

MIXODECTIDAE, MICROSYOPIDAE,
AND THE INSECTIVORE-PRIMATE
TRANSITION

FREDERICK S. SZALAY

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 140 : ARTICLE 4 NEW YORK : 1969

MIXODECTIDAE, MICROSYOPIDAE, AND THE INSECTIVORE-PRIMATE TRANSITION

FREDERICK S. SZALAY

*National Science Foundation Postdoctoral Fellow
Department of Vertebrate Paleontology
The American Museum of Natural History*

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 140 : ARTICLE 4 NEW YORK : 1969

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 140, article 4, pages 193-330, text
figures 1-28, plates 17-57, tables 1-21

Issued February 17, 1969

Price: \$9.00 a copy

CONTENTS

INTRODUCTION	197
Acknowledgments	197
Abbreviations	198
Eutherian Tooth Nomenclature	198
Butler's Field Theory	199
Historical Review: 1871-1937	203
Historical Review: 1938-1966	207
STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE OF THE MIXODECTIDAE	210
Order Insectivora Bowdich, 1821	210
Superfamily Mixodectoidea (Cope, 1883) Simpson 1945	210
Family Mixodectidae Cope, 1883	211
<i>Mixodectes</i> Cope, 1883	211
<i>Mixodectes pungens</i> Cope, 1883	213
<i>Mixodectes malaris</i> (Cope, 1883) Matthew, 1937	215
<i>Elpidophorus</i> Simpson, 1927	218
<i>Elpidophorus elegans</i> Simpson, 1927	219
<i>Elpidophorus minor</i> Simpson, 1937	223
<i>Eudaemonema</i> Simpson, 1935	224
<i>Eudaemonema cuspidata</i> Simpson, 1935	225
<i>Dracontolestes</i> Gazin, 1941	227
<i>Dracontolestes aphantus</i> Gazin, 1941	228
<i>Remiculus</i> D. E. Russell, 1964	228
<i>Remiculus deutschii</i> D. E. Russell, 1964	229
Supposed Puercan Mixodectids	230
"Mixodectid a" of Gazin, 1941	230
"Mixodectid ? b" of Gazin, 1941	231
"Mixodectidae, n. gen. and sp." of Van Valen and Sloan, 1965	231
Cranial Characters of the Mixodectidae	231
Tooth Occlusion	233
Trends in Mixodectids	235
Mixodectid Affinities	237
Status of Mixodectid-Plagiomenid Relationships	240
STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE OF THE MICROSYOPIDAE	245
Order ?Primates Linnaeus, 1758	247
Suborder Uncertain	247
Family Microsyopidae Osborn and Wortman, 1892	247
<i>Microsyops</i> Leidy, 1872	248
<i>Microsyops wilsoni</i> , New Species	249
<i>Microsyops alfi</i> (McKenna, 1960), New Combination	254
<i>Microsyops angustidens</i> (Matthew, 1915), New Combination	255
<i>Microsyops latidens</i> (Cope, 1882), New Combination	258
<i>Microsyops scottianus</i> Cope, 1881	262
<i>Microsyops lundeliusi</i> (White, 1952) McKenna, 1966	263

<i>Microsyops</i> from the Huerfano Formation	267
<i>Microsyops elegans</i> (Marsh, 1871) Leidy, 1872	269
<i>Microsyops annectens</i> (Marsh, 1872) Osborn 1902	270
<i>Microsyops</i> sp.	272
<i>Microsyops kratos</i> Stock, 1938	273
<i>Craseops</i> Stock, 1934	274
<i>Craseops sylvestris</i> Stock, 1934	274
Order Primates Linnaeus, 1758	275
Suborder Uncertain	275
Family ?Microsyopidae Osborn and Wortman, 1892	275
<i>Navajovius</i> Matthew and Granger, 1921	275
<i>Navajovius kohlhaasae</i> Matthew and Granger, 1921	278
<i>Navajovius? mckennai</i> , New Species	280
Supposed Microsyopids from Europe	281
Is <i>Alsaticopithecus</i> Hürzeler (1947) a Microsyopid?	281
The Cranial Anatomy of <i>Microsyops</i>	284
The Skull of <i>Microsyops</i>	284
Skull Fragment of <i>Microsyops annectens</i>	287
The Skull of <i>Microsyops latidens</i>	288
Mandible	290
The Endocranial Cast of <i>Microsyops</i>	291
Comparative Aspects of the Microsyopid Cranium	294
Postcranial Remains of Microsyopids	302
Tooth Occlusion	303
Notes on Mastication in Microsyopids	303
Trends in Microsyopids	305
Dental Convergence of Microsyopids and Contemporaneous Artiodactyls	310
Microsyopid Affinities	310
THE INSECTIVORE-PRIMATE TRANSITION	312
Notes on Some Insectivora	312
The Apatemyidae	314
The Tupaiidae	314
The Paromomyidae	315
The Plesiadapidae and Carpolestidae	317
The Picrodontidae	318
Ordinal Characters and Ancestry of the Earliest Prosimians	318
Selection and the Insectivore-Primate Transition	319
SUMMARY	323
REFERENCES	324

INTRODUCTION

THE PRESENT STUDY is an attempt to answer the following questions: (a) are the Paleocene mixodectids and the Eocene microsyopids as intimately related to each other as has been commonly presumed, or not; and (b), if not, what is the relative degree of affinity between these mammals? It became apparent that, to supply a satisfactory answer to these questions, many other, equally important ones had to be asked and at least in part answered. It was necessary to study in some detail all Cretaceous and early Tertiary insectivores, insectivore-derived groups, and the earliest known Paleocene prosimians.

A detailed study of virtually all the known specimens of mixodectids and microsyopids confirmed the view suggested by several previous workers, namely, that these mammals belong to two validly separable eutherian families. Furthermore, as the study progressed and the morphology of other pertinent insectivores and all Paleocene prosimians was reviewed, it became apparent that there was no special genetic affinity between mixodectids and microsyopids. Although the ordinal allocation of the Mixodectidae entails no taxonomic difficulties, that of the Microsyopidae proved to be a thought-provoking and at the same time also a frustrating taxonomic problem. Although with a query, I place the Microsyopidae in the Primates, because there is no direct or indirect evidence against doing so, and the known facts seem to support such a move. Negative evidence against this action is supplied by the ear region of late Paleocene *Plesiadapis*, the lack of cranial remains of unspecialized early or middle Paleocene prosimians, and, of course, a paucity of knowledge of the Paleocene ancestry of the microsyopids. Allocating the microsyopids to the Primates is supported by the available evidence and, as a taxonomic procedure, is more desirable and research-provoking than burying this family in the adaptively dissimilar Insectivora.

As an integral part of the present study, a brief discussion of the insectivore-primate transition is presented in this paper. This is primarily a biological evaluation of the meager evidence, with obvious implications for

the insectivore-primate taxonomic boundary. It applies to the virtually undocumented insectivore-primate transition that occurred probably during the second half of the Cretaceous.

Under descriptions of the species, only the teeth are treated. Specimens showing other than dental features are so rare (hence valuable) that they are described under special headings that deal with various parts of the skeleton.

Contrary to the usual practice of plotting parameters for only one tooth of a species, I have attempted to do so for as many of the upper and lower molars and fourth premolars of each species as the sample permitted. My purpose is to provide an additional aid for future research on mixodectids and microsyopids. As new species are discovered by recognizable elements of the dentition, parameters may be easily plotted and compared with the homologous teeth of related species.

ACKNOWLEDGMENTS

My first thanks belong to Dr. Malcolm C. McKenna, for being an inspiring sponsor and for fostering an atmosphere of keen research interest. His careful and penetrating criticism has substantially improved this manuscript.

Dr. Edwin H. Colbert, former Chairman of the Department of Vertebrate Paleontology of the American Museum of Natural History, generously permitted the extensive use of the unequalled collections of that museum.

Dr. Bobb Schaeffer, Chairman of the Department of Vertebrate Paleontology, has taught me a deep and active appreciation of evolutionary biology without which fossils remain mute relics of the geological record.

I have profited from a critical reading of the manuscript by Dr. Karl F. Koopman and Dr. Bobb Schaeffer.

For fruitful discussions, my thanks are also due to Dr. Walter J. Bock, Mrs. Sylvia F. Graham, Mr. Stephen J. Gould, Dr. Max K. Hecht, Dr. Giles T. Mac Intyre, Dr. Mal-

colm C. McKenna, Dr. James S. Mellett, Dr. Leonard B. Radinsky, Dr. Bobb Schaeffer, and Dr. Leigh Van Valen. For many favors and help during this study, my special thanks are extended to Mr. Martin Cassidy, Mr. Louis Monaco, Mr. Walter Sorensen, Mr. Gilbert Stucker, and Mr. George Whitaker.

Frequent discussions with Mr. Chester Tarka on the psychology of perception as it relates to scientific illustrations are sincerely appreciated.

The following persons and institutions have generously allowed the study of fossil specimens: Mr. Raymond Alf, the Raymond M. Alf Museum, Claremont, California; Dr. Craig C. Black and Dr. Mary Dawson, Carnegie Museum, Pittsburgh; Dr. William C. Clemens, the University of Kansas Museum of Natural History, Lawrence; Dr. C. Lewis Gazin, the United States National Museum of the Smithsonian Institution, Washington, D. C.; Dr. Glenn L. Jepsen, Princeton University, Princeton, New Jersey; Dr. James R. Macdonald, Los Angeles County Museum Los Angeles, California; Dr. Bryan Patterson, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; Dr. Peter Robinson, University of Colorado, Boulder; Dr. Elwyn L. Simons, Peabody Museum of Natural History, Yale University, New Haven, Connecticut; and Dr. Robert W. Wilson, South Dakota School of Mines, Rapid City.

Help in the preparation of the manuscript and unfailing patience from my wife, Mrs. Jeanne Szalay, are deeply appreciated.

The research was supported by my tenure of a two-year fellowship from the National Institutes of Health.

ABBREVIATIONS

The following abbreviations are used throughout the text:

INSTITUTIONS

A.M.N.H., the American Museum of Natural History, Department of Vertebrate Paleontology
B.M., British Museum (Natural History), London
L.A.C.M., Los Angeles County Museum, Los Angeles
M.N.H.N., Muséum National d'Histoire Naturelle, Paris
N.M.C., National Museum of Canada, Ottawa

P.U., Princeton University, Princeton
S.D.S.M., South Dakota School of Mines, Rapid City
U.C.M., University of Colorado Museum, Boulder
U.C.M.P., University of California Museum of Paleontology, Berkeley
U.M., University of Minnesota, Minneapolis
U.S.N.M., United States National Museum, Smithsonian Institution, Division of Vertebrate Paleontology, Washington, D. C.
U.S.N.M. (D.M.), United States National Museum, Smithsonian Institution, Department of Mammalogy, Washington, D. C.
Y.P.M., Peabody Museum of Natural History, Yale University, New Haven

MEASUREMENTS AND STATISTICS

AW, anterior width
L, length
N, number of specimens included in sample
OR, observed range
PW, posterior width
S, standard deviation
S², variance
V, coefficient of variation
 \bar{X} , mean

EUTHERIAN TOOTH NOMENCLATURE

Mac Intyre (1966) and Van Valen (1966) have discussed most of the important points pertaining to the nomenclature of details of the teeth of primitive eutherian mammals. Their papers have added considerably to the refinement of a very important descriptive tool of paleomammalogy: a stable tooth nomenclature. It is regrettable, however, that there has been no agreement, or, rather, no communication, between these closely associated workers in naming some homologous structures of teeth. Most standard terms for the details of the crown patterns of teeth date back to the Cope-Osborn theory of trituberculy. It is obvious that any attempt to change the foundations of this nomenclature would be of highly questionable value.¹

¹ Vandebroek (1961) has suggested a radically new nomenclature based on the premise that the historical appearance of the therian cusps, cuspules, and other features can be deciphered from their sequence of appearance in ontogeny. In the light of what is known at present of the relation of ontogeny to phylogeny, this premise is erroneous. Furthermore, even if Vandebroek will prove to be correct as to the historical appearance of various parts of the therian tooth, to change so drastically a nomenclature that has been firmly entrenched in the literature for almost a century is not justifiable.

Mac Intyre (1966) and Van Valen (1966) both firmly base their nomenclature on the Cope-Osborn terms. They differ from each other in the naming of previously unnamed details. I believe that many of Van Valen's names for previously unnamed details on the teeth are very useful, although some of them do not adhere to the Cope-Osborn terminology. Van Valen's "protofossa," "prefossid," and "postfossid," and Mac Intyre's "protocone fossa" and "talonid shelf" can be, and have been in the past, called "trigon basin," "trigonid basin," and "talonid basin" (Mac Intyre uses the last term), respectively. The last three terms have been used throughout the literature with a perfectly clear meaning. The naming of the various crests leading to the cusps and cuspules is very useful for the obvious purpose of clearer and more succinct descriptions. The term "crista," qualified by various topographic adjectives, is appropriate for these crests. Although the paracrista, centrocrista, and metacrista are simply segments of the ectoloph, the differentiation is still helpful. The anterior and posterior segments of the centrocrista are also called here the "postparacrista" and "premetacrista," respectively. I prefer to call Van Valen's various "wings" "cristae," because these structures are crests. Van Valen's "ectostylid" is very likely a remnant of the ectocingulid that appears as a vestige in some species. Calling the various crests of the lower teeth "cristids," qualified by topographic modifiers, has the great advantage of a clear connotation of exactly where these crests are, i.e., on the lower teeth.

In table 1 I have attempted to reconcile and synthesize the differences between the tooth nomenclature of Van Valen and that of Mac Intyre. The grouping of various names into four categories can facilitate the understanding of this nomenclature. The four categories are: cusps and cuspules, crests, cingula (cingulid for the lower teeth), and basins. I follow Van Valen's definition of the following directional terms: "anterior," "posterior," "lingual," "apical," "basal," "central," and "marginal." I prefer the term "buccal" to "labial," because the former word is less apt to confuse either a printer or a reader with the word "lingual." Van Valen's terms "prevallum" and "postvallum,"

and "prevallid" and "postvallid," are precise and greatly enhance exactitude in description.

The term introduced here as "talonid notch," a gap that separates the lingual portions of the trigonid and the talonid, is highly diagnostic on the generic level and is of great descriptive value.

I describe premolars (mainly P_4^1) with the following terminology, here defined:

PREMOLARIFORM: On lower tooth only protoconid, with no homologizable cusps on the incipient talonid; upper tooth consisting only of the paracone and protocone.

PREMOLARIFORM-SEMIMOLARIFORM: On lower tooth small paraconid or metaconid or both; on upper tooth both paracone and protocone and either one of the conules and an incipient metacone.

SEMIMOLARIFORM: All three cusps present on the trigonid although in different proportions from those of M_1 , talonid somewhat smaller and cusps and cuspules less developed than on that of M_1 ; on upper tooth paracone, metacone, protocone, and incipient conule or conules.

The molariform premolar is essentially like M_1^1 , with only slight differences.

In the present paper the term "hypocone" includes the "pseudohypocone" of various students of primates.

BUTLER'S FIELD THEORY

Throughout the text reference is made to Butler's (1937, 1939) theory on the morphogenetic fields involved in the development of the dentition. The theory is well known as the field theory. Although this hypothesis is widely referred to and understood among mammalian paleontologists, it is appropriate to summarize and briefly paraphrase it here.

The tooth buds of the primary dentition (i.e., the deciduous premolars and the molars) do not necessarily appear in the embryo in the same order as they erupt. Their eruption appears to depend on the rate of growth of the tooth.¹ The primitive therian primary dentition usually displays a spec-

¹ The details of a mammalian tooth crown originate during ontogeny from the folding of a sheet of epithelium. This epithelium becomes the internal surface of an ectodermal enamel organ. This ectodermal organ is the original tooth bud on the dental lamina. For a thorough review of the known facts and interpretations of the ontogeny of the molar pattern, see Butler (1956a).

TABLE 1
TOOTH NOMENCLATURE USED BY MAC INTYRE (1966), VAN VALEN (1966),
AND IN THE PRESENT PAPER

Mac Intyre	Van Valen	This Paper (see Text Fig. 1)
UPPER TEETH		
CUSPS AND CUSPULES		
Parastyle	Parastyle	Parastyle
Stylocone	Stylocone	Stylocone
Mesostyle	Mesostyle	Mesostyle
Metastyle	Metastyle	Metastyle
Paracone	Paracone	Paracone
Metacone	Metacone	Metacone
Metaconule	Metaconule	Metaconule
Paraconule	Paraconule	Paraconule
Mesoconule	—	—
Protocone	Protocone	Protocone
Hypocone	Hypocone	Hypocone
Pericone	Pericone	Pericone
CRESTS		
—	Paracrista	(Pre) paracrista
—	Centrocrista	Centrocrista (= postparacrista and premetacrista)
—	—	Ectoloph (= preparacrista, centrocrista, and postmetacrista)
—	Metacrista	(Post) metacrista
—	Preprotocrista	Preprotocrista
—	Postprotocrista	Postprotocrista
—	Preparaconule wing	Preparaconule crista
—	Postparaconule wing	Postparaconule crista
—	Premetaconule wing	Premetaconule crista
—	Postmetaconule wing	Postmetaconule crista
CINGULA		
Stylar cingulum	Ectocingulum	Ectocingulum
Anterior lingual cingulum	Precingulum	Precingulum
Posterior lingual cingulum	Postcingulum	Postcingulum
—	—	Paracingulum
—	—	Metacingulum
BASINS (AND DEPRESSIONS)		
Protocone basin	Protofossa	Trigon basin
Stylar shelf	Stylar shelf	Stylar shelf
—	Ectoflexus	Ectoflexus
LOWER TEETH		
CUSPS AND CUSPULES		
Paraconid	Paraconid	Paraconid
Metaconid	Metaconid	Metaconid
Protoconid	Protoconid	Protoconid
Periconid	—	Periconid
Prehypoconid	Mesoconid	Mesoconid
Hypoconid	Hypoconid	Hypoconid
Posthypoconid	—	—

TABLE 1—(Continued)

Mac Intyre	Van Valen	This Paper (see Text Fig. 1)
Hypoconulid	Hypoconulid	Hypoconulid
Preentoconid	Entoconulid	Entoconulid
Entoconid	Entoconid	Entoconid
—	Metastylid	Metastylid
—	Protostylid	Protostylid
—	Ectostylid	—
CRESTS		
—	Paralophid	Paracristid (paralophid)
—	Protolophid	Protocristid (protolophid)
—	Entocristid	Entocristid
—	Postcristid	Postcristid
Crista obliqua	Crista obliqua	Cristid obliqua
CINGULIDS		
Anterior labial cingulum	—	Precingulid
—	—	Postcingulid
—	—	Ectocingulid
BASINS (AND DEPRESSIONS)		
Talonid basin	Postfossid	Talonid basin
Trigon shelf	Prefossid	Trigonid basin
Sulcus obliqua	Hypoflexid	Hypoflexid
Carnassial notch	—	Trigonid notch
—	—	Talonid notch

trum of characters from one tooth to another. In making a special reference to primates, Butler (1963, pp. 7–13) explained this dental spectrum as follows: "The general nature of the spectrum, the changes that go on within it as one passes from one end to the other, are always essentially the same, though of course there are differences in detail. This spectrum could be explained if it were supposed that there exists in the embryo a continuous morphogenetic field or gradient, which controls the development of the tooth germs within it. Each tooth germ would develop according to its position in relation to the field as a whole, i.e., according to its local environment. It is likely that there is a stage in the development of the tooth germ when it is competent to react to the field; as a result it becomes determined, i.e., it will go on developing in a predetermined direction even if transplanted or explanted. We do not yet know when this process of determination takes place; it may be even before the tooth germ is histologically recognizable.

"One could imagine a continuous field which has been, as it were, sampled at intervals represented by the position of the tooth germs. If the sampling is done at a slightly different place, the resultant tooth pattern will be slightly different. This would be most obvious in regions where the field is changing rapidly, for example, at the level where the molar pattern first appears: here teeth will be more or less molariform according to their position.

"This additional variation would be due to genes that influenced the shape and size of the field (in relation to individual tooth germs). It is reasonable to believe that such 'field' genes exist, analogous to those that control the regional differentiation of the vertebral column.

