lingual/length, labial	—	—	1.15	1.19	—
M^1					
Width (anterior)	—	—	—	—	5.7
Width (posterior)	—	—	—	5.1	5.05
Grind width (anterior)	—	—	—	5.1	4.85
Width (anterior)/width (posterior)	—	—	—	—	1.13

cusps is here less except for the parastyle, which is about the same size in both M^1 and M^2 . General wear on both these teeth is approximately equal but may be slightly heavier on M^2 (A.M.N.H. No. 35364), which does not necessarily mean eruption out of normal sequence but could signify nearly simultaneous eruption, with slightly different functional relationships accounting for the differential. In a heavily worn specimen (A.M.N.H. No. 35360), nearly all the enamel has been worn off the central basin of both molars, but the attrition on M^1 was heavier between the paracone and metacone and around the hypocone area than in M^2 , and in most other specimens M^2 is less worn. The significance of other wear facets is discussed above in connection with the lower teeth.

Two specimens of lower teeth were collected in the Crazy Mountain field from localities other than the Gidley quarry. One of these, U.S.N.M. No. 12151, has no specific

locality data but is recorded from "Sweetgrass County, Montana." This is a fragment of the left dentary, with M_1 and the roots of M_2 . The lower carnassial is well preserved and resembles the majority of the Gidley quarry specimens. It has no unusual features, but the absence of the variable small lingual cingulum at the base of the paraconid should be noted. The matrix that still conceals the labial side of this specimen does not differ visibly from samples of Gidley quarry matrix, and it seems possible that this specimen came from that locality. Nevertheless, it is here considered of indefinite location.

From the Silberling quarry (locality 1), U.S.N.M. No. 6146 is a fragment of left dentary, with P_{3-4} preserved nearly unworn but minus a few fragments, together with the alveoli for P_2 and part of P_1 alveolus and including part of the symphysis. Only one measurement, P_4 width, differs (though not significantly, $0.02 < P < 0.05$) from the large

Gidley quarry sample. There is a mental foramen below the posterior root of P_3 and the edge of another below the posterior root of P_1 (where the specimen was broken off). There was a diastema of 0.7 mm. between P_1 and P_2 , and the alveoli for P_2 measure 2.6 mm. in total length. The anterior basal cusps of P_3 has been broken away. The differences between this specimen and those from the Gidley quarry are insignificant in spite of the fact that the Silberling quarry is 65 feet higher in the section. They provide a concrete example of how such a difference in level can mean little or nothing even when specimens are compared in minute detail, if normal variability is assumed.

Three specimens of upper teeth were collected in the Crazy Mountain field from localities other than the Gidley quarry. U.S.N.M. Nos. 6147 (a P^4) and 9875 (an M_1) are from the Silberling quarry (locality 1). U.S.N.M. No. 16870 is recorded from the Crazy Mountain field but without exact locality data. This specimen consists of right P^4-M^1 , with the roots embedded in a fragment of hard, greenish matrix, different from the soft, buff-colored matrix on the specimens from the other quarries mentioned above. The teeth fall well within the range of variation observed in the Gidley quarry sample. On P^4 , the styler cingulum extends to the apex of the parastyle, and the posterior crest on that cuspsule is continuous with the anterior crest

on the paracone. The metacone of M^1 is a trifle taller than in some of the Gidley quarry specimens, but there are no other noteworthy peculiarities of this individual.¹

The specimens from the Silberling quarry are also within the range of individual variation for the Gidley quarry, and the only peculiarities that appear worthy of mention are the reduced M^1 metacone and the enlarged lingual cingulum, which is complete but less rugose than usual, although it bears a small, distinct hypocone.

Skeleton: The dentary is not complete in any one specimen, but the major portions of this bone are shown by enough specimens to permit a partial reconstruction. The following description is based mainly on U.S.N.M. No. 9303 (the only one showing the condyle and most of the base of the coronoid process), A.M.N.H. No. 35376 and U.S.N.M. No. 9302 (which show part of the ascending ramus), A.M.N.H. Nos. 35372 and 35373 (which show most of the horizontal ramus), and A.M.N.H. No. 35375 (which shows most of the symphyseal region). The first specimen listed is broken off just anterior to

¹ Simpson (1937a, p. 37) listed "an upper tooth" from locality 24 at the 800-foot level of the upper Lebo. In view of his customary precision of language, it is unlikely that U.S.N.M. No. 16870 was intended, since it has two teeth. No such upper tooth was found in either the American Museum of Natural History or United States National Museum collections.

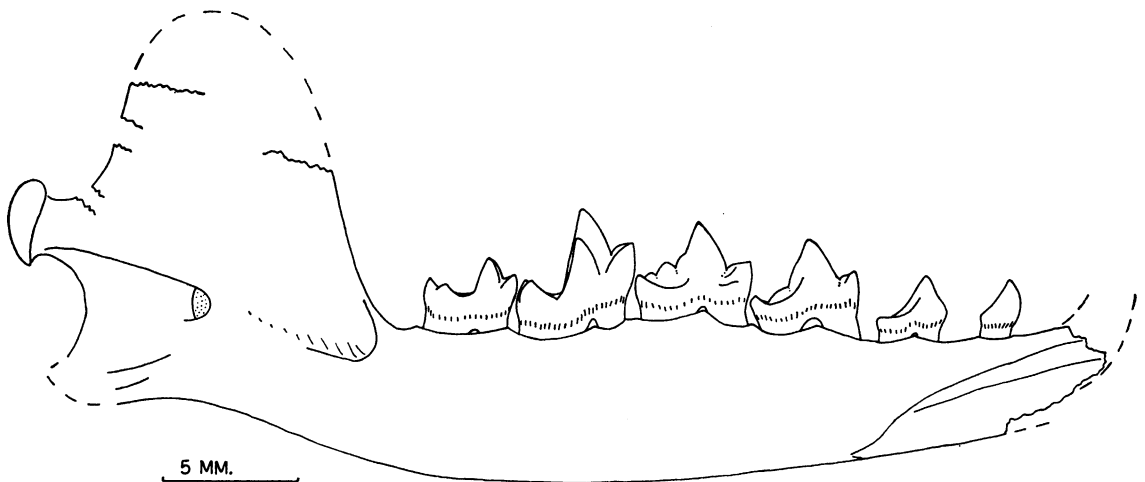


FIG. 19. *Protictis (Bryanictis) microlestes*. Reconstruction of left lower dentition and jaw. Compare plates 13 and 17.

M₂; the last is broken just posterior to M₁. When the lengths of these two are added together, the total is very close to 40 mm. The missing part of the anterior end can hardly have added more than 1 or 2 mm., so that the total length of the jaw was about 41 or 42 mm.

The symphysis is sloping and elongate, extending back to the level of P₂, and the symphyseal surface is marked by rounded irregularities which articulated with corresponding grooves and ridges in the opposite symphysis, as usual in primitive mammals. The ventroposterior end of the symphysis trails out in an elongate, narrow crest for the mylohyoid and geniohyoid muscles which becomes obsolete below P₃. There is no obvious break here in the ventral curve. The ventral edge of the symphysis is barely convex, and the nearly straight ventral border of the jaw continues to a point below M₁ where the jaw is deepest.

From here to a point just below the dental foramen, the ventral edge rises rather sharply in a convex curve, straightens, and becomes concave as it approaches the angular process.

No complete angular process is known, but parts preserved in U.S.N.M. No. 9303 show that this process was present and distinct. On the medial surface of the angle, a prominent ridge begins near the ventral edge of the dental foramen and, curving slightly posteriad and becoming rapidly more pronounced, passes ventroposteriad toward the (presumably pointed) end of the angle which was broken off. This prominent ridge was evidently for the insertion of strong pterygoid muscles. A smaller, parallel ridge runs ventral to this and evidently was for part of the same muscles. The preserved parts of the lateral surface of the angle are flat and smooth and grade dorsally into the masseteric fossa without any clear demarcation immediately above the angle. The usual posterior vertical crest below the condyle is here a thin, rather sharp-edged lamina which is slightly chipped well above the angle and is broken off where the pterygoid crest passes posteriad toward the missing point of the angle. Dorsally, this crest turns sharply posteriad and becomes indefinite as it approaches the condyle.

The condyle projects posteriad about 3.5 mm. from the vertical part of the sharp crest below it. The articular surface is smoothly

hemicylindrical and is about 2.2 mm. in diameter. A small part of the pointed lateral end has been lost, and the remainder measures 4.5 mm. in width. The medial half of the articular surface is drawn downward into a rounded flange which has a slightly flattened surface posteroventrally. This feature is not unusual in carnivores and can be observed (in more pronounced form) in canids such as coyotes. More to the point, the condition seen in U.S.N.M. No. 9303 is not very different from that of *P. (Protictis) haydenianus* (A.M.N.H. No. 35390), described above. It may be observed here that the pterygoid ridge is present but relatively weaker in the larger species than it is in *P. (Bryanictis) microlestes*, and the vertical crest below the condyle is relatively thinner in this smaller species, as it is in *P. (Simpsonictis)*.

A strong, rounded ridge of bone passes anteroventrad and a little ventrad from the condyle on the medial side of the jaw. This becomes lower and sharper anteriorly and, although interrupted by a broken area, evidently was continuous with the low crest marking the ventral limit of the temporal muscle. Such a crest has been observed in *P. (Simpsonictis) tenuis*, described above, but in that species the tubercle at the anterior end is slightly more pronounced. In *P. (B.) microlestes*, the tubercle is only a slight thickening at the ventral end of a nearly vertical crest which meets the horizontal crest at the base of the coronoid process behind M₂. This medial vertical crest is absent or indefinite in *P. (Simpsonictis)* and *P. (Protictis)*.

On the opposite, lateral face of the coronoid process, there is a conspicuous crista coronoidea in most specimens. The anterior edge of the coronoid process shows a definite vertical groove (which becomes shallower dorsally) between the crista coronoidea and its counterpart just described. The masseteric fossa is deep and well marked anteriorly by the crista coronoidea and posteroventrally by the crista condyloidea, which extends from the condyle anteroventrad but becomes indefinite above the angle. A somewhat weaker, more rounded crest marks the anteroventral border of this fossa, but this, too, becomes ill defined as it approaches the angular process. The coronoid process is about 12 mm. long at the base; it is somewhat broken in U.S.N.M.

No. 9309, so the shape is slightly distorted. The anterior edge is nearly vertical in U.S.N.M. No. 9302 and A.M.N.H. Nos. 35376 and 35372, which show this part undistorted. Its full extent is, however, nowhere preserved.

On the lateral surface, there are two conspicuous mental foramina of approximately equal size below P_1 and P_3 ; the former is directed anterodorsad, and the latter faces more nearly dorsad.

Most known fragments of maxilla are so badly broken as to be nearly featureless, but three (A.M.N.H. Nos. 35360 and 35361 and U.S.N.M. No. 9300) show most or all of the large infraorbital foramen (about 1 mm. wide by 2 mm. high) which opens above the posterior root of P^3 . Small portions of the edge of the orbit are preserved in U.S.N.M. No. 9300 and A.M.N.H. No. 35360, but these show no specialized features. At the lowest part, the orbit is only 4.5 mm. from the alveoli of M^1 ; posterior to this point, a little of the irregular maxillojugal suture surface is visible.

The bone is excavated into distinct but rather variable, shallow cavities between the roots of P^2 - P^4 , the deepest being above P^3 . This is a trivial if peculiar character, seen in *Viverravus minutus* and *P. (P.) haydenianus* to a lesser degree.

No postcranial bones have been identified.

DISCUSSION: The unusually large sample of this species from the Gidley quarry was almost certainly drawn from a single local population. The validity of this assumption is defended in the General Discussion section below. At any rate, this is an unusually homogeneous sample of fossil carnivores. Aside from the quantitative data given in tables 9 and 10, much information on the qualitative characters of the dentition, particularly on the variation in minor cusps and crests, has been gained. As this sample was the first examined in detail during this study, objective evaluation of smaller or less coherent samples was made possible.

Description of wear patterns has permitted some reasonable deductions about occlusion which can be confirmed in this sample by more direct observations. Some of the more complete dentitions were selected for matching sizes and approximate state of wear.

Manipulation of such matched (but not associated) dentitions shows the following relationships during active occlusion:

1. Lingually, (a) the protocone of P^3 meets the paraconid of P_4 ; (b) the protocone of P^4 passes lingual to the hypocone of P_4 into the talonid basin; (c) the protocone of M^1 passes labial to the entoconid of M_1 ; and (d) the protocone of M^2 meets the entoconid of M_2 .

2. Labially, (a) the paracone of P^3 shears past the paraconid of P_4 and the posterior cingulum cuspule of P_3 ; (b) the paracone of P^4 shears past the paraconid of M_1 , and the tip of the P^4 paraconid shears along the posterior labial cingulum of P_4 ; (c) the paracone of M^1 passes between the M_1 protoconid and M_1 hypoconid; and (d) the metaconid of M_1 passes between the M_1 hypoconid and the M_2 protoconid.

3. The protocones of P^3 - M^2 do not touch the talonid basins of P_3 - M_2 but meet cusps and crests or shear past them.

4. As the jaws are brought together, the carnassials pass each other in such a way that there is a distinct lateral shift. This results in a movement of the M_1 paraconid such that, beginning in direct opposition to the P^4 paracone, it eventually falls lingual and anterior to that position when the teeth are in full occlusion. The M_1 paraconid thus ends up almost directly behind the P^4 protocone. The protoconid of M_1 similarly shifts from an initial position at the posterolabial corner of P^4 to a final position anterior to the M^1 paraconule.

Study of wear patterns and occlusion in this sample permitted some reasonable deductions about missing teeth in other species (such as *P. tenuis*) and even clarified the interpretation of wear patterns in other genera (such as *Ictidopappus*). If the range of variation shown may be taken as typical of other species, then it is possible to retain most of the specimens of *P. (Protictis)* in one species, but the distinctness of the two species of *P. (Bryanictis)* is made inescapable. One good sample thus helps to solve several problems. Decisive solution of some other problems must await the collection of similarly extensive samples for comparison.

For example, there are some specimens which, although clearly members of the subgenus *P. (Bryanictis)*, are yet not quite

adequate for decisive assignment to a particular species.

Protictis (Bryanictis) cf. microlestes

Plate 19, figures 1, 4, 5, 8, 11, 12

DISTRIBUTION: Late Paleocene (early Tiffanian), Fort Union Formation, Shotgun Member; NE. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 31, T. 6 N., R. 3 E., Wind River basin, Fremont County, Wyoming.

HYPODGM: Uncatalogued M_1 and P^3 - 4 in 1960 Harvard-University of Wyoming collection.

MEASUREMENTS: See table 12.

DESCRIPTION: The right M_1 is generally similar in size and shape to a specimen (A.M.N.H. No. 35377) near the lower size limit of the Gidley quarry *P. (B.) microlestes* sample. The Shotgun specimen has a broader anterior labial cingulum, a slightly larger entoconid, and a smaller hypoconulid; the talonid basin appears somewhat smoother and more concave than that of the Gidley quarry specimens used for comparison.

The wear patterns on M_1 are not well developed, but the usual shear facet on the anterior face of the trigonid is clearly visible, and a small shear facet has formed on the posterior edge of the metaconid. The usual cingulum between the base of the protoconid and the base of the hypoconid shows only minute traces of the wear facet observable in the Gidley quarry sample [and in all specimens of *P. (Simpsonictis)* also]. There is a faint wear facet along the edge of the postero-labial cingulum and a similarly weakly worn area at the edge of the anterior labial cingulum.

Very small wear craters are visible at the summits of the protoconid, metaconid, hypoconulid, and entoconid. The summit of the hypocone, the full length of the crista obliqua, and its posterior continuation to the hypoconulid all show a prominent, characteristically formed groove where the dentine is exposed between two enamel ridges. A much slighter area of apical wear appears near the summit of the paraconid and extends part way toward the carnassial notch. There is no visible wear on the posterior face of the protoconid.

The P^3 is well worn, but it resembles the P^3 in a Gidley quarry specimen (A.M.N.H.

TABLE 12

MEASUREMENTS (IN MILLIMETERS) OF *Protictis (Bryanictis) cf. microlestes* FROM THE SHOTGUN MEMBER, WYOMING

M_1	
Length	4.3
Width (anterior)	2.55
Width (posterior)	2.4
Grind width (anterior)	2.2
Length of talonid	1.7
Length of trigonid	2.4
Length of paraconid	1.5
Length of metaconid	1.1
Length/width (anterior)	1.69
Width (posterior)/length of talonid	1.41
P^3	
Length	3.8
Width	1.8
P^4	
Length, labial	4.55
Width	3.5
Metastyle	1.8
Length, lingual	5.5
Length, labial/width	1.30
Length, lingual/length, labial	1.24

No. 35360) in its general form. It has two roots, lacks a protocone, but shows a distinct metastyle and metacone behind the paracone; there is a small parastyle. This tooth is well within the size range of P^3 in *P. (B.) microlestes*.

The right P^4 is a complete tooth crown, very little worn. Only the scars of the three roots remain, but these show nothing remarkable and appear to be exactly as in the Gidley quarry P^4 sample. The size and outline of the crown are very close to A.M.N.H. No. 35363 from the Gidley quarry, except for some slight differences in the shape of the parastyle and protocone crests. These features are highly variable within the Gidley quarry sample and do not seem to be particularly diagnostic.

The upper carnassial is little worn, but it shows the usual shear facets along the edge of the metastyle blade and the paracone. The tips of all cusps show the usual small wear craters, and the posterior labial cingulum is worn along the anterior half of its edge but not visibly worn posterior to the point below the paracone apex. A small, lightly worn shear facet appears on the lingual side of the pro-

tocone between the lingual cingulum and the lingual crest on that cusp. Finally, a small dimple appears at the extreme posterior end of the tooth, obviously caused by the M^1 parastyle corner.

DISCUSSION: These teeth were collected by McGrew and Patterson in 1960 and very kindly turned over to me for study. Final disposition of the collection between the University of Wyoming and the Harvard Museum of Comparative Zoölogy has not been made, so the collection is uncatalogued.

Comparisons (using Student's t -test) of the measurements of these teeth with the Gidley quarry sample of *P. (B.) microlestes* show that, although the P^4 and M_1 are at or near the lower limits of the ranges observed in the Gidley quarry sample, there are no significant differences from the mean of that sample in P^4 . In M_1 , the Shotgun specimen has a shorter trigonid ($0.01 < P < 0.02$) and is also narrower anteriorly ($0.02 < P < 0.05$). These differences indicate that the Shotgun specimens probably represent a population distinguishable from *P. (B.) microlestes*, but the distinction, if any, does not demand taxonomic recognition at this time. The qualitative differences are similarly vague, tending to confirm the view that these specimens are not quite separable from the type species yet are not quite identical.

The available evidence does not indicate that the Shotgun specimens have any close ties with *P. (B.) vanvaleni*, and the few slight clues now known suggest that such a special relationship is mildly improbable.

If the assignments suggested here are not contradicted by subsequent evidence, these specimens would extend the range of *P. (Bryanictis)* stratigraphically and provide the first published record of this subgenus in Wyoming.

***Protictis (Bryanictis) vanvaleni*,¹**
new species

Plate 16, figure 6; plate 17, figures 5, 8;
plate 18, figure 1; text figure 20

TYPE: A.M.N.H. No. 16031, a left dentary fragment, with P^4 and partial M_1 ; collected by William Stein, August 1, 1912.

¹ Named for Dr. Leigh Van Valen, who brought the type specimen to my attention.

DISTRIBUTION: Middle Paleocene (Torrejonian), Nacimiento Formation, Torrejon beds; east fork of Torrejon Arroyo,² San Juan basin, New Mexico.

HYPODIGM: Type only.

DIAGNOSIS: Differs from *P. (B.) microlestes* in having metaconid lingual to protoconid on P^4 and wider P^4 talonid, with entoconid, hypoconulid, and hypoconid; and relatively lower metaconid and smaller, more transversely directed paraconid of M_1 . Over-all size similar to that of *P. (B.) microlestes*.

MEASUREMENTS (IN MM.): P^4 : length, 4.6; width, 2.35; length/width, 1.95. M_1 : width (anterior), 2.8; length of trigonid, 2.9; length of paraconid, 1.6; length of metaconid, 1.3. Depth below P^4 : 5.8. Depth below M_1 : 5.8.

DESCRIPTION: Dentition: Viewed from the labial side, the P^4 bears a striking resemblance to that tooth in *P. (B.) microlestes* except for the slightly lower, more leaf-shaped main cusp (protoconid), slightly smaller anterior basal cusp (paraconid), and the great reduction of the anterior basal cingulum. From the lingual side, however, the aspect of this tooth is notably different. In *P. (B.) microlestes*, the labial cingulum may continue around the base of the main cusp, or it may rise part way toward the summit of the main cusp. In *P. (B.) vanvaleni*, this crest is essentially similar, but it fades into the posterior edge of the median accessory cusp (metaconid), which continues as a rounded elevation to the summit of that cusp (see text fig. 20).

Although the base of this cusp is a distinct, outstanding feature of the tooth, the summit is not tall and sharp but appears as a slight elevation of the crest, which becomes sharper

² This was "locality 11" of Sinclair and Granger (1914, p. 316) and was shown by Matthew (1937, pl. 65) as part of the "type locality of the Torrejon." This locality probably includes a considerable area in or near T. 20 N., R. 4 W., Sandoval County, New Mexico. A.M.N.H. No. 16031 was collected here and given field number 150. Granger's 1912 field book records A.M.N.H. Nos. 16003 "*Claenodon*," 16011 "*leptacid*," 15990 "*Chriacus*," 15973 "*?Protoselene*," and 15983 "*Tricentes*" as Stein's other specimens for that day and place. Wilson (1956, p. 83) cites *Claenodon* as a characteristic "upper-zone" fossil of the Torrejonian. Sinclair and Granger (1914, p. 311) stated that "the collections . . . of 1896 and 1912 were from the upper horizon of Escavada, Torrejon and intervening arroyos." The type of *P. (B.) vanvaleni* hence probably came from the "upper-zone" Torrejonian.

at that point, turns abruptly labiad, and rises to the apex of the main cusp (protoconid). However, because the enamel has become transparent during fossilization, the underlying form of the dentine shows that this structure is a genuine cusp and no mere crenulation in the enamel.

The usual anteroposterior line of sharp crests begins at the apex of the anterobasal cusp (paraconid), passes diagonally to a well-developed carnassiform notch, and rises again as a prominent blade to the summit of the main cusp (protoconid). From this point, a corresponding posterior crest (somewhat less prominent but still quite bladelike) falls to the carnassiform notch between the protoconid and the posterior accessory cusp (hypoconid). This latter cusp is low, and the crest curves linguad as it passes over its apex and down to a small carnassiform notch at the base of the posterior cingulum cuspsule. From this notch, the crest rises to the apex of that cuspsule (which corresponds to a molar hypoconulid in position), where it joins with the posterior cingulum. There is a small cuspsule (lingual to the posterior cingulum cuspsule) which is at the rounded posterolingual corner of the talonid. This cuspsule corresponds to the entoconid of the molars in position and forms a small peak on the posterior cingulum where the crest turns anteriad and becomes the lingual cingulum crest. The talonid basin enclosed by these cuspidate crests is fairly deep and quite smooth, without the rugosities seen in some specimens of *P. (B.) microlestes*; it is wholly unworn.

There is, to be sure, very little wear anywhere on these teeth, and the individual must have died young. The apex of the paraconid is chipped and may have been slightly worn. Typical, but very small, wear craters can be seen near the apex of the protoconid and at the extreme tip of the hypoconid. A small wear facet (caused by the P^4 paracone) appears on the posterolabial face of the hypoconid, and a larger but not pronounced wear facet shows that the P^4 paracone also passed down the labial slope of the posterior cingulum, just as in *P. (B.) microlestes*.

The surviving parts of M_1 also show little more wear than P_4 . The tips of the paraconid and metaconid have only the beginnings of wear craters. There is a minute wear facet on

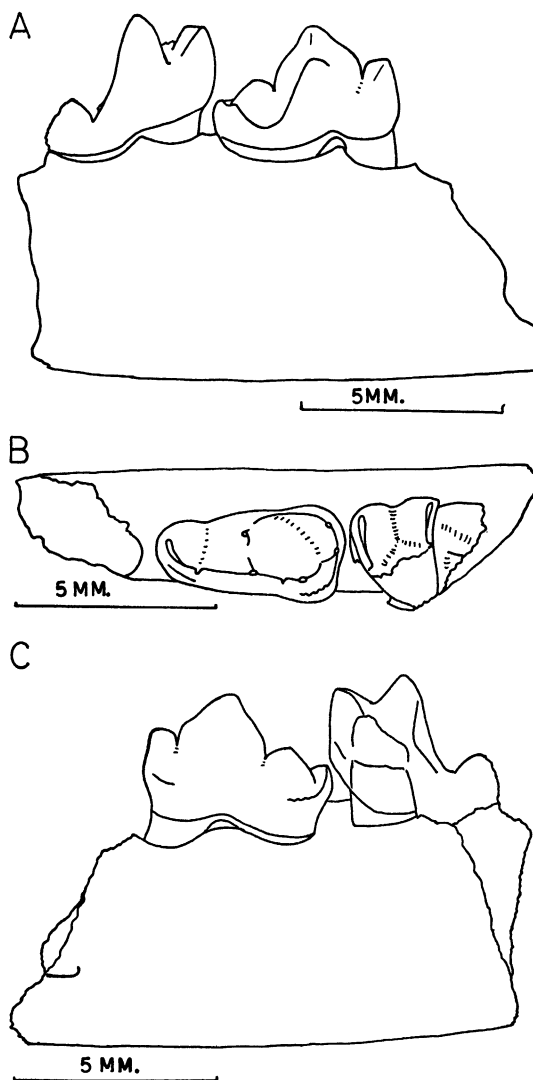


FIG. 20. *Protictis (Bryanictis) vanvaleni*. A.M.N.H. No. 16031. Diagrams of type specimen. A. Lingual aspect. B. Occlusal aspect. C. Labial aspect. Compare plate 16, figure 6; plate 17, figures 5, 8; and plate 18, figure 1.

the anterior edge of the paraconid, and the posterior face of the metaconid shows a more extensive wear facet which hints of more contact here with M^1 than had occurred anteriorly with P^4 , but further extrapolation from these facts is unsafe until more of the dentition is known.

There has been extensive postmortem damage to M_1 . The protoconid has been broken off, and most of the talonid is missing,

while the labial face of the trigonid is represented by a mere flake of enamel. The enamel has spalled off most of the anterior face of the protoconid, so that only the most lingual end of the anterobasal cingulum remains. Except for the differences noted in the diagnosis above, the first lower molar in this species appears to have been generally similar to that of *P. (B.) microlestes*.

Skeleton: The only known skeletal part of this species is the fragment of dentary remaining with the teeth. This small piece of bone is broken off vertically behind M_1 and obliquely in front of P_4 , so the ventral edge is longest. In general, it is identical with corresponding parts in *P. (B.) microlestes*, with a similar conspicuous mental foramen below the posterior root of P_3 .

DISCUSSION: The measurable dimensions are all within the observed range of *P. (B.) microlestes* except for slightly greater P_4 width and slightly smaller P_4 length/width ratio. The differences are not significant by Student's *t*-tests ($0.02 < P < 0.05$ and $0.05 < P < 0.10$, respectively) and would not require separation of this species. The qualitative differences of this species from the type species, however, outweigh the quantitative data, even though *P. (B.) vanvaleni* now is represented solely by a single (admittedly unsatisfactory) specimen.

The high degree of variability in minor details of premolar cuspidation seen in the Gidley quarry sample of *P. (B.) microlestes* is limited to accentuation or reduction of certain features. The highest variability occurs in the anterior premolars and last molars. The characters of the carnassials and P_4 are considerably more constant. This is entirely to be expected because there was undoubtedly stronger centripetal selection operating on those parts of the dentition that are intimately connected with the shearing mechanism and on those parts that must interlock precisely. Moreover, the striking differences in P_4 that are cited here as convenient taxonomic characters were probably less important to these animals than the more subtle differences in the carnassial trigonid. The latter imply a probable difference in the shearing mechanism—a slightly lower degree of carnassial specialization than that attained by *P. (B.) microlestes* and, it is reasonable to

assume, some ecological difference of rather uncertain nature.

It should be noted that no ecological difference is assumed between Montana and New Mexico in Paleocene time. The postulated slight difference in ecology between the two species is based solely on the observable morphological differences. No support is claimed from the geographic separation of the type collecting areas, either. Single subspecies of small carnivores¹ today range from southern Montana to northern New Mexico, although these animals are of course not precisely comparable to the fossil forms.

The assumption that the observable morphological differences reflect a genuine genetic difference between two populations is, as usual in paleontology, not supported by such extensive information as might be wished. However, having started from the assumption that the Torrejon specimen was merely an extreme variant of the Montana species, I have come to conclude that this specimen differs in ways that are not compatible with the normal variation within a species. Also, alternate hypotheses have been considered: (1) this isolated pair of teeth might be part of a milk dentition; and (2) since only one individual is represented, it is possible that it represents a wide aberration, perhaps a teratological specimen or a freak.

The second possibility may be dealt with immediately. If this individual were congenitally deformed, it would be logical to expect a distortion of the cusps, such as will be described in an Eocene *Didymictis* specimen (A.M.N.H. No. 3182a), rather than the addition of cusps that are not distorted but really well formed. The enamel is smooth, and the cusps are regular and well proportioned. Until a second specimen is found, this hypothesis remains possible, but from the appearance of the specimen it seems quite improbable.

No milk dentitions have been described for miacids, and very few for fossil mammals generally. Fortunately, some identifiable miacid juveniles have come to light during the course of this study. A fine specimen of a

¹ Hall (1951) showed *Mustela erminea muricus* covering such a range and *Mustela frenata longicauda* and *M. f. nevadensis* having a geographic distribution nearly as wide.

miacine collected in the Washakie Formation by William Turnbull will be described by him, and a rather poor specimen showing Eocene *Didymictis* milk teeth will be described in a later section of this study.

A specimen of *Vassacyon* will also be described later in this study which shows some unerupted permanent teeth in a juvenile jaw. Unfortunately, the deciduous teeth were not found. This specimen, however, shows the same shallow, thick jaw that may be seen in juveniles of modern carnivores. The bone appears rather spongy around the roots and highly vascular elsewhere, and the teeth are obviously in mint condition except where postmortem damage has occurred.

The bone of the Eocene *Didymictis protenus* (U.S.N.M. No. 19484) is too shattered to show its original character, but dP_{3-4} and M_1 are in place. The dP_3 is not molarized as is the P_4 of *P. (B.) vanvaleni*, and dP_4 in *D. protenus* is much more molarized than P_4 in *P. (B.) vanvaleni*. The *D. protenus* dP_4 also differs markedly from M_1 in *P. (B.) vanvaleni*. A more detailed discussion would be out of place here; it suffices to say that the teeth of the *P. (B.) vanvaleni* type are not like known miacid milk teeth and that the jaw bone is deep, narrow, and fully adult in aspect. Finally, a roentgenogram of the specimen has been made, and no replacement teeth are present.

To turn from the question of the validity of the taxon to its possible significance, there are some particularly interesting points to be discussed.

Proctictis (Bryanictis) vanvaleni is the only new miacid to be described from the Torrejon formation since *P. (Proctictis) haydenianus* was described by Cope in 1882.¹ It is to be expected that more such small forms will be found in the future, because modern methods of washing and screening sediments are more likely to reveal them.

The type of *P. (B.) vanvaleni*, in addition to its importance as a new element in the known Torrejon fauna, provides some information useful in the identification of premolar

cusps. I have previously expressed doubts about the propriety of using molar-cusp names for the cusps of premolars (Mac Intyre, 1962). However, study of this specimen has altered my opinion, because it shows so clearly which of the premolar cusps correspond to cusps on the molars.

It now appears justifiable, on the grounds of convenience and succinctness, to refer to premolar cusps by molar-cusp names whenever such usage will reduce ambiguity and increase clarity. However, use of these names must explicitly exclude any implication that the development of premolar-cusp patterns bears any necessary relationship to the previous evolution of molar cusps. On the contrary, the molarization of premolars, which appears to have occurred independently in diverse lines of mammals, obviously results from a forward extension of the morphogenetic field influencing molar-cusp patterns, and the resulting shapes of the premolars are governed by the shape of the molars nearest to them. Unfortunately, there is no important experimental evidence as to the specific mode of operation of morphogenetic fields upon dentitions, but it seems reasonable to assume that such fields operate here much as they do in other parts of the anatomy during embryonic development. Hence it is herein assumed that cusps appearing on premolars owe their existence to the same basic forces, suitably modified, that operate to produce the molar cusps in any individual instance. For this reason, it is unnecessary to become involved in controversy over which cusps are "really primary" or represent the "primitive reptilian cone." The cusp names are of merely geographic significance and may be applied within any specific series without necessarily implying that a genuine homology with other groups is involved. If, then, it is possible to show that a premolar [such as the P_4 of *P. (B.) vanvaleni*] has developed a cusp pattern similar to that of the molars in the same dentition, it seems to me that one can reasonably apply the convenient and universally accepted names for molar cusps in that particular instance. I also think that no broad and general theoretical extrapolations should be made from such cases, because the course of evolution may have been quite different in diverse groups.

¹ Wilson (1951, 1956) has reported three undescribed new species from the Torrejon. Dr. Wilson has been kind enough to include brief descriptions of his unpublished species in a letter to me, and none of them appears to be *P. (B.) vanvaleni*.

In the specific case now at hand, it seems perfectly reasonable to call the anterobasal cuspule the paraconid, the main cusp the protoconid, the first posterior accessory cusp the hypoconid, the posterior cingulum cuspule the hypoconulid, the lingual accessory cusp the metaconid, and the small postero-lingual cuspule the entoconid (see text fig. 1). Obvious homologies of upper teeth are also used here. Furthermore, it seems reasonable, by a modest extrapolation of this usage, to apply these names to similar cusps appearing in the premolars of other viverravine miacids, because these are obviously a close-knit group of species and genera and because there is a definite similarity in the premolars of this group. Further extension to the *Miacinae* could be defended on the same grounds, but there are a few dubious cases in which it might be better to retain the more cumbersome but less dubious neutral descriptive terms. Extension of the terms to other carni-

vores may also be justifiable, but whenever there is any uncertainty the descriptive terms have been retained.

Furthermore, the peculiar labiad curve of cusps and crests that often¹ may be seen in miacid premolars becomes understandable if one assumes that the molarization field influences their form. To draw a somewhat shaky analogy, it seems almost as if some premolars had a potential metaconid "buried" in the lingual flank of the protoconid.

Finally, it must be said that the cusp homologies between molars and premolars suggested by Scott (1892) are not true for miacids, and they probably should not be applied to other carnivores either, although such terms or some modification have been adopted by others (e.g., Teilhard de Chardin, 1915).

¹ The degree of curvature is as variable as other features of the dentition and may be comparatively strong or weak within single samples.

GENERAL DISCUSSION

ECOLOGICAL ADAPTATIONS

THE ECOLOGICAL NICHES filled by the miacids of the middle Paleocene can be deduced to a limited degree from the associated fauna and the dental adaptations of the different species. In all the communities represented by middle Torrejonian fossil assemblages, a number of small herbivorous or omnivorous animals occurred which might have been the natural prey of the miacids described in the present paper.

In the environment represented by the Gidley quarry, for example, there is an abundance of multituberculates, primates, and insectivores that are as small as or smaller than *Protictis* (*Simpsonictis*) *tenuis* (see Simpson, 1937a). The evident adaptations of the dentition for piercing and the diminutive size of this species suggest insectivorous habits. The variety of plants indicates a jungle environment and implies the presence of insects, although none are reported as fossils. There can be little doubt that *P. (S.) tenuis* could and did prey on insects and soft-bodied invertebrates as well as on other vertebrates. It must be remembered that an insectivore (in any sense of the term) is, after all, essentially carnivorous. Although normally specializing in smaller prey, modern shrews will kill and eat mice larger than themselves, as is well known. Also, present-day small carnivores are known to eat insects occasionally (see Hall, 1951, pp. 176, 216). It is also worth noting that there is some overlap in size between various members of the orders Carnivora and Insectivora.

These remarks should not be interpreted as implying a special relationship between *P. (Simpsonictis)* and the order Insectivora. As shown in the discussion of *P. (S.) tenuis*, that species did have a functional carnassial system and was undoubtedly a true carnivore, although much less specialized in that direction than some of the contemporary miacids, especially *Ictidopappus mustelinus*.

Undoubtedly the most hypercarnivorous of the middle Paleocene miacids was *Ictidopappus mustelinus*. The teeth of this species have a pattern basically similar to that of the various species of *Protictis* but simplified by

the absence of cingula and minor cuspules. The nearly connate paracone and metacone of the sharply transverse upper molars, the widely open P^4-M^1 embrasure, and the low, elongate M_1 trigonid (in other words, the large angle γ) are correlated with the large canines and short, powerfully constructed jaws. This was clearly a specialized predator comparable to the modern weasels. Such a degree of specialization is unexpected in such an early form and contrasts not only with contemporary *Protictis* species but also with the early *Viverravus* of the Wasatchian. Indeed, *I. mustelinus* is more specialized in some ways than the middle or late Graybull species, *V. acutus*, and is certainly more specialized than the *Viverravus* species (not *V. acutus*) now known from the earliest Wasatchian.

The relative rarity of *I. mustelinus* in collections may be due to a real scarcity of members of this species at the time represented by the Gidley quarry, but it could also be due to the possibility that the normal habitat of this species was far from the areas of deposition. If it was normally an upland species and not very numerous as well, we are not likely to find many more specimens, so a detailed study of the available material is supplied in the Systematics section.

The relative abundance of *P. (Bryanictis)* in the Gidley quarry contrasts with its absence (or, at least, relative scarcity) in the San Juan basin and the scattered localities in the lower parts of the upper Lebo. This distribution is not wholly explicable on the basis of collecting accidents. The quarry sediments were probably deposited in swampy forests. The various "lower" localities represent flood-plain deposits, which Simpson (1937a, pp. 62-63) considered similar to the New Mexico Torrejon facies. It seems likely that species in this subgenus were forest dwellers and perhaps arboreal. The dentition and jaw structure show more definitely carnivorous adaptations than does that of *P. (S.) tenuis*. Comparison with *P. (Protictis)*, on the other hand, indicates some differences in specialization, but, although the differences are obvious, their significance is elusive. In the interpretation of these differences,

much depends upon which conditions are considered primitive (as discussed below). *Protictis* (*Protictis*) and *P. (Bryanictis)* show many characters, many of them probably primitive, that are probably correlated with carnivorous-omnivorous habits. Both forms appear to have been more or less generalized predators. The main difference might well have been in habitat. *Protictis* (*Protictis*) is relatively rare in the Crazy Mountain field and relatively abundant in the San Juan basin. It appears possible that *P. (Protictis)* lived in more open areas, or perhaps it was more terrestrial in habits, but in the absence of more complete postcranial material these possibilities remain speculative.

There was evidently some diversity within both lines. *Protictis* (*B.*) *vanvaleni* may have been slightly more omnivorous than *P. (B.) microlestes* (it is noteworthy that, if analogy may be made with other carnivores, the former would be more specialized than the latter in this respect). The rare, rather bulky teeth referable to *P. (Protictis)* from the lower levels of the upper Lebo are similarly to be contrasted with the rather smaller but also rare *P. (P.) haydenianus* from the Gidley and Silberling quarries.

These robust scraps are unusually interesting, because they suggest a trend toward the robust, more hypocarnivorous *Didymictis* of Tiffanian and later times.

The situation in the Lebo *P. (Protictis)* samples provides an interesting comparison with the case of *Metachriacus provocator* discussed by Simpson (1937a, p. 49). This oxyclaenine arctocyonid occurs at lower levels than its smaller relative, *M. punitor*—a circumstance that Simpson attributes to a difference in facies between the earlier, scattered localities and the later quarry sites.

TAXONOMY

The philosophy of a classification, its primary concepts and basic ideas, are what Simpson (1961) has redefined as "taxonomy." In the classification of the Miacidae, two alternative outlooks have been espoused by different students of the group. These may be categorized as the horizontal (which tends to regard the miacids as a subdivision of the creodonts) and the vertical (which groups

the miacids with the later true Carnivora Fissipeda).

In any particular case, a choice between the vertical or horizontal schemes depends largely on individual preferences and circumstances. In numerous papers, Matthew consistently favored a horizontal scheme, and Osborn just as consistently espoused vertical classifications (although not especially for miacids). In my opinion, a horizontal classification is perhaps slightly clearer when one is dealing with organisms on a single time level. Other things being equal, the horizontal scheme allows greater convenience for practical sorting of specimens, and the Linnean system was originally adapted to the sorting out of organisms from one time level—the Recent.

But other things are hardly ever equal in reality, and no classification is wholly vertical or horizontal. Some compromise is always necessary, particularly when one is working with the time dimension added to the others.

For example, at or near the pelycosaur level, the position of the Therapsida is pretty clearly with the Reptilia. There is of course no doubt that the Mammalia¹ arose from some of the later Therapsida, but there is as yet no conclusive evidence as to which of the most mammal-like of the advanced therapsid families really gave rise to the unmistakably mammalian Theria. In this case the evidence is in favor of a horizontal classification of the Therapsida as Reptilia.

If we had all the connecting links that relate the various groups of condylarths or those that lead from the eohippus stock to tapirs, chalicotheres, rhinoceroses, and titanotheres, a horizontal classification of *Hyra-*

¹ As our knowledge increases, the dividing line between therapsid reptiles and primitive mammals must become more arbitrary. Since the monotremes and the various groups of non-therian but mammal-like fossils are exceptional in many ways and have no clear connection with the vast majority of undoubted mammals, living and extinct, it seems to me that a restriction of the class Mammalia to the clearly mammalian Theria would serve the interests of clarity and stability in the future, while not really obscuring the true relationships of the various near-mammalian genera. I hope to pursue this discussion elsewhere in detail, but it seems proper to explain here what I mean by "Mammalia," as this is not the widely accepted definition of the class.