"There would also be another set of 'pattern' genes, influencing the way in which the tooth germs react to any given level of the field. These would control the full molar pattern, for example. All the tooth germs of the series must have the same genetic constitu-

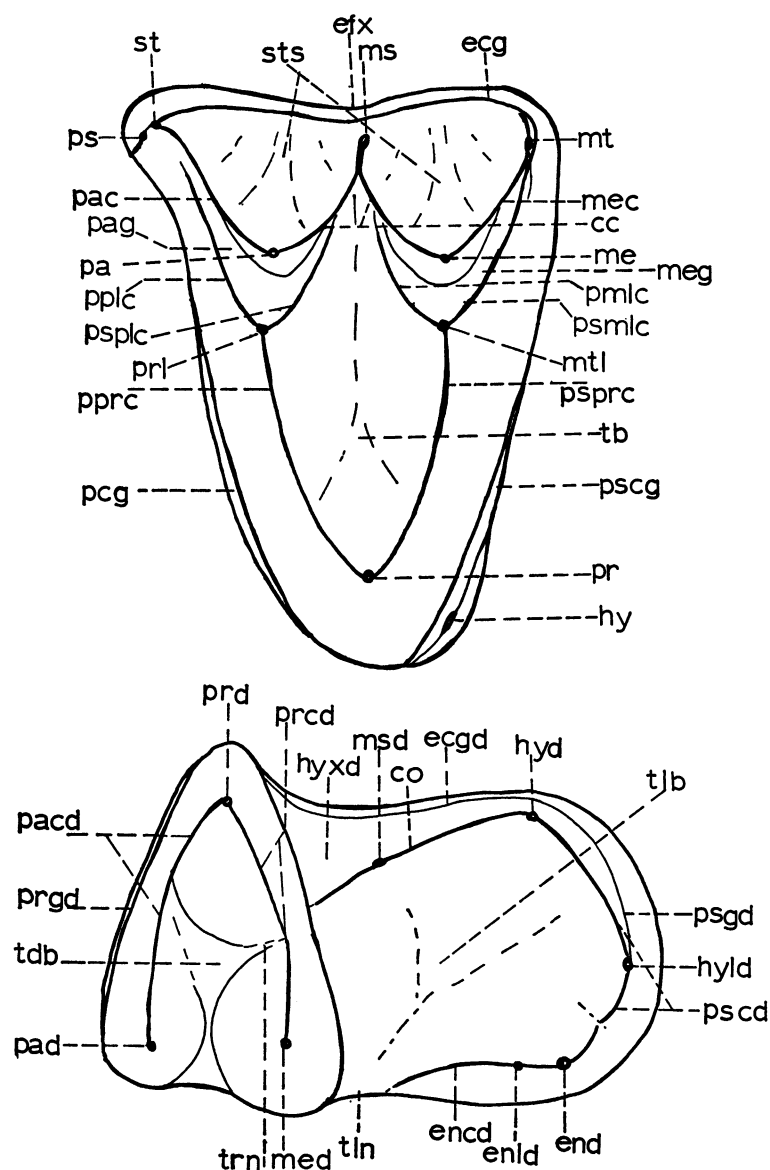


FIG. 1. Hypothetical upper and lower molars, illustrating the tooth nomenclature used in this paper.

Abbreviations: cc, centrocrista (divisible into the postparacrista and premetacrista); co, cristid obliqua; ecg, ectocingulum; ecgd, ectocingulid; efx, ectoflexus; encd, entocristid; enld, entoconulid; end, entoconid; hy, hypocone; hyd, hypoconid; hyld, hypoconulid; hyxd, hypoflexid; me, metacone; mec, metacrista (or postmetacrista); med, metaconid; meg, metacingulum; ms, mesostyle; msd, mesoconid; mt, metaconule; mtl, metaconule; pa, paracone; pac, paracrista (or preparacrista); pacd, paracristid; pad, paraconid; pag, paracingulum; pcg, precingulum; pmlc, premetaconule crista; pplc, preparaconule crista; pprc, preprotocrista; pr, protocone; prcd, protocristid; prd, protoconid; prl, paraconule; prgd, precingulid; ps, parastyle; pscd, postcristid; pscg, postcingulum; psd, postcingulid; psmc, postmetaconule crista; psplc, postparaconule crista; psprc, postprotocrista; st, stylocone; sts, stylar shelf; tb, trigon basin; tdb, trigonid basin; tlb, talonid basin; tln, talonid notch; trn, trigonid notch.

tion, because they are all parts of a single individual, and therefore they can be regarded as equipotential: all could, if situated in the appropriate part of the field, become molars, canines and incisors. What they do become, i.e. how their genetic constitution expresses itself phenotypically, depends on the position of teeth in the series. There is no tooth on which all the elements of the pattern are developed to a maximal extent, not even the first molar: each element reaches its maximal development at a characteristic position in the series. In some cases the character might be present only on one tooth, or on a few adjacent teeth. This is true for variant characters as well as for those that are normally present: a supernumerary cusp with maximal expression on M_3 would have a different genetic basis from a topographically similar cusp with a maximal incidence on M_1 .

HISTORICAL REVIEW: 1871-1937

Because the history of the taxa now clearly allocated either to the Mixodectidae or to the Microsyopidae is inseparably interwoven, this subject is dealt with as a unit.

The names of species and genera listed in the historical review are the original names used by the authors of pertinent past literature. Using the original names of many synonymous concepts, which are clarified under the section on taxonomy, allows a non-anachronistic evaluation of the ideas of previous workers in a time-sequential historical framework.

The main debate over these groups, since the first knowledge of their existence in the late nineteenth century, involved their possible relation to either insectivores or to basal primate stocks. The unsettled question consequently embraced (as it still does) the dilemma of the primate-non-primate boundary.

In 1871 Marsh described two species in the same paper: *Limnotherium elegans* and *Hyopsodus gracilis*. As discussed in more detail under *Microsyops* (see below, p. 249), Leidy (1872) recognized that *Hyopsodus gracilis* represented a new genus, which he named *Microsyops*. Leidy classified the recognized microsyopid (he did not erect the family, however) as a mammal belonging to a broad

group called the "Odd-toed pachyderms."

Several years later the family Mixodectidae was erected by Cope (1883a) based on the genus *Mixodectes* which was described in the same paper. Cope (1883b) gave an extended description of *Indrodon*¹ and allocated the genus to the family Anaptomorphidae (p. 318) "...suborder perhaps Lemuroidea, as indicated by the dentition only." Cope in that paper doubted the lemuroid affinities of the Adapidae, and he considered the mixodectids and anaptomorphids the only Eocene lemuroids. Cope's two families of lemuroids included the following genera: Mixodectidae ("superior premolars three")

Tricentes

Necrolemur

Mixodectes

Microsyops

Cynodontomys

Anaptomorphidae ("superior premolars two")

Indrodon

Anaptomorphus

In 1884 Cope was not certain of the position of *Mixodectes* but still considered it to be near *Cynodontomys*. In another paper (1884b) he placed *Microsyops* in the suborder Mesodonta (p. 216), but later (p. 239 of the same publication) under the suborder Prosimiae he listed this genus in the Mixodectidae, along with *Mixodectes* and *Cynodontomys*. He transferred *Necrolemur* to the Anaptomorphidae under which *Indrodon* was not mentioned.² The next year, in 1885, Cope changed his mind about the adapids' not being lemuroids and listed them as the most primitive of the three families that he considered lemuroids (deriving this latter broad taxon from the condylarths). In Cope's hierarchy, relative primitiveness was based on the presence of four premolars in the adapids as opposed to the three found in mixodectids and the two present in the anaptomorphids.

Schlosser (1887-1890) included *Mixodectes* and *Cynodontomys* in his concept of the Lemuridae. From a hypothetical ancestor, which he derived from *Mixodectes*, he de-

¹ In spite of having described *Indrodon* in 1883, Cope in 1884 (1884a) treated this taxon, as well as *Tricentes*, as a "new genus and species."

² It may be of interest to mention here that, according to oral tradition in vertebrate paleontology, Cope wrote papers that he never reread prior to publication.

rived *Cynodontomys*, *Anaptomorphus*, *Necrolemur*, *Tarsius*, *Plesiadapis*, and *Omomys*. He queried the last two genera, apparently questioning the correctness of their arrangement.

Osborn and Wortman (1892) considered *Cynodontomys* a primate in their study of the fossil mammals of the Wasatch and Wind River beds. Matthew (1897) maintained, from skeletal material, that *Indrodon* was a generalized primate. He also noted that the upper molars of this genus were very similar to teeth supposedly belonging to *Mixodectes*. In association with a lower jaw of *Mixodectes pungens* some skeletal elements were discovered. One such skeletal element, an astragalus,¹ induced Matthew to remove *Mixodectes* from the Primates and place it in the Rodentia, with a question mark. Matthew (1897, p. 267) wrote: "The strong resemblance of the astragalus of *Mixodectes* to those of the sciuriform rodents is in harmony with the indications of the teeth, which show progress towards a type with scalpriform incisors and four molariform teeth in the lower jaw, short crowned with peripheral cusps. . . . It is better to place it as a sciuriform rodent of the most primitive type." It appears, then, that the original impetus to view *Mixodectes* as a rodent came from the supposed association of the astragalus; from that Matthew deduced rodent-like characters in the dentition.

In 1902 Osborn published the only comprehensive treatment in the literature devoted to the mixodectids known up to that time. His concept of the Mixodectidae was broad and included the microsyopids, which have been treated independently by several later students. Osborn noted the similarity (pp. 170-171) between an upper molar of *Indrodon malaris* and one of *Mixodectes*, and wrote that the former was surely not an anaptomorph. The allocation of a skeleton (A.M.N.H. No. 823) that Osborn and Earle (1895, pp. 16-20) had associated with *Indrodon* was claimed to have been an error. Osborn in 1902 believed that the skeleton belonged to a primate,² be-

cause he had noted that its astragalus was not rodent-like. He then accepted the rodent affinities of *Mixodectes* as had been proposed by Matthew in 1897. Osborn erected a suborder within the Rodentia, suborder Proglires, under which he listed *Mixodectes*, *Microsyops*, and *Olbodotes* (the last-named was described as a new genus in the 1902 paper). He enumerated seven features that he believed showed rodent affinities in the mixodectids. On the other hand, he also cited characters, such as the persistence of canines, the absence of diastemata, and the "... absence of any evidence (except the levelling of the premolars) of adaptation for antero-posterior or orthal motion of the jaw" (p. 204), which were against rodent affinities. Osborn's definition of the Mixodectidae (p. 203) follows: "Characters.—Median lower incisors close to symphysis, enlarged and elongating (unlike Tillodontia, in which second incisor is enlarged), lateral incisors early reduced; canines persistent (unlike Rodentia); no diastemata (unlike Rodentia), first and second premolars rapidly reduced; third premolar slowly reduced, fourth premolar progressively molariform (as in Tillodontia and Rodentia); lower molars with narrow, slightly elevated trigonid, but early reduce paraconid; talonid broad, hypoconulid small, except in third lower molar; superior molars tritubercular. A feature of the jaw is the sharp definition of a ridge descending from the coronoid and defining the masseteric insertion anteriorly." From this definition of the family, it would seem that Osborn considered the middle Paleocene *Mixodectes* directly related to the middle Eocene *Microsyops*. On the basis of the features that he considered either persistent or reduced, he apparently viewed *Microsyops* as an advanced descendant of the primitive, ancestral *Mixodectes*. In mentioning the tillodonts, Osborn may have suggested, implicitly, without committing himself in print, possible affinities of the mixodectids to these mammals, a personal view that he never directly stated.

In the same paper Osborn described *Olbodotes copei* from a specimen previously referred to *Mixodectes* (Matthew pointed out in 1937 that the specimen was *M. crassiusculus*). In spite of the fact that an upper molar (asso-

¹ This astragalus (A.M.N.H. No. 703, previously catalogued with A.M.N.H. No. 2451) has recently been found to belong to *Prodiacodon*, not to *Mixodectes* (see Szalay, 1966).

² Matthew (1909a, p. 512) referred this specimen to *Mioclaenus acolytus*, a condylarth.

ciated with the type of *Olbodotes*) suggested to him the mixodectid affinities of *Indrodon*, he placed *Indrodon* with *Cynodontomys* and *Microsyops* as *incertae sedis*. He considered *Cynodontomys* separate from *Microsyops* only for lack of better evidence to the contrary. One must conclude concerning Osborn's views (1902), that, although he considered all the sundry genera noted above to be broadly related to one another, he had no real trust in their close affinities.

Wortman (1903, p. 163), in his monographic work on primates, divided the order into three suborders: the Cheiromyoidea, the Lemuroidea, and the Anthropeidea. In his family Microsyopidae, which he allocated to the Cheiromyoidea (p. 203), he included *Mixodectes*, *Olbodotes*, *Microsyops*, *Cynodontomys*, and *Smilodectes*, the last a then newly described Eocene primate. Wortman was aware that his microsyopids might not be true primates in spite of his allocating them to the Cheiromyoidea. He placed very little trust in the true association of the "rodent-like" astragalus with *Mixodectes pungens* and consequently rejected the conclusions of Matthew (1897) and Osborn (1902). Wortman then proceeded to give his view, demonstrating that the animals in question were not rodents. His main argument, in his rather vehement refutation of the rodent affinities of microsyopids, was the basic difference in the mode of addition of the cusps to the premolars and "presumably" to the molars in rodents and primates. As an example for the rodents he used *Paramys*, and he concluded that microsyopids follow the cusp-addition pattern of the primates and not that of the rodents. The animosity that existed between Wortman and Osborn during the period when the paper was written is reflected in the emotional treatment of this topic. Wortman, as zestfully as he refuted Osborn, committed himself to the other extreme (p. 218): "Among the Lemuroidea on the other hand, the great similarity of the molar crowns to those of the Microsyopidae is apparent at a glance."

Matthew (1909b), in his contribution to Osborn's (1909) "Cenozoic mammal horizons of western North America," placed the Mixodectidae (*Mixodectes* and *Indrodon*) in the Insectivora, but he noted in a footnote that,

according to Osborn, the group is of "Order Proglires of uncertain relationship" (p. 92). The Microsyopidae (*Cynodontomys* and *Microsyops*) were allocated to the Primates. However, in a footnote, Matthew expressed the possibility that this family was the same as that of the mixodectid insectivores.

Matthew's ideas on the affinities of the mixodectid-microsyopid complex continued to evolve. Matthew, Gregory, and Mosen-thal (1910) grouped the mixodectids, *sensu lato*, under the suborder Proglires (they designated this suborder as "diprotodont rodent-like insectivores"). These authors (chiefly Matthew) also allocated the Apatemyidae (at that time consisting of *Apatemys*, *Uintsorex*, and *Trogolemur*) and Adapisoricidae (*Adapisorex* and *Adapisoriculus*, both from the early Eocene of Europe) to the Proglires.

Matthew (1915 p. 433) spoke of the Mixodectidae, *sensu lato*, under the Primates as a group which, when better known, might be considered primates. He further noted, of *Cynodontomys* and *Microsyops*, that they might not belong to the family (p. 466): "The lower molars are unquestionably much like those of *Mixodectes*, but there the resemblance ends. The upper molars are by no means so close; the premolars are of wholly different type, and the homologies of the enlarged front teeth may not be the same." In this paper Matthew asserted that *Metoldobotes* from the Fayum of Egypt was not a mixodectid "... and cannot therefore afford any confirmatory evidence as to their [the Mixodectidae] insectivore affinities as Schlosser affirms that it does" (p. 467).

Stehlin (1912-1916, vol. 41, p. 1503) held that the mixodectids and microsyopids were not closely related, but he maintained that both groups were primates.

Matthew (1918), accepting Stehlin's conclusions, considered the mixodectids and microsyopids as separate families. He suggested that insectivore nature of the *Mixodectes* astragalus and the two-rooted canine of *Microsyops* indicate strong insectivore affinities. Matthew was fully aware of the doubtful nature of the evidence, but he believed it to be sounder practice to allocate, as he put it, "... primitive groups of doubtful affinities in a generalized and broadly inclusive order, such as I consider the Insectiv-

ora to be, rather than in a more compact specialized order such as the primates" (1918, p. 568).

A new genus, *Elpidophorus*, was described by Simpson in 1927 from the Paskapoo Formation of Alberta, Canada, which he tentatively referred to the Oxyclaenidae (= Arcocyonidae). In spite of the fact that at this time Simpson could not find any similarity to any other genus, he noted that the animal might be an insectivore, without listing any special reasons for his suggestion.

Seven years later Stock (1934) described another new mammal, *Craseops*, from the Sespe upper Eocene of California. He cautiously referred it to the Microsyopinae without any mention of higher categories or possible relationships except to *Cynodontomys* and *Microsyops*.

Eudaemonema, a new genus from the middle Paleocene of Montana, was described by Simpson (1935b) as a mixodectid insectivore. In one of his papers (1936) on the new fauna from the Fort Union Formation of Montana, Simpson recognized *Elpidophorus* as undoubtedly a mixodectid and noted that distinguishing genera among the mixodectids on the basis of the lower molars alone is extremely difficult. *Cynodontomys* was considered to be the closest ally of *Elpidophorus*. The molarization of upper and lower premolars in *Cynodontomys* was thought to be advanced; the prominent paraconid of P_4 was viewed as an aberrant specialization. Simpson (1936, p. 15) further discussed the possible immediate relationship of *Elpidophorus* with the Mixodectidae, *sensu lato*, and he went on to evaluate the role of *Elpidophorus* and *Eudaemonema* in the new concept of the family Mixodectidae. He noted (p. 15): "The discovery of *Elpidophorus* and *Eudaemonema* tends to enhance the probability that *Mixodectes* and its allies are really related to *Cynodontomys* and *Microsyops*, yet it also shows that the group is a complex one and that our knowledge is of isolated stages of several different phyla and not of a single structural sequence." He suggested that the separation of the family into the Mixodectinae and the Microsyopinae breaks down in the light of the new genera discovered. Simpson noted many similarities between the Plagiomenidae and *Elpidophorus*, although

he did not consider the latter genus ancestral to the problematical plagiomenids. His allocation of the mixodectids to the Insectivora was by default rather than by any convincing evidence or strong preference.

In 1937 two outstanding papers were published on early Tertiary mammals. Both, the posthumous monograph by Matthew (1937) and the Paleocene faunal study of Simpson (1937), contributed to the knowledge of mixodectids and microsyopids. Matthew (1937) was convinced (with new material of the *Mixodectes* upper dentition in hand) that mixodectids were distinct from microsyopids and plesiadapids.

He listed some of the similarities of the upper teeth of *Mixodectes* to those of *Chriacus* and *Protoselene*, and also some of the differences. He remarked that the fourth premolar of *Mixodectes* differed very much from the creodont type, being nearer to that of condylarths, primates, and insectivores. In his diagnosis, he wrote of *Mixodectes* (p. 220): "The position of this genus is uncertain, but may be near to *Cynodontomys* Cope, which I have provisionally placed among the Prosimiae." Matthew also synonymized the species of *Indrodon* and *Olbodotes* with those of *Mixodectes*.

Simpson (1937) suggested that the primate-like dentitions of mixodectids, *sensu lato*, were not a good clue in any determination of affinities because, as he said (p. 127): "... they refer to single characters of various different primates that are, in just these characters, highly aberrant among the primates as a whole. Aside from such points, which can almost be discarded categorically as more likely to be convergent than not, I detect no primate resemblances in the teeth that go beyond the general Paleocene tuberculosectional pattern common to many different orders at this time." Simpson denied that the mixodectids had any truly distinctive primate characters. On the contrary, he cited some features that are virtually unknown among primates. Simpson considered the known mixodectids to represent four different lines of phyletic descent in the family. These four lineages, the dentition of which he compared in detail, were *Mixodectes* and *Indrodon*, *Eudaemonema*, *Elpidophorus*, and *Cynodontomys* and *Microsyops*. It

is worthwhile to repeat Simpson's evaluation of these mammals: "It is probable that the mixodectids include a related group of phyla that diverged from the primitive placental stock, and apparently from the Insectivora in a more limited sense, at a very early date. Had such a sideline evolved more rapidly, or had it run a longer span and occupied a more important place in mammalian history, it would be more conveniently defined as an order, as, for instance, are the tillodonts, which probably had a very similar history, but developed more striking specializations. Since, in fact, the mixodectids were a short lived and relatively unimportant group, it is most convenient simply to classify them in the order Insectivora, from which they probably arose" (1937, p. 128). Simpson repeated what he had earlier stated (1936) concerning the artificiality of the Mixodectinae and Microsyopinae in a perspective which embraced *Eudaemonema* and *Elpidophorus*. After discussing the mixodectids, he made a case for plagiomenid affinities of the family. However, he stated: "On the other hand the following characters [which were listed] show that the relationship cannot be very close. if it exists at all" (Simpson, 1937, p. 131).

HISTORICAL REVIEW: 1938-1966

From 1938 to 1966 much factual information has been added to our knowledge of mixodectids and microsyopids. Apart from the new genera described by Gazin (1941), Hürzeler (1947), and D. E. Russell (1964), however, there has been no satisfactory synthesis of either the taxonomy or the evolution of the mammals in question. McKenna's (1960) work has served to focus attention again on the problematical status of the mixodectids and microsyopids.

In 1941 Gazin described a new genus, *Dracontolestes*, from the Paleocene of central Utah. He considered this form nearest to *Elpidophorus*.

Simpson (1945), in his classification of mammals, named a new superfamily, Mixodectoidea¹ (= Mixodectoidae Hay, 1930) and included in it Osborn and Wortman's (1892)

Microsyopidae, within the Mixodectidae. He expressed disbelief (as in 1937) in the primate affinities of these mammals, and in accordance with his 1937 views he considered them insectivores of unclear relationships.

In 1947 another new form, *Alsaticopithecus*, was described by Hürzeler from the lower Lutetian in Alsace. He placed the genus in the Primates, *incertae sedis*. McKenna (1960) later included *Alsaticopithecus* in the Microsyopidae.

Saban, in his 1954 and 1958 papers on insectivores, considered the mixodectids as one family, which also included the microsyopids. He erected the suborder Mixodectomorpha in 1954 and included in it the Mixodectoidea of Simpson and the Apatemyoidea, a new superfamily designated by him in the same paper. Saban derived the mixodectids directly from the pantotheres.

McDowell (1958, p. 206) noted the lepidactid and rodent-like features of the mixodectid astragalus, but saw no other resemblance of the family to any other group of mammals. He excluded the Mixodectidae, *sensu stricto*, from the Lipotyphla (his 1958 sense).

McKenna (1960) believed that the known mixodectids fell into three groups:

1. *Mixodectes* (including *Indrodon* and *Olbodotes*) and *Dracontolestes*
2. *Cynodontomys*, *Microsyops*, *Craseops*, and *Alsaticopithecus*
3. *Elpidophorus* and *Edaemonema*

He asserted that the reason Simpson (1937) had maintained that *Elpidophorus* was related to *Cynodontomys* [and consequently found that Matthew's (1915) subfamilies were artificial] was partly the misidentification of P₄ and M₁ of *Cynodontomys angustidens* as P₃ and P₄. This misidentification, said McKenna, led Simpson to believe that the posterior premolars in primitive microsyopids were molariform. McKenna claimed that the possession of molarized premolars or molar mesostyles (he noted that *Elpidophorus*, *Eudaemonema*, and plagiomenids had them) can be convergent and may not necessarily indicate direct relationships. In the 1960 paper he very firmly denied that there was any structural intermediacy between mixodectids and microsyopids, as was shown by *Elpidophorus* and *Eudaemonema*, and con-

¹ According to the Code (Stoll and others, 1961, Article 36), Cope in 1883, not Simpson in 1945, is the author of this superfamily.

sidered this lack the major stumbling block in the way of uniting the mixodectids with the microsyopids. In essence, McKenna (1960) placed the microsyopids among the primates, suggesting plesiadapid ancestry for the former group, and allocated the mixodectids to the Menotyphla. As mentioned above, he referred *Alsaticopithecus* to the Microsyopidae, deriving that genus and *Cynodontomys* from a common ancestor. *Eudaemonema* was placed in the Tupaioidea, *incertae sedis*,¹ and *Elpidophorus* was thought of as a questionable plesiadapid. He believed that *Microsyops* was descended from *Cynodontomys* and that *Microsyops* in turn was ancestral to *Craseops*.

Gazin (1962) retained *Cynodontomys* in the Mixodectidae, hence not agreeing on the separation of the group into two families. On the contrary, Simons (1962a) considered the microsyopids (*sensu* McKenna, 1960) as a group of borderline primates, together with the amphiemurids and apatemyids. His opinion was based on the views of McKenna (1960).

McKenna (1963a), in a paper on early primate origins, suggested the derivation of plesiadapids and microsyopids from unspecialized leptictid ancestors. He wrote that, despite the dental resemblances of microsyopids to plesiadapids, the ear region is similar to "... a primitive leptictid insectivore level of organization" (p. 71).

Three years later McKenna (1966), in discussing the origin of primates, treated the Microsyopidae and Mixodectidae together as two separate but closely related families in the Insectivora. Such an approach is quite a departure from his 1960 treatment. He maintained that, on the basis of the dentition, particularly the mode of premolar molarization, the Microsyopidae and Mixodectidae could be validly separated into two groups, "... though derived from the same general ancestry." On the basis of the microsyopid ear region, which he considered leptictid-like and more similar to that of juvenile tupaiids than to that of the late Paleocene *Plesiadapis*, he believed that the microsyopids were in-

sectivores and that the Mixodectidae were an insectivore family near the primates.

In early 1964, D. E. Russell described a new genus, *Remiculus*, from the late Paleocene of France (Thanetian).

The section below shows a synoptic comparison of the major classifications of the mixodectids and microsyopids. Of the workers listed, probably Teilhard de Chardin and Saban had no firsthand knowledge of these mammals.

A synoptic comparison of classifications and opinions concerning the taxonomy of mixodectids and microsyopids follows:

COPE (1884A)

- Primates
 - Lemuroidea
 - Mixodectidae
 - Tricentes*
 - Necrolemur*
 - Mixodectes*
 - Microsyops*
 - Cynodontomys*
 - Anaptomorphidae
 - Indrodon*
 - Anaptomorphus*

COPE (1884B)

- Primates
 - Suborder Mesodonta
 - Omomys*
 - Microsyops*
 - Pantolestes*
 - Tomitherium*
 - Pelycodus*
 - Sarcolemur*
 - Hyopsodus*
 - Apheliscus*
 - Anaptomorphus*²
 - Adapis*
 - Opisthotomus*
 - Suborder Prosimiae
 - Mixodectidae
 - Mixodectes*
 - Cynodontomys*
 - Anaptomorphidae
 - Anaptomorphus*
 - Necrolemur*

OSBORN (1902)

- Rodentia
 - Suborder Proglires
 - Mixodectidae
 - Olbodotes*
 - Mixodectes*

¹ Since 1960 McKenna (personal communication) has ceased to think that such placement of *Eudaemonema* is valid.

² Also included by Cope in the Prosimiae.

Cynodontomys
Microsyops

MATTHEW (1909B)

Insectivora

Mixodectidae
Mixodectes
Indrodon

Primates

Microsyopidae
Cynodontomys
Microsyops

MATTHEW, GREGORY, AND MOSENTHAL (1910)

Insectivora

Suborder Proglire

Mixodectidae
Mixodectes
Olbodotes
Indrodon
Cynodontomys
Microsyops

Apatemyidae

Apatemys
Uintasorex
Trogolemur

Adapisoricidae

Adapisorex
Adapisoriculus

MATTHEW (1915)

Insectivora

Mixodectidae
Mixodectinae
Mixodectes (*Olbodotes*)
Indrodon
Microsyopinae
Cynodontomys
Microsyops

TEILHARD DE CHARDIN (1916-1921)

Chiromyidae

Mixodectes
Cynodontomys
Plesiadapis (including *Nothodectes* and
Chiromyoides)
Phenacolemur
Trogolemur

Uintasorex

Heterohyus (including *Necrosorex*, *Hetero-*
ochiromys, and ?*Amphichiromys*)

Apatemys

Stehlinella;

Chiromys (= *Cheiomys* = *Daubentonina*)

SIMPSON (1945)

Insectivora

Superfamily Mixodectoidea
Mixodectidae (including Microsyopidae)

Mixodectes
Indrodon
Eudaemonema
Dracontolestes
Elpidophorus
Cynodontomys
Microsyops
Craseops

SABAN (1954, 1958)

Insectivora

Suborder Mixodectomorpha¹

Mixodectoidea

Mixodectidae

(All genera listed under family in Simp-
son, 1945)

McKENNA (1960)

Insectivora

Menotyphla

Mixodectidae

Mixodectes
Indrodon
"Oldobotes" (= *Olbodotes*)
Dracontolestes

Tupaioidea *incertae sedis*

Eudaemonema

Primates

Microsyopidae

Cynodontomys
Microsyops
Craseops
Alsaticopithecus
?Plesiadapidae *incertae sedis*
Elpidophorus

¹ Saban also included the Apatemyoidea in this new suborder.

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE OF THE MIXODECTIDAE

THE MIXODECTIDS, as recognized today, are an exclusively Paleocene group of mammals known from North America and Europe. The stratigraphy of the continental Paleocene of North America and Europe has been thoroughly discussed by authors too numerous to be enumerated here. In addition to Matthew (1937) and Simpson (1937), Dorr (1952) gave a detailed correlation chart of the North American Paleocene and Eocene. Some recent contributions to Paleocene correlation are those of Gazin (1961), Mac Intyre (1966), D. E. Russell (1964; 1967), Simpson (1959a), and Wilson (1951; 1956).

Both the Dragonian and the Clarkforkian are omitted as North American Land-Mammal Ages. The Dragonian is considered to be a part of the Puercan for the reasons given by Evernden, Savage, Curtis, and James (1964, p. 152). I follow Roger Wood (personal communication), who has extensively studied the Clark Fork "assemblage," in abandoning the Clarkforkian as a land-mammal age.

The earliest undoubted mixodectid is *Dracontolestes aphantus*, reported by Gazin (1941) from the Dragon local fauna from the Uinta Basin. The concept of the proposed Dragonian as a North American Land-Mammal Age was based on this rather poorly known fauna, and, as noted above, I prefer at the present time to consider the Dragon assemblage as late Puercan in age.

Mixodectes malaris, the smaller of the two species of the genus, occurs in the *Deltatherium* zone (older than the *Pantolambda* zone of the Nacimiento Formation of the San Juan Basin, New Mexico) and also in the Swain Quarry in the lower part of the Fort Union Formation in the Washakie Basin, Wyoming (see Szalay, 1965, for locality data). The sample from the *Deltatherium* zone is fair-sized. Although the partly sorted sample from the Swain Quarry consists of only a few isolated upper and lower teeth, it appears beyond doubt that the two populations, which are geographically well separated, represent the same species.

Mixodectes pungens, the larger species, is known only from the Paleocene of the San

Juan Basin, New Mexico. The exact records of the provenance of the specimens are not known, although no evidence indicates that *M. malaris* and *M. pungens* were ever found sympatrically. Because Wilson (1951) reported only *M. malaris* from his localities 9 and 13, both in the *Delthatherium* zone, and reported no specimens of *M. pungens*, it is likely that all the specimens of the latter species were collected from the younger *Pantolambda* zone.

Eudaemonema cuspidata is known from the Torrejonian Gidley Quarry of the Fort Union Formation of the Crazy Mountain Field of Montana and also from bed 17 (see Keefer and Troyer, 1964) of the Shotgun Member of the Fort Union Formation, Wyoming.

The known Torrejonian species, *Mixodectes malaris*, *Mixodectes pungens*, and *Eudaemonema cuspidata*, do not occur at the same locality, so, strictly speaking, are not in the same fauna. A possible explanation of this allopatry may lie partly in ecological and facies differences of the faunas in which they occur, as noted under the discussion of *Eudaemonema cuspidata*.

The youngest North American mixodectid is the Tiffanian *Elpidophorus*. The older, but less well known, of the two species, *E. minor*, occurs at the Silberling Quarry (Torrejonian) of the Fort Union Formation at the Crazy Mountain Field, Montana, whereas the better-known and younger *E. elegans* is known from Scarritt Quarry of the same formation and field and also from the Paskapoo Formation of Alberta, Canada.

The Thanetian *Remiculus* from Europe is known from the Lemoine Quarry at Cernayles-Reims, France. Donald E. Russell has informed me that specimens of *Remiculus*, probably representing a new species other than *R. deutschii*, have been collected at a new Paleocene locality in France.

ORDER INSECTIVORA BOWDICH, 1821

SUPERFAMILY MIXODECTOIDEA

(COPE, 1883) SIMPSON, 1945

Mixodectoidae HAY, 1930, p. 445.

Mixodectoidea SIMPSON, 1945, p. 53.

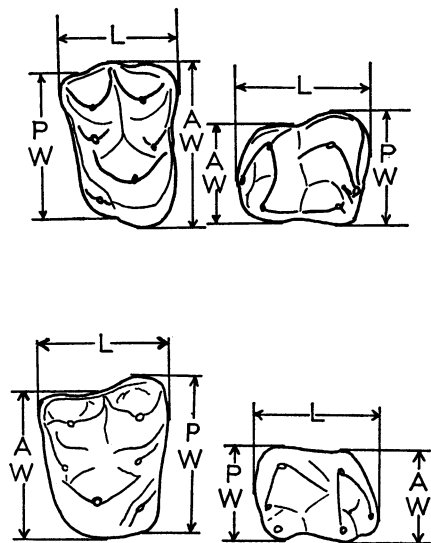


FIG. 2. Line drawings of the upper and lower molars of *Elpidophorus* (above) and *Microsyops* (below) to illustrate the points at which measurements of length (L), anterior width (AW), and posterior width (PW) were taken on mixodectid and microsyopid molars.

INCLUDED FAMILIES: Mixodectidae Cope (1883b, p. 80).

KNOWN DISTRIBUTION: Same as for family.

DIAGNOSIS: Same as for family.

FAMILY MIXODECTIDAE COPE, 1883

Mixodectidae COPE, 1883b, p. 80.

Oldobotidae SCHLOSSER, 1907, p. 222.

TYPE GENUS: *Mixodectes* Cope, 1883 (= *Indrodon* Cope, 1883, and *Olbodotes* Osborn, 1902).

INCLUDED GENERA: The type genus and *Eudaemonema*, *Dracontolestes*, *Elpidophorus*, and *Remiculus*.

KNOWN DISTRIBUTION: From the late Puercan to Tiffanian in North America and the Thanetian in Europe.

DIAGNOSIS: Eutherian mammals with two pairs of characteristically enlarged upper and lower incisors; median pair usually larger than lateral one; canines and more anterior premolars reduced in certain genera; long and wide paracrista and metacrista characteristic of all genera; presence of a mesostyle and closely twinned large entoconid and smaller hypoconulid, with a balance of other characters, also apparently diagnostic. Size from that of a rat to that of a beaver.

Mixodectids appear to differ from apatemyids in having a mesostyle, the entoconid and hypoconulid characteristically in proximity, and the talonids relatively more elevated lingually. Whereas the enlarged apatemyid lower incisor extended far back in the horizontal ramus, the analogous tooth of mixodectids seems, in no instance, to have extended farther than approximately the posterior border of the mandibular symphysis.

Mixodectids clearly differ from known leptictids and pantolestids in the presence of enlarged incisors and a wider styler shelf, and in the greater importance of shear on the paracrista and metacrista.

Members of the Mixodectidae differ from primitive members of the Microsyopidae, but converge to the more advanced species of the latter family, in the following characters: the presence of a mesostyle, a large styler shelf (secondarily greatly enlarged in *Craseops*, for example), and, in the primitive members, a molarized fourth premolar. Mixodectids differ from all microsyopids in having a more shearing paracrista and metacrista and a more transversely aligned centrocrista.

MIXODECTES COPE, 1883

Mixodectes COPE, 1883a, p. 559.

Indrodon COPE, 1883c, p. 318.

Olbodotes OSBORN, 1902, p. 205.

TYPE SPECIES: *Mixodectes pungens* Cope, 1883.

INCLUDED SPECIES: *Mixodectes pungens* and *M. malaris*.

KNOWN DISTRIBUTION: The Torrejonian of western North America (Wyoming, New Mexico).

GENERIC DIAGNOSIS: *Mixodectes* differs from both *Eudaemonema* and *Elpidophorus* in lacking the canine and P₁; the individual teeth of *Mixodectes* are relatively larger than those of the latter two genera, and it has a premolariform fourth premolar in contrast to the semimolariform-molariform homologue of *Eudaemonema* and *Elpidophorus*. *Mixodectes* is also distinguishable from the latter two genera in having a lingual notch of different shape.

Mixodectes can be distinguished from *Eudaemonema* by a precingulid on the lower molars. In *Mixodectes* the cristid obliqua

joins the posterior wall of the trigonid more buccally than in *Eudaemonema*.

Mixodectes differs from *Elpidophorus* in having the lower teeth less anterolingually precumbent. *Mixodectes* has a talonid on M_3 relatively wider than the trigonid; in *Elpidophorus* the trigonid of M_3 is wider than the talonid. The hypocone is relatively much larger than that in *Elpidophorus*. The trigon basins of *Elpidophorus* are relatively shallower. The paraconule and metaconule are relatively much weaker than those in *Elpidophorus*.

The hypoconulid lobe of M_3 leans lingually, like that of *Eudaemonema* but unlike the homologous structure of *Dracontolestes*; the hypoconulid lobe is approximately vertical to the base of the tooth. The lingual portion of the trigonid is relatively less constricted anteroposteriorly than in *Dracontolestes*.

Mixodectes lacks the strong and characteristic parastylar area that extends anteriorly in *Remiculus*.

Dental formula: $I_{1(2)}^{1(2)} P_{234}^{234} M_{123}^{123}$.

DISCUSSION: The genus is based on *Mixodectes pungens* which is almost identical morphologically with *M. malaris*, and clearly differs from it only in being larger in size. Matthew (1937, p. 220) quoted the diagnosis of Cope of *Mixodectes* and *Indrodon*; his survey and discussion of the genus *Mixodectes* are entirely satisfactory in all respects, so they are not reprinted here.

The homologies of the upper dentition of *Mixodectes* are inferred only from the very fragmentary type specimen of *Mixodectes malaris*. The interpretation presented here differs from that of Cope (1883a), that of Matthew (1937, who apparently followed Cope by merely quoting and not commenting on the type description of *Indrodon* by Cope), and that of Osborn (1902). Cope (1883a) believed that there were three upper incisors, the canine, and three premolars in front of the molars. Osborn (1902, fig. 33) published a drawing of the type specimen of *Indrodon* (= *Mixodectes*) *malaris*, agreeing to the same number of teeth preceding the molars as Cope had claimed, but labeling Cope's third incisor a canine and Cope's canine the P^2 . I believe that the "tooth" both Cope and Osborn (and Matthew, who followed Cope)

called an incisor is calcite filling between the broken basal remains of the two enlarged upper incisors. These two incisors were very widely splayed when the type skull was crushed. There was no canine, as far as the badly crushed skull permits me to judge. The upper dentition of *Elpidophorus*, as known from the alveoli of the anterior upper teeth (A.M.N.H. No. 35963; see also pl. 27, figs. 7 and 8), indirectly strongly reinforces the present interpretation of the homologies of the upper dentition of *Mixodectes*.

The homologies of the anterior lower teeth have also been questionable. Matthew (1897, fig. 1) illustrated the type specimen of *Mixodectes pungens* and labeled the two anterior-most teeth as the incisor and the canine, respectively. Osborn (1902, figs. 30, 31) reprinted Matthew's figure but (in fig. 30) questioned the identification of the anterior teeth as the incisor and the canine. In the other figure (fig. 31; see pl. 17 of the present paper) Osborn merely labeled the two anterior teeth as "i." and "c.," without a query. The most probable homologies of the two enlarged lower teeth, namely, that they are two incisors, became evident to me after looking at specimens of *Eudaemonema* (see pl. 25 and the discussion below under *Eudaemonema*).

The premolars are P_2 , P_3 , and P_4 , as both Matthew (1897) and Osborn (1902) correctly indicated. I also agree with Osborn's homologies of the upper premolars which are the same as the lowers.

Simpson's (1937, p. 133) remark that the metaconule of the upper molars of *Mixodectes* are almost lacking is incorrect, having been based on an examination of badly worn specimens.

Olbodotes Osborn was based on a specimen of *Mixodectes pungens*, in which Osborn (1902, pp. 205–206) misconstrued the crushed alveolus of the median lower incisor as being two alveoli. The lateral wall of the alveolus of the median incisor was pressed medially, and this crushing resulted in the extra "alveolus." This condition is clearly illustrated by Osborn's (1902, fig. 29) figure of the type of *Olbodotes copei*. Matthew (1937) synonymized *Olbodotes copei* with both *M. pungens* and *M. crassiusculus*, but maintained *M. crassiusculus* as a valid species. Quite recently, how-

ever, McKenna (1960, p. 29) has referred to "*Oldobotes*" (= *Olbodotes*) as the most primitive genus of the family.

Matthew (1937, p. 224) noted the incorrect association of the P^4 with M^{1-3} of *M. malaris* of A.M.N.H. No. 833 which was figured by Osborn (1902, fig. 34) as *Indrodon* sp. This specimen, however, does not represent an "... otherwise unknown genus of Mixodectidae not closely allied to *Indrodon* or *Mixodectes*," as Matthew stated (see pl. 21, figs. 10 and 11, present paper). Although Matthew in his last major work fully synonymized *Indrodon* with *Mixodectes*, he nevertheless used the name in the same work as that of a valid genus. Simpson (1945) also accepted *Indrodon* as a valid genus.

Saban (1958, p. 856) stated, under *Mixodectes*, that "... Le genre *Metoldobotes* [misspelled form of *Metoldobotes*] Schlosser, 1910, de l'Oligocène du Fayum (Egypte), est un *Mixodectes*."¹ As early as 1915, Matthew (p. 467) had rejected any similarity of *Metoldobotes* to any mixodectid. Patterson (1965) placed the Fayum genus in the Macroscelidinae of the African macroscelidids, an action that is certainly correct. *Metoldobotes* has no affinity with mixodectids beyond the fact that both are eutherian mammals.

***Mixodectes pungens* Cope, 1883**

Plate 17, figures 1-4, plates 18-20, plate 21,
figures 1-3, plate 22, figures 5, 6;
text figure 3

Mixodectes pungens COPE, 1883a, p. 559.

Mixodectes crassiusculus COPE, 1883a, p. 560.

Olbodotes copei OSBORN, 1902, p. 205.

TYPE: A.M.N.H. No. 3081, fragmentary left mandible with P_2 - M_3 ; collected from Nacimiento beds (presumably from the *Pantolambda* zone) of the San Juan Basin, New Mexico.

HYPODIGM: The type and A.M.N.H. Nos. 2385, 2432, 2434, 2451, 2480a, 2557b, 3082, 3083, 3085, 3087, 3088, 3997, 8227, 8233,

12381, 15988, 16012, 16015-16017, 16018, 16020-16022, 16038, 16531, 16532, 16593-16597, 16727, 17033, 17071, 17032, 17723, 22651, 22652, 25576, 45775-45779, 45795-45800; U.S.N.M. Nos. 15389, 15391-15399, 15501, and uncatalogued specimens with original Nos. 155, 156, 164; all collected from the Nacimiento Formation in the San Juan Basin, New Mexico.

SPECIFIC DIAGNOSIS: Although *M. pungens* is distinctly larger than *M. malaris*, the morphology of the dentition of the two species is virtually identical.

DESCRIPTION: As the hypodigm indicates, this species is known from a relatively large number of specimens, although they are mostly fragmentary mandibles with only one or two teeth. Of the two lower incisors the median one is more enlarged than the one lateral to it. The condition seen in A.M.N.H. No. 2557b (see pl. 17, figs. 1-4), namely, the extreme elevation of the median incisor in relation to the mandible and the incisor lateral to it, is exaggerated by the cementing of the median incisor to the mandible in an obviously unnatural position. This must have been done prior to Osborn's (1902) paper, since the specimen is figured there.

The roots of the incisors are transversely flattened; the crown of the lateral incisor ($I_{2(?)}$) is known with some accuracy only in *M. malaris*. $I_{2(?)}$ is flattened against $I_{1(?)}$. The canine and P_1 are absent. P_2 is single-rooted; P_2 and P_3 are simple and premolariform, with a tall protoconid and an incipient posterior heel. P_4 is premolariform, with a strong and high protoconid, a vestigial (rather than an incipient) paracristid, and in some cases a vestigial, tiny paraconid; there is no precingulid. The talonid is small, and there are no cusps or cuspules that can be made homologous with those of the molars. P_4 is the tallest and the most robust of the premolar series.