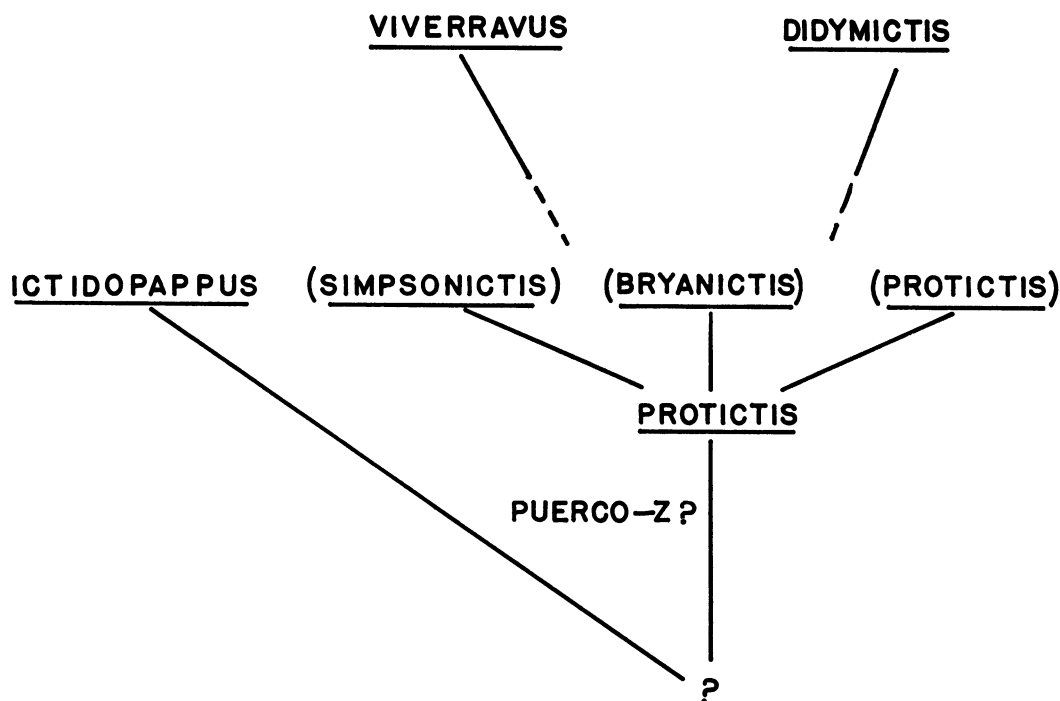


FIG. 21. Dendrogram indicating approximate relationships of taxa discussed in this paper.

cotherium to the Condylarthra would certainly be more fitting. Our vertical classification of the horses would then begin where we could see a definite specialization into truly horse-like forms, and so on for the others. The necessary links to the older groups have not been found, however, whereas we do have a closely allied sequence of forms leading up to the true horses but not such close links to the other perissodactyls. From both theoretical and practical standpoints, the present assignment of *Hyracotherium* to the horse clade seems logical, even though it could be placed in the Condylarthra with almost equal justice.

For the same reasons, assignment of the miacids to the Creodonta seems less useful than acknowledging their closer affiliation with the fissipedes. As our knowledge stands now, the miacids are clearly distinct when they are first found, and there is an increasing resemblance between some of the later fissipede groups and certain miacid lines as the Eocene-Oligocene transition is approached. If we go toward the beginnings of the Cenozoic, on the other hand, we are not yet faced with the happy dilemma of finding a creature

exactly intermediate between the miacids and their ancestors.

If we are ever faced with that dilemma, the choice will be influenced heavily by convenience and stability, and the vertical classification will probably be retained at that time as it is now.

VIVERRAVINE RELATIONSHIPS

The middle Paleocene species of Viverravinae are clearly most closely related to the viverravine genera typical of the Eocene: *Viverravus* and *Didymictis*. These two genera arose from *Protictis* in North America well before the end of Paleocene times. It is not now possible to state which species of *Protictis* is the direct ancestor of *Didymictis*, but it was certainly not a species of *P. (Simpsonictis)*. It is likewise not yet possible to say which *Protictis* species gave rise to *Viverravus*, but it is hardly likely that the first members of the latter genus arose from *P. (Protictis)*. Contrary to Simpson's (1937a, p. 208) suggestion, I see no special resemblance between *Viverravus* and *Ictidopappus* except for certain

parallel developments that might be expected to occur in hypercarnivores.

It is possible that some of the modern families of Carnivora were derived from the Viverravinae, but those groups with known ancestors possessing third molars were evidently derived from the Miacinae. It is unlikely that any of the later carnivores arose from *Didymictis*, however, as that genus became extinct near the beginning of the middle Eocene without known issue. The further relationships of the Eocene Viverravinae may be more profitably discussed when detailed studies (now in progress) are complete.

Text figure 21 illustrates the above relationships diagrammatically.

MIACID RELATIONSHIPS

The general relationships of the Miacidae are still clearest and closest with their descendants, the later families of the Fissipeda. Such is true even though the precise connections between the known miacid genera and the first recognizable Felidae, Mustelidae, Viverridae, and Canidae have yet to be demonstrated (with the exception of the Canidae, which were derived from *Miacis* without much doubt).

The detailed relationships of the Pinnepedia are not clear, but derivation from one or more of the Oligocene or later families of Carnivora now appears more likely than direct origin from the Miacidae.

The relationship of the Miacidae to the other groups now in the superorder Ferae and the broader relationships of the Ferae to the other kinds of placental mammals present much larger and more difficult problems. It is certain that the later fissipedes are derived from the Miacidae, but here we face the problem of the derivation of the Miacidae themselves.

MIACIDS AND CREODONTS: The long-held view that the miacids are about as close to the Creodonta¹ as they are to the Carnivora,

while far from being discredited, is now at least debatable. At present, it appears that the miacid-creodont relationship may be either closer or more distant than has hitherto been supposed.

There is a basic question involved here. Simply stated it is: What is a carnivore? More realistically, the question is what groups of mammals, considering all known living and fossil forms, shall we agree to include in the order Carnivora and the superorder Ferae? More specifically, what are the common denominators of *Viverravus*, *Ailuropoda*, *Andrewsarchus*, *Oxyaena*, *Proteles*, *Acinonyx*, and *Loxolophus* (to cite a few of the extremes involved) and all the other genera commonly accepted as Carnivora? There is certainly no serious disagreement as to the position of the living genera in this order, despite their diversity, and, even though all are not literally meat-eaters, their union within one order has an ultimate reality.

The primary adaptations of primitive carnivores are generally associated with predation on comparatively large prey. Because of the broad range of adaptation seen in specialized carnivores, it is impossible to frame a definition of the superorder Ferae that will at once include both primitive and specialized members of this superorder and exclude members of all other orders of mammals. For example, it is next to impossible to make general statements about carnivore dentitions except to say that the cheek teeth are never

this group have always included the Oxyaenidae and Hyaenodontiade. Van Valen (personal communication) believes that there are some groups usually classed as Insectivora or Marsupialia (*Deltatheridium*, *Didelphodus*, and *Cimolestes*, for example) that should be included, and he removes some of the families (such as the Arctocyoniidae) from the Creodonta, rejecting that name to describe the altered concept. As I have been primarily concerned with miacids while he was working on other groups, I shall not comment upon his taxonomic conclusions except to say that we are in substantial agreement on many points, particularly on the closer affinities of some "insectivores" with the carnivores (*sensu lato*). But I see no compelling reason to abandon the name Creodonta, which is still useful for referring to the Oxyaenidae and Hyaenodontidae whether or not all their relatives are included in the group. In practice, it is used here to mean these two families and their immediate common ancestry (which probably constitute a distinct order within the Ferae), without prejudice regarding other possible relations.

¹ As originally proposed by Cope (1875), the Creodonta were a suborder of the Insectivora. Included were *Ambloctonus* and *Oxyaena* (Oxyaenidae), "*Stypolophus*" (= *Sinopa*; Hyaenodontidae), and *Didymictis* (Miacidae). Subsequent emendations have greatly altered, expanded, and sometimes contracted this original arrangement, but the more authoritative students of

hypsodont. Indeed, the primitive characters of carnivores are, in general, the same characters that are probably primitive for Eutheria generally. These are: dental formula 3/3, 1/1, 4/4, 3/3; canines relatively large and simple; premolars not strongly molarized; brachydont molars with cusp pattern as in the Forestburg therians (Patterson, 1956); fibula in contact with tarsus, not fused to tibia; ulna in contact with carpus, not fused to radius; phalanges and metapodials relatively short; digits 5-5; scaphoid, lunar, and centrale free; astragalus with ball-shaped, rounded, or oval head on distinct neck at oblique angle to body, trochlear facet not deeply grooved, foramen astragali present; ungual phalanges not fissured. None of these is either an inclusive or exclusive character, and they provide scant support for a comprehensive diagnosis.

But the aim of modern taxonomy is to classify animals, not characters (a fact some taxonomists lose sight of even now). Characters can be useful in the distinguishing of real groups, but the distinction between groups or the unity within them need not be obscured because no single character can be found to serve as a convenient marker at every stage of evolution. It is enough for a character or a complex of characters to demonstrate that primitive members of one group are distinct from primitive members of another. If evolution results in the loss from descendants of some key characteristic useful in the distinguishing of their primitive ancestors from other primitive organisms, the continuity of evolutionary lines (if it is reasonably clear) is sufficient evidence for maintaining the unity of a higher category, if other factors make this convenient.

Hence, the superorder Ferae (as presently constituted) may be considered a natural group even though there are no exclusive and inclusive characters. If (following Patterson and McGrew, 1962, footnote 1) we consider that the arctocyonids are not distinguishable from the condylarths (both being relatively primitive omnivorous or herbivorous eutherians without demonstrably close connections with the predaceous Ferae), at least one characteristic of primitive carnivores can be mentioned. That characteristic is the possession of some molar teeth in which shearing is accentuated. By this criterion, the Miaci-

dae, Oxyaenidae, Hyaenodontidae, and possibly the Mesonychidae can be retained in the superorder Ferae without straining the concept, and the families of Recent Carnivora that appeared recognizably in the early Oligocene and subsequently diverged so widely remain in that order by virtue of their obvious community of origin within the Miacidae.

All this is not, of course, proof that the creodonts and the miacids do in fact share a common ancestry closer than either has with, say, primates. In regard to this aspect of the problem, it might be well to consider what the common ancestry of the two subfamilies of the Miacidae might have been like.

Suppose we assume that the unknown ancestral miacids were more or less like the known Paleocene Viverravinae dentally (except that the ancestors had M_3^3). If the conditions seen in the skull and postcranial skeleton of known miacids are synthesized and extrapolated backward slightly, it is possible to enumerate some characters that are here considered primitive for the family Miacidae. The following is a list of the major characters that one might expect to find in the common ancestry of the two miacid subfamilies:

A. Dentition

1. Incisors 3/3, relatively small and subequal.
2. Canines 1/1, moderately enlarged, single-rooted, recurved, and sharply pointed.
3. Premolars 4/4, sharp and increasing in size and complexity from P_1 to P_4 .
 - a. P_4 probably with protoconid, paraconid, hypoconid, and hypoconulid on crest concave lingually. Length of P_4 subequal to M_1 length.
 - b. P^4 probably with paracone, protocone, and possibly metacone. Protocone probably displaced slightly forward. Some shear on metastyle area. Parastyle probably present.
4. Molars 3/3, with relatively high, sharp cusps and crests divided by carnassiform notches.
 - a. Upper molars with wide styler areas, distinct small stylocone, tall paracone, shorter metacone, and intermediate protocone. If present, lingual cingula small, separate, and subequal. Conules present on M^{1-2} at least. M^{1-2} subequal; M^3 slightly reduced.
 - b. Lower molars with high trigonids and

non-shearing, moderately basined talonids somewhat smaller than trigonids. All primitive cusps distinct. M^{1-2} subequal. All molars shearing, but M_{1-2} versus P^4 - M^1 dominant.

B. Skull form generally elongate and opossum-like dorsally.

1. Braincase relatively small and tubular, sharply constricted behind orbits.
2. Median sagittal and nuchal crests well developed.
3. Zygomatic arches strong but not exaggerated.
4. Facial and cranial regions about equal in length.
5. Ear region not covered by well-ossified bulla; ectotympanic loosely attached; entotympanic not ossified.
6. Skull foramina essentially similar to those of living viverrids but with distinct foramina for median entocarotid, vidian, and promontory arteries. Small stapedial artery present and passing through stapes. Large infraorbital canal.
7. Groove or notch in premaxilla between I^3 and C^1 for tip of C_1 .
8. No postorbital ring but possibly a post-orbital process.

C. Lower jaws generally elongate and foxlike.

1. Symphysis long, sloping without visible "chin" or strong interlocking processes.
2. Body moderately deep and approximately straight.
3. Ascending ramus at small angle to body.
4. Coronoid process high, rounded at tip.
5. Condyle wide, near level of trigonids.
6. Angle low, strong, not very elongate, essentially straight but hooked at tip.

D. Postcranial skeleton generally primitive as in many small, generalized insectivores, condylarths, and other primitive mammals.

No suggested miacid thus far described is both primitive enough and ancient enough to fit this concept of a primitive ancestor. It is entirely possible that such an ancestor is already known but unperceived from isolated teeth in collections of mammalian fossils from the late Cretaceous. It is quite probable that a really primitive ancestor may be nearly unrecognizable as such, since it may very well lack any more than faint signs of the typical P^4 - M_1 carnassial specialization. For this reason, almost any primitive eutherian with high-cusped first and second molars approximately coequal and with P_4^4 partly (but

not wholly) molarized may be a possible ancestor. The upper-molar pattern of primitive miacids is not far from the generalized therian pattern exhibited by the early Cretaceous therians described by Patterson (1956). By a slight reduction of the stylocone and addition of small lingual cingula on the flanks of the protocone, a generalized miacid pattern could be produced from these most primitive tribosphenic upper molars. The alteration necessary to produce a miacid-like lower-molar pattern from some of the Forestburg specimens is even smaller—a slight broadening of the talonid basin and a slight elongation of the trigonid with a little emphasis on the paraconid.

One specimen from the Forestburg, Texas Cretaceous, C.N.H.M. No. PM931, illustrated by Patterson (1956, fig. 2a) is similar to a miacid P^4 . The paracone is lower, hence relatively stouter than in *Deltatheridium* and its allies. The parastyle is well developed, with three faint ridges running to the lingual and buccal cingula and toward the paracone. The labial cingulum is low and runs nearly to the posterior edge of the tooth, being broadest where the crown is "pinched" opposite the carnassial notch between the paracone and metastyle-metacone ridge. The metastyle is still visible as a bulge or thickening of this ridge and is slightly lingual to the fainter thickening of the elongated metastyle behind it.

The cingulum running lingual to the parastyle continues around the anterior and lingual faces of the tooth. A part has been broken off just posterior to the attachment of the anterior root and lingual to the apex of the paracone.

If this broken part represents a slight expansion of the lingual cingulum, it would be in the right position for a protocone to develop just medial to the paracone and thus anterior to the middle of the tooth.

It would be rash to assert that this tooth belonged to a Cretaceous miacid or even that it represents a primitive premiacid. It might be a P^3 and not a P^4 at all. A somewhat more realistic appraisal could be made if there were more associated material, but it is quite clear that the pattern of a shearing ridge posterior to the paracone and running obliquely toward the posterolabial corner of the tooth can be

seen here as it is in the Miacidae, but on a considerably less specialized level and at a time much earlier than one might anticipate for the origin of specialized carnivores. Rather than indicating early derivation of the miacids from such remote ancestors, I prefer to use this as an example of the persistently primitive nature of the miacids—a primitive nature proclaimed by their long retention of many essentially primitive features of the skeleton as well as of the dentition.

Russell (1954) has pointed out the close resemblance between arctocyonid and condylarth molar patterns and the basic similarity between miacid, oxyaenid, and hyaenodontid molars, suggesting that the common ancestor of all the latter three probably had miacid-like molars. Such is undoubtedly true insofar as the miacids preserved, with relatively slight changes, the pattern seen in early Cretaceous Theria. However, the resemblance between the miacids and the classic creodont families cannot now be shown to be due to any special relationship (although such seems not improbable), and the contention that the common ancestors of the three families would be members of the family Miacidae is not supported by the evidence now available. If such close common ancestry did exist, it appears to me that these still hypothetical animals would be closer to primitive Hyaenodontidae than to anything that could be properly called a miacid.

The miacid molar pattern is, indeed, more primitive than that of known hyaenodontids, but the latter are basically more primitive in their over-all nature and particularly in the fact that all their molars are shearing teeth.

The retention of this little-altered primitive pattern in miacid molars is explicable on functional grounds. The emphasis on a single pair of teeth in the shearing mechanism obviated the changes observable in forms in which two or three pairs of molars functioned as shearing teeth. Thylacine marsupials and primitive hyaenodontids are two obvious examples. In such forms, the second and third (and in marsupials the fourth) lower molars provide the main shears against M^{1-2} (and M^3 in marsupials), and the latter become modified by extension of the posterior edge and by partial or complete fusion of the paracone and metacone as the dentition be-

comes more specialized. The emphasis upon shear minimizes the importance of the crushing mechanism, and the talonids of the lower molars are reduced in such non-miacid carnivores.

With the forward shift of the primary shearing function in miacids to P^4 from the successive shears on all molars (trigonids shearing in all interdental embrasures), the upper molars retained most of the primitive crushing or grinding function, and there was a slow change of M^{1-2} to decrease the interlocking of cusps that would otherwise tend to interfere with the ectal jaw motion associated with grinding. At the same time, the shearing mechanism was fully functional and could become more efficient without reduction of the grinding mechanism.

In the predatory creodonts, there was little of the grinding function retained in the molar teeth. In both oxyaenids and hyaenodontids, the general trend was toward more and more strictly hypercarnivorous forms, culminating in some genera with superficially very catlike dentitions.

Despite the fact that the major shearing teeth are different in miacids, hyaenodontids, and oxyaenids, the resemblances among these primitive predators have customarily been taken as evidence of real relationship. The evidences of this relationship do not necessarily appear in the more specialized forms that are most abundant in the fossil record. The question of miacid and creodont ancestry may be more profitably investigated among the relatively small (but fortunately no longer quite so rare) mammals of the Mesozoic-Cenozoic transition.

MIACIDS AND CRETACEOUS MAMMALS: The first unmistakable miacid fossils appear in the Dragon¹ local fauna of central Utah (see

¹ The two specimens of *P. (Protictis) haydenianus* from Dragon Canyon were collected by McKenna in 1957 and are not the same as the three reported by Gazin (1939, 1941). Gazin's specimens were: U.S.N.M. No. 15763, a P_4 or P_3 , minus roots and the anterior end of the crown (not *Protictis* or *Didymictis* and probably not a miacid); U.S.N.M. No. 15774, a P^4 or P^3 (surely not a miacid tooth); and U.S.N.M. Field No. 5-35, an uncatalogued carnassial trigonid. This last fragment is part of a highly specialized shearing tooth, evidently representing an animal somewhat smaller than *P. (P.) haydenianus* but larger than *Ictidopappus mustelinus*. If, as I suspect, the isolated carnassial fragment rep-

text fig. 4, D. and pl. 3, fig. 4, pl. 8, figs. 2, 5). These are already clearly distinguishable from the creodonts and evidently had a considerable evolutionary history behind them even then. If we discount Puerco-Z as ambiguous, there are no clear antecedents in the Puerco fauna for these first miacids, and until recently there was little suggestion that any known pre-Puercan mammals could possibly have been ancestral to the miacids.

In recent years, collections from the Wyoming Lance Formation (see text fig. 4, L.C.) by University of California expeditions and from the Montana Hell Creek beds (text fig. 4, H.C.) by University of Minnesota expeditions have provided large numbers of isolated teeth and bones, together with several associated dentitions of latest Cretaceous mammals. Most of these animals have been known hitherto only from isolated teeth, and a number of them are new to science. The material is so rich and varied that it will undoubtedly be some time before the full fauna¹ can be described.

Dr. William Clemens is describing the Lance mammals, Dr. Robert E. Sloan is writing on the Hell Creek mammals, Dr. Leigh Van Valen is working on fundamental relationships among assorted primitive mammals, and Dr. Malcolm C. McKenna is writing studies of primitive primate-insectivores, and all these persons are cooperating in the study of these important and complex problems.

The information available to me at this time has been derived from conversations with Drs. Clemens, McKenna, Sloan, and Van Valen, access to some of their manuscripts, and inspection of some of their new fossils. It is a pleasure to acknowledge the generous spirit of cooperation that permitted this part of the paper. The conclusions drawn here are, of course, tentative and may be

resents a new oxyaenid creodont, this would be the earliest reported member of that family, even though the Dragon local fauna is now generally believed to be more nearly equivalent to a local facies of the Torrejon fauna than it was originally. As these specimens are not strictly relevant to the present study, they have been turned over to Van Valen for study and fuller description.

¹ The word "fauna" is used in the sense customary among paleontologists, so refers to an assemblage of fossils that represents the once-living assemblage of animals (the real fauna) inferred therefrom.

subject to correction after more detailed descriptions of these fossils become generally available.

From the Lance Creek type area, Clemens has (among other things) a nearly complete jaw and lower dentition (and a maxilla with P^4-M^2) of a small and very primitive, creodont-like, paleoryctid insectivore, *Cimolestes*. This genus is more primitive than the known Mongolian Eutheria. Originally described (from isolated teeth) as a marsupial, it was recognized by Clemens as a true placental on the basis of his new material, and all those presently doing original research on this and similar primitive mammals agree that this view is correct. Its relationships involve a technical problem of nomenclature (see Clemens, McKenna, Russell, Sloan, and Van Valen, 1964), but this is not especially germane to the present discussion. *Cimolestes* is most important as a probable direct ancestor of the Creodonta as they have been defined here. Its relevance to the miacids is discussed below.