On the lower molars there is a precingulid, and the metaconid is the tallest of the trigonid cusps. On the talonid the hypoconulid and entoconid are closely twinned; the entoconid is much more distinct and taller than the hypoconulid. The base of the hypoconid extends farther buccally than that of the protoconid. The mesoconid is pronounced and

¹ Schlosser (1910), in introducing the name *Metoldobotes* (without diagnosis or description), obviously committed a *lapsus calami*, meaning to write *Metolbodotes* and expressing what he thought was a similarity to *Olbodotes* (a synonym of *Mixodectes*) of Osborn, 1902. In 1911 Schlosser used *Metolbodotes*. The "misspelled" *Metoldobotes* has, however, priority over the "correct" *Metolbodotes*.

TABLE 2
NUMERICAL DATA FOR SPECIMENS OF *Mixodectes pungens* FROM THE
NACIMIENTO FORMATION OF SAN JUAN BASIN, NEW MEXICO

	N	OR	\bar{X}	S ²	S	V
P ₃						
L	4	2.4-3.0	2.75	—	—	—
PW	4	1.65-2.2	1.99	—	—	—
P ₄						
L	22	3.8-5.2	4.58	.095	.308	6.72
PW	24	2.8-3.7	3.06	.066	.257	8.39
M ₁						
L	17	4.4-5.0	4.67	.025	.159	3.40
PW	16	3.4-4.2	3.77	.040	.202	5.35
AW	17	2.9-3.5	3.46	.030	.173	5.00
M ₂						
L	19	4.5-5.5	4.83	.062	.249	5.15
PW	21	3.5-4.3	3.96	.070	.265	6.69
AW	20	3.0-3.9	3.44	.065	.256	7.44
M ₃						
L	19	5.3-6.5	5.82	.144	.374	6.42
PW	22	3.2-4.1	3.69	.071	.266	7.20
AW	17	2.8-3.6	3.23	.073	.271	8.39
P ³						
L	2	3.3-3.4	3.35	—	—	—
PW	2	2.4-3.4	2.90	—	—	—
P ⁴						
L	9	3.5-6.1	4.34	1.013	1.005	23.15
PW	9	4.0-5.9	5.20	.386	.620	11.92
M ¹						
L	4	4.2-4.7	4.52	.056	.236	5.22
PW	3	5.7-5.9	5.80	.010	.100	1.72
AW	3	5.1-5.6	5.40	.070	.264	4.88
M ²						
L	4	4.2-4.8	4.65	.090	.300	6.45
PW	4	5.7-6.9	6.20	.313	.557	8.98
AW	4	5.4-6.6	5.97	.243	.490	8.20
M ³						
L	2	3.6-4.8	4.20	—	—	—
PW	2	5.0-5.7	5.35	—	—	—

close to the point where the cristid obliqua joins the protocristid. The talonid notch is V-shaped; the bottom of the notch is slightly rounded, and a sharp, low crest runs antero-posteriorly, slightly obstructing the opening of the talonid lingually. The talonids are invariably wider transversely than the trigonids.

There are no known skull fragments that would indicate the nature and number of the upper incisors in *M. pungens*, but there is little doubt that the upper incisors are similar to those in *M. malaris*. P⁴ is premolariform

with a strong paracone and protocone with a distinct preprotocrista and postprotocrista, which run anterobuccally and posteriorly from the apex of the protocone. A homologue of the centrocrista runs posteriorly, then turns sharply anterobuccally. P⁴ has a slight precingulum and postcingulum.

On the molars there is a rather broad stylar shelf divided into an anterior and posterior portion by a strong mesostyle. The hypocone is strong on M¹ and M² but absent from M³; all the molars bear precingula and postcingula. There is a parastylar area, very con-

stricted anteroposteriorly but long transversely. An anterobuccal cuspule on the ectocingulum and preparacrista junction is the stylocone, without much doubt. As stated, the ectocingulum is present, but it is vestigial and discontinuous.

DISCUSSION: Cope (1883a) described two species of *Mixodectes*, *M. pungens* and "*M. crassiusculus*," in the same paper, both type specimens having been collected from the same formation. These two specimens (A.M.N.H. Nos. 3081 and 3085) of the original Cope collection completely lack reliable locality data, but there is little doubt that both were found in the Nacimiento Formation. Matthew (1937) cited the same locality for both "species" but gave the horizon as middle Paleocene for *M. pungens* and late Paleocene for "*M. crassiusculus*." He quoted fully Cope's description of both "species." The differences given by Cope (1883a) were the supposed larger size of "*M. crassiusculus*" and the relatively greater length of the last molar of this "species" than that in *M. pungens*. Both distinctions disappear when one examines all the known specimens of *M. pungens*. The scatter diagrams (see text fig. 3) of M_2 and M_3 do not even suggest the possibility of two distinct size classes that could be used as an argument for the validity of "*M. crassiusculus*." It is quite clear that the type of the latter taxon of Cope is only a large representative of *M. pungens*.

A.M.N.H. No. 4078 (see pl. 27, figs. 9 and 10) is an unusual, isolated upper molar of *Mixodectes* that deserves special mention. The size of the tooth is approximately intermediate between that of *M. pungens* and that of *M. malaris*, but, apart from its unusual size, the specimen differs from these two species of *Mixodectes* in its much more expanded posterobuccal corner above the metacone. This peculiarity resulted from the expansion of the ectocingulum in the area. Whether this specimen represents a new taxon or is an aberrant tooth of *M. pungens* cannot be determined, although the latter appears more probable.

***Mixodectes malaris* (Cope, 1883) Matthew, 1937**

Plate 17, figures 5–10, plate 21, figures 4–11,
plate 22, figures 1–4; text figure 3

Indrodon malaris COPE, 1883c, p. 318.

Mixodectes malaris: MATTHEW, 1937, p. 223.

TYPE: A.M.N.H. No. 3080, exceptionally badly shattered palate and mandible; left upper dentition is recognizable. The type was collected from the *Deltatherium* zone of Osborn (1929, vol. 1) in the Nacimiento Formation of the San Juan Basin, New Mexico. The species is also known from the Fort Union Formation of the Washakie Basin, Wyoming.

HYPODIGM: The type and A.M.N.H. Nos. 833, 3032B, 3080, 4023, 16027, 16584, 16726, 17064, 17066, 17068; U.K.M.N.H. Nos. 7744–7747, 7914, 9516, 9539–9545, 9547–9550, 10591, 13751, 13816, 14009, 14022, 16013, 16019, 16028.

The locality data of the specimens in the collection of the American Museum of Natural History are poor, although it is fairly certain that all the specimens referred to *M. malaris* were collected in the San Juan Basin of New Mexico, from Nacimiento ("Torrejon") beds at various localities and at different times. The more recent collection made by the University of Kansas Museum of Natural History (Wilson, 1951, 1956) has accurate locality data.

SPECIFIC DIAGNOSIS: *Mixodectes malaris* differs from *M. pungens* in being smaller. The former species seems to have a talonid on M_3 that is relatively narrower transversely.

DESCRIPTION: More is known of the enlarged lower teeth of *Mixodectes malaris* than of those of *M. pungens* (see pl. 17, figs. 5–8). Little is known of the crown of the median incisor, but that of $I_{2(?)}$ has a transversely flattened lateral tuberosity on about the same level as the apices of the teeth posterior to it.

With a few exceptions, which are listed below, the lower dentition of *M. malaris* is virtually identical to that of *M. pungens*. On some specimens the talonid of P_4 is quite prominent, with a definite talonid basin. An occasional tiny cuspule on the talonid cannot be recognized to be homologous with any particular cusp or cuspule. The talonid of M_3 is considerably (both absolutely and relatively) narrower transversely than that of the preceding M_2 .

In the discussion of the genus, reference is made to the upper incisors, which are best

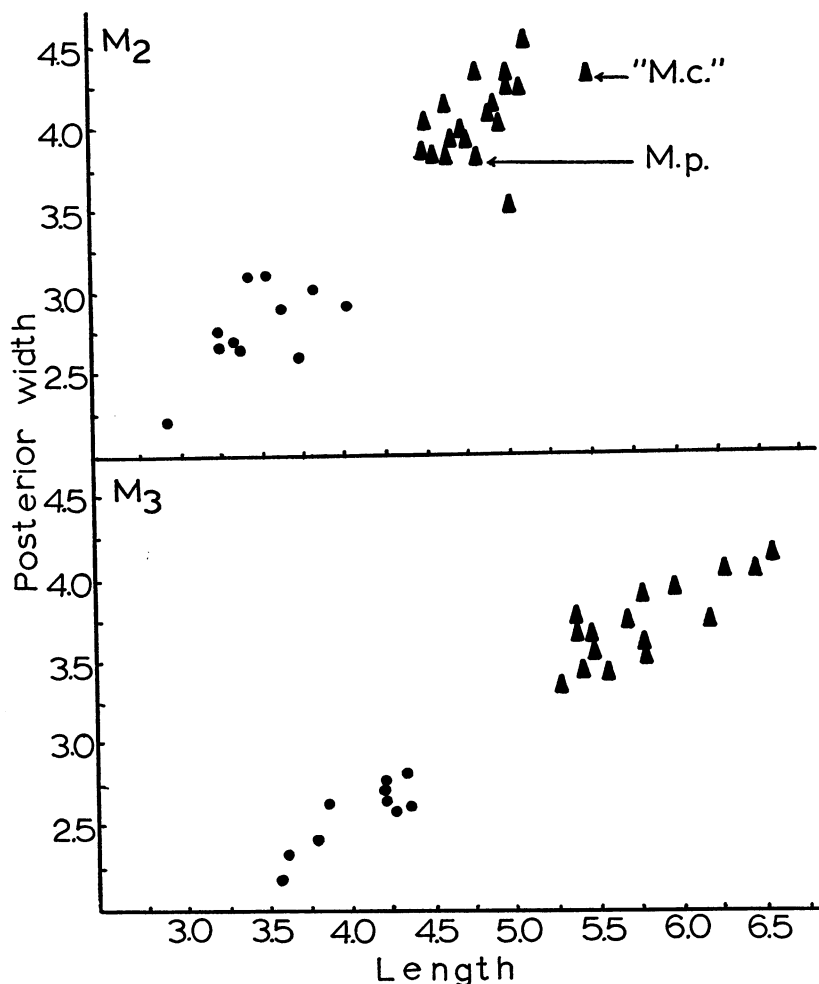


FIG. 3. Scatter diagram of the posterior width/length of most of the known specimens of *Mixodectes pungens* (black triangles) from various localities from the Nacimiento Formation of the San Juan Basin, New Mexico, and of *Mixodectes malaris* (black dots) from the *Deltatherium* zone of the Nacimiento Formation and the Fort Union Formation of the Washakie Basin, Wyoming.

Abbreviations: "M.c.," type specimen of "*Mixodectes crassiusculus*"; M.p., type specimen of *Mixodectes pungens*.

known from the type specimen. There seems to be little doubt that two enlarged lower incisors were present in the species, as in the maxilla of the type. The number of antemolar upper teeth is known only from the type specimen; in addition to the two enlarged incisors there are three antemolar teeth: P^4 , $P^3(?)$, and a tooth with a high buccal cusp (paracone) and lingual shelf, having a general caniniform-premolariform aspect. The anterior upper dentition is rather poorly known, and

the number of antemolar teeth of the species is also not certain. P^3 is also known from two badly broken specimens (U.K.M.N.H. No. 9539; see pl. 17, figs. 9 and 10). The base of the tooth is badly encrusted with the notorious Torrejon matrix, although it seems fairly clear that the base of the tooth was triangular in outline. A crista runs down posteriorly from the apex of the paracone. U.K.M.N.H. No. 13816 shows a faint lingual cingulum around the lingual shelf of P^3 ; there

seems to be no trace of a protocone on this shelf.

The upper molars of *Mixodectes malaris* (see pls. 21 and 22) are very similar to those of *M. pungens*, and consistent differences in the morphology between the two species cannot be noted.

DISCUSSION: Specimens of *Mixodectes malaris* collected by R. W. Wilson for the University of Kansas Museum of Natural History greatly expanded our knowledge of the species and also of the genus *Mixodectes*. On the

basis of the collected material, it is difficult to determine the differences between *M. malaris* from locality 9 and those from locality 13 of the University of Kansas (Wilson, 1951). Because Wilson's (1951) paper was a preliminary report, he did not note the basis for identifying specimens from locality 9 as cf. *M. malaris* and those from locality 13 as *M. malaris*. U.K.M.N.H. No. 13816, a fragmentary palate in extremely hard matrix, in particular (pl. 22), shows that the molars lack an ectocingulum posterior to the meso-

TABLE 3

NUMERICAL DATA FOR SPECIMENS OF *Mixodectes malaris* FROM THE *Deltatherium* ZONE OF THE NACIMIENTO FORMATION, SAN JUAN BASIN, NEW MEXICO, AND SWAIN QUARRY OF FORT UNION FORMATION, WASHAKIE BASIN, WYOMING

	N	OR	X	S ²	S	V
P ₃						
L	3	1.8-2.1	1.93	—	—	—
PW	3	1.25-1.5	1.36	.016	.125	9.19
P ₄						
L	12	2.9-3.3	3.15	.049	.222	7.04
PW	12	1.8-2.4	2.11	.034	.183	8.67
M ₁						
L	6	3.1-3.7	3.44	.050	.224	6.51
PW	8	2.45-3.0	2.61	.033	.182	6.97
AW	6	2.0-2.4	2.20	.028	.167	7.59
M ₂						
L	9	3.2-4.0	3.48	.075	.273	7.84
PW	11	2.65-3.1	2.85	.029	.170	5.96
AW	11	2.2-3.3	2.50	.097	.311	12.44
M ₃						
L	8	3.6-4.4	3.96	.147	.382	9.64
PW	9	2.25-2.8	2.49	.052	.228	9.15
AW	8	1.95-2.45	2.21	.038	.195	8.82
P ₃						
L	2	1.85-1.9	1.87	—	—	—
PW	1	—	1.45	—	—	—
P ₄						
L	1	—	2.65	—	—	—
PW	1	—	3.50	—	—	—
M ₁						
L	2	3.2-3.4	3.30	—	—	—
PW	2	4.1-4.4	4.25	—	—	—
AW	2	3.9-4.1	4.00	—	—	—
M ₂						
L	2	3.35-3.5	3.42	—	—	—
PW	2	4.1-4.35	4.22	—	—	—
AW	2	4.2-4.5	4.35	—	—	—
M ₃						
L	8	3.05-3.7	3.37	.064	.252	7.47
PW	8	3.6-4.1	3.87	.034	.185	4.78

style, but A.M.N.H. No. 833 of the Cope collection has a fairly clearly defined ectocingulum at that point (see pl. 21, figs. 10 and 11). A Torrejonian mammal assemblage from the Fort Union Formation in the Washakie Basin collected by the American Museum of Natural History in 1963 and 1964 (see Szalay, 1965) yielded, among many other specimens, about nine well-preserved upper molars of *M. malaris* which resolve this minor taxonomic difficulty. Among the nine molars, all from the same locality, the conditions exhibited by both U.K.M.N.H. No. 13816 and A.M.N.H. No. 833 are represented. In the Fort Union collection there are specimens without an ectocingulum posterior to the mesostyle and also specimens with an ectocingulum. Unfortunately lower teeth from the Fort Union Formation, Swain Quarry, are not abundant enough (only two M_3 's) to be compared meaningfully with the sample from the Nacimiento Formation.

The known specimens presently allocated to *Mixodectes malaris* come from several different localities and two different formations. Although they appear to be homogeneous as far as dental morphology and the size range of the teeth are concerned, there are some subtle clues concerning the relative thickness of the known mandibular fragments which cannot be successfully correlated with the age of the individuals (i.e., juvenile, adult, and senile, and the complete spectrum between these artificial categories, as can be inferred from dental wear). On the other hand, there is no meaningful way that I can determine to base more than one species on the available sample. Differences in the thickness of various mandibles may well reflect the fact that the individuals involved may have belonged to different demes of the same species living at the various localities. It is quite conceivable, however, that the degree of variation in the depth of the mandible is within the confines of intraspecific variation for *M. malaris*. The well-defined size distribution (see table 3 and text fig. 3) and the relatively similar morphology of the teeth from one locality to those of another may very well mean that the scattered sample of these animals, here recognized as a single paleontological species, represents the remains of a once truly biological species that inhabited

an area stretching at least from southern Wyoming to the southern half of New Mexico.

ELPIDOPHORUS SIMPSON, 1927

Elpidophorus SIMPSON, 1927, p. 5.

TYPE SPECIES: *Elpidophorus elegans* Simpson, 1927.

INCLUDED SPECIES: The type and *Elpidophorus minor*.¹

KNOWN DISTRIBUTION: The Tiffanian and Torrejonian of western North America.

GENERIC DIAGNOSIS: *Elpidophorus* differs from *Eudaemonema*, *Mixodectes*, and *Dracontolestes* in that the lower teeth lean much more anterolingually. *Elpidophorus* has much stronger cingulids on the lower teeth than any of the other recognized genera of the family. The premolars of this genus are the most molariform in all mixodectids. The trigonid basin of the molars is shallower than that of *Eudaemonema*, *Mixodectes*, and *Dracontolestes*. The genus differs from other known genera of mixodectids in having the talonid of M_3 narrower transversely than the trigonid of the same tooth.

Elpidophorus differs from both *Eudaemonema* and *Mixodectes* in having much smaller hypocones on the upper molars.

The portion of the postcristid between the hypoconid and the hypoconulid runs roughly in a straight line, but in the other known genera of mixodectids, least so in *Remiculus*, the homologous cristid is curved. *Elpidophorus* has a much more bulbous paraconule and metaconule than other known mixodectids.

Elpidophorus differs from *Eudaemonema* in having more molariform P_3^3 and differs from *Mixodectes* in having canines and first premolars.

Dental formula: $I^{1(?)2(?)}$, C, P_{1234}^{1234} , M_{123}^{123} .

DISCUSSION: A.M.N.H. No. 35963 (see pl. 27, figs. 7 and 8) is an almost complete maxilla-premaxilla fragment of *Elpidophorus elegans*, and it is the only specimen to show the nature of the teeth anterior to the premolars adequately. Although a premaxilla-maxilla

¹ *Elpidophorus patratius* is a synonym of *E. elegans*, as is discussed below. *Elpidophorus minutulus*, described by Dorr (1958), is a specimen of the erinaceoid *Leptacodon* cf. *L. ladae*, as discovered by Peter Robinson (personal communication) and confirmed by me after examining the specimen from the Hoback Formation.

suture cannot be ascertained, it is very likely that the tooth posterior to the two enlarged incisors is the canine and not the third incisor. The area posterior to the presumed canine (only the root is preserved) is fragmentary, and it is possible that this area held a very reduced canine anterior to the P^1 , which would make the canine, as presently identified, the third incisor. A close examination of plate 27 will reveal the problem involved.

It seems fairly reasonable to assume that the association of a unique upper incisor, along with several isolated teeth of *Elpidophorus*, with A.M.N.H. No. 33857, a mandible of *Elpidophorus elegans*, is reliable. The incisor is far too large to belong to any known paromomyid, and, although the tooth bears great adaptive similarity to the known upper incisors of *Plesiadapis*, a brief examination shows that convergence is involved. The tooth associated with *Elpidophorus* is distinct. The three-pronged incisor of *Elpidophorus* also shows adaptive convergent similarity to the upper incisor of *Saxonella* (and that of the multituberculate *Eucosmodon*). A distinct feature of the associated incisor is a crown that is laterally broader and more spatulate than that of *Plesiadapis* and that of *Saxonella*. There is a laterally placed lobe or cusp on the mixodectid incisor, but the analogous structure is on the posterior surface of the more transversely constricted crown of the plesiadapid incisor. Text figure 4 and plate 26 (figs. 3–6) of this paper, and figures 355–359 in Stehlin (1912–1916) and those in Matthew (1917), should be consulted for a critical comparison of the incisor structure of *Elpidophorus* and that of *Plesiadapis*. D. E. Russell (1964, pl. 8) figured upper incisors of *Saxonella*, presumably correctly associated.

It may be noted here that Simpson (1936, p. 15) suggested that the closest ally of *Elpidophorus* was *Cynodontomys*, although he immediately remarked that *Elpidophorus* could not be ancestral to the latter. Although the most primitive species of *Cynodontomys* (= *Microsyops*) were not then known, whatever was known of the Eocene genus did not justify the statement. Simpson suggested *Eudaemonema* as an ideal ancestor for both, but pointed out that the very large hypocone of *Eudaemonema* barred this genus from being

a probable ancestor. The degree of resemblance of *Elpidophorus* to *Eudaemonema* is discussed under *Eudaemonema*.

McKenna (1960, p. 79) removed *Elpidophorus* from the Mixodectidae and placed it in the ?*Plesiadapidae*, *incertae sedis*. He did not justify his action by any argument or discussion. It is appropriate to point out here that *Elpidophorus* is unlike *Mixodectes* and *Eudaemonema* in many respects, the latter two genera representing the Mixodectidae, *sensu stricto*. There are no known mandibles of *Elpidophorus* in which the condition of the dentition anterior to the canine is shown. Judged from the upper incisors, the lowers were presumably also enlarged, but proof for mixodectid-like enlarged lower incisors is still wanting. The P^2 – P_4 anteroposterior shear of *Elpidophorus*, described in detail under tooth occlusion, is unique among mixodectids, although it may have been present in *Remiculus*. M_3 of *Elpidophorus*, with a narrow talonid, is unusual for a mixodectid and more common in primates. In spite of the unique morphology of *Elpidophorus* in comparison with that of *Mixodectes* and *Eudaemonema*, it is almost certainly a mixodectid and only superficially resembles plesiadapids. *Elpidophorus* is certainly not a primate.

Elpidophorus elegans Simpson, 1927

Plate 24, figures 1, 2, plate 26, figures 3–10, plate 27, figures 1–8; text figures 4 and 5

Elpidophorus elegans SIMPSON, 1927, p. 5.

Elpidophorus patratius SIMPSON, 1936, p. 11.

TYPE: A.M.N.H. No. 15541, fragment of right ramus of a young specimen, with M_{1-2} . The type was collected from the Paskapoo Formation, Red Deer River, Alberta.

HYPODIGM: A.M.N.H. Nos. 15541, 15542, 33856–33863, 33899–33902, 35963. In addition to the type locality, the species occurs in the Scarritt Quarry in Montana.

SPECIFIC DIAGNOSIS: *Elpidophorus elegans* is larger than *E. minor*. The main morphological difference of the former species from the latter is the apparent lack of a mesoconid in *E. minor*. Because only the type specimen is known in the latter species, this distinction may disappear once additional specimens are collected. *Elpidophorus elegans* appears to have a cuspule on the portion of

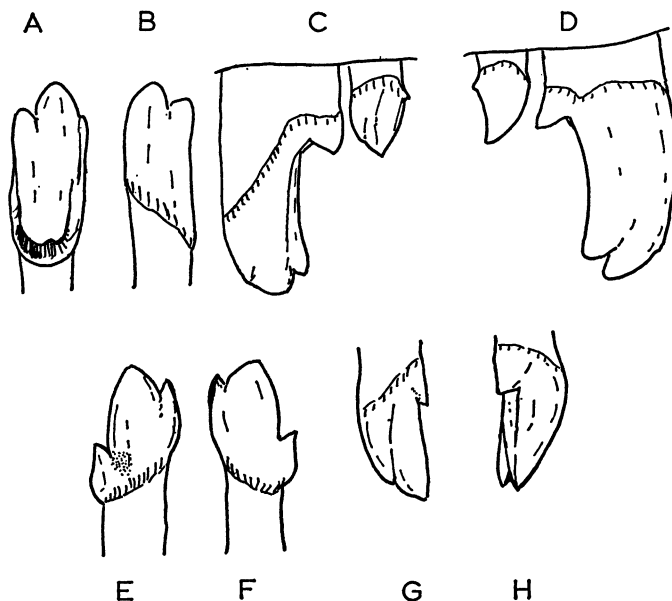


FIG. 4. Comparative aspects of upper incisors of *Plesiadapis* and *Elpidophorus*. A-D. *Plesiadapis gidleyi* (A.M.N.H. No. 17404) from Mason Pocket. E-H. *Elpidophorus elegans* (A.M.N.H. No. 33857) from Scarritt Quarry. The adaptively similar incisors are the result of convergence. On C and D the incisor of *Plesiadapis*, posterior to the enlarged incisor, is shown.

the postcristid between the hypoconid and hypoconulid.

DESCRIPTION: Nothing is known of the lower incisors of *E. elegans*. In addition to the two lower jaw fragments with the lower molars from the Paskapoo beds, A.M.N.H. Nos. 15541 and 15542, the lower dentition is best known from A.M.N.H. 33856 (pl. 27, figs. 1, 2; pl. 26, figs. 7, 8), a right mandible from the Scarritt Quarry. No teeth are known in detail anterior to P_2 . P_2 is almost as wide transversely as long, has a sharp cristid running anteroposteriorly, and an incipient but almost complete cingulid is evident around the teeth.

P_3 is very wide transversely and has an incipient but recognizable paraconid. A strong cingulid is continuous around the tooth. Posteriorly this cingulid is strongly thickened and it is rather high. P_4 is almost completely molariform, and its trigonid is anteroposteriorly longer, not so compressed but more robust, than the trigonids of the molars. The trigonid is widely open anterolingually, and

its cusps are wide-based, their size approximately the same, although the metaconid is the strongest and the paraconid is the smallest. The talonid is smaller than the talonids of the molars and lacks a hypoconulid. The tooth has the precingulid, postcingulid, and buccal cingulid continuous.

On the lower molars the talonids are much wider transversely than the trigonids, and the trigonid basin is closed off on all sides. The molars lean strongly anterolingually. The metaconid is the tallest cusp. A not very prominent mesoconid is present, and a cuspule similar in size to the latter is found on the postcristid between the hypoconid and hypoconulid. The hypoconulid is rather small, and it is well below the level of the more lingual and much more prominent entoconid. The enamel is wrinkled and rugose at the base of the posterior wall of the trigonid. A precingulid, postcingulid, and buccal cingulid border the molars as in the fourth premolar. The cingulid is occasionally missing at the buccal base of the hypoconid.

The talonid of M_3 is less wide than the trigonid, an unusual feature not found in other mixodectids. In *Remiculus* the M_3 is not known.

The lingual notch on the lower molars is V-shaped, with the angle between the arms of the V between 80 and 90 degrees. There is a small extension of the posterolingual base of the metaconid, which is converted into a vertical, thin crest which partially closes off the talonid basin lingually.

The enlarged, presumably median upper incisor (pl. 26, figs. 3-6; text fig. 4) was found in Scarritt Quarry in association with A.M.N.H. No. 33857, which is a mandible and several isolated teeth of *E. elegans*. The crown, resting on a long and stout root, is wide transversely, anteroposteriorly somewhat flattened, with three distinct lobules. These lobules on the spatulate-shaped crown are as follows: the lateral one is the smallest and is the most dorsally situated on the crown; the median (most medial of the three cusps) one is the largest, broadest,

and extends down the most ventrally. This cuspsule is considerably smaller than the adjacent middle one. The horizontal section of the root is more or less circular in outline.

A.M.N.H. No. 35963 is a left premaxilla-maxilla fragment showing at least alveoli of the entire upper dentition (pl. 27, figs. 7 and 8). The most anterior incisor, which was probably the most median one also, is represented by half of the alveolus. This alveolus is much wider in diameter than the one of the incisor following it. The third tooth was presumably the canine, much smaller than either of the incisors. Only the root of the canine is preserved. It cannot be determined whether P^1 was single- or double-rooted.

P.U. No. 17637 shows the morphology of the second upper premolar (see pl. 27, figs. 4-6). This tooth is double-rooted, almost completely rounded, and has a rather tall, sharp-crested paracone. In addition to the latter specimen, which shows well-preserved P^3 and P^4 , is P.U. No. 17639, in which P^3 - M^3 are excellently preserved, showing the inter-

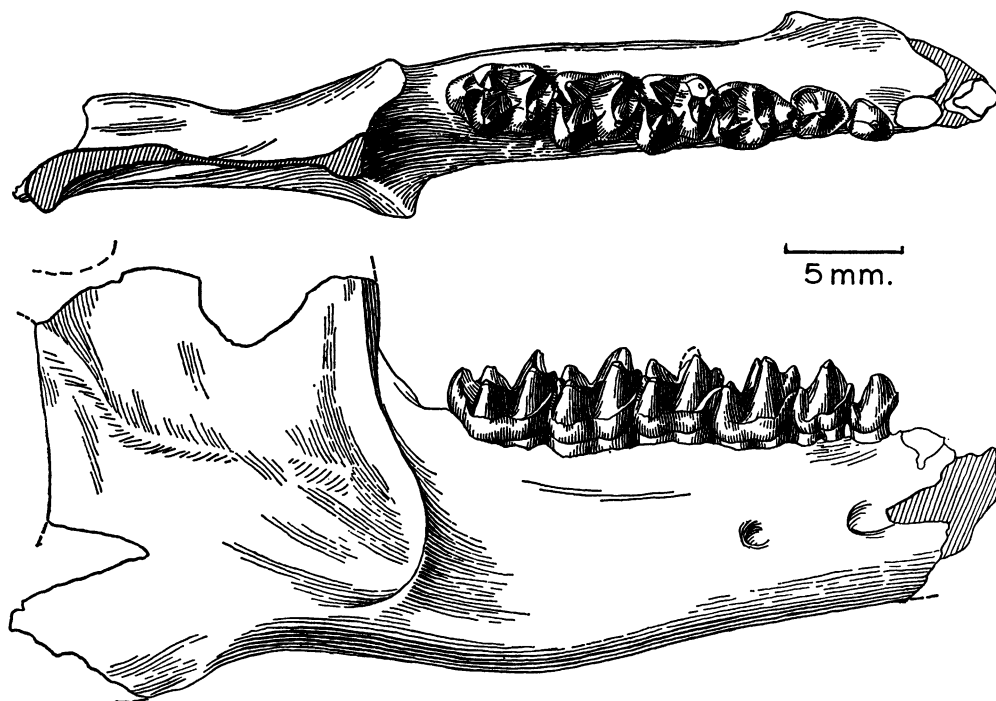


FIG. 5. *Elpidophorus elegans*, almost complete right mandible with P_2 - M_3 , A.M.N.H. No. 33856, Tiffanian Scarritt Quarry, Montana. *Top*: Occlusal view. *Bottom*: Lateral view. Slightly modified from Simpson (1936). $\times 6$.

TABLE 4

NUMERICAL DATA FOR SPECIMENS OF *Elpidophorus elegans* FROM THE PASKAPOO FORMATION OF ALBERTA AND FROM THE SILBERLING QUARRY OF THE FORT UNION FORMATION, MONTANA

	N	OR	\bar{X}	S ²	S	V
P ₁						
L	2	—	1.80	—	—	—
PW	1	—	1.40	—	—	—
P ₂						
L	1	—	2.60	—	—	—
PW	1	—	2.30	—	—	—
P ₃						
L	4	3.2-3.6	3.42	.043	.206	6.02
PW	4	2.4-3.0	2.65	.063	.252	9.50
AW	4	2.5-2.7	2.60	.007	.081	3.11
M ₁						
L	6	3.2-3.7	3.55	.035	.187	5.26
PW	5	3.2-3.5	3.32	.017	.130	3.91
AW	5	3.0-3.2	3.06	.008	.089	2.90
M ₂						
L	4	3.2-4.0	3.62	.123	.350	9.66
PW	4	3.4-3.6	3.47	.009	.096	2.76
AW	5	3.1-3.4	3.26	.013	.114	3.49
M ₃						
L	6	4.3-4.8	4.57	.267	.518	11.33
PW	6	2.6-2.9	2.78	.014	.117	4.20
AW	5	2.6-3.1	2.92	.047	.216	7.39
P ²						
L	2	1.9-2.3	2.10	—	—	—
PW	2	1.65-1.7	1.67	—	—	—
P ³						
L	3	3.35-3.9	3.55	—	—	—
PW	2	3.75-3.8	3.77	—	—	—
P ⁴						
L	5	3.6-3.95	3.79	.021	.145	3.82
AW	4	4.5-4.9	4.72	.029	.171	3.62
M ¹						
L	4	3.7-4.0	3.82	.016	.125	3.27
PW	3	4.3-5.3	4.90	.280	.529	10.79
AW	4	4.9-5.6	5.20	.100	.316	6.07
M ²						
L	4	3.6-3.9	3.77	.023	.150	3.97
PW	2	4.8	4.80	—	—	—
AW	3	5.2-6.0	5.50	.190	.436	7.92
M ³						
L	2	2.8-3.2	3.00	.080	.283	9.43
PW	1	—	4.40	—	—	—
AW	2	4.9-5.0	4.95	.005	.070	1.41

relationship of the dental battery posterior to P² (pl. 27, figs. 1-3). P³ has three roots, a prominent paracone, and a less tall metacone, the latter two forming an anteroposterior shearing surface that works against the paracristid of the P₄. There are a parastyle and

a rather small protocone. P³ is roughly triangular in outline. P⁴ is a semimolariform tooth, lacking a mesostyle, and, although it has a robust paraconule and metaconule, it also lacks the postparaconule crista and the premetaconule crista. In some species a cingu-

lum surrounds the entire tooth. It may be noted that both the P^3 and P^4 are as long as the first or the second molar.

The molars have very strong, robust, bulbous conules; the paracone and metacone are about equal in size. The bulbous, broad-based, relatively low protocone is on the anterior half of the tooth, lingual to the paracone. The trigon basin of the molars is rather shallow. Both the paracrista and the metacrista run long and transversely and the two elements of the centrocrista, which also run transversely, are continuous with the very strong mesostyle. An enamel fold runs down on the buccal slopes of both the paracone and the metacone onto a relatively wide stylar shelf. Strong parastyles are present on the molars. The hypocone is rather small and unimportant.

M^1 is a slightly smaller tooth than M^2 , and the paracone of M^1 has a relatively smaller stylar shelf. M^3 has an exceptionally large parastyle, whereas the mesostyle and the metacone are rounded off posterobuccally.

DISCUSSION: The specimens described as "*Elpidophorus patratius*" from the Scarritt Quarry of Montana by Simpson (1936) clearly belong to *Elpidophorus elegans*, described by him in 1927. There is no meaningful difference in morphology and size range between the Paskapoo specimens from Alberta (A.M. N.H. Nos. 15541 and 15542) and the sample from Scarritt Quarry. Various features cited by Simpson (1936, p. 11) in the specific diagnosis of "*E. patratius*" are either incorrect or appear meaningless in the light of the fact that only one of each of the lower molars is known from the Paskapoo Formation. The range of individual variation of the teeth from Scarritt Quarry clearly encompasses the supposed specific differences between the Alberta and Montana individuals. In diagnosing "*E. patratius*," Simpson cited the jaw of *E. elegans* as being more shallow than that of the Montana sample. The type of *E. elegans* was an immature individual in which the thickness of the mandible had not reached its full development, as is clearly indicated by the position of the alveoli for M_3 relative to the coronoid process in comparison with the condition in the paratype (A.M.N.H. No. 15542) from the same locality. The mandible of the latter specimen is much deeper than

that of the type, in spite of dorsoventral crushing of the paratype. The relation of M_3 to the coronoid process on the paratype mandible is exactly the same as that of any M_3 in mandibles of adult specimens from Montana. In the Paskapoo type the M_3 was relatively closer to the coronoid process than in the paratype or in other Montana specimens. The relatively poorer development of the masseteric fossa on the type compared with the same structure on the paratype and the Montana specimens also supports the view that the claim of a specific difference between the Alberta and Montana sample was due to the failure to consider the less mature condition of the type mandible.

Elpidophorus minor Simpson, 1937

Plate 24, figures 3-6

Elpidophorus minor SIMPSON, 1937, p. 133.

TYPE: P.U. No. 14201, fragmentary left mandible with P_3 - M_2 .

HYPODIGM: Type only; collected from the Torrejonian Silberling Quarry, Crazy Mountain Field, Montana.

SPECIFIC DIAGNOSIS: This species is most clearly distinct from *E. elegans* in its smaller size and in lacking a mesoconid. The cuspule that is present on the postcristid between the hypoconid and hypoconulid on *E. elegans* is absent from the type of *E. minor*.

The dimensions (in millimeters) of the type are as follows:

	P_3	P_4	M_1	M_2
L	2.05	2.85	2.80	3.10
PW	1.40	1.80	2.50	2.85
AW	—	1.80	2.30	2.65

DESCRIPTION: This poorly known species is similar to *E. elegans* in the details of its known structure. The effect of the field of molarization is approximately the same in both species. As noted, only the type specimen is known, which drastically limits our knowledge of the dentition.

The P_4 has a large and a smaller cuspule on the postcristid between the entoconid and hypoconid. *Elpidophorus elegans* lacks these unidentifiable cuspules, but, on the basis of the type specimen only, the nature of the talonid of P_4 in *E. minor* cannot be accurate. The lower cheek teeth seem to lean slightly

less anterolingually than do those of *E. elegans*. On the molar talonids of *E. minor* there is neither a mesoconid nor the cuspule found between the hypoconid and hypoconulid of *E. elegans*. The enamel appears to be less wrinkled on the molars than on those of the latter species. The lingual notch is of exactly the same shape in both species, i.e., V-shaped. The small crest observed in *E. elegans* at the base of the metaconid to close off the talonid is also found in *E. minor*.

DISCUSSION: Simpson's (1937) diagnosis of this species, based on the type specimen, is not very meaningful if one considers the variation in *E. elegans*. *Elpidophorus minor* precedes *E. elegans* in time, and lacks a few features (e. g., the mesoconid) that the younger species has. It is best to quote Simpson on his opinion of *E. minor* (pp. 134-135): "The species is very distinct from the later *E. patratius* of this field, and it will probably prove to be generically different, but they are certainly allied and the present data do not seem to warrant generic definition. *E. minor* resembles *Eudaemonema* more than does *E. patratius*, but it is closer to the latter than to *E. cuspidata* and shows the *Elpidophorus* line to have been distinct at this time."

On the basis of what is known of the lower dentition, I cannot agree with Simpson that *Elpidophorus minor* is probably generically distinct from *E. elegans*. It is slightly more primitive, but otherwise is a morphologically standard species of the same genus. Additional specimens, particularly of the upper dentition, of course, may alter the view expressed here.

EUDAEMONEMA SIMPSON, 1935

Eudaemonema SIMPSON, 1935b, p. 231.

TYPE SPECIES: *Eudaemonema cuspidata* Simpson, 1935.

INCLUDED SPECIES: Type species only.

KNOWN DISTRIBUTION: The Torrejonian of western North America (Wyoming, Montana).

GENERIC DIAGNOSIS: *Eudaemonema* differs from *Mixodectes* in its dental formula, semimolariform-molariform P_4^4 , and relatively transversely wider and anteroposteriorly more constricted upper molars. The lower teeth differ from those of *Mixodectes* in their lack of a precingulid, in their relatively

smaller size, and in having a relatively larger mesoconid. The cusps of the lower molars, although very similar to those of *Mixodectes*, are more pointed and more distinct.

Eudaemonema differs from both *Mixodectes* and *Dracontolestes* in having a more lingual joining of the cristid obliqua with the posterior wall of the trigonid than do the two latter genera. *Eudaemonema* lacks a precingulid, but *Dracontolestes* has one. The hypoconulid leans lingually on the M_3 of *Eudaemonema* but not on that of *Dracontolestes*.

Eudaemonema differs from *Elpidophorus* in lacking cingulids on the lower teeth. *Elpidophorus* has premolariform-semimolariform P_3^3 , whereas these teeth in *Eudaemonema* are premolariform. *Eudaemonema* has strong hypocones on M_1^{1-2} compared to the weak hypocones on the molars of *Elpidophorus*. In *Eudaemonema* the paraconules are larger than the metaconules; not so in *Elpidophorus*, in which the very strong conules are of about equal size.

Eudaemonema differs from *Remiculus* in having much larger hypocones, in having the paraconule larger than the metaconule, and in having larger mesoconids on the lower molars.

Dental formula: $I_{1(?)2(?)}^{1(?)2(?)}$, C, P_{1234}^{1234} , M_{123}^{123} .

DISCUSSION: When Simpson (1935b, p. 231) briefly described *Eudaemonema*, he noted that "... the ... genus is so distinctive that it may not belong in this family, but it compares more nearly with *Mixodectes*, *Cynodontomys*, and their respective allies than with other genera known to me." Later, Simpson (1937) used *Eudaemonema* and *Elpidophorus* to argue against Matthew's (1915) "splitting" of the "mixodectids" into the Mixodectinae and the Microsyopinae.

Simpson recognized, I believe correctly, that the retention of the canines and the first premolars in *Eudaemonema* is primitive in comparison with *Mixodectes*. On the other hand, he noted, I believe incorrectly, that the premolars of *Eudaemonema* are more advanced (i.e., semimolariform compared with a supposedly primitive premolariform ancestral condition) than those of *Mixodectes*. The nature of the origin of the mixodectid dentition is discussed below in more detail.

McKenna (1960) rejected mixodectid af-

finities for *Eudaemonema* (and also for *Elpidophorus*, although he did not think that the two genera were related, or that they belonged to the same family) and placed the genus in the Tupaioidea, *incertae sedis*.

D. E. Russell (1964) rejected McKenna's (1960) removal of *Eudaemonema* and *Elpidophorus* from the Mixodectidae. Russell cited detailed evidence to demonstrate the close similarity of *Remiculus* to *Eudaemonema*. Recently Van Valen (1965a, p. 140) stated that the closest relatives of *Eudaemonema* are "... without much question, the late Paleocene genera *Elpidophorus* and *Remiculus*." The controversy as to whether *Eudaemonema* is a mixodectid or not is no longer meaningful; there is general agreement that the genus is an undoubted mixodectid. In my opinion, the genus is very probably the most characteristic known mixodectid in respect to all known aspects of the fairly well-known dentition, a view that is discussed below. I question (as did McKenna, 1960) the supposed close similarity of *Eudaemonema* and *Elpidophorus*, first stated by Simpson (1936), not as resolutely as later by Van Valen (1965a). Simpson's conclusion was mainly based on the nature of the premolars and the presumably similar tooth formulas of the two genera. Although both *Eudaemonema* and *Elpidophorus* have semimolariform-molariform fourth premolars, these teeth in the two taxa are quite different and function differently. The molar pattern of the two genera are not similar.

These differences of the molars are cited in the generic diagnosis. On the other hand the molar teeth of *Eudaemonema* and *Mixodectes* are constructed similarly, much more similarly, in my opinion, than those of *Eudaemonema* and *Elpidophorus*. *Remiculus*, as is discussed under that genus in greater detail, seems closer to *Eudaemonema* than to *Elpidophorus*. In the case of *Eudaemonema* and *Mixodectes* I prefer to favor the similarity of the molar patterns as indicative of a resemblance (and relationship) closer than the more primitive dental formula shared by *Eudaemonema* and *Elpidophorus*.