The Hell Creek beds of Montana have yielded (Sloan, 1964; Sloan and Van Valen, 1965) a fauna equivalent to the type Lance of Wyoming as well as other faunas from slightly different levels. The rich Bug Creek Anthills locality (with several sites at the same stratigraphic level along a single stream channel) has yielded a *Cimolestes* maxilla with P^3-4 among many isolated teeth of the same species, two species of the long-known erinaceoid insectivore *Gypsonictops*, a new genus of arctocyoniid condylarth called *Protungulatum*, and a new genus of leptictid insectivore, *Procerberus*, together with some previously unknown multituberculates as well as many specimens of previously known Cretaceous mammals, reptiles, and fishes—all well below the stratigraphic position of the last *Triceratops* and bearing witness to the diversity and abundance of mammals at that time. It should be understood that *Procerberus* is not necessarily restricted to the leptictids in its affinities, nor is *Cimolestes* quite the same thing as the familiar, more specialized Hyaenodontidae or Paleoryctidae, but the references are certainly correct in the broad sense, and they are so accepted here.

Comparison of *Cimolestes* with the oldest known miacids shows that the chief differ-

ences lie in the molars. In *Cimolestes*, M_{1-3} are subequal, all with high, shearing trigonids and clearly basined talonids bearing all the usual cusps prominently. The premolars are much as in *Sinopa* and *Prolimnocyon*, with no definite hypoconid, no apparent basining, and with the median crest essentially straight and sharp. The canines were larger than the incisors, judged from the alveoli, and I_1-P_1 all were single-rooted. The jaw is elongate and rather slender anteriorly, with a long, sloping symphysis quite chinless. The body is noticeably dorsally flexed below M_1 toward the ascending ramus. Close in size to *Protictis* (*Bryanictis*) *microlestes*, but with a striking resemblance in appearance to *P. (Simpsonictis)* *tenuis*, the late Cretaceous genus seems generally intermediate in morphology between *Protictis* and *Sinopa*. *Cimolestes* differs from the Mongolian Cretaceous genus *Deltatheridium* in the presence of P_1^1 , the absence of a chin, the wider molar talonids and the more transverse upper molars, with slightly greater paracone-metacone separation, and the presence of a protocone on P_4 ; *Cimolestes* also lacks the extremely elongated M_3 talonid seen in *Deltatheridium*. The lingual cingula, usually well developed in miacids but not in creodonts, are barely present in *Cimolestes* upper molars. All in all, the suggestion that *Cimolestes* or something very close to it could have been the common ancestor of both creodonts and miacids does not stretch credulity too far.

Part of the problem in unraveling the ancestral relationships of miacids lies in two possible interpretations of the fourth premolar. If a simple fourth premolar is primitive among these mammals, then the P_4 of *Cimolestes* is primitive and could have become more molariform in its descendants. If a molarized P_4 is primitive, the ancestral condition for miacids may be represented by the Cretaceous leptacid *Procerberus*.

In this connection, it has been generally assumed that the last premolariform tooth of therian mammals is homologous throughout the Pantotheria, Metatheria, and Eutheria. However, premolars are usually defined by replacement, not morphology, and the detection of replacement patterns in fossils depends on the rare occurrence of specimens which show it. If enough complete

dentitions were available, some clues might be derived from wear patterns in adult dentitions. The fact is that, at present, we know nothing about tooth replacement in pantotheres. In metatherians, the replacement of only one molariform tooth by P_3^3 leaves us uninformed about the possible homologies involved here as well.

If we may assume that the two kinds of cheek teeth can be differentiated on the basis of morphology (the few available examples of miacid tooth replacement certainly permit this in that family), disregarding the difficulties in identification of premolars in Mesozoic mammals, then the primitive shape for therian last lower premolars was not molariform but comparatively simple, as in oxyclaenine condylarths, primitive creodonts, and the genera *Cimolestes* and *Oodectes*. Progressive complication presumably involved enlargement of the small paraconid and the beginnings of basining in the talonid, with the first indications of an incipient hypoconid present as a posterior accessory cusp, as in *P. (Simpsonictis)* *tenuis*. The next step would be the addition of a metaconid, presaged by a shift of the anteroposterior crest from the midline to a more labial position, as in all *Protictis* species. Development of a rudimentary metaconid, as in *Ictidopappus mustelinus* with only a trace, Puerco-Z with a more definite bulge, and *P. (Bryanictis)* *vanvaleni* with an unmistakable cusp, would follow in this hypothetical morphological sequence.

Unfortunately the temporal sequence is not right for this hypothesis.

The genus *Oodectes* is a miacine that appears first in the late Wasatchian fossil record. The putative succeeding steps are all present in various middle Paleocene viverravines that are nearly or exactly contemporaries. The enigmatic tooth called Puerco-Z cannot be the most primitive among miacids. In development of the metaconid, it resembles the most specialized of the middle Paleocene forms, *Ictidopappus*, and both of these are intermediate between the extremes represented by *P. (B.) microlestes* (no metaconid on P_4) and *P. (B.) vanvaleni* (prominent P_4 metaconid). Such is true even if we assume that the presence of a metaconid is primitive and that specialization was in the direction of progressive reduction and loss of this cusp,

as suggested by Van Valen (personal communication). With such an assumption, then *P. (B.) vanvaleni* among the miacids exhibits the most primitive condition and *P. (S.) tenuis* is the most specialized of the middle Paleocene miacids. Even so, Puerco-Z and *Ictidopappus mustelinus* would still be intermediate.

The upper P^4 of primitive miacids appears to be partly molarized, as is that tooth in *Cimolestes*, *Procerberus*, *Protungulatum*, and *Gypsonictops* among the Cretaceous mammals. In *Cimolestes*, molarization of this tooth is least, with a small metacone¹ and a slight shear on the metastyle crest against M_1 . The protocone is not extended forward, however, and the tooth is generally more like the P^4 of creodonts than that of miacids in general appearance. As in the Forestburg therian upper premolar, all viverravines, and some miacines, there is a large parastyle—presumably a primitive feature on P^4 . If the carnassial notch of the miacid P^4 lies between paracone and metacone, then possibly it was derived from an ancestor with a P^4 like that of *Cimolestes* by the forward shift of the protocone and the union of metacone and metastyle into the typical miacid bladelike crest. Incidentally, in the Djadochta genus *Deltatheridium*, P^4 has neither protocone nor metacone, and P_4 lacks a paraconid.

If, on the other hand, a molarized lower P_4 is primitive, *Cimolestes*, *Deltatheridium*, and their allies would represent specialized derivatives from the condition seen in *Procerberus*, and the primitive creodonts, together with *P. (Simpsonictis) tenuis*, would illustrate secondarily simplified premolars. *Procerberus* is about the size of *P. (S.) tenuis*, hence somewhat smaller than *Cimolestes*. The upper molars in *Procerberus* have a more separate paracone and metacone than those of *Cimolestes* and more distinct lingual cingula, but a narrower stylar shelf than those of either *Cimolestes* or the Paleocene miacids. The molar cusps are generally lower in *Procerberus*

than in these miacids or *Cimolestes*. The stylocone is not visible, and the stylocone-paracone crest is short and not prominent.

The evidence from the Forestburg therians shows plainly that a prominent stylocone, a broad stylar shelf, and a nearly equilaterally triangular crown outline are primitive among therian molars. *Procerberus* has the most nearly equilateral crown shape, followed by *Deltatheridium* and *Cimolestes* with more transverse molars, but also with broader stylar shelves and more distinct stylocones.

The paracone and metacone of the Forestburg therians are fully separate, as they are in *Procerberus* and most miacids except *Ictidopappus*, so that a connate paracone-metacone (also in *Cimolestes* and *Deltatheridium*) is evidently a specialization associated with accentuation of the shearing function of molars. Emphasis of the grinding function, as seen in most miacid molars (and in molars of other groups such as the condylarths), would be likely to lead to a loss of the interdental embrasures as the molars became relatively longer and narrower. Undeniably, either pattern can evolve from the other.

The evidence of the fourth lower premolars can be interpreted either as an increase of molarization or as a simplification in the various groups of small predators, and, in my opinion, we do not know what sort of premolar pattern is really primitive. The older view that a simple P_4 is primitive for therians in general can be maintained subject to revision with discovery of new evidence (which may not be far off). On this basis, if the miacids had an ancestor among the known Lance mammals, *Cimolestes* seems somewhat more likely than *Procerberus*. The transverse shape of *Cimolestes* upper molars and the absence of a stylocone and the narrower stylar shelf on the upper molars in *Procerberus* are, however, peculiar features that one would not expect to find in a miacid ancestor.

Moreover, if one of these or any other American Lance mammal was really ancestral to the miacids, it surely would have been ancestral to the Miacinae, which then (presumably during the early Paleocene) would have given rise to the Viverravinae. It would then be reasonable to expect a record of the Miacinae somewhere in the Paleocene of North America.

¹ The problem of molar-premolar cusp names is discussed above under *Protictis (Bryanictis) vanvaleni*. It is worth repeating that the application of molar-cusp names to the cusps of premolars does not carry the implication that the history of molar cusps can be deduced from the patterns of molarization seen in premolars.

There is no such record.

No one has suggested that the known miacines of the earliest Eocene were derived from the Viverravinae. Such derivation is improbable on morphological grounds and not solely because of the absence of M_3^3 from the viverravines. Examples of the reacquisition of a lost tooth or even of the symmetrical addition of new teeth are not unknown. For example, the peculiar genus *Otocyon* has added M_4^3 to the usual canid dental formula, and Kurtén (1963) has shown that M_2 is present in about 10 per cent of Recent *Felis lynx* from northern Europe. But there is nothing about the dentition of the oldest known miacines (*Miacis* and *Uintacyon* are certainly, and *Vassacyon* and *Vulpavus* are probably,

present in the beginning of the Eocene) to suggest that they had lost and then regained M_3^3 .

If a particular fossil group is proposed as a possible common ancestor of the Miacidae, it must antedate the Dragon local fauna (and probably the Puercan also). It must be found in a place that permits explanation of the unheralded appearance of the Miacinae at the very beginning of the Eocene (in Europe and North America) as well as the presence of the Viverravinae in North America during the Paleocene.

In short, a putative miacid ancestor must be not only morphologically possible but also stratigraphically and geographically plausible.

We have not got it yet.

SUMMARY

VIVERRAVINE MIACIDS have been found in all the larger collections of fossil mammals from the middle and late Paleocene rocks of North America. These oldest known fissipede carnivores are described in detail, the classification is revised, and notes on their probable ecology and known geographic and stratigraphic distribution are included. A list of characters believed primitive for miacids is presented, together with some discussion of possible miacid ancestry.

Two genera, *Ictidopappus* Simpson, 1935, and *Protictis* Matthew, 1937, are recognized, the latter being raised in rank and including *P. (Protictis)* Matthew, 1937, *P. (Simpsonictis)* Mac Intyre, 1962, and a new subgenus, *P. (Bryanictis)*, which unites *P. (B.) microlestes* (Simpson, 1935) and a new species, *P. (B.) vanvaleni*. The removal of *Protictis* from *Didymictis* is discussed; both the Eocene viverravine genera (*Viverravus* and *Didymictis*) were derived from *Protictis*.

Several probably new (but unnamed) Pa-

leocene Viverravinae are also described, including a single tooth from the Puerco beds of New Mexico which may represent the oldest known miacid. This specimen (called Puerco-Z informally) is tentatively referred to *Ictidopappus*. If this assignment is correct, *Ictidopappus* ranged from northern New Mexico (about latitude 36° N.) to southern Montana (about latitude 46° N.) and from early to middle Paleocene time. The middle Paleocene *Protictis* (*Protictis*) and *P. (Bryanictis)* have been found over the same range, and *P. (Simpsonictis)* occurs from southern Montana to central Wyoming.

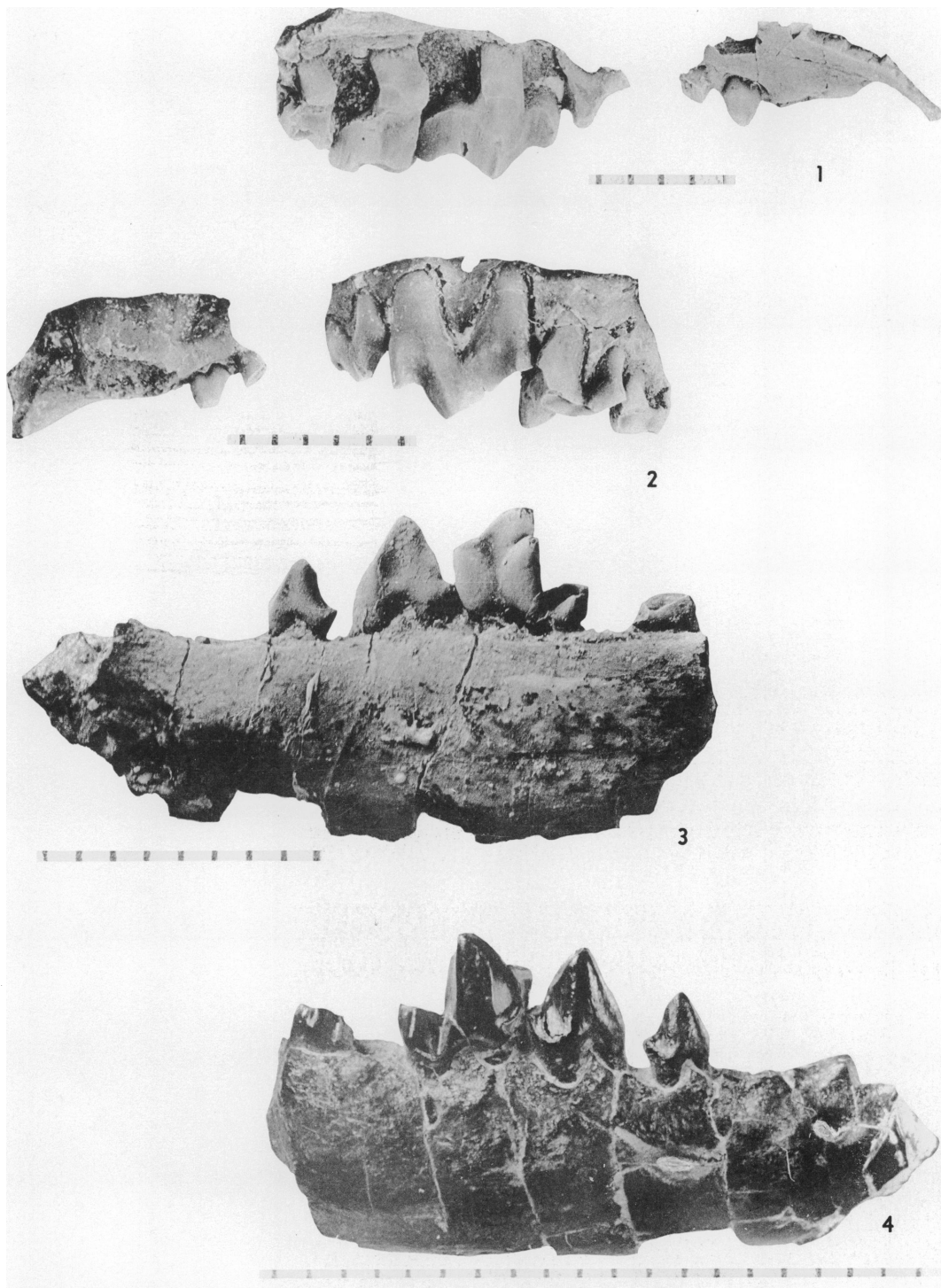
The possible miacid relationships to the earliest creodonts and leptictid insectivores recently collected in the late Cretaceous of North America are considered, but, as it is impossible to derive the known Miacinae from any known Paleocene Viverravinae, derivation of the Miacidae from any known American Cretaceous genus is rejected.

REFERENCES

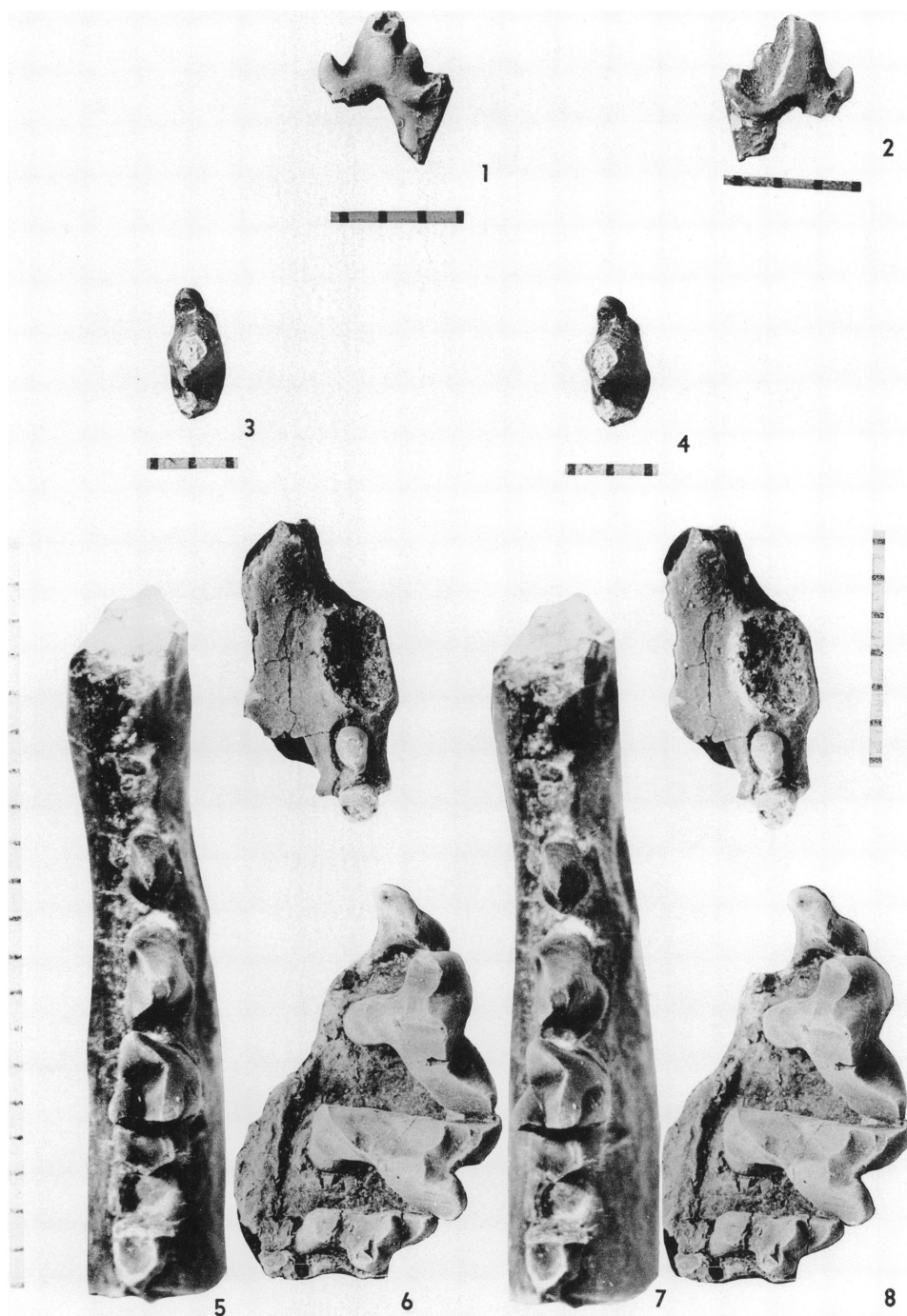
- BUTLER, PERCY M.
1956. The ontogeny of molar pattern. *Biol. Rev., Cambridge Phil. Soc.*, vol. 31, pp. 30-70, figs. 1-12.
- CLEMENS, WILLIAM, MALCOLM C. MCKENNA, DONALD E. RUSSELL, ROBERT E. SLOAN, AND LEIGH VAN VALEN
1964. Cimolestidae Marsh, 1889 (Mammalia): Proposed suppression under the plenary powers. *Z.N.(S.)* 1630. *Bull. Zool. Nomenclature*, vol. 21, pt. 5, p. 363.
- COPE, EDWARD DRINKER
1875. On the supposed Carnivora of the Eocene of the Rocky Mountains. *Proc. Acad. Nat. Sci. Philadelphia*, vol. 27, pp. 444-448; also issued as *Paleont. Bull.* (1875), no. 20, pp. 1-4.
1882. Synopsis of the Vertebrata of the Puerco Eocene epoch. *Proc. Amer. Phil. Soc.*, vol. 20, pp. 461-471; also issued as *Paleont. Bull.* (1882), no. 35, pp. 461-471.
1884a. The Vertebrata of the Tertiary formations of the west. Book I. Rept. U. S. Geol. Surv. Terr. (F. V. Hayden, geol. in charge), vol. 3, pp. i-xxxv, 1-1009, pls. 1-75.
1884b. Second addition to the knowledge of the Puerco epoch. *Proc. Amer. Phil. Soc.*, vol. 21 (1883), pp. 309-324; also issued as *Paleont. Bull.* (1884), no. 37, pp. 309-324.
- CRUSAFONT-PAIRÓ, M., AND J. TRUYOLS-SANTONJA
1956. A biometric study of the evolution of fissipede carnivores. (Translated by George Gaylord Simpson.) *Evolution*, vol. 10, pp. 314-332, figs. 1-14.
- DORR, JOHN A.
1952. Early Cenozoic stratigraphy and vertebrate paleontology of the Hoback basin, Wyoming. *Bull. Geol. Soc. Amer.*, vol. 63, pp. 59-94, figs. 1-7, pls. 1-7.
- ELLENBERGER, W., AND H. BAUM
1891. *Anatomie des Hundes*. Berlin, Paul Parey, pp. i-xxiv, 1-646, figs. 1-208, pls. 1-37.
- GAZIN, C. LEWIS
1939. A further contribution to the Dragon Paleocene fauna of central Utah. *Jour. Washington Acad. Sci.*, vol. 29, pp. 273-286, figs. 1-10.
1941. The mammalian faunas of the Paleocene of central Utah, with notes on the geology. *Proc. U. S. Natl. Mus.*, vol. 91, no. 3121, pp. 1-53, figs. 1-29, pls. 1-2.
1956. Paleocene mammalian faunas of the Bison basin in south-central Wyoming. *Smithsonian Misc. Coll.*, vol. 131, no. 6, pp. i-iv, 1-57, figs. 1-2, pls. 1-16.
1961. Occurrences of Paleocene Mammalia in Tertiary basins of Wyoming. *Wyoming Geol. Assoc. Guidebook*, 16th Ann. Field Conf., Green River, Washakie, Wind River, and Powder River Basins, pp. 47-52, fig. 1.
- GRANGER, WALTER
1917. Notes on Paleocene and lower Eocene mammal horizons of northern New Mexico and southern Colorado. *Bull. Amer. Mus. Nat. Hist.*, vol. 37, pp. 821-830, fig. 1, pls. 97-98.
- GREGORY, WILLIAM KING, AND MILO HELLMAN
1939. On the evolution and major classification of the civets (Viverridae) and allied fossil and recent Carnivora: a phylogenetic study of the skull and dentition. *Proc. Amer. Phil. Soc.*, vol. 81, pp. 309-392, figs. 1-33, pls. 1-6.
- HALL, E. RAYMOND
1951. American weasels. *Univ. Kansas Publ., Mus. Nat. Hist.*, vol. 4, pp. 1-466, figs. 1-31, pls. 1-41.
- HAY, OLIVER PERRY
1902. Bibliography and catalogue of the fossil Vertebrata of North America. *Bull. U. S. Geol. Surv.*, no. 179, pp. 1-868.
1929-1930. Second bibliography and catalogue of the fossil Vertebrata of North America. *Carnegie Inst. Washington Publ.*, no. 390, vol. 1 (1929), pp. i-viii, 1-916; vol. 2 (1930), pp. i-xiv, 1-1074.
- JEPSEN, GLENN LOWELL
1940. Paleocene faunas of the Polecat Bench formation, Park County, Wyoming. Pt. 1. *Proc. Amer. Phil. Soc.*, vol. 83, pp. 217-341, figs. 1-22, pls. 1-5.
- KEEFER, WILLIAM R.
1961. Waltman Shale and Shotgun members of Fort Union formation (Paleocene) in Wind River basin, Wyoming. *Bull. Amer. Assoc. Petrol. Geol.*, vol. 45, pp. 1310-1323, figs. 1-5.
- KEEFER, WILLIAM R., AND MAX L. TROYER
1956. Stratigraphy of the upper Cretaceous and lower Tertiary rocks of the Shotgun Butte area, Fremont County, Wyoming. Washington, D. C., United States Geological Survey, chart OC-56.
1964. Geology of the Shotgun Butte area, Fremont County, Wyoming. *Bull. U. S.*