Eudaemonema cuspidata Simpson, 1935

Plate 25, plate 26, figures 1, 2

Eudaemonema cuspidata SIMPSON, 1935b, p. 231.

TYPE: U.S.N.M. No. 9314, left mandible with canine and P_2-M_3 , collected from the Gidley Quarry of the Fort Union Formation, Montana.

HYPODIGM: A.M.N.H. Nos. 35817-35840, 35845; U.S.N.M. Nos. 9311, 9313-9317, 9558, 9670, 9811. The hypodigm was collected from the Torrejonian Gidley Quarry; the species also occurs in a collection made by M. C. McKenna from bed 17 of the Shotgun Member of the Fort Union Formation, Wyoming (see Keefer and Troyer, 1964, for exact locality).

SPECIFIC DIAGNOSIS: Same as the generic diagnosis; only known species of the genus.

DESCRIPTION: There are no specimens in which the lower incisors are preserved, although several specimens, particularly U.S. N.M. Nos. 9314 and 9317 (see the former on pl. 25, figs. 1-4), have the alveoli of these teeth well preserved. These specimens show that the teeth were enlarged, procumbent, the median tooth larger than the one lateral to it, and that the roots were transversely flattened as in *Mixodectes*.

The type is the only specimen that shows adequately the structure of almost all the lower teeth (see pl. 25, figs. 1-4).

The slightly procumbent lower canine is larger than the following P_1 and has a root round in cross section, although the crown that bears the anteroposteriorly running cristid is transversely flattened.

Judged from the alveolus of P_1 , this tooth is only slightly smaller than P_2 . The crown of P_1 , broken off from the type, is not known. The crown of P_2 is very similar to that of the canine in being somewhat constricted transversely and in having the anteroposteriorly running cristid. P_3 is double-rooted, the posterior root being stouter than the anterior one; the crown is completely premolariform. On the semimolariform-molariform P_4 the protoconid and the metaconid are partly confluent, the protoconid being discernibly taller than the metaconid. An incipient paraconid is definitely present; the hypoconulid is fully developed, although the entoconid is low and much smaller than the tall entoconid of the molars. There is no trace of the mesoconid on the cristid obliqua of P_4 .

The largest and tallest cusp of the molar trigonids is the metaconid, the protoconid

being somewhat smaller and less tall. The paraconid is not a distinct cusp *per se*, but it is rather the anterolingual end portion of a somewhat posterolingually sloping shelf closing off the trigonid basin anteriorly. This described condition of the paraconid and the relation of the cusps and cuspules are exactly paralleled in *Mixodectes*. Anterobuccal to the talonid of the molars the hypoflexid is large.

The cristid obliqua, which bears a very prominent mesoconid, joins the protocristid at about the lingual limit of the protoconid. On M_1 and M_2 the entoconid is much larger and taller than the hypoconulid, but on M_3 the hypoconulid lobe is slightly larger than that formed by the entoconid. There are no cingulids on the lower teeth except an occasional (either incipient or vestigial) trace of

TABLE 5
NUMERICAL DATA FOR SPECIMENS OF *Eudaemonema cuspidata* FROM THE
GIDLEY QUARRY OF THE FORT UNION FORMATION, MONTANA

	N	OR	\bar{X}	S ²	S	V
P ₂						
L	1	—	1.50	—	—	—
PW	1	—	1.30	—	—	—
P ₃						
L	5	1.9–2.1	1.96	.008	.089	4.54
PW	5	1.1–1.5	1.38	.028	.167	12.10
P ₄						
L	9	2.6–3.1	2.81	.031	.176	6.26
PW	7	1.7–2.0	1.87	.016	.125	6.68
AW	8	1.6–2.0	1.85	.026	.160	8.65
M ₁						
L	11	3.0–3.5	3.26	.030	.175	5.36
PW	10	2.3–2.8	2.56	.020	.143	5.58
AW	11	2.2–2.6	2.46	.013	.112	4.55
M ₂						
L	11	3.0–3.6	3.33	.036	.189	5.67
PW	11	2.4–3.0	2.65	.031	.175	6.60
AW	10	2.1–2.7	2.44	.034	.183	7.50
M ₃						
L	10	3.8–4.2	3.98	.013	.115	2.89
PW	10	2.3–2.5	2.42	.006	.078	3.22
AW	10	2.0–2.5	2.34	.023	.150	6.41
P ³						
L	2	1.7–1.8	1.75	.005	.070	4.00
PW	1	—	2.20	—	—	—
P ⁴						
L	2	2.8–2.9	2.85	.005	.070	2.45
PW	2	—	3.90	.005	.070	1.79
M ¹						
L	5	3.0–3.5	3.28	.037	.192	5.85
PW	5	4.7–5.1	4.88	.022	.148	3.03
AW	5	4.4–5.0	4.58	.062	.249	5.43
M ²						
L	6	3.3–3.7	3.42	.026	.160	4.67
PW	6	4.5–5.2	4.92	.055	.233	4.73
AW	6	4.3–5.0	4.62	.084	.289	6.25
M ³						
L	3	2.7–3.8	3.20	.323	.565	17.65
PW	3	3.5–4.3	3.83	.173	.412	10.75

the buccal cingulid buccal to the hypoflexid. The lingual notch on the lower molars is much closer in shape to a U than to a V.

No specimens are known that show the dentition anterior to P³. P³ and P⁴ are known only in A.M.N.H. No. 35834, a rather poorly preserved left maxilla (see pl. 26, figs. 1 and 2). The rather small, triangular P³ bears a tall and large paracone and on the unimportant lingual half of the tooth a small protocone. P⁴ is about twice as wide transversely as long and has a distinctly large paracone and metacone. P⁴ bears a parastyle, a faint ectocingulum, incipient paraconules and metaconules, and precingula and postcingula.

The upper molars are rather well known from fair specimens (A.M.N.H. Nos. 35830 and 35817; see pl. 25). The parastyle (it may include the stylocone; see particularly M¹ of A.M.N.H. No. 35830) is strong, and it forms a functional buccal cusp. The styler shelf is broad, and a very strong mesostyle partitions it into a distinct anterior and a smaller posterior portion. The ectocingulum shows the same type of variation as that of *Mixodectes*: in some specimens it is faint and discontinuous but is well defined in others. A slight enamel fold runs down on the buccal side of the paracone and the metacone. A metastyle is present on M¹⁻² but absent from M³, on which the posterobuccal corner of the tooth is smoothly rounded off at the base of the metacone. On each of the molars the paraconule is somewhat stronger than the metaconule, and the paracingulum and metacingulum are strongly defined. The hypocones of M¹ and M², which originate on the postcingula, are large at their base but come to a point that is directed anterobuccally. M³ lacks the hypocone. The precingulum and postcingulum are strong. The two cingula may or may not meet lingually, and the two extremes of this condition are well shown in A.M.N.H. Nos. 35817 and 35830; in the former the precingulum and postcingulum do not meet, although in the latter the cingula form an uninterrupted lingual ledge on the molars (see pl. 25, figs. 5, 6, 8, and 9).

In an over-all view of the known upper dentition, the tooth row from P³ (and probably from the first of the premolars, to judge from the size relationship of the lower homo-

logues) becomes wider transversely at each succeeding tooth all the way back to M².

DISCUSSION: *Eudaemonema* is a monotypic genus, and most of the pertinent information is discussed under the genus. *Eudaemonema cuspidata* occurs in the Torrejonian Gidley Quarry of the Fort Union Formation in Montana and also in the Shotgun Member of the same formation in Wyoming. The species does not occur in the classic Torrejonian localities in the Nacimiento Formation of New Mexico nor in the Torrejonian Swain Quarry of the lower part of the Fort Union Formation in the Washakie Basin of Wyoming. At the localities cited where *Eudaemonema cuspidata* does not occur we find *Mixodectes malaris*, and vice versa (*Mixodectes pungens* has been reported only from the San Juan Basin in New Mexico). Whether this particular distribution of the Torrejonian mixodectids is simply the reflection of different facies or whether it means that *Mixodectes* and *Eudaemonema* were ecologically incompatible are questions not yet solved.

DRACONTOLESTES GAZIN, 1941

Dracontolestes GAZIN, 1941, p. 13.

TYPE SPECIES: *Dracontolestes aphantus* Gazin, 1941.

INCLUDED SPECIES: The type species only.

KNOWN DISTRIBUTION: Late Puercan of western North America (Utah).

GENERIC DIAGNOSIS: *Dracontolestes* differs from *Mixodectes* in the shape of the lingual notch and in having an anteroposteriorly more constricted trigonid. The large hypoconulid lobe on M₃ does not lean lingually as it does in *Mixodectes* and *Eudaemonema*.

Dracontolestes differs from *Eudaemonema* in having a precingulid. In *Dracontolestes* the cristid obliqua joins the postvallid more buccally than in *Eudaemonema* and *Remiculus*.

Dracontolestes differs from *Elpidophorus* in having the talonid wider than the trigonid on M₃ and in having less anterolingually tilted lower molars.

Dracontolestes differs from *Remiculus* in having the entoconid and hypoconulid less separated, a much smaller hypoconulid, an anteroposteriorly much more constricted

trigonid, and the lower molars much less tilted anterolingually.

DISCUSSION: When Gazin (1941) described the genus, he compared it extensively with *Eudaemonema* and *Elpidophorus* but did not mention *Mixodectes*. He summed up his views of *Dracontolestes* (p. 14) as follows: "This new form is possibly closest to the *Elpidophorus* line, but differs most notably in the less accentuated elevation of the inner cusps and in the more widely basined talonids. The differences from *Eudaemonema* that are significant, although not striking, in determining the relationship of this form lie principally in the position of the paraconid and in the distinctly closed talonid basin."

I disagree with Gazin (1941) about the closest relationships of *Dracontolestes*. This poorly known genus is probably the earliest known mixodectid, and it is the closest, if not directly ancestral, form to *Mixodectes* or *Eudaemonema* or both. The supposed difference noted by Gazin, that *Dracontolestes* has wider talonids than *Elpidophorus*, is applicable only to M_3 . The first and second molars of *Elpidophorus* probably have the relatively widest talonids among known mixodectids. *Dracontolestes* also differs fundamentally from *Elpidophorus* in the general orientation of the lower teeth. The lower dentition of *Dracontolestes*, and also that of *Eudaemonema* and that of *Mixodectes*, show no tendency toward leaning anterolingually as do (strongly) the lower molars of *Elpidophorus* and *Remiculus*. The strong ectocingulid and postcingulid of *Elpidophorus* and *Remiculus* are not represented on *Dracontolestes* or on *Eudaemonema* and *Mixodectes*.

***Dracontolestes aphantus* Gazin, 1941**

Plate 23, figures 1-4

Dracontolestes aphantus GAZIN, 1941, p. 13.

TYPE: U.S.N.M. No. 16180, fragment of left ramus with M_3 and the talonid of M_2 .

HYPODIGM: The type and U.S.N.M. No. 15719, both collected from the Joes Valley Member, North Horn Formation, Emery County, Utah. See Gazin (1941) for exact locality data.

SPECIFIC DIAGNOSIS: Only known species of the genus. The dimensions (in millimeters) of the type specimen are:

	M_2^1	M_3
L	2.4	3.45
PW	2.3	2.0
AW	—	2.0

DESCRIPTION: Only M_3 and the talonid of M_2 are known. A precingulid is definitely present, and the paraconid, although distinct, forms a narrow shelf close to the anterior wall of the metaconid. The latter cuspid is slightly the highest of the trigonid cusps.

A mesoconid is clearly present on the talonid of M_2 and somewhat less distinct on M_3 . The hypoconulid is small, and it is tightly butted against the entoconid. The talonid basin is slightly closed off with a low extension of the entocristid. The hypoconulid lobe on M_3 does not lean either buccally or lingually. The talonid of M_2 appears to be relatively wider than that of M_3 (the two known specimens are too poor to be accurately determined). The posterior outline of the lingual notch is posteriorly inclined, whereas the anterior portion tends to be vertical.

DISCUSSION: I agree with Gazin (1941, p. 14) in referring U.S.N.M. No. 15719 to *Dracontolestes aphantus*.

REMICULUS D. E. RUSSELL, 1964

Remiculus D. E. RUSSELL, 1964, p. 72.

TYPE SPECIES: *Remiculus deutschii* D. E. Russell, 1964.

INCLUDED SPECIES: Type species only.

KNOWN DISTRIBUTION: Thanetian of Europe.

GENERIC DIAGNOSIS: *Remiculus* is unique among mixodectids in having a relatively large stylar area, a distinct stylocone, and probably the broadest stylar shelf. It also appears to be the only genus among mixodectids that has a distinct paraconid and not a "paraconid shelf" as is usually the case. The trigonids of this genus appear to be more procumbent than those of other mixodectids, with the probable exception of *Elpidophorus*.

Remiculus (if the lower teeth are correctly allocated to the type species) differs from *Dracontolestes* and *Mixodectes* in its lack of a mesoconid (or, if present, its very small size) and in having a more lingual joining of the

¹ Because the outline of the broken trigonid of this tooth shows up well, fairly accurate measurements were possible.

cristid obliqua with the posterior wall of the trigonid than in the latter genera.

Remiculus differs conspicuously from both *Eudaemonema* and *Mixodectes* in the relatively smaller size of the hypocone. The paracone and metacone are of about equal size in *Remiculus*, but in *Eudaemonema* the paracone tends to be larger. The paracone and metacone of *Elpidophorus* are relatively bulbous and relatively much larger than those of *Remiculus*.

Remiculus differs from *Eudaemonema* in the very small size of a mesoconid or its absence altogether. The latter genus has an exceptionally large mesoconid.

DISCUSSION: In general, D. E. Russell (1964, pp. 73-74) pointed out the major resemblance, and lack of it, of *Eudaemonema* and *Elpidophorus* to *Remiculus*. I believe that Russell was correct in stating that *Remiculus* is closer to *Eudaemonema* than it is to *Elpidophorus*.

Both the lower and upper teeth of *Remiculus* possess characters that are probably very primitive among the mixodectids, namely, a semimolariform-molariform P_4 (if the tooth allocated to the species is correctly referred), with a well-formed talonid; a distinct paraconid (not a shelf, as in other mixodectids); a relatively small mesoconid, or none; a curved, posteriorly convex postcristid (unlike the straight postcristid of *Elpidophorus*); a relatively large parastylar area; a very broad stylar shelf; a stylocone, and tall and pointed paracone and metacone; distinct but not exaggerated precingulum and postcingulum; small hypocone well below the apex of the protocone; and molars that are very wide transversely.

The present restudy of *Dracontolestes* and *Remiculus* differs somewhat from D. E. Russell's interpretation (1964). Russell implied that the similarity between *Remiculus* and *Dracontolestes* is very close and that the only important difference was in the orientation of the cristid obliqua in these genera. He maintained that the cristid obliqua in *Dracontolestes* joins the protolophid (i.e., the posterior wall of the trigonid) much more buccally than in *Remiculus*, *Eudaemonema*, and *Elpidophorus*. In addition to the feature noted by Russell, I find the mesoconid smaller, the hypoconulid relatively larger and

more separated from the entoconid, the cristid obliqua relatively lower, and the lower molars much more anterolingually procumbent than these features are in *Dracontolestes*. Unfortunately the meager evidence available for both *Dracontolestes* and *Remiculus* does not permit any more meaningful synthesis concerning their affinities within the family. It appears probable, however, that *Remiculus* (if a mixodectid) is the most primitive one known insofar as the structure of the molars is concerned.

Remiculus deutschii D. E. Russell, 1964

Plate 23, figures 5-8

Remiculus deutschii D. E. RUSSELL, 1964, p. 72.

TYPE: M.N.H.N. No. CR312, left M^2 .

HYPODIGM: See specimens referred to the species by D. E. Russell (1964, p. 72). All known specimens were collected in the Thanetian Lemoine Quarry at Cernay-les-Reims, France.

SPECIFIC DIAGNOSIS: Only known species of the genus. The following measurements (in millimeters) are from D. E. Russell (1964):

	L	W
M.N.H.N. No. CR1196, M^1	2.9	3.4
M.N.H.N. No. CR312, M_2	3.0	3.9
M.N.H.N. No. CR286, M^2	2.5	3.5
M.N.H.N. No. CR4415, P_4	2.9	1.8
M.N.H.N. No. CR1170, M_1	3.1	2.1
M.N.H.N. No. CR928, M_1	4.0	2.8
M.N.H.N. No. CR274, M_2	2.7	1.9
M.N.H.N. No. CR4417, M_2	3.0	2.2

Judged from the measurements of M.N. H.N. Nos. CR312 and CR1196, it may be that M^2 of *Remiculus* is larger than M^1 , as it is in *Eudaemonema*.

DESCRIPTION: D. E. Russell (1964) has thoroughly described all the specimens referred to this species. In the light of some new knowledge about mixodectids and a slightly different emphasis on form and function of some features, however, I find it necessary to redescribe the dentition of *Remiculus deutschii*. All my observations are based on stereophotographs of the specimens illustrated by Russell (1964) and refuged in this paper through his kind permission.

Of the upper dentition, only M^1 and M^2 are known. M^1 apparently can be distinguished from the molar following it by its

smaller parastyle and relatively shorter length and width. On M^2 the parastyle is large and extends anterobuccally. The stylar shelf of *Remiculus* is exceptionally wide, and the mesostyle tends to be on the posterior half of the tooth. There is a stylocone at the point where the paracrista meets the ectocingulum. A small but very distinct cusplule is present posterior to the mesostyle. This cusplule is essentially part of the ectocingulum; it is present in some specimens of both species of *Mixodectes*. Both the paracrista and the metacrista are long and very wide transversely, and both halves of the centro-crista run rather transversely and connect to the mesostyle. Curiously, the paracone and the metacone tend to point posteriorly, whereas the apex of the protocone is oriented anteriorly. The apex of the protocone is closer to the paraconule than to the metaconule, a feature clearly present, for example, in plagiomenids. The precingulum and postcingulum are weak but present; the hypocone is rather small. The paraconule and metaconule are of about equal size, fairly large, but not so bulbous as in *Elpidophorus*.

With caution D. E. Russell (1964, p. 72) referred to the known specimens of the lower teeth of *Remiculus* as "*attribution incertainne*." The only known P_4 is a worn specimen, but it is clear that the tooth was semimolariform-molariform. The badly worn but discernible hypoconulid and entoconid are characteristically close to each other and displaced somewhat lingually so that the allocation of the specimen is a highly probable one. The metaconid is worn off, and its height in relation to the protoconid cannot be judged. The wear on this tooth is strange, since the protoconid is relatively very little worn compared with the virtually obliterated metaconid. The paraconid is small and seems to be confluent with the strong precingulid.

On the trigonid of the lower molars the protoconid and the metaconid are about equal in height. The paraconid is distinct on the trigonid as a cusp, and not as a shelf as in *Mixodectes* and *Eudaemonema*. The precingulid is strong, but I cannot determine accurately from the stereophotographs whether the small buccal cingulid that borders the hypoflexid continues anteriorly to connect with the precingulid. This is very

probably a variable feature, as is the intensity of cingula in *Eudaemonema*. The hypoflexid is very pronounced, mainly because of the great procumbency of the lower molars and the fact that the cristid obliqua meets the posterior wall of the trigonid lingually, almost as lingually as the notch on the protocrisid. If there was a mesoconid on the cristid obliqua, it was exceptionally small. There are not enough specimens (and those known are all slightly worn at the area in question) to make this determination certain. The talonid basin is closed off by a slight extension of the enamel both from the base of the anterior metaconid and the posterior entoconid. The lingual notch between the trigonid and the talonid is V-shaped but with a slightly rounded bottom to the V.

SUPPOSED PUERCAN MIXODECTIDS

"MIXODECTID A" OF GAZIN, 1941

Plate 24, figures 7-10

Judging from the single tooth reported from the Dragon local fauna, I cannot confirm or deny Gazin's allocation of this specimen to the Mixodectidae. The lower molar (U.S. N.M. No. 16220) is rather strongly procumbent anterolingually. There is a precingulid on the trigonid, but the crucial features of the trigonid itself cannot be evaluated because the protoconid and the metaconid are broken off. The paraconid is small and shelf-like. The cristid obliqua joins the protocrisid approximately at the middle of the latter. It cannot be determined, because of breakage and wear, whether a mesoconid was present or not. The hypoflexid is large, and the hypoconulid is extremely small. The entoconid is relatively smaller than in any mixodectid known to me.

Gazin compared the tooth with teeth of *Elpidophorus* and *Eudaemonema*. The comparison of the single molar talonid with that of various mixodectids, remains, however, inconclusive. The specimen is as different from all known mixodectids as can be determined from a broken tooth. It seems to bear more similarity to hyopsodontids than to mixodectids. The dimensions (in millimeters) of U.S.N.M. No. 16220 are: L, 3.2; PW, 2.8; AW, 2.8.

"MIXODECTID ? B" OF GAZIN, 1941

Plate 23, figures 10, 11

Gazin (1941) reported a broken maxilla fragment with one complete but badly worn molar from the Wagonroad local fauna. The specimen, U.S.N.M. No. 16200, was inaccurately illustrated; it is refigured here on figures 10 and 11 of plate 23.

I believe Gazin came as close to identifying the specimen as seems possible now. The unbroken but badly worn upper molar is truly an enigma. The presence or absence of a mesostyle so characteristic of known mixodectids cannot be determined because of heavy wear on the styler shelf, although from the pattern of wear it seems improbable that there was a mesostyle. There appear to have been rather long and transversely wide paracrista and metacrista, characteristic of mixodectids, erinaceoids, and didelphodontines. The strong and lingually continuous precingulid and postcingulid and the enormous hypocone are especially reminiscent of *Eudaemonema*. I find it unjustifiable either to name the specimen as a new taxon or to allocate the specimen to a genus or to a family. Additional material is necessary before any formal taxonomic step in relation to this Wagonroad specimen can be taken.

The dimensions of the unbroken upper molar are: L, 3.5; PW, 5.1; AW, 4.75.

"MIXODECTIDAE, N. GEN. AND SP." OF
VAN VALEN AND SLOAN, 1965

Van Valen and Sloan (1965) reported the presence of a new genus of mixodectids at the Purgatory Hill locality of the Tullock Formation, approximately late Puercan in age. I have examined the specimen that was supposed to become the type and the remainder of the hypodigm; all these specimens are referable to species of *Protungulatum* of Purgatory Hill, the genus described by Sloan and Van Valen in 1965. The condylarth *Protungulatum* bears no meaningful similarity to mixodectids.

CRANIAL CHARACTERS OF THE
MIXODECTIDAE

No complete skulls of any species that are recognized as mixodectid are known. It is not possible at the present time to give

a coherent account of even the major features of the mixodectid skull from the bits of information extracted from a few fragmentary specimens.

A.M.N.H. No. 35834 is a left maxillary fragment of *Eudaemonema* from the Gidley Quarry. The infraorbital foramen is rather well preserved above P³. The opening is approximately as high as the crown height of P³ from the base of the enamel to the tip of the paracone. It is difficult to determine the extent to which the foramen was transversely flattened. The same foramen of P. U. No. 17637, a left maxillary fragment of *Elpidophorus elegans*, is well preserved. The opening on this specimen is above the P³ of *Elpidophorus*, which is relatively much more molariform than that of *Eudaemonema*. This foramen of *Elpidophorus* appears to be more extensive than that of *Eudaemonema*, although it must be remembered that the comparison is based on one specimen of each taxon. The condition of the infraorbital foramen is not known in any other species of mixodectid.

A.M.N.H. No. 16038 is a skull fragment associated with an identifiable P₄ of *Mixodectes pungens*. The specimen (pl. 21 figs. 1, 2) is the dorsal portion of the posterior segment of the facial skull and the anterior segment of the cerebral cranium. The only surely recognizable feature of this specimen is a rather strong sagittal crest, which originated from two strong temporal lines above the area where the olfactory fossa must have been. I suspect that the skull of *Mixodectes* had superior postorbital processes. Such an inference is based on the somewhat thickened temporal lines well in front of the origin of the sagittal crest itself. It is apparent from both A.M.N.H. Nos. 16038 and 16593 that the skull was constricted between the facial and cerebral segments. The latter specimen allows a few observations concerning the general shape and proportions of the skull in *Mixodectes pungens* (see pl. 21, fig. 3). The transverse palatal width is approximately four-fifths of the reconstructed length of the upper dentition (or, rather, of the palate). The animal must have had a relatively short and broad muzzle in comparison, for example, with a leptictid such as *Prodiacodon* or *Leptictis*. The sharp narrowing of the palate

occurs at P^3 which is more median than P^4 . A.M.N.H. No. 16593 confirms the presence of a strong sagittal crest.

THE MANDIBLE

The mandible is fairly well known in *Eudaemonema cuspidata*, *Elpidophorus elegans*, and *Mixodectes pungens*. The symphysis is unfused in *Eudaemonema* and *Mixodectes*. Simpson (1936, p. 14) stated that the symphysis in *Elpidophorus* (A.M.N.H. Nos. 33856, 33857, and 33899) is much more strongly sutured than the symphysis of either *Eudaemonema* or *Mixodectes*. I cannot state with any degree of certainty whether the symphysis in *Elpidophorus* was mobile or not, although it is very probable that the two mandibles of both *Eudaemonema* and *Mixodectes* could move independently during certain phases of mastication.

The mixodectid mandible is rather deep and stout. The strong and thick horizontal ramus bears considerable adaptive resemblance to that of recent lemurids. There is a striking contrast between the mandible of leptictid insectivores, rather shallow and relatively long, and the shorter and more massive mixodectid one. It is very likely that the heavy and shortened mixodectid horizontal ramus is the result of herbivorous-frugivorous habitus in contrast to the probably more insectivorous mode of life of leptictids.

In the well-preserved horizontal rami of *Elpidophorus elegans* (A.M.N.H. Nos. 33856, 33857, and 33899) there are two not very large mental foramina and occasionally several tiny ones. The posterior foramen is either under P_3 or the anterior root of P_2 . The more anterior one is either under P^2 or slightly anterior to this position. In *Eudaemonema* (A.M.N.H. Nos. 35818 and 35829; U.S.N.M. Nos. 9314 and 9317) there are also two major mental foramina in the same minor range of variation of position as seen in *Elpidophorus*. In both species of *Mixodectes* I can detect only one foramen, which is either under P^2 or under the anterior half of P_3 (see pl. 19, figs. 1, 2, for A.M.N.H. No. 3081; see also A.M.N.H. No. 16018; for *M. malaris* the same condition is shown in U.K. M.N.H. No. 9540). The reduction of a foramen (providing the two mental foramina represent the primitive number) may be cor-

related with the relative shortening of the horizontal ramus in comparison with *Eudaemonema*, for example. Only in *Mixodectes pungens* (U.S.N.M. No. 15396, see pl. 20, figs. 1-4) is there evidence for the position of the mandibular articular condyle. In this species, it seems to have been just barely above the level of the tooth row. As can be seen on plate 20, however, U.S.N.M. No. 15396 has only the base of the condyle preserved. In *Elpidophorus elegans* the condyle may have been relatively slightly higher than in *Mixodectes*. There are some very faint indications on A.M.N.H. No. 33856 (see pl. 24, figs. 1, 2) that the articular condyle may have been on the level indicated on a line drawing of the same specimen (text fig. 5).

Although the masseteric fossa is rather well defined in all mixodectid mandibles in which this feature is preserved, apparently it was more accentuated in *Elpidophorus* than the other genera in which this character is known. A.M.N.H. No. 33857, a mandible of *Elpidophorus elegans* belonging to a relatively young individual, judged from tooth wear, shows an extremely excavated pocket at the anterior part of the masseteric fossa.

There is a characteristic, triangular muscle scar on the anteromedial base of the coronoid process in the mandibles of all specimens of mixodectids. This scar very likely represents the point of insertion for a portion of the temporalis muscle. A homologue of this scar can be seen in almost all early Tertiary insectivore and primate specimens.

In general, it appears that on all mandibles that preserve at least some of the posterior part the base of the angular process was very broad, indicating exceptionally strong pterygoid muscles. No mixodectid mandible is sufficiently well preserved to show the extent and shape of the angle of the mandible.

On the medial side of the ascending ramus a prominent internal pterygoid crest is present in *Eudaemonema*, *Mixodectes*, and *Elpidophorus*, mixodectids that are represented by mandibles in addition to teeth. In *Eudaemonema* and *Elpidophorus* this crest tends to be horizontal, and it is very long. In *Mixodectes* it is much shorter and much more vertical, a change that may be correlated in some way with the relative shortening of the mandible.

On the lateral side of the ascending ramus of A.M.N.H. No. 33856, a right mandible of *Elpidophorus elegans*, there is a long, slightly oblique crest on about the same level as the tooth row. The crest, probably the temporalis profundus crest, runs from the middle of the masseteric fossa to the posterior border of the mandible.

Nothing is known of the postcranial skeleton of mixodectids. The supposed astragalus and femur of *Mixodectes pungens* figured by Osborn (1902, fig. 28) were incorrectly associated with a mandible of *Mixodectes*. These postcranial elements belong to the Torrejonian leptictid *Prodiacodon* (see Szalay, 1966).

TOOTH OCCLUSION

There are some fundamental similarities in the occlusal patterns of mixodectids, palaeoryctids, primitive erinaceoids, leptictids, microsypids, paramomyids, and plesiadapids. The similarities and differences strikingly reflect a community of a probably broad common origin as well as the adaptive differences (and similarities) between these families.

As Van Valen (1966, p. 47) has noted for *Didelphodus*, the occlusion of the mixodectids conveniently can be treated under two not drastically different modes: shearing and grinding. Alternations between the two modes probably occurred, depending on the food and the age of the individual animal. Shear may lose some of its effectiveness as the dentition becomes heavily worn, and this dentition may then serve as primarily an effective grinding device. Only the cutting edges of enamel on the opposing crests are the result of direct tooth-on-tooth contact. The remaining homologous wear facets are largely due to wear by food between the occluding teeth.

There are two alternative ways that can be profitably followed to describe the occlusion: (a) artificially separate wear facets and treat under two headings, the shearing mode and the grinding mode, or (b) describe the wear facets and their occurrence in individuals of different ages, correlate them on the upper and lower teeth, and then comment on the mode responsible for the wear. The former alternative is preferred here, because

it easily lends itself to an organized treatment. The plates in this paper have been selected to show the best available representative sample of the various conditions and stages of wear of the dentitions of the species treated.

Mixodectes and *Eudaemonema* are discussed together because no consistent, major differences have been detected between their respective occlusions. In referring to either of the two genera, I mean either *M. malaris* and *M. pungens*, on the one hand, or *E. cuspidata*, on the other hand. There are greater individual differences in occlusion between individual specimens of either species of *Mixodectes* than an average between the two species. The relative degree of wear from M_1^1 to M_3^3 also fluctuates a great deal, although more often than not the anterior molar is more worn than the one following it.

It is possible to occlude partial maxillae and mandibles and obtain a rather accurate idea, in addition to what is suggested by the actual wear facets, as to which elements of the upper and lower molars were involved in shear. Whenever shear took place, it did so on only one side of the mandible at one time. The shearing occlusion (like that in carnivorous mammals) was a unilateral one; while one side was shearing, the other was not in occlusal contact. Most of the shearing surfaces (i.e., the edges of the various crests) between the upper and lower teeth were roughly transverse in direction. The prevallid-postvallum shear of the molars involved the metacrista, postmetaconule crista, and paracristid, and the prevallum-postvallid shear involved the paracrista, preparaconule crista, and the protocristid. At the time when the trigonid was thrust into the space between the adjacent upper molars, the protocone pounded food into the general area of the talonid basin, and the hypocone crushed into the low shelf formed by the reduced paraconid. When the mandible was at its lateralmost point of the lateral excursion, the portions of the centrocrista on the paracone and metacone sheared against the cristid obliqua and the posterobuccal portion of the postcristid, respectively. The prevallid shear and the postvallid shear did not take place at the same time. When there was prevallid-postvallum contact there was also shear between

the cristid obliqua and the paracone portion of the centrocrista. The paracone commonly grooved out the area of hypoflexid either during this latter contact or during the postvallid-prevallum shear or perhaps during both. Only after slight posterior movement of the mandible relative to the former position was it possible for postvallid-prevallum shear and shear between the premetacrista and the posterobuccal portion of the postcristid to be accomplished.

Very strong wear can be observed in the area slightly buccal to the entoconid and hypoconulid, and occasionally in the deepest part of the talonid. Heavy bands of wear on the lower molars also appear on the cristid obliqua and on the postcristid, in addition to the food wear on the buccal walls of the latter two crests. Apical wear on both the lower and upper teeth is invariably in the line of wear with the various crests connected with the apices of the cusps, and not isolated on the apex itself. In addition to the shear facets on the upper molars, virtually all the crests, including the mesostyle, show wear in most specimens.

It is quite clear that all the wear facets described above are not due to an orderly, crisp occlusion; most of them resulted from food wear as the lower and upper molars moved across one another mediolaterally (ectental) and to some degree anteroposteriorly (propalinal) with food between the opposing tooth rows. In older individuals the trigonid becomes completely worn down to the same level as the talonid, and there is a continuous, smooth, and broad exposure of a slightly concave dentine surface on the buccal half of the tooth from anterior to posterior (pl. 22, figs. 5, 6). It is likely that, when an individual reached this stage of molar wear, the mode of mastication was an irregular mixture of ectental and propalinal grinding, with shear only on the buccal and lingual edges of the opposing molars.

The slightly stronger parastyle, larger hypocone, slightly transversely wider upper teeth, and larger mesoconid of *Eudaemonema* do not seem to make a noticeable difference in affecting the kind of molar occlusion seen in *Mixodectes*. Although the number of individual specimens available of *Mixodectes* is much larger than that of *Eudaemonema*, the

excessive wear on several specimens of *Mixodectes* but not on specimens of *Eudaemonema* may reflect characteristic differences between the two genera and not collecting bias. The less tall and more squared teeth of *Mixodectes* may very well reflect a more frugivorous type of diet than the taller-cusped, transversely wider molars of *Eudaemonema*.

The most striking and noticeable wear on the premolars of *Mixodectes* is on the posterolingual slope of the protoconid of P_4 and on the homologue of the centrocrista and paracrista on P^4 . The centrocrista of P^4 shears against the paracristid and precingulid of M_1 , and the paracrista of P^4 excavates (rather than shears) the posterolingual slope of the P_4 during postvallid-prevallum shear of the molars.

The P_4^4 interaction in *Eudaemonema* is essentially the same as that of the occluding molars, although the prevallid shear on P_4 is considerably reduced compared with that of the molars. Virtually nothing is known of the occlusal relations of the incisors and the premolars anterior to P_4^4 in either *Mixodectes* or *Eudaemonema*.

With the exception of the premolars, the observations recorded on the occlusion and wear in *Mixodectes* and *Eudaemonema* apply with equal weight to *Elpidophorus*. The notable difference between the last-named and the first two genera lies in the presence of a relatively anteroposterior shear between the paracristid on P_4 and the tip of the paracone and metacone of P^3 . This shear is possible because the paracristid of P_4 is relatively elongated anteroposteriorly (as seen in many erinaceoids) and also because P^3 is rather long, slightly longer in its anteroposterior dimension than either P^4 or the individual upper molars.

The only known upper incisor of a mixodectid is that of *Elpidophorus* (see pl. 26, figs. 3-6, and text fig. 4). This upper incisor shows traces of wear on the medial side of the first cusp (the most medial one) and signs of rather heavy excavation (presumably by food between it and the tip of the large medial lower incisor) on the posterior surface of the crown in a concave depression very slightly below the enamel-dentine border. Because of the poor preservation of the crown, no other wear can be ascertained.

TABLE 6
MORPHOLOGICAL DIFFERENCES BETWEEN THE TEETH OF MIXODECTIDAE
AND THOSE OF MICROSYOPIDAE

Mixodectidae	Microsyopidae
In all species a broad stylar shelf and a mesostyle, strongly suggesting that these structures are primitive	From most primitive species a stylar shelf and a mesostyle completely lacking; a large stylar shelf appearing secondarily in late Eocene <i>Craseops</i>
Cusps on both trigon and trigonid tall and piercing, less so in <i>Elpidophorus</i> than in other genera	Cusps on teeth rather low and bulbous; relative to size of teeth, cusps lower than in mixodectids
Metaconid invariably highest cusp on trigonid	Metaconid in no case highest cusp; metaconid and protoconid invariably about equal in height
Two upper and two lower enlarged incisors	Only one enlarged anterior tooth in lower and upper dentitions in <i>Microsyops</i>
Anteriormost enlarged upper incisor apparently spatulate, with small cuspsules as in eucosmodontine multituberculates or in plesiadapids	Enlarged upper incisor a caniniform tooth with no indication of accessory cuspsules or spatulation
Crown of enlarged lower teeth rather constricted transversely; two incisors pressed closely together	Only enlarged lower tooth rather broad at base of crown; in general enlarged lower tooth, as well as upper one, of quite different construction than in mixodectids

TRENDS IN MIXODECTIDS

Because of a lack of reasonably well-preserved skulls or postcranial elements in the family, remarks are necessarily restricted to the characters of the dentition. There are few well-established ancestor-descendent lineages in the Mixodectidae; consequently any deciphering of trends is conjectural.

Elpidophorus minor to *E. elegans* may be considered as representing a phyletic line of rather brief duration, although the extreme paucity of specimens of *E. minor* (a single fragmentary mandible with four teeth) prevents any far-reaching conclusions.

There is little doubt that *Mixodectes*, *Eudaemonema*, *Remiculus*, and *Elpidophorus* represent four distinct lineages, although all four can be easily classified in one family. Of all these genera, it appears that *Remiculus* and *Eudaemonema* display the most primitive molar patterns. The large stylar shelf, the stylocone, the mesostyle, the long and transverse paracrista and metacrista, and the tall metaconid may be primitive features for the Mixodectidae. Whether the Thanetian *Remiculus* has enlarged upper and lower incisors as do *Eudaemonema* or *Mixodectes* has yet to be discovered.

It has been repeatedly noted throughout the mixodectid section of this paper that *Mixodectes* and *Eudaemonema* bear strong resemblances to each other in spite of the differences of the molar and premolar morphology and the reduced number of teeth in the former genus. In its dental formula *Mixodectes* is probably the most aberrant of the genera known from the complete dentition. In spite of the reduced canine and first lower premolar, which are present in *Eudaemonema* and *Elpidophorus*, *Mixodectes* and *Eudaemonema* show the condition of the enlarged lower incisors and the same general pattern of the lower and upper molars. The upper incisors are very poorly known in *Mixodectes* and unknown in *Eudaemonema*. It is likely that, as a result of the reduction of the lower canine and the the first premolar in *Mixodectes*, P_4^4 and the molars became relatively more enlarged in relation to the mass of the mandible in that genus than did those in *Eudaemonema*. Although the individual molars are relatively larger and more robust than those of *Eudaemonema* or *Elpidophorus*, the mandible of *Mixodectes* is not heavier than mandibles of the former genera.

Reduction of teeth in *Mixodectes* is diffi-

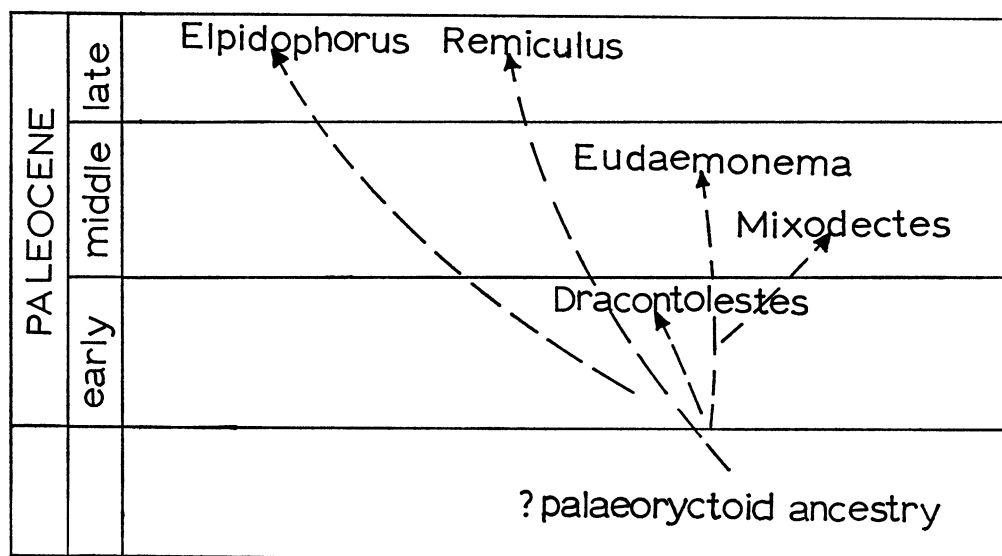


FIG. 6. Conjectural phylogeny of North American and European Paleocene mixodectids.

cult to explain. The loss of the canine (and also probably of P_1) may be due indirectly to the condition of intense incisivation, resulting in large and robust enlarged incisors and a corresponding lessening of the influence of the field of caninization, or a possible posterior shift of the caninization resulting in a premolariform P_4 , or both. The relative size increase of the molars, in comparison with the situation in *Eudaemonema*, which may be very similar to the ancestor of *Mixodectes*, can be explained by the selective advantage of a greater surface area to compensate for the loss of the grinding surface of the presumably primitive semimolariform P_4 of mixodectids.

Whether the late Puercan *Dracontolestes* is in the direct ancestry of either *Mixodectes* or *Eudaemonema* is a futile point to debate when one considers how poorly *Dracontolestes* is known. Nonetheless, if there is any connection between the Puercan genus and any of the Torrejonian genera, then it may be pointed out that the large hypoconulid lobe of the M_3 of both Torrejonian genera leans relatively more lingually than it does in *Dracontolestes*. *Dracontolestes*, as well as *Mixodectes*, has a precingulid, but *Eudaemonema* lacks this feature. Although the approximately synchronous *Mixodectes* and *Eudaemonema* represent slightly different

phyletic lines, these two genera are closer to each other than either is to any other mixodectid, or other mixodectids are to one another.

The molar morphology of *Elpidophorus* shows this genus to be the most advanced of mixodectids. Enlarged lower incisors of the genus are not known, although there were two enlarged upper incisors and a complete eutherian postincisor series. As described under the genus, the larger of the upper incisors (the medial one) is the only mixodectid upper incisor known. The outstanding differences of *Elpidophorus* from other mixodectids, which clearly indicates that this genus represents an independent lineage, are cited under the generic diagnosis.

If some of the common features of *Remiculus* and *Eudaemonema* are taken to represent a hypothetical primitive condition among mixodectids, then a few remarks concerning the possible changes that resulted in the morphology of *Elpidophorus* may be useful. In general, the premolars of *Elpidophorus* were more intensely molarized than those of any other known mixodectid. This molarization is shown particularly on P^3 , which is a three-rooted, triangular tooth with a small metacone in addition to the paracone. The cusps on the molars are relatively less tall and blunter than those of other mixo-

dectids. The very small to absent hypocone may be a primitive feature, as is suggested by the similar condition of *Remiculus*. There is anteroposterior shear between the buccal wall of the paracristid of P_4 and the lingual walls of the cusps of P^3 . There is no such shear in either *Mixodectes* or *Eudaemonema*. Neither a mandible nor a maxilla of *Remiculus* is known, so only the isolated upper and lower molars, and possibly a lower fourth premolar, can be compared with these teeth in other mixodectids.