- Geol. Surv., no. 1157, pp. i-v, 1-123, figs. 1-16, pls. 1-3.
- KURTÉN, BJÖRN
1963. Return of a lost structure in the evolution of the felid dentition. Soc. Sci. Fennica, Commentationes Biol., vol. 26, no. 4, pp. 1-12, figs. 1-2.
- LOVE, J. D., PAUL O. MCGREW, AND H. D. THOMAS
1963. Relationship of latest Cretaceous and Tertiary deposition and deformation to oil and gas in Wyoming. Mem. Amer. Assoc. Petrol. Geol., Tulsa, no. 2, pp. 196-208, figs. 1-9.
- MCGREW, PAUL O., AND BRYAN PATTERSON
1962. A picrodontid insectivore (?) from the Paleocene of Wyoming. Breviora, Mus. Comp. Zool., no. 175, pp. 1-9, figs. 1-2.
- MAC INTYRE, GILES T.
1962. *Simpsonictis*, a new genus of viverravine miacid (Mammalia, Carnivora). Amer. Mus. Novitates, no. 2118, pp. 1-4, figs. 1-3.
- MCKENNA, MALCOM C.
1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. California Publ. Geol. Sci., vol. 37, no. 1, pp. 1-130, figs. 1-64.
- MATTHEW, WILLIAM DILLER
1897. A revision of the Puerco fauna. Bull. Amer. Mus. Nat. Hist., vol. 9, pp. 259-323, figs. 1-20.
1899. A provisional classification of the freshwater Tertiary of the west. *Ibid.*, vol. 12, pp. 19-77.
1901. Additional observations on the Creodonta. *Ibid.*, vol. 14, pp. 1-38, figs. 1-17.
1909. The Carnivora and Insectivora of the Bridger basin, middle Eocene. Mem. Amer. Mus. Nat. Hist., vol. 9, pt. 6, pp. 289-567, figs. 1-118, pls. 42-52.
1915. A revision of the lower Eocene Wasatch and Wind River faunas. Part I.—Order Ferae (Carnivora), suborder Creodonta; Part II.—Order Condylarthra, family Hyopsodontidae. Bull. Amer. Mus. Nat. Hist., vol. 34, pp. 4-103, figs. 1-87; pp. 311-328, figs. 1-10.
1929. Creodonta. In The Encyclopaedia Britannica. Fourteenth edition. London, Encyclopaedia Britannica Co., Ltd., vol. 6, pp. 667-668.
1937. Paleocene faunas of the San Juan basin, New Mexico. Trans. Amer. Phil. Soc., new ser., vol. 30, pp. i-viii, 1-510, figs. 1-85, pls. 1-65.
- PATTERSON, BRYAN
1951. Early Cretaceous mammals from northern Texas. Amer. Jour. Sci., vol. 249, pp. 31-46, figs. 1-3.
1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. Fieldiana: Geol., vol. 13, pp. 1-105, figs. 1-17.
- PATTERSON, BRYAN, AND PAUL O. MCGREW
1962. A new arctocyonid from the Paleocene of Wyoming. Breviora, Mus. Comp. Zool., no. 174, pp. 1-10, figs. 1-3.
- RUSSELL, LORIS S.
1954. Evidence of tooth structure on the relationships of the early groups of Carnivora. Evolution, vol. 8, pp. 166-171, figs. 1-7.
- SCHLOSSER, MAX
1886. Über das Verhältnis der Cope'schen Creodonta zu den übrigen Fleischfressern. Morph. Jahrb., vol. 12, pp. 287-298.
- SCOTT, WILLIAM BERRYMAN
1892. The evolution of the premolar teeth in the Mammalia. Proc. Acad. Nat. Sci. Philadelphia, vol. 44, pp. 405-444, figs. 1-8.
- SIMPSON, GEORGE GAYLORD
1931. A new classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 59, pp. 259-293.
1935. New Paleocene mammals from the Fort Union of Montana. Proc. U. S. Natl. Mus., vol. 83, pp. 221-244.
1937a. The Fort Union of the Crazy Mountain field, Montana, and its mammalian faunas. Bull. U. S. Natl. Mus., no. 169, pp. i-x, 1-287, figs. 1-80, pls. 1-10.
1937b. Notes on the Clark Fork, upper Paleocene, fauna. Amer. Mus. Novitates, no. 954, pp. 1-24, figs. 1-6.
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i-xvi, 1-350.
1948. The Eocene of the San Juan basin, New Mexico. Amer. Jour. Sci., vol. 246, pp. 257-282, 363-385, figs. 1-4.
1950. Cenozoic formations and vertebrate faunas. In Colbert, Edwin H., and others, Guidebook for the fourth field conference of the Society of Vertebrate Paleontology in northwestern New Mexico. [New York], the American Museum of Natural History and the University of New Mexico, pp. 74-85.
1959. Fossil mammals from the type area of

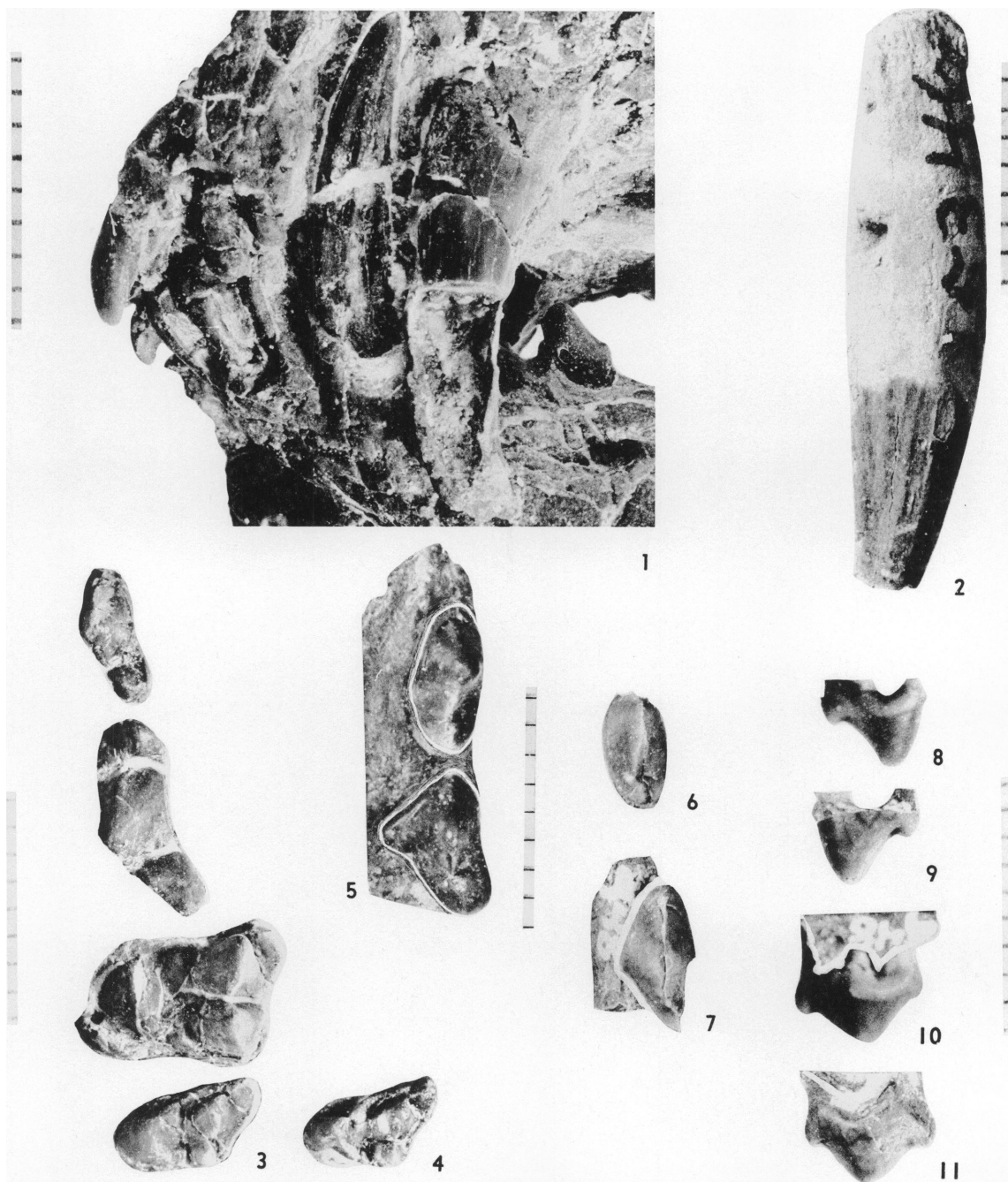
- the Puerco and Nacimiento strata, Paleocene of New Mexico. *Amer. Mus. Novitates*, no. 1957, pp. 1-22, figs. 1-6.
1961. *Principles of animal taxonomy*. New York, Columbia University Press, pp. i-xii, 1-247, figs. 1-30.
- SIMPSON, GEORGE GAYLORD, ANNE ROE, AND RICHARD C. LEWONTIN
1960. *Quantitative zoology*. Revised edition. New York, Harcourt, Brace and Co., pp. i-vii, 1-440, figs. 1-64.
- SINCLAIR, WILLIAM JOHN, AND WALTER GRANGER
1914. Paleocene deposits of the San Juan basin, New Mexico. *Bull. Amer. Mus. Nat. Hist.*, vol. 33, pp. 297-316, figs. 1-2, pls. 20-27.
- SLOAN, ROBERT E.
1964. Paleocology of the Cretaceous-Tertiary transition in Montana. *Science*, vol. 146, no. 3642, p. 430.
- SLOAN, ROBERT E., AND LEIGH VAN VALEN
1965. Cretaceous mammals from Montana. *Science*, vol. 148, no. 3667, pp. 220-227, figs. 1-6.
- STUCKER, GILBERT F.
1961. Salvaging fossils by jet. *Curator*, vol. 4, pp. 332-340, figs. 1-6.
- TEILHARD DE CHARDIN, PIERRE
1915. Les carnassiers des Phosphorites du Quercy. *Ann. Paléont. Paris*, vol. 9 (1914-1915), pp. 103-192, figs. 1-13, pls. 12-20.
- TROYER, MAX L., AND WILLIAM R. KEEFER
1955. *Geology of the Shotgun Butte area, Fremont County, Wyoming*. Washington, D. C., United States Geological Survey, map OM 172.
- WILSON, ROBERT W.
1951. Preliminary survey of a Paleocene faunule from the Angels peak area, New Mexico. *Univ. Kansas Publ., Mus. Nat. Hist.*, vol. 5, pp. 1-11, 1 fig.
1956. A new multituberculate from the Paleocene Torrejon fauna of New Mexico. *Trans. Kansas Acad. Sci.*, vol. 59, pp. 76-84, fig. 1.
- WOOD, HORACE ELMER, 2ND, RALPH W. CHANEY, JOHN CLARK, EDWIN H. COLBERT, GLENN L. JEPSEN, JOHN B. REESIDE, JR., AND CHESTER STOCK
1941. Nomenclature and correlation of the North American continental Tertiary. *Bull. Geol. Soc. Amer.*, vol. 52, pp. 1-48, pl. 1.
- WORTMAN, JACOB LAWSON
1901. Studies of Eocene Mammalia in the Marsh collection, Peabody Museum. *Amer. Jour. Sci.*, ser. 4, vol. 11, pp. 333-348, figs. 1-6, pl. 5, pp. 437-450, figs. 7-17, pl. 6; vol. 12, pp. 143-154, figs. 18-30, pp. 193-206, figs. 31-43, pp. 281-296, fig. 44, pls. 1-4, pp. 377-382, figs. 45-48, pp. 421-432, figs. 49-60, pls. 8-9.
- WORTMAN, JACOB LAWSON, AND WILLIAM DILLER MATTHEW
1899. The ancestry of certain members of the Canidae, the Viverridae, and Procyonidae. *Bull. Amer. Mus. Nat. Hist.*, vol. 12, pp. 109-139, figs. 1-10, pl. 6.



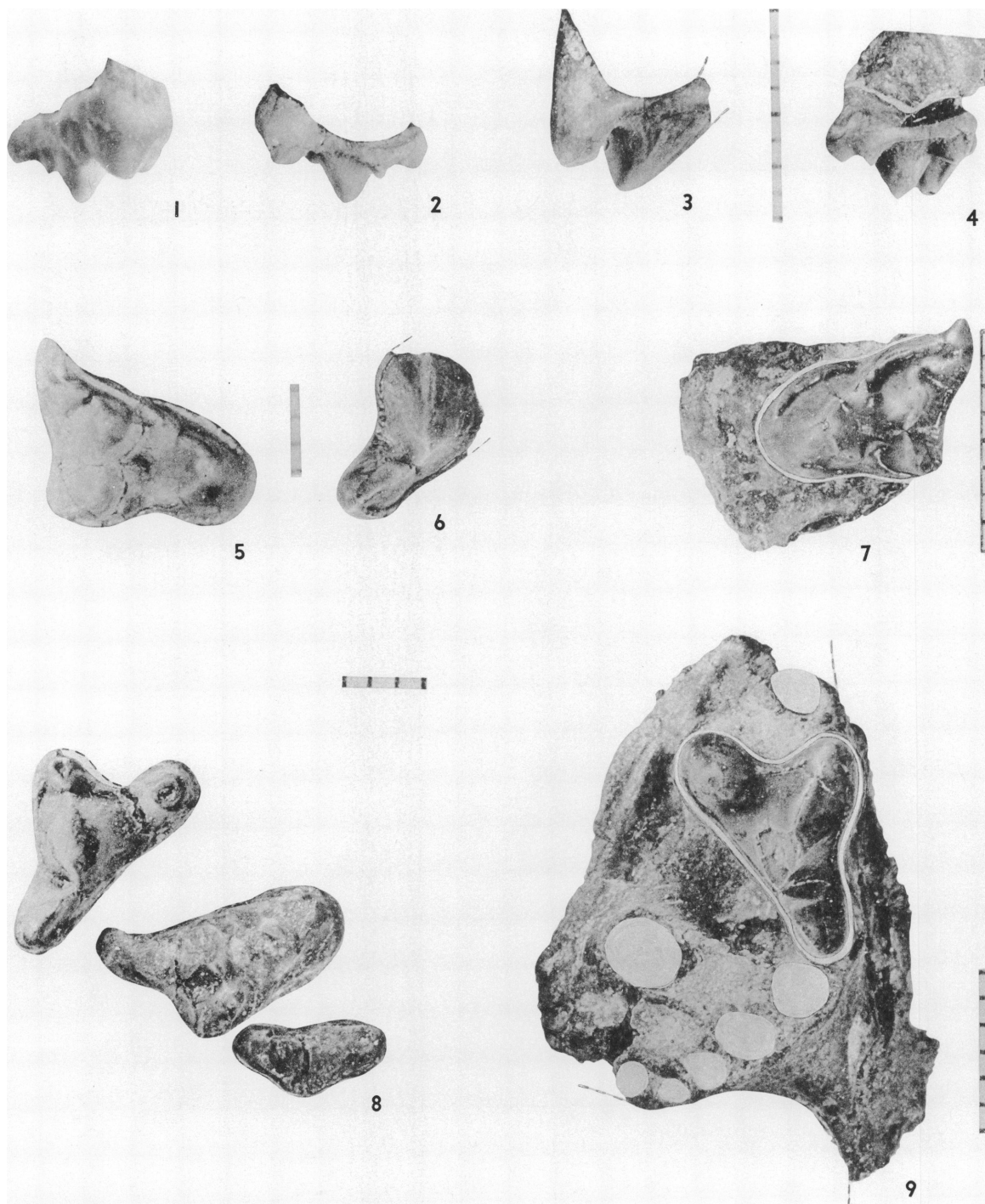
Ichidopappus mustelinus. 1, 2. U.S.N.M. No. 9295, two fragments of left maxilla, with P¹, anterior root of P², and crowns of P³-M². 3, 4. U.S.N.M. No. 9296 (type), right dentary, with P₃-M₂. 1, 3. Lingual aspects. 2, 4. Labial aspects. About $\times 5$



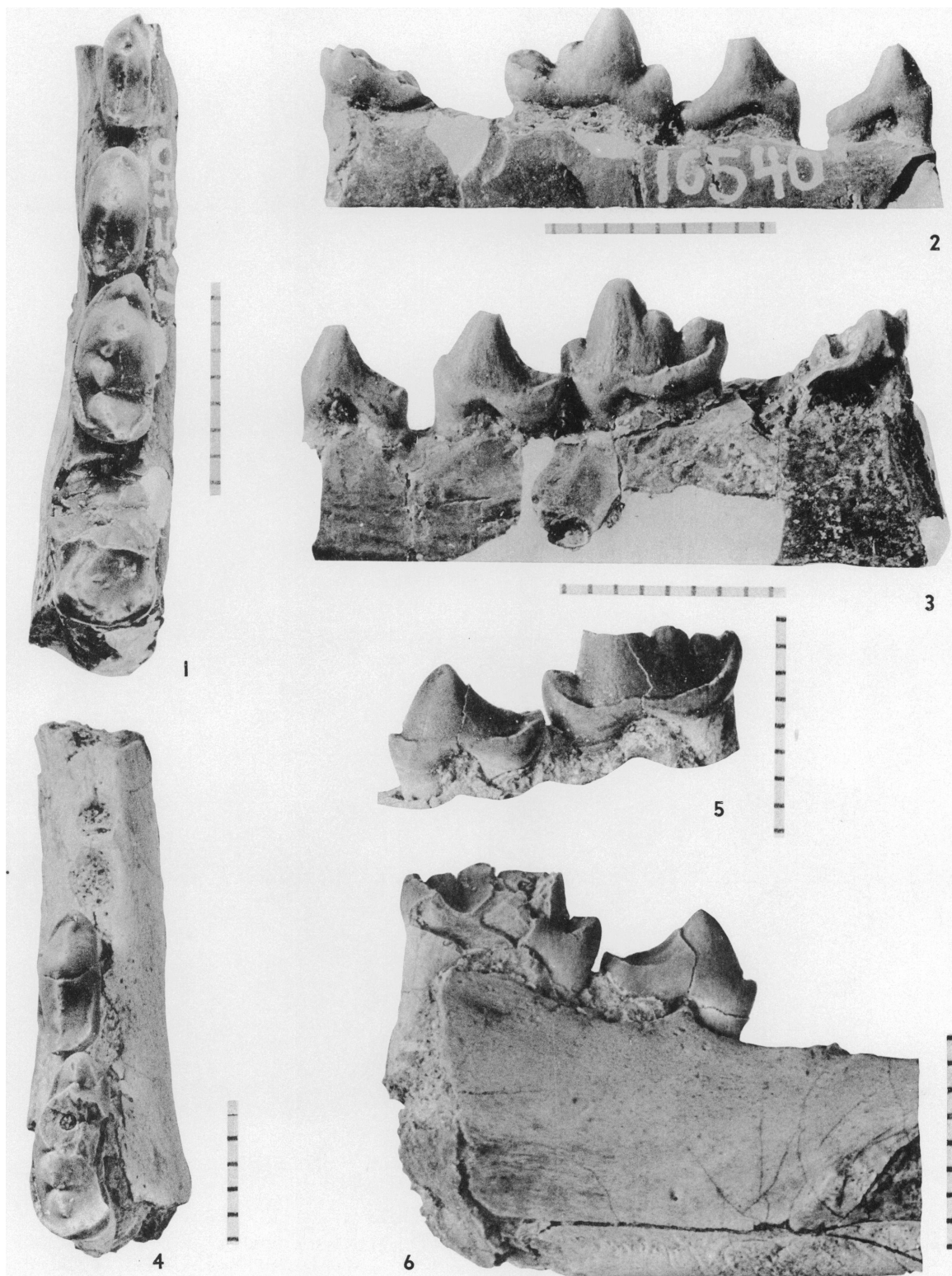
1-4. ?Cf. *Ictidopappus* (Puerco-Z). A.M.N.H. No. 58409, isolated right lower premolar. 5-8. *Ictidopappus mustelinus*. 5, 7. U.S.N.M. No. 9296 (type). 6, 8. U.S.N.M. No. 9295. 1. Lingual aspect. 2. Labial aspect. 3-8. Stereoscopic occlusal aspects. About $\times 5$



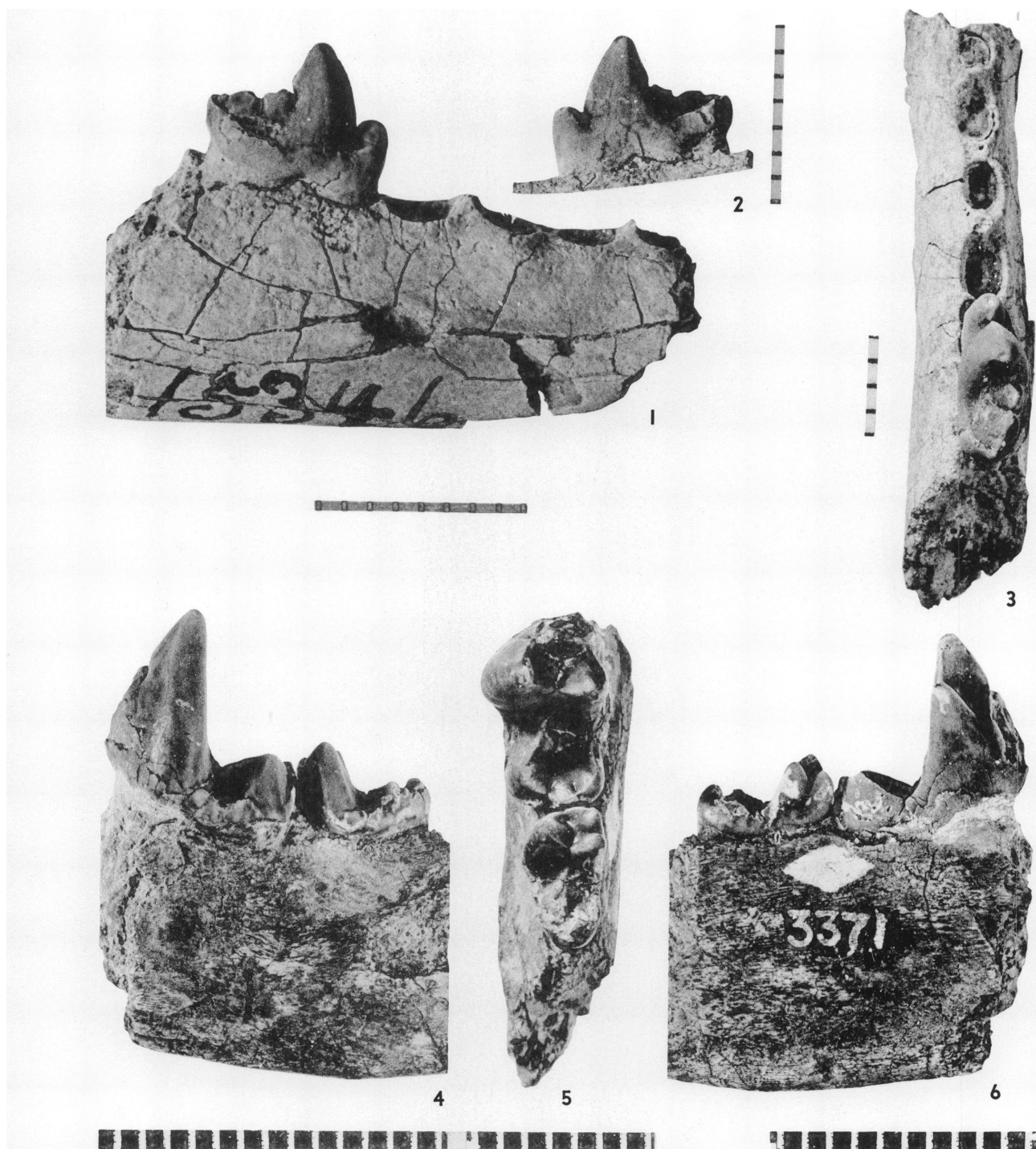
Protictis (Protictis) haydenianus. 1. A.M.N.H. No. 3374, left I^1-C^1 and I^1-P^1 in occlusion. 2. U.S.-N.M. No. 15346, right C^1 . 3. A.M.N.H. No. 3374, left P^3-M^2 . The outlines of P^3-M^1 show typically distorted outlines caused by partial concealment in matrix and by damage. Compare with 5 on this plate and with 7 and 9 on plate 4. See text for discussion of M^2 . 4. U.Cal.M.P. No. 51682 (Dragon Canyon), left M^2 . 5. A.M.N.H. No. 35862 (Gidley quarry), left P^2-3 . 6-11. A.M.N.H. No. 948. The occlusal outlines in 6 and 7 are slightly distorted by damage to the anterior end of P^2 and to the posterolabial edge of P^3 ; the lingual sides are complete. 6, 8, 9. Left P^2 . 7, 10, 11. Left P^3 . 1, 2, 9, 11. Labial aspects. 3-7. Occlusal aspects. 8, 10. Lingual aspects. 1. About $\times 4.9$. 2. About $\times 4.3$. 3, 4, 8-11. About $\times 4$. 5-7. About $\times 4.2$.



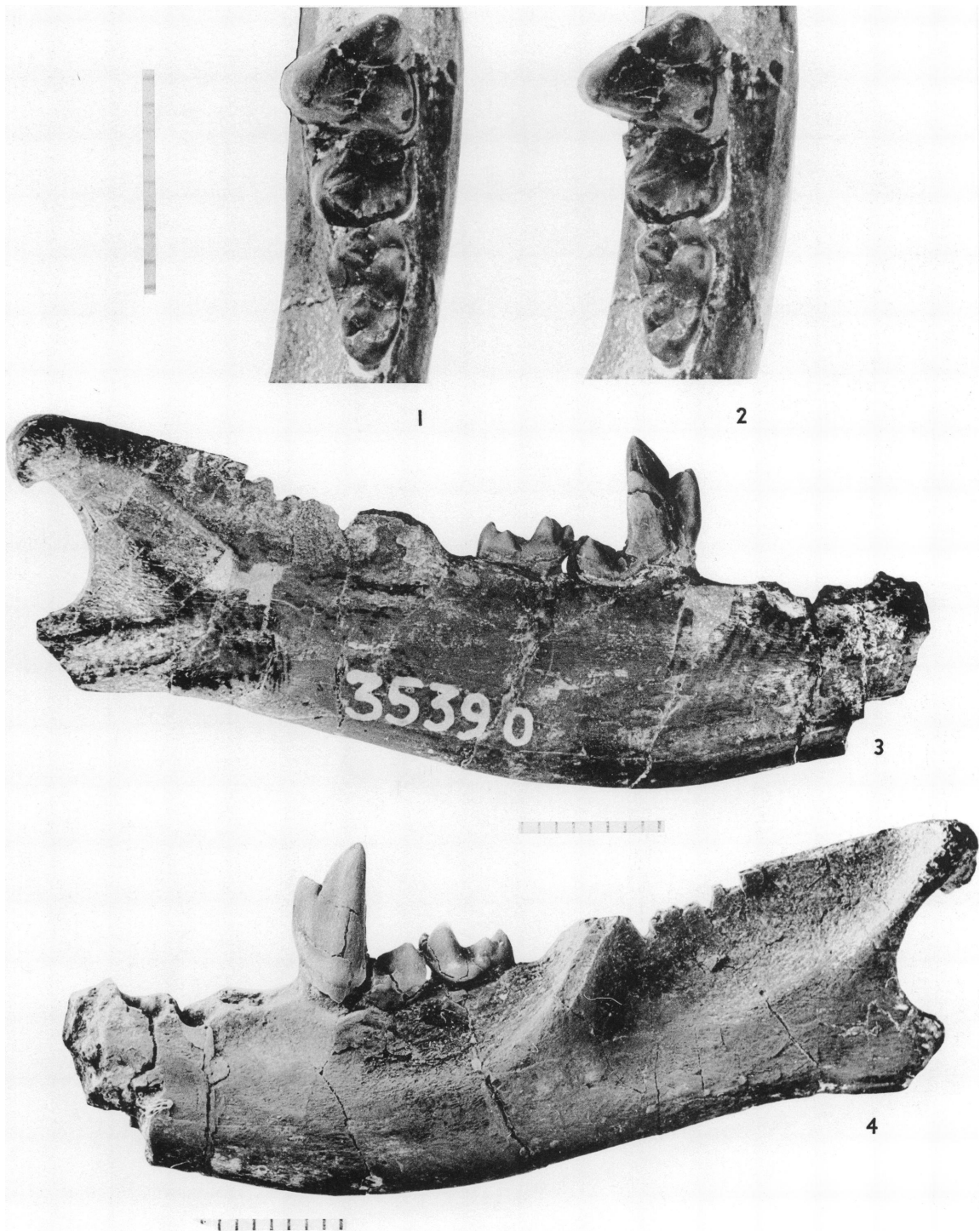
Protictis (Protictis) haydenianus. 1-7. A.M.N.H. No. 948. 1, 2, 5. Right M^1 . 3, 6. Right P^4 fragment. 4, 7. Left M^1 . 8. A.M.N.H. No. 17059, right P^4-M^2 . The unnatural relationship of P^4 to M^1 is the result of a postmortem shift within the nodule containing this specimen; the relationships of M^1-2 are relatively undisturbed, but the cusps of both are damaged. (1-8 all from Bohannon Canyon.) 9. U.S.N.M. No. 6145 (Silberling quarry), left P^4 and alveoli of M^1-2 , showing normal relationships. 1. Lingual aspect. 2-4. Labial aspects. 5-9. Occlusal aspects. About $\times 4$



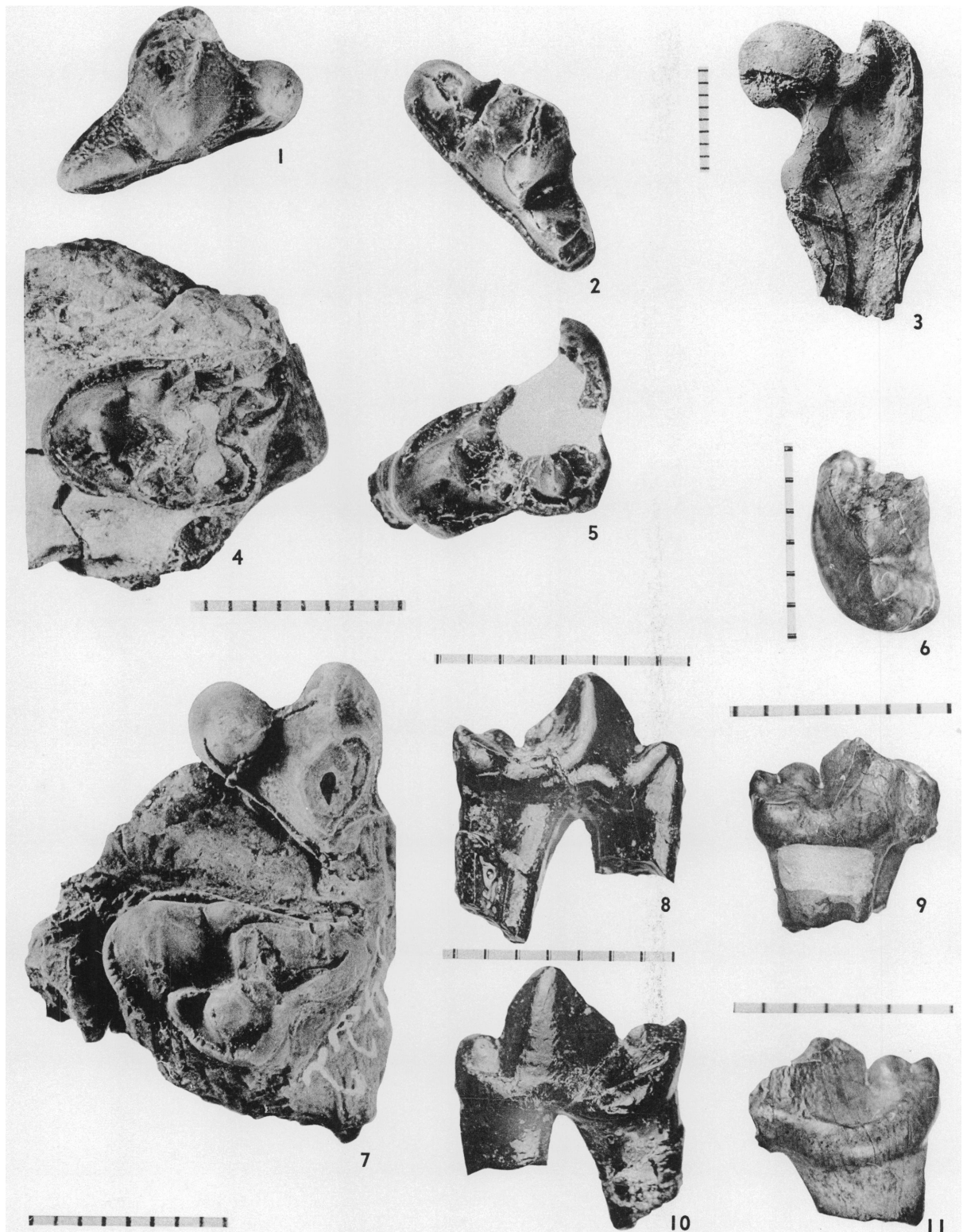
Protictis (Protictis) haydenianus. 1-3. A.M.N.H. No. 16540, left dentary, with P_{2-4} and M_1 talonid. 4-6. U.S.N.M. No. 15354, left dentary with P_{3-4} . 1, 4. Occlusal aspects. 2, 6. Lingual aspects. 3, 5. Labial aspects. About $\times 4$



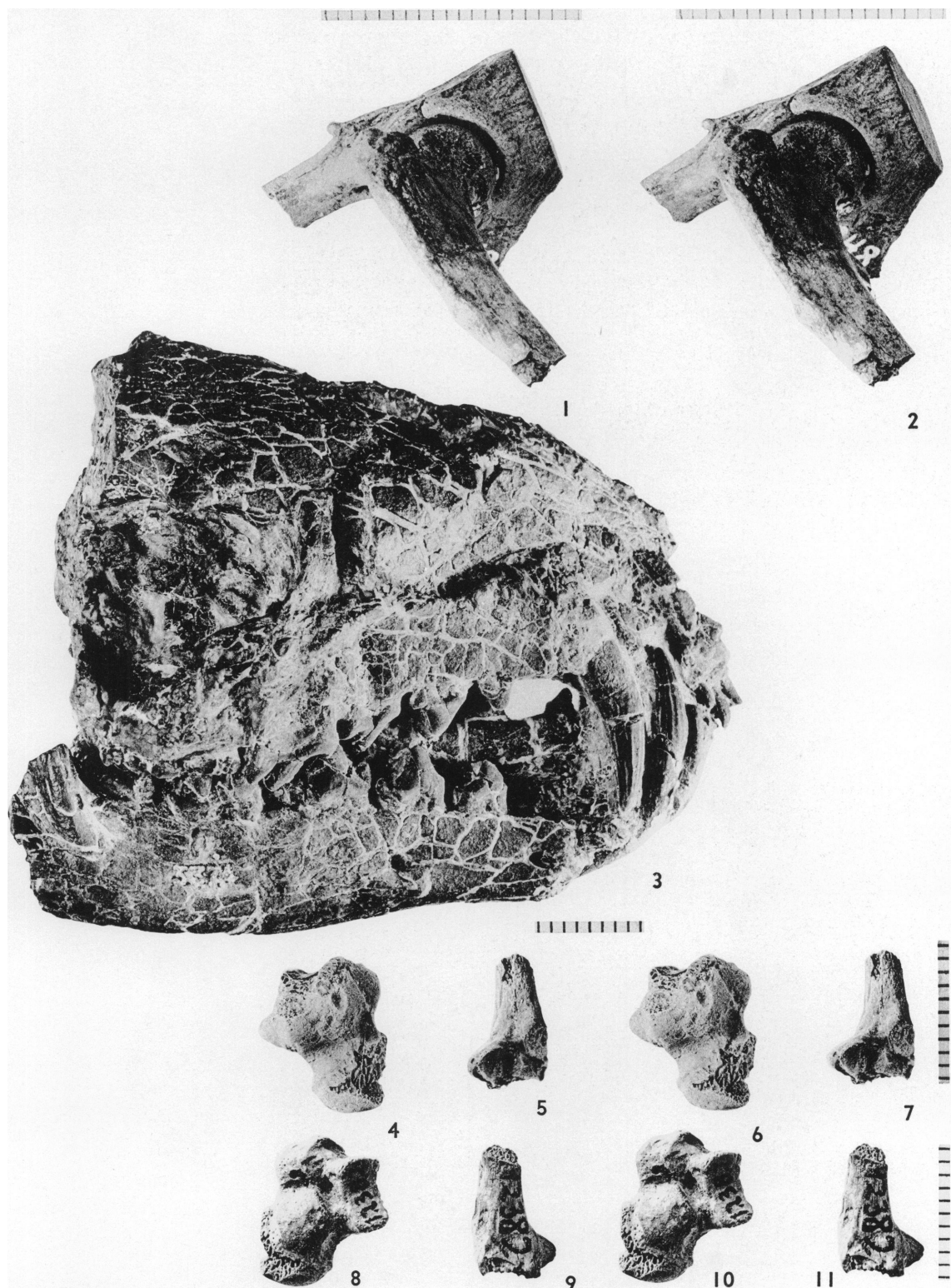
Protictis (Protictis) haydenianus. 1-3. U.S.N.M. No. 15346, right dentary, with P₄. 4-6. A.M.N.H. No. 3371 (type of "*Didymictus primus*" Cope), left dentary, with M₁₋₂, M₁ paraconid broken off. 1, 4. Labial aspects. 2, 6. Lingual aspects. 3, 5. Occlusal aspects. About $\times 4$



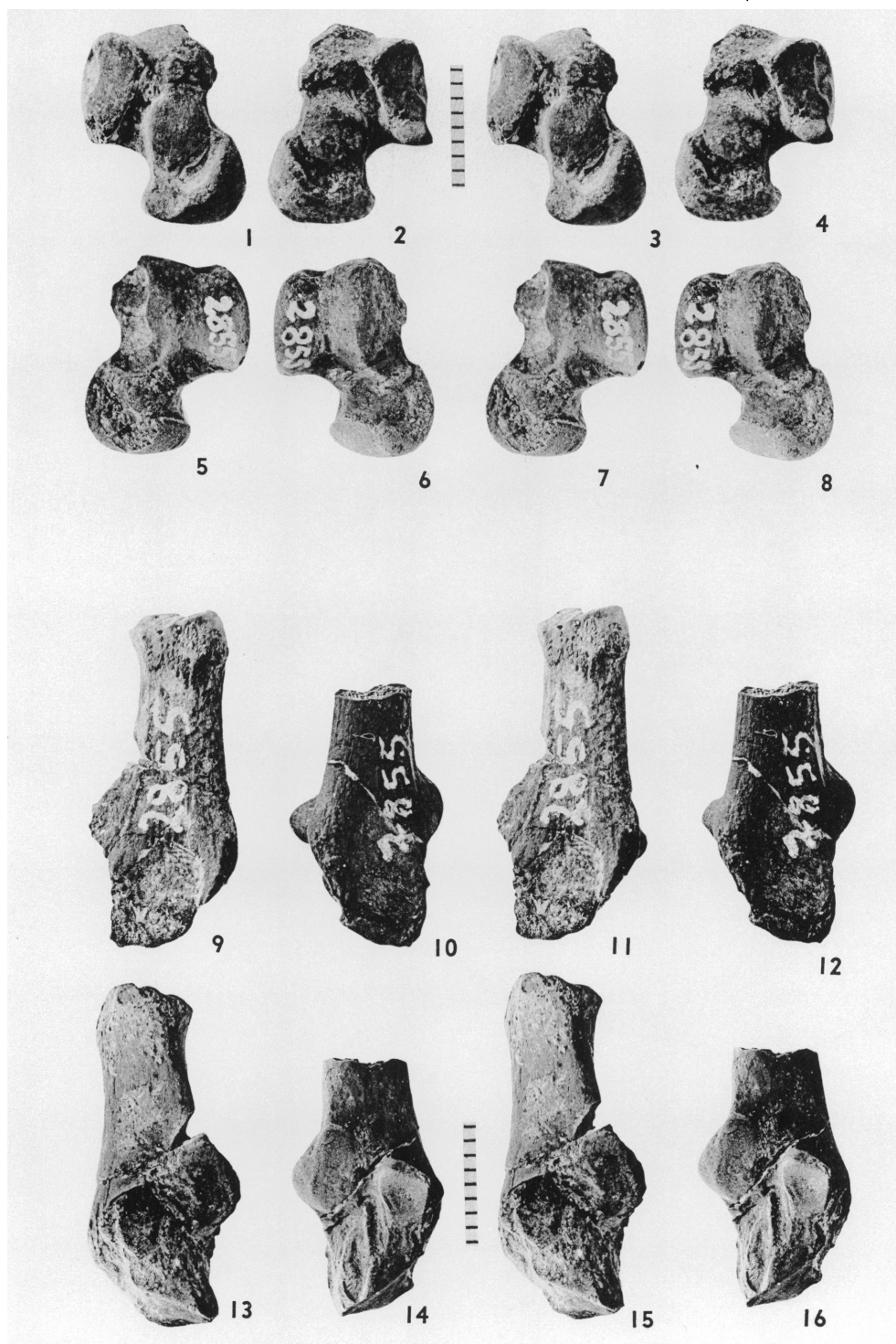
Protictis (*Protictis*) *haydenianus*. A.M.N.H. No. 35390 (Gidley quarry), left dentary, with M_{1-2} . This is the only known specimen of the subgenus with the articular and angular processes preserved. Part of the angle has been broken off. 1, 2. Stereoscopic occlusal aspect. 3. Lingual aspect. 4. Labial aspect. 1, 2. $\times 4$. 3, 4. $\times 2.7$



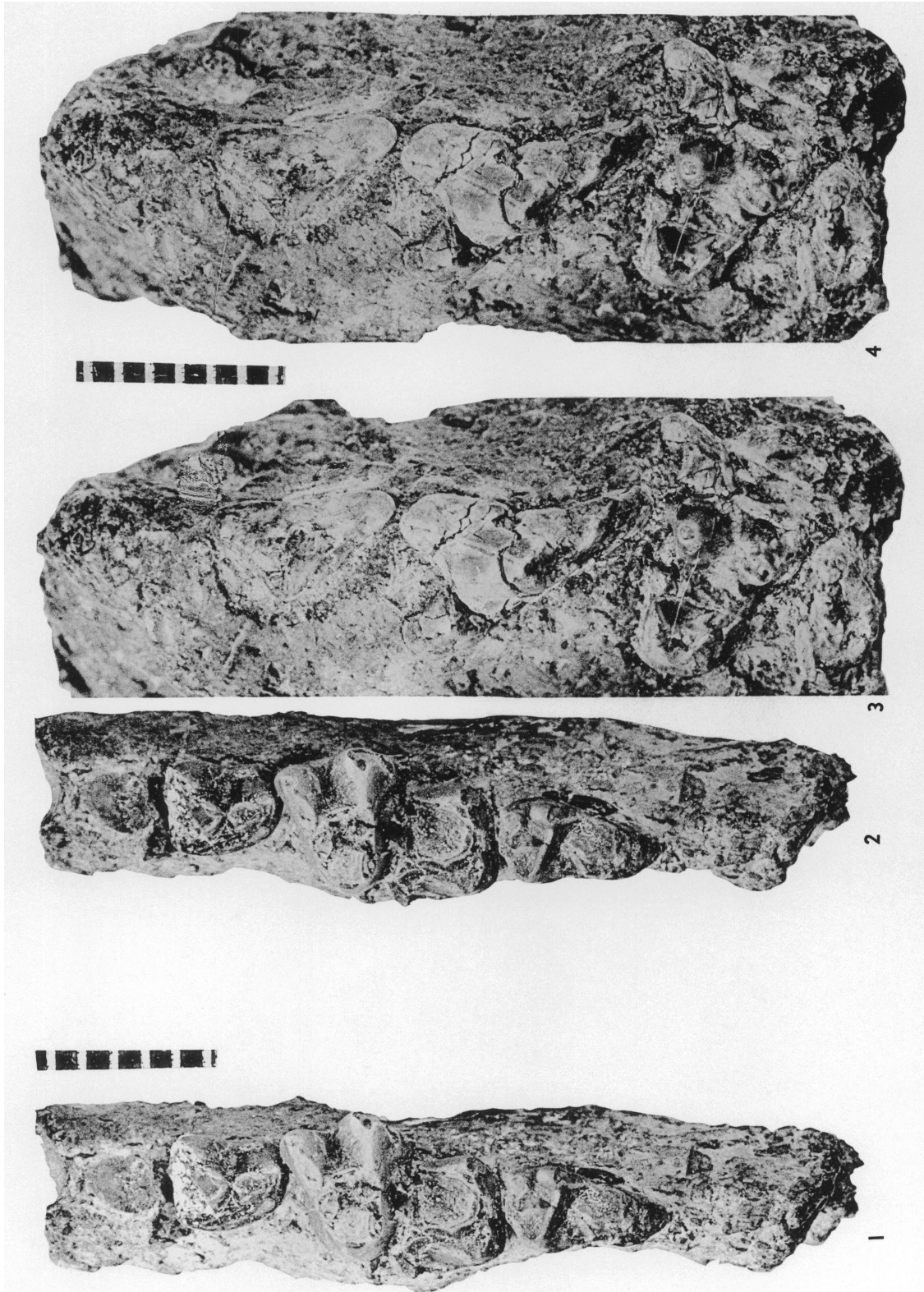
1, 4, 6, 7, 9, 11. *Protictis (Protictis)* sp. 1, 4. U.S.N.M. No. 6143 (locality ?50, Lebo Formation), P⁴-M¹. 6, 9, 11. U.S.N.M. No. 9930 (locality 51, Lebo Formation), talonid fragment of left P₄. 7. A.M.N.H. No. 35422 (locality 81, Lebo Formation), left P⁴-M¹. 2, 3, 5, 8, 10. *Protictis (Protictis) haydenianus*. 2, 5. U.Cal.M.P. No. 47252 (Dragon Canyon), P⁴-M¹. 3. A.M.N.H. No. 948, proximal end of femur. 8, 10. A.M.N.H. No. 35391 (Gidley quarry), left P₄. 1, 2, 4-7. Occlusal aspects. 3. Posterior aspect. 8, 9. Lingual aspects. 10, 11. Labial aspects. 1, 2, 4, 5, 7. About $\times 4$. 3. $\times 2$. 6, 8-11. About $\times 5$



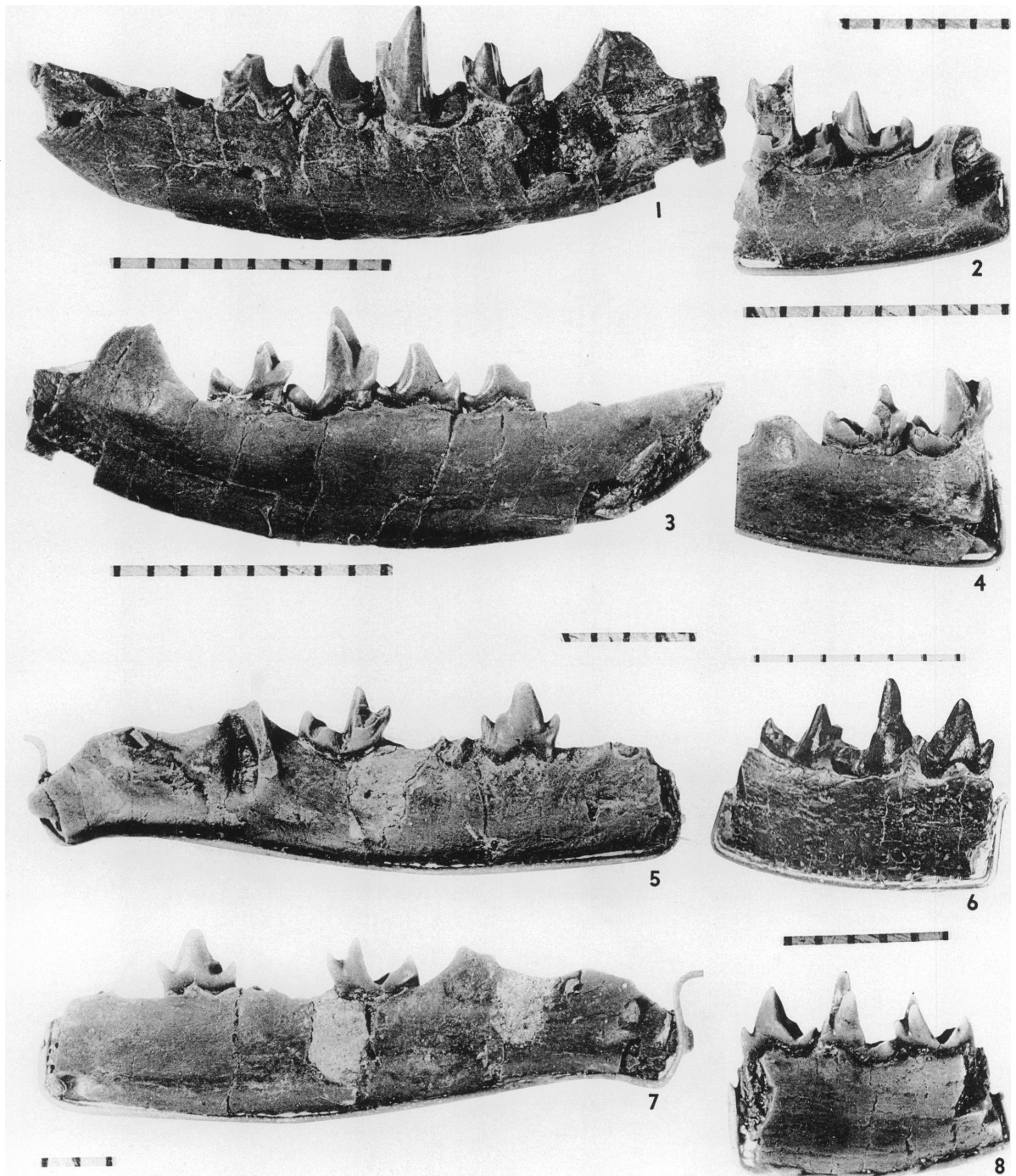
Protictis (Protictis) haydenianus. 1, 2. A.M.N.H. No. 948, reconstructed pelvic and femoral fragments. 3. A.M.N.H. No. 3374, front of skull and jaws. 4-11. A.M.N.H. No. 2382. 4, 6, 8, 10. Right astragalus. 5, 7, 9, 11. Left calcaneum fragment. 1, 2. Stereoscopic lateral aspect. 4-7. Stereoscopic dorsal aspects. 8-11. Ventral aspects. 1, 2. About $\times 2$. 3-11. $\times 2$



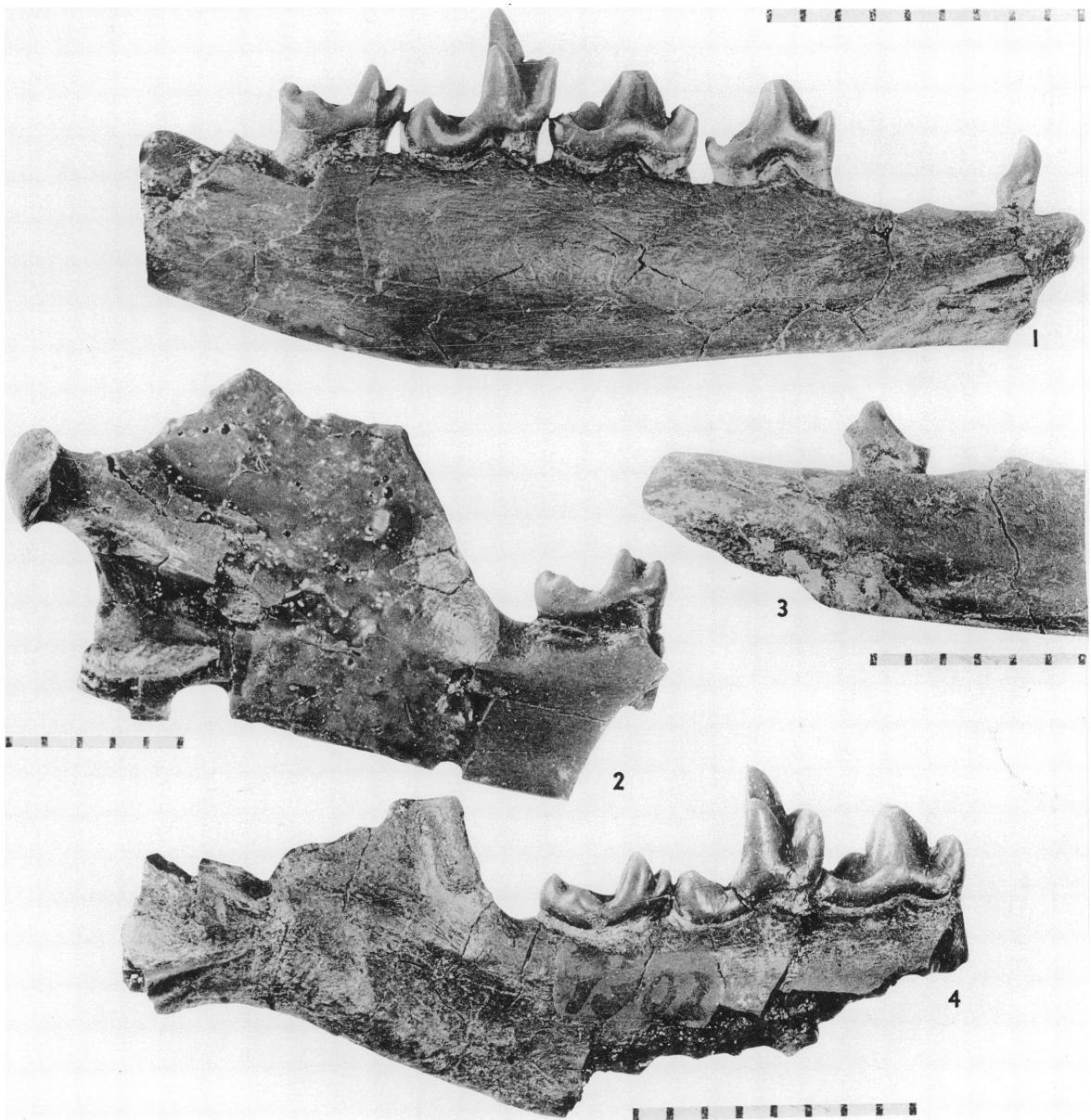
Didymictis protenus. A.M.N.H. No. 2855. 1, 3, 5, 7. Left astragalus. 2, 4, 6, 8. Right astragalus. 9, 11, 13, 15. Left calcaneum. 10, 12, 14, 16. Right calcaneum. This specimen represents an early Eocene viverravine (from the Graybull local fauna) for comparison with plate 9, figures 4-11. Comparable parts shown in plates 9 and 10 were cut from the same photographs and are shown at the same scale. 1-4, 9-12. Stereoscopic ventral aspects. 5-8, 13-16. Dorsal aspects. All about $\times 2$



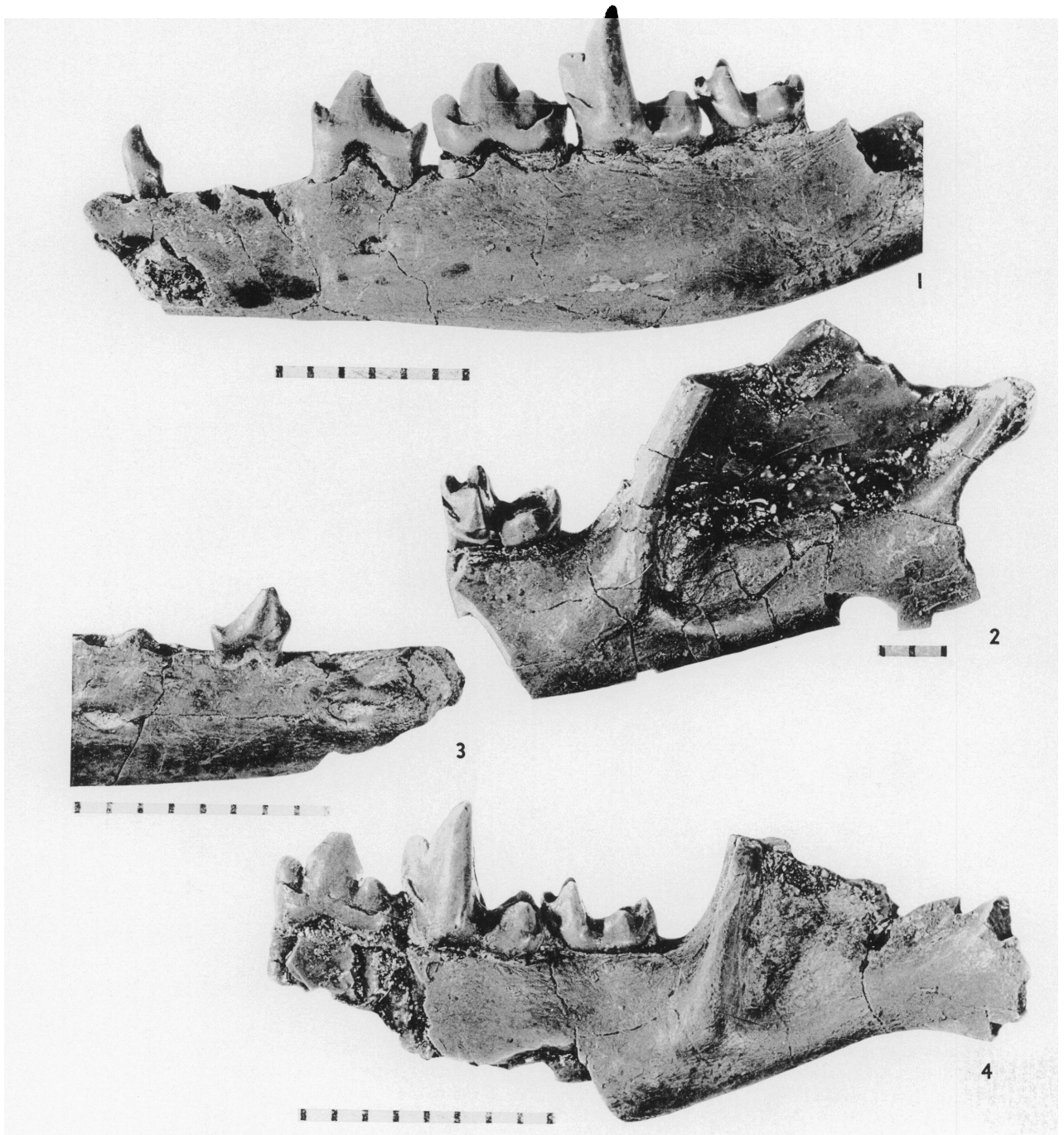
Protictis (Protictis) haydenianus. A.M.N.H. No. 3368 (type). 1, 2. Left P_4-M_2 . 3, 4. Left P^a-M^a . Stereoscopic occlusal aspects. $\times 5$



Protictis (Simpsonictis) tenuis. 1, 3. A.M.N.H. No. 35348, left dentary, with P_3 - M_2 . 2, 4. A.M.N.H. No. 35349, left dentary, with M_{1-2} . 5, 7. A.M.N.H. No. 35350, right dentary, with P_4 and M_2 . This specimen is the only one known illustrating the dental foramen in this species. The posterior end preserves a portion of the vertical lamina between condyle and angle. 6, 8. A.M.N.H. No. 35347, right dentary, with P_4 - M_2 . 1, 2, 5, 6. Labial aspects. 3, 4, 7, 8. Lingual aspects. All about $\times 5$



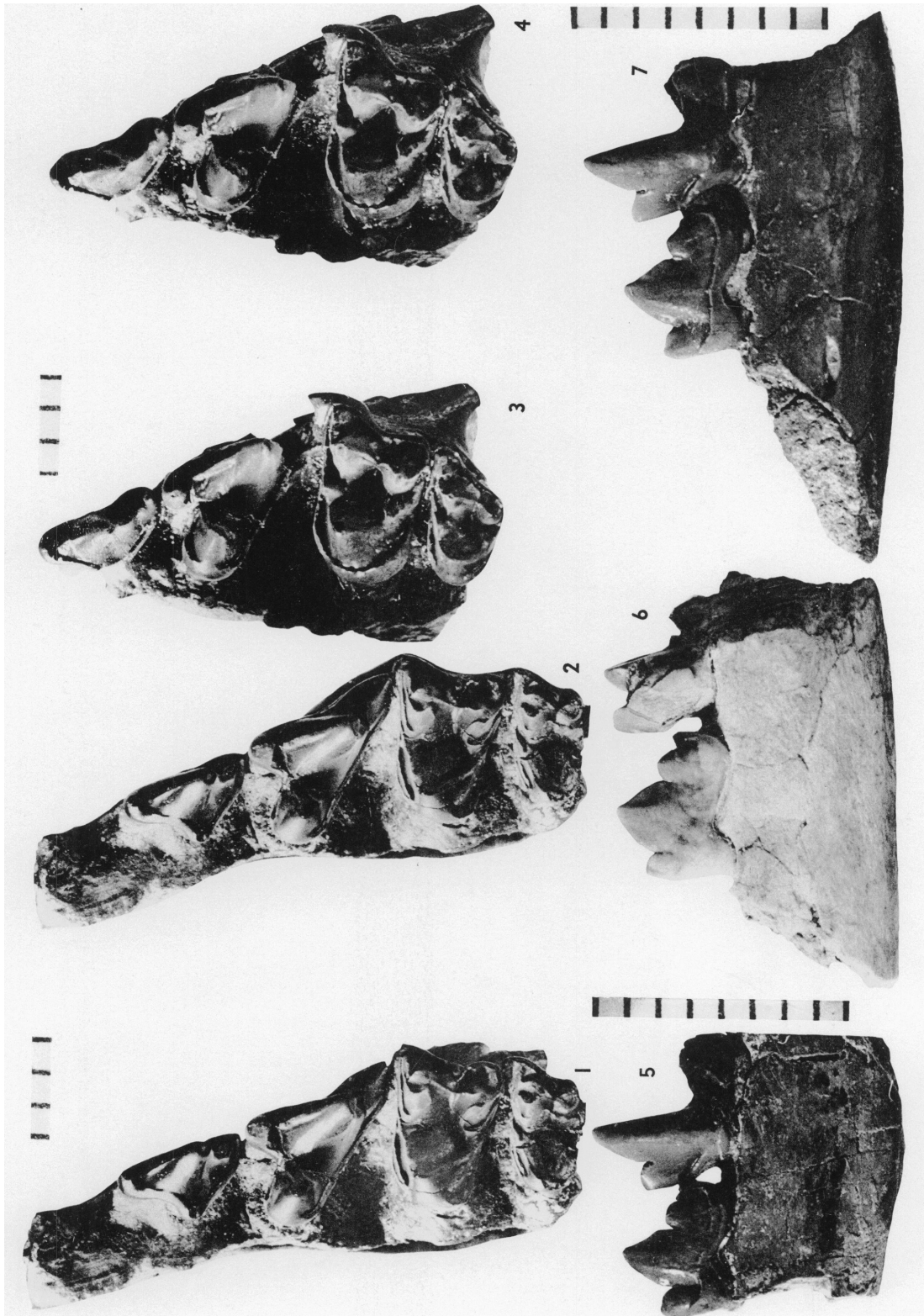
Protictis (Bryanictus) microlestes. 1. A.M.N.H. No. 35373, left dentary, with P_1 and P_3-M_2 . This is the only P_1 of this species known. 2. U.S.N.M. No. 9303, left dentary, with M_2 . This is the only articular condyle of this species known. 3. Part of A.M.N.H. No. 35378, right dentary and P_2 . 4. U.S.N.M. No. 9302, left dentary, with P_4-M_2 . The remainder of the coronoid process is less distorted and less complete than in U.S.N.M. No. 9303, above. Both specimens illustrate the dental foramen. Lingual aspects. About $\times 5$



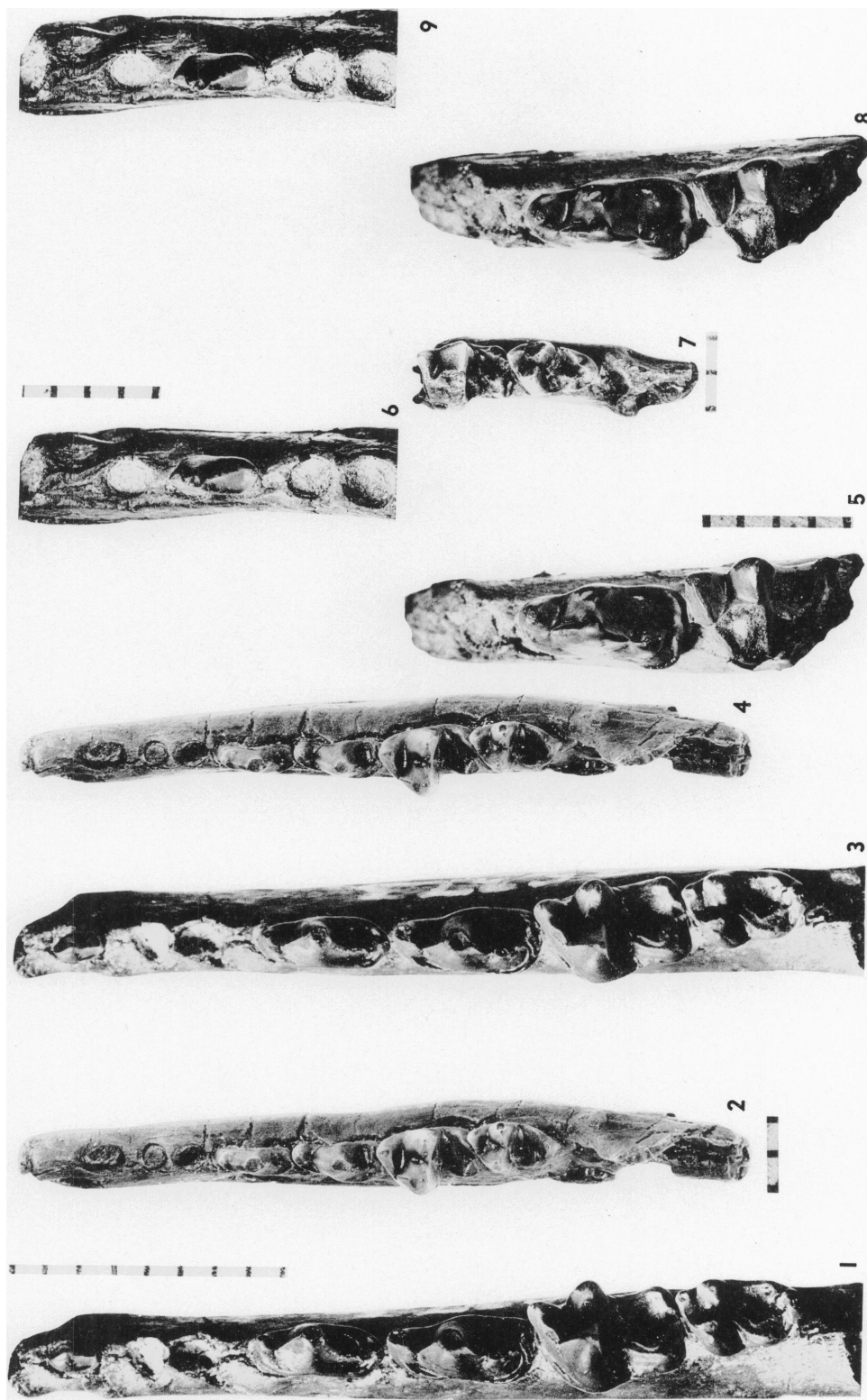
Protictis (Bryanictus) microlestes. 1. A.M.N.H. No. 35373. 2. U.S.N.M. No. 9303. 3. A.M.N.H. No. 35378. 4. U.S.N.M. No. 9302. Mental foramina are visible below P_1 and P_3 . Labial aspects of lower jaws and teeth. About $\times 5$



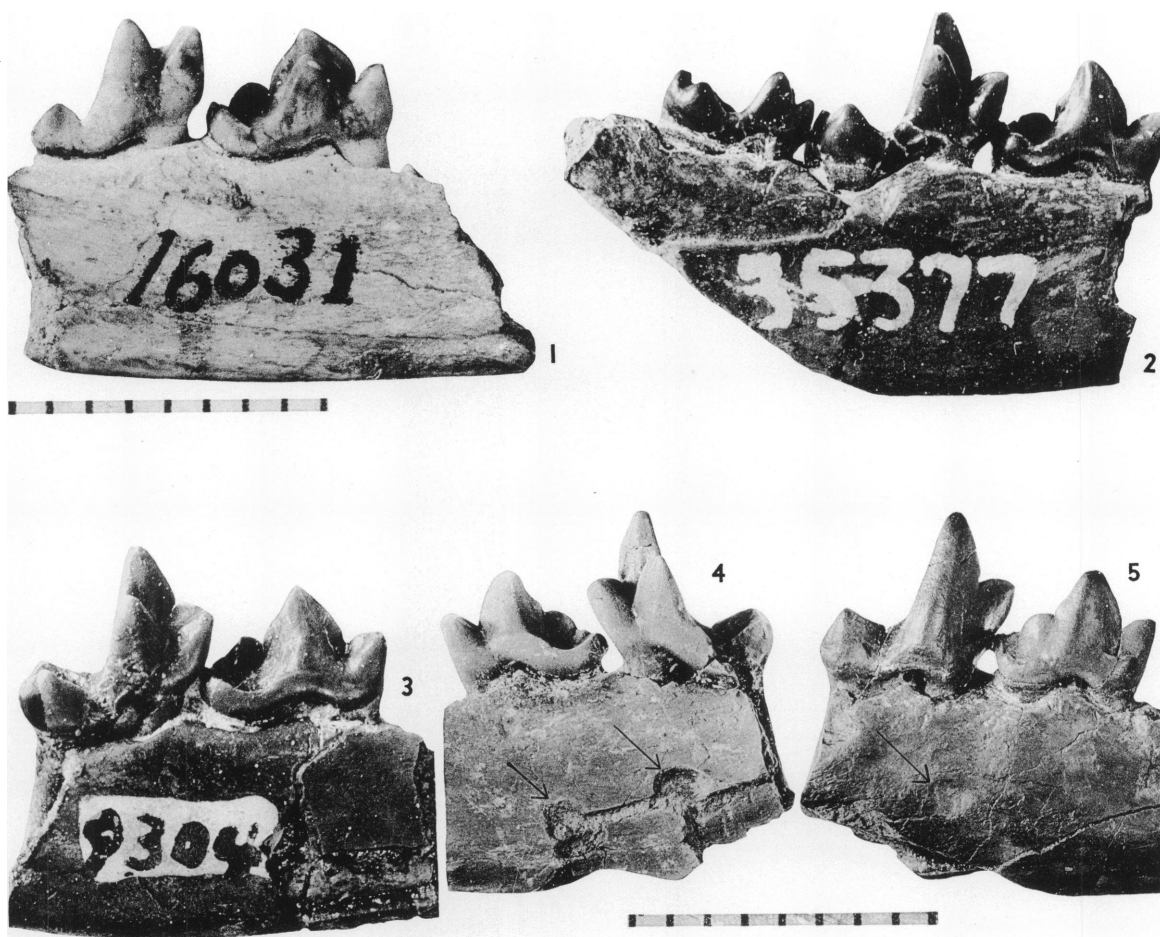
Protictis (Bryaniictis) microlestes. 1, 2. U.S.N.M. No. 9299, left maxilla, with P^3 - M^2 . 3, 4. A.M.N.H. No. 35360, left maxilla, with P^3 - M^2 and infraorbital foramen above P^3 . 5, 6. A.M.N.H. No. 35370, right P^4 , with cingulum complete around protocone. 7, 8. A.M.N.H. No. 35363, right P^4 - M^1 . 1, 3. Lingual aspects. 2, 4. Lingual aspects. 5-8. Stereoscopic occlusal aspects. About $\times 5$



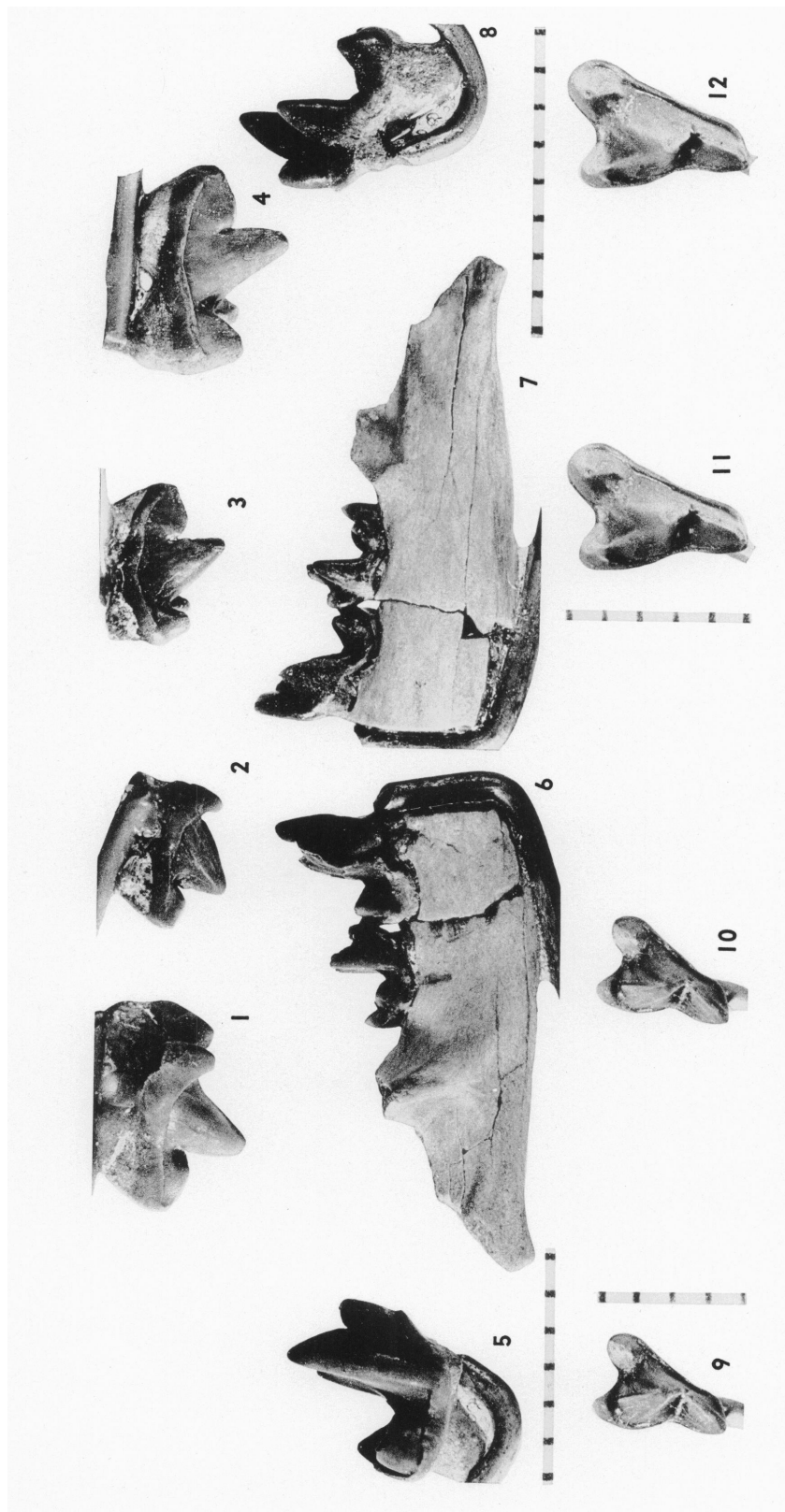
1-5, 7. *Protictis* (*Bryanictis*) *microlestes*. 1, 2. A.M.N.H. No. 35360. 3, 4. U.S.N.M. No. 9299. 5. A.M.N.H. No. 35377. 7. U.S.N.M. No. 9304. 6. *Protictis* (*Bryanictis*) *vanvaleni*. A.M.N.H. No. 16031 (type). 1-4. Stereoscopic occlusal aspects, showing different degrees of wear and cingulum development. 5-7. Labial aspects, comparing the two species. About $\times 5$



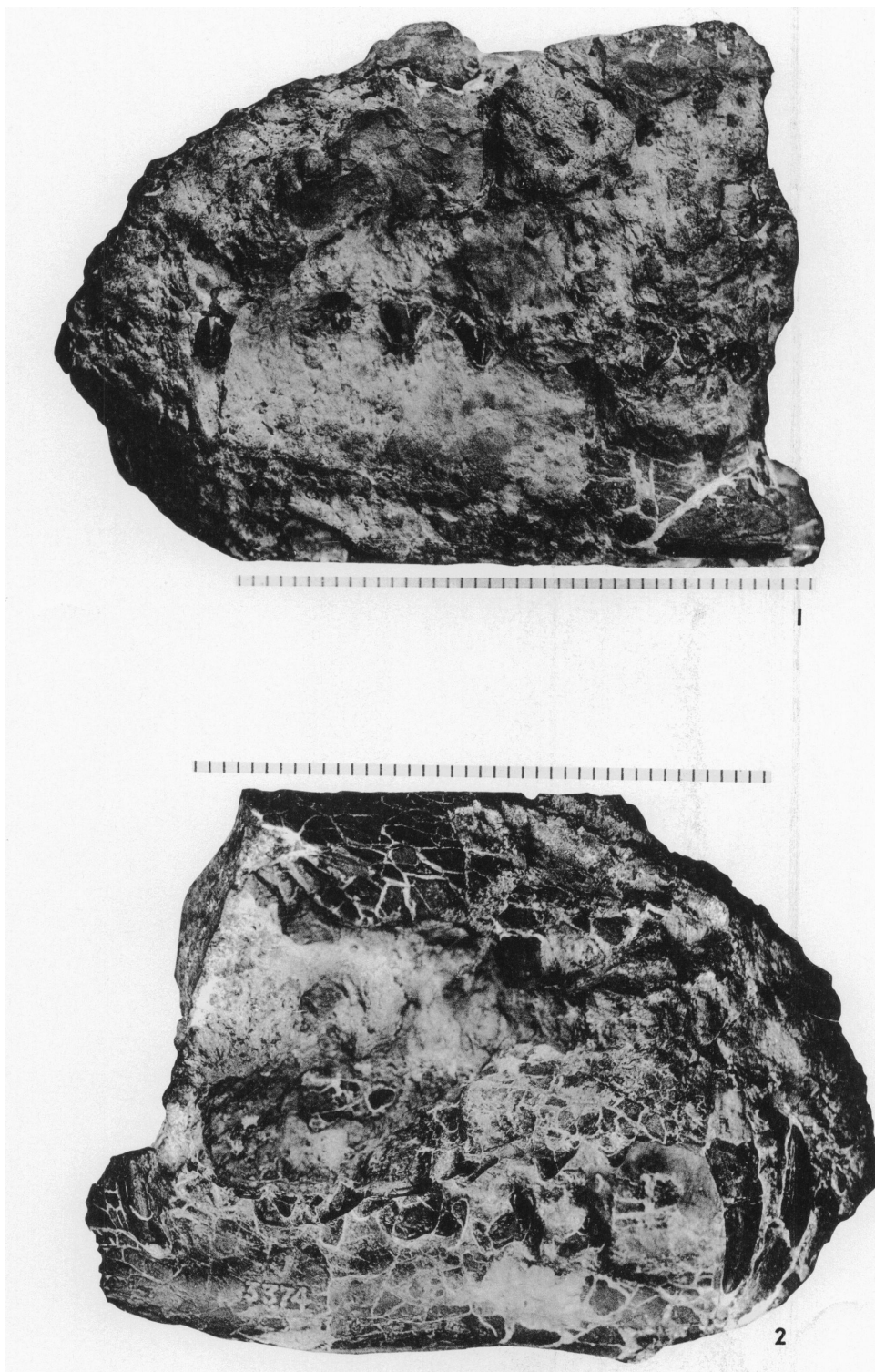
1, 3, 6, 9. *Proictis (Bryanictis) microlestes*. 1, 3. A.M.N.H. No. 35373, left P₁, P₃-M₂. 6, 9. A.M.N.H. No. 35378, right P₂, 2, 4, 7. *Proictis (Simpsonictis) tenuis*. 2, 4. A.M.N.H. No. 35348, left P₃-M₂. 7. A.M.N.H. No. 35349, left M₁-2. 5, 8. *Proictis (Bryanictis) vanvaleni*, A.M.N.H. No. 16031 (type), left P₄-M₁. Stereoscopic occlusal aspects of lower teeth. $\times 5$



1. *Protictis (Bryanictus) vanvaleni*. A.M.N.H. No. 16031 (type), left P_4 - M_1 , showing metaconid on molarized P_4 . 2-5. *Protictis (Bryanictus) microlestes*. 2. A.M.N.H. No. 35377, left P_4 - M_2 . 3. U.S.N.M. No. 9304, left P_4 - M_2 . 4, 5. A.M.N.H. No. 35378, right P_4 - M_1 , with part of dentary, showing two tooth marks on lingual side and opposing indentation on labial side indicated by arrows. 1-3 are from the same negative, printed at the same scale. 1-4. Lingual aspects. 5. Labial aspect. All about $\times 5$



Various uncatalogued specimens in the Harvard-University of Wyoming collections. 1, 4, 5, 8, 11, 12. *Protictis* (*Bryanictis*) cf. *microlestes* (Shotgun Member). 1, 4, 11, 12. Right P⁴. 5, 8. Right M¹. 2, 3, 9, 10. Cf. *Protictis* (*Simpsonictis*) (Shotgun Member), right P⁴. 6, 7. *Protictis* (*Simpsonictis*) cf. *lenius* (Bison basin Saddle locality), right dentary with M₁₋₂. 1, 2, 5, 6. Labial aspects. 3, 4, 7, 8. Lingual aspects. 9-12. Stereoscopic occlusal aspects. About $\times 5$



Protictis (Protictis) haydenianus. A.M.N.H. No. 3374, fore part of skull and jaws, showing specimen at the beginning of preparation with Airbrasive apparatus. 1. Left side, largely buried in flinty matrix. 2. Right side, showing parts described by Cope. About $\times 2$