MIXODECTID AFFINITIES

One of the most important conclusions of this study is that the families Mixodectidae and Microsyopidae are not closely related and almost certainly originated from different ancestral families and very probably from different superfamilies. This conclusion would not be altered even if the microsyopids were recognized as non-primates in the future. Owing to this basic distinctness (demonstrated and discussed below) between mixodectids and microsyopids, most of the earlier views, opinions, and conclusions concerning the mixodectids in a broad sense, i.e., lumping the two families into one, are necessarily unclear, not pertinent, and of no value in the picture that emerges here.

Before the affinities of the mixodectids are examined, it is important to discuss the facts that have resulted in the separation of the Eocene microsyopids from the Paleocene mixodectids. The most obvious morphological differences between the teeth of the two families are listed in table 6. The functional differences in the mode of occlusion are discussed in more detail.

In addition to the major differences cited in table 6, one may mention the relatively large hypocones of *Eudaemonema* and *Mixodectes* (but also the relatively small hypocone in *Remiculus*) and the unimportant hypocone in microsyopids. It is likely that molariform P_4^4 are primitive in mixodectids, but the opposite is almost certainly true of microsyopids as they are presently understood.

There are important differences in the mode of occlusion and the nature and extent of shear of the molar teeth of mixodectids from those of the molar teeth in the microsyopids. It is a seemingly small but very im-

portant fact with far-reaching functional implications that the centrocrista is somewhat an inverted V in shape in mixodectids but runs almost directly anteroposteriorly on the buccal half of the upper molars of microsyopids, paromomyids, *Pronothodectes*, *Saxonnella*, i.e., in primitive prosimians, and also in leptictids and the most primitive condylarths such as *Protungulatum*.

It does not appear likely that the difference in the alignment of the centrocrista in mixodectids and microsyopids is due to the presence of a large mesostyle in the mixodectids. As *Microsyops* gradually developed a mesostyle, the relatively anteroposterior position of the centrocrista was not greatly altered. The differences in the centrocrista in the two families are accompanied by corresponding differences in the structure of the lower molars, namely, in the shape of the cristid obliqua. In mixodectids the angle between the cristid obliqua and the anterobuccal portion of the postcristid is rather acute, resulting in an abrupt, sharp break in the plane of the buccal wall anterior and posterior to the hypoconid. In microsyopids, as in undoubted primitive prosimians, the angle formed between the plane of the cristid obliqua and the postcristid is wide, and consequently the buccal wall of the talonids is rather gently rounded.

The functional consequences of the two situations described for the two families are a more transverse shear in the mixodectids, and a reduced transverse shear and a more anteroposterior shear in the microsyopids and early Tertiary prosimians. This latter shear results from the contact of the centrocrista and the cristid obliqua and the anterobuccal part of the postcristid.

Other differences between the mixodectid and microsyopid molars have important effects on the occlusion. In microsyopids the paracrista and metacrista are relatively shorter, and the trigonid is relatively narrower transversely in relation to the talonid. These differences can be effectively correlated with the respective, but totally interdependent, functions that these parts of the teeth perform in the two families.

In mixodectids the trigonid is relatively large compared with the talonid; the trigonid is rather wide transversely and also antero-

posteriorly elongate. In the prevallid-postvallum shear and the prevallum-postvallid shear there are rather long crest surfaces involved between the paracrista-preprotocrista and the protocristid, and the metacrista-postprotocrista and the paracristid, respectively. The shear is approximately transverse in relation to the surface of the teeth or in relation to the midline of the skull itself. The only economical way to elongate the paracrista and metacrista for enlarged shearing surfaces is to run the two crests transversely along the width of the upper molars. Extensive transverse shear on the molars was probably primitive in the Theria, as is exhibited on *Pappotherium*, palaeoryctids, and primitive erinaceoids.

The situation described above for mixodectids does not hold true in microsyopids. In microsyopids, as in early Tertiary prosimians in general, the paracone and metacone are relatively well separated, having a long centrocrista between them and the paracrista and the metacrista are reduced in size and consequently in the importance of their function. The correlation with the relatively large talonid and the reduced, primarily crushing low trigonid of the lower molars is obvious. Unlike mixodectids, microsyopids relied on more anteroposterior shear, as opposed to transverse shear, although there is considerable reduction in the importance of shear in microsyopids from a primitive eutherian condition in which shear played a more important role.

The functional explanation of the morphological differences between the molar patterns of the two families may be roughly summarized as follows: 1. In mixodectids the prevallid-postvallum shear and the postvallid-prevallum shear are much more important than in microsyopids. 2. The anteroposteriorly elongate centrocrista and the almost reduced paracrista and metacrista, correlated with corresponding features on the lower molars, result in relatively more important anteroposterior shear in microsyopids. Occlusion in microsyopids and other primitive prosimians is similar. Shear in microsyopids is less important than in mixodectids, and what shear does take place does so more horizontally than vertically.

Possible affinities or similarities of mixo-

dectids with a number of eutherian groups are discussed, although conclusive evidence for the origin of the family from any other family is lacking. Early Tertiary palaeoryctoids, erinaceoids, leptictids, tupaiids, apatemyids, and pantolestids are the groups that may have bearing on the origins of the mixodectids, although none of these families, with the possible exception of as yet unknown or unrecognized Cretaceous palaeoryctoids or erinaceoids, gave rise to the Mixodectoidea.

The general resemblance of lower molars of mixodectids to those of leptictids, and a probably primitive molariform fourth premolar, such as it appears to be in the latter family, suggest close leptictid ties. In Cretaceous leptictids, such as *Gypsonictops*, and in all the Tertiary species of that family, the paracrista and the metacrista are reduced, and the shear on these crests is limited. In mixodectids the opposite holds true, although it is possible that moderate vertical shear has secondarily evolved from a leptictid ancestry. At present a detailed comparison of mixodectids with pantolestids and apatemyids is not justified, because there is little meaningful resemblance in the details of the molar dentition of any of these three families. It would be tempting to speculate about a special affinity between mixodectids and apatemyids, because there are two anterior lower and upper enlarged incisors (P.U. No. 17465) in primitive apatemyids as in mixodectids. It appears most probable at present, however, that this may be due to convergence.

One of the greatest obstacles against postulating an erinaceoid origin for mixodectids is the lack of both erinaceoid and mixodectid fossils from the Cretaceous or even adequate specimens from the early Paleocene. The Paleocene leptacodonts, the later geolabidines, and *Scenopagus* give only an unclear picture of Cretaceous erinaceoids.

A tupaiid-mixodectid relationship is equally possible (until mixodectid basicrania are known), as is the idea that mixodectids are erinaceoid- or palaeoryctoid-derived, although complete lack of well-characterized early Tertiary tupaiids necessarily weakens the latter suggestion. If *Adapisoriculus? germanicus* Russell, 1964, is accepted as a Paleocene tupaiid, as suggested by Van Valen (1965a),

then a meaningful mixodectid-tupaïid relationship may be seen. In Recent tupaïids, in *Adapisoriculus minimus* and *Adapisoriculus? germanicus* of the European Paleocene, and in the Paleocene mixodectids, the hypoconulid is strongly displaced in a lingual direction toward the entoconid, although such displacement occurred to a different degree in the tupaïids from that in the mixodectids. Although the entoconid and the hypoconulid in tupaïids are about equal in size, in mixodectids the entoconid is invariably the larger and more robust cusp. Nothing in the structure of the trigonids in mixodectids, *Adapisoriculus*, and tupaïids contradicts close relationship. There is considerable enlargement of the two pairs of lower incisors in Recent tupaïines, these incisors being not dissimilar to those of mixodectids. The first and second lower incisors of *Tupaia* and *Urogale* are rather similar to those of mixodectids, although the latter may have the incisors very slightly more enlarged. The first and second tupaïine incisors have flattened roots, and the second incisor closely flanks the first one. The third incisor is vestigial. In *Ptilocercus* (see pl. 31, figs. 7–10) the third incisor is also the smallest of the incisors. The facts enumerated above suggest, but certainly do not supply evidence for, a probable tupaïid-mixodectid relationship.

Regardless of the correctness or falsity of a mixodectid relationship with the tupaïids, the similarity between mixodectids (*Remiculus* in particular) and *Adapisoriculus* is striking. A large stylar shelf, prominent parastyle, long paracrista and metacrista, and a mesostyle (it can be discerned only on *Adapisoriculus minimus*, not on *Adapisoriculus? germanicus*) are shared by both groups. The lower teeth show considerable similarity, particularly the proximity of the hypoconulid to the entoconid, as is pointed out above. D. E. Russell (1964, p. 57) discussed the possible affinities of *Adapisoriculus? germanicus* and concluded that *Adapisoriculus* might be a metatherian. Van Valen (1965a) wrote that such an allocation was not probable.

It appears that families closely allied to the mixodectids are not known or recognized from anywhere as yet. It seems probable, however, that future discoveries of other elements than dentitions, particularly speci-

mens showing basicranial morphology, will change this state of affairs.

The enlarged apatemyid lower incisors are exceptionally long-rooted and extend posteriorly into the horizontal ramus as far as the last lower molar. The enlarged incisors of mixodectids do not extend back into the mandible as do those of apatemyids, rodents, lagomorphs, or multituberculates, but are implanted in the alveoli as canines would be, i.e., for part of the depth of the mandible only.

Primitive molars of apatemyids bear little resemblance to those of mixodectids. The posterior portion of the stylar shelf is broad, the paracone and metacone are about equal in size, the paraconule and metaconule are very small and unimportant, the former being higher than the latter (i.e., when the tooth is examined with its ventral surface facing toward the observer). The protoconid and metaconid are about equal in height. The trigonid basin is large and prominent. The entoconid is reduced, and the talonid is wide open lingually as a result of the very low entocristid.

McDowell (1958, p. 206) commented on the teeth of *Apheliscus* that they were "... reconcilable with those of *Mixodectes*." No evidence known to me lends support to such a statement. In addition to McDowell, Gazin (1959b, p. 5) noted, concerning *Apheliscus* and *Phenacodactylus*, that "Among the insectivores outside of the Pantolestidae I find a rather more remote relationship to the mixodectids indicated." I believe McKenna (1960, pp. 110–114) was correct in referring *Apheliscus* to the hyopsodont Condylarthra.

The suggested affinity of *Metoldobotes* Schlosser, 1910, to the Mixodectidae by Schlosser (1911), and later inexplicably supported by Saban (1958, p. 856), was firmly rejected by Matthew (1915). Patterson (1965) has shown beyond any doubt that the Fayum genus is a macroscelidid. The Macrosclididae, beyond infraclass affinities, show no undoubted relationship to the mixodectids or to any of the other early Tertiary mammals (Patterson, 1965).

A note must be made here of Saban's (1954) suborder Mixodectomorpha of the Insectivora. The suborder defined by Saban (1958) included the Mixodectoidea Simpson,

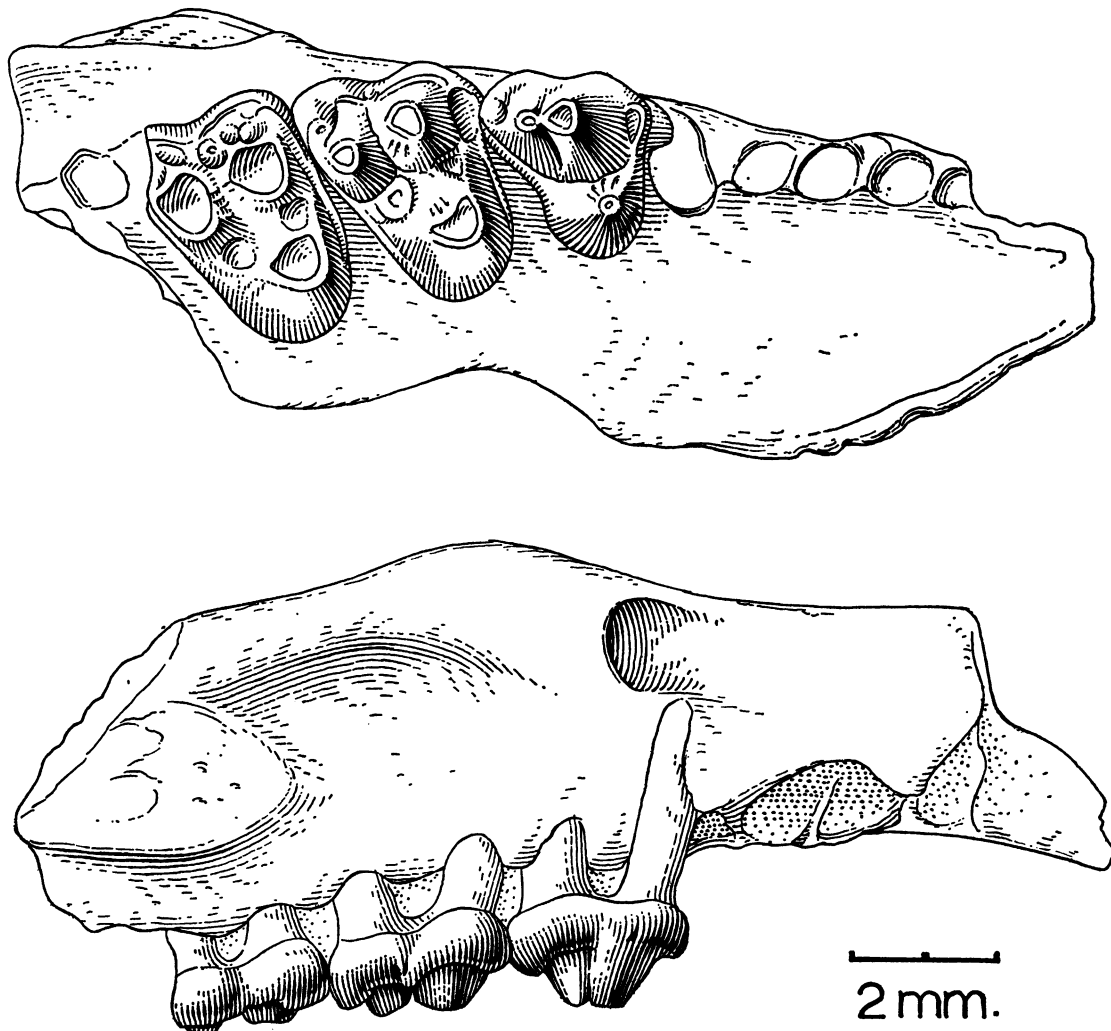


FIG. 7. *Plantietherium mirabile*, almost complete right maxilla with P^8-M^1 , C.M. No. 11671, from the Fort Union Formation at Eagle Coal Mine, Bear Creek, Montana. Above: Occlusal view. Below: Lateral view. Compare with figures 13–15 of plate 29. $\times 10$.

1945, and the Apatamyoidea Saban, 1954. The latter author derived his Mixodectomorpha directly from pantotheres. Undisputed pantotheres occur only in the middle and late Jurassic. Some of the latest radiometric dates (Casey, 1964; Holmes, 1959; Kulp, 1961; and others) place the Jurassic-Cretaceous time boundary 136 million to 135 million years ago. The earliest Paleocene is approximated (Evernden, Savage, Curtis, and James, 1964) to have begun about 64 million years ago. Deriving mixodectids and apatemyids from undisputed pantotheres means the casual bridging of more than 70

million years, a time interval during which the evolutionary history of therian mammals is recorded only in the most unsatisfactory fashion. It must be concluded that the Mixodectomorpha as an insectivore suborder is an artificial and unwarranted category that should be allowed to slip into the oblivion of historical curiosities.

STATUS OF MIXODECTID- PLAGIOMENID RELATIONSHIPS

In the context of a brief examination of the possible relationships of the enigmatic family Plagiomenidae Matthew, 1918, to the

Mixodectidae, the opportunity is taken here to present illustrations and brief descriptions of some new material and of some specimens that have already been discussed but inadequately figured in the literature.

Matthew's family Plagiomenidae was based on the monotypic genus *Plagiomene* from the Gray Bull beds of the Big Horn Basin. New information is presented here on the upper premolar dentition of *Plagiomene*. In addition to *Plagiomene*, the monotypic Paleocene *Planetetherium*¹ is the only other undoubted plagiomenid reported in the literature since Matthew's naming of the family. In the light of all presently available evidence Matthew's (1918, pp. 598-600) original observation that the plagiomenids are the most similar to the recent dermopterans is still the most reasonable view of the relationship of the family, and A.M.N.H. No. 15208, described and illustrated here, strengthens Matthew's suggestion.

A.M.N.H. No. 15208, a well-preserved palate, shows the right side of the upper dentition (pl. 28, figs. 3-6) in virtually perfect condition, in spite of the complete obliteration of the bone around it, owing to concretionary preservation. Five antemolar teeth are preserved: P⁴ is entirely molariform; P³ is equal in width to P⁴, with a distinct parastyle, paracone, metacone, and metastyle but completely lacking the characteristic styler cusps of the molars and the fourth premolar. P² resembles a slightly simplified buccal half of P³. The apparently single-rooted P¹ shows the same exact, but much less accentuated, subdivision of the crown as do P² and the buccal half of P³. Whether the tooth preceding P¹ is the canine or an incisor cannot be determined; the crown of this tooth has a very tiny anterior cuspule, a larger middle one with a longer anterior and posterior slope, and a somewhat elongated posterior crest or cuspule.

The entire upper dentition of *Plagiomene* shows a gradual morphological gradation of the teeth from the molars to the most anterior tooth known. In addition to the unique features of the styler cusps, the complete lack of a hypocone and the position of the

protocone directly lingual to the paracone also characterize both *Planetetherium* and *Plagiomene*. In the two Recent genera² of dermopterans, *Galeopithecus* and *Galeopterus*, there are five antemolar upper teeth, the first three of which are characterized by a subdivision of the crown into lobules in the deciduous and permanent teeth of *Galeopterus* and the deciduous ones of *Galeopithecus*. In the latter genus the replacement teeth have lost this apparently primitive feature which occurs in the fossil record in *Plagiomene*, in *Galeopterus*, and in the deciduous dentition of *Galeopithecus*. The permanent upper and the lower second and third premolars of *Galeopithecus* have sharp-crested paracones and protoconids, respectively, without any subdivision into lobules as seen in their deciduous homologues or in the identical teeth, both deciduous and replacement, of *Galeopterus*.

Although both P⁴ and P³ of the plagiomenids are more molariform than their homologues in Recent colugos, and there are some differences between the teeth that deserve family distinction at present, the family appears to be the earliest representative of the Dermoptera.

An additional feature that seems to add strength to the argument for plagiomenid-galeopithecid relationship should be noted. Recent dermopterans are herbivorous mammals that feed mainly on green vegetable matter, flowers, leaves, and to some degree fruits. Their teeth display primarily apical wear. Most of the specimens of plagiomenid teeth known to me show primarily apical wear on the cusps,³ which strongly suggests

² After having examined a series of skulls and dentitions (both permanent and deciduous) of the two valid species of living dermopterans, I have concluded that Cabrera (1925) was correct in recognizing two genera instead of one. The two species, *Galeopterus variegatus* from the Malay Archipelago and *Galeopithecus volans* from the Philippine Islands, show generic differences in the morphology of the dentition. These differences are sharply defined in both premolars and molars and clearly separate the two equal-sized species. Also, *Galeopterus* has a more inflated ear region than does *Galeopithecus*. From the point of view of general classification of the mammals, which deals with the living as well as fossil taxa, this generic distinction is well based and important; it is far from an attempt to oversplit the living colugos.

³ There are, however, large discrepancies in the wear and shear facets among individual specimens of the

¹ Figures 9A and B in the original description of *Planetetherium* (Simpson, 1928) represent P³ and P⁴, respectively, not P⁴ and M² as labeled in the publication.

a herbivorous diet similar to that of Recent colugos.

The broader affinities of the Plagiomenidae, whether they are related to the Recent colugos or not, are very poorly understood. The presence of the four molariform teeth, the stylar cusps, and the very strong overall similarity of *Planetetherium* and *Plagiomena* to the Lance marsupial *Glasbius*, suggested to me (see also Clemens, 1966) that plagiomenids may be metatherians. Thorough cleaning of A.M.N.H. No. 22206, a very well-preserved partial mandible of *Planetetherium mirabile* (see pl. 28, figs. 1 and 2) revealed a slightly inflected angle, but this condition is far from that usually seen in marsupials. Although the usually observed degree of inflection of the mandibular angle may not be all-pervasive among early Metatheria, on present evidence it appears that the similarity of plagiomenids to *Glasbius* is convergent and not indicative of affinity.

Possible relationship has been proposed of the Plagiomenidae to the poorly known family Paroxyclaenidae by Van Valen (1965c).

A brief note is made here of the enigmatic genus *Thylacaelurus* from the Kishenehn Formation (latest Eocene or early Oligocene) of Canada described by L. S. Russell (1954) as a didelphid marsupial. McKenna (in Van Valen, 1965c) first suggested eutherian affinities of this genus, and Van Valen (1967), who is in favor of plagiomenid affinities of *Thylacaelurus*, erected the subfamily Thylacaelurinae within the Plagiomenidae. I disagree with Van Valen's allocation of the genus to the Plagiomenidae, a mere difference of opinion that is discussed below, but I oppose the naming of a subfamily based on a genus of which the family ties are obscure.

L. S. Russell's (1954) illustration of N.M.C. No. 8910 is unclear, and it was necessary to present the illustration shown in this paper. Text figure 8 was originally prepared for, and checked for accuracy by, Dr. M. C. McKenna, who has generously turned it

over to me. My comparative and descriptive remarks are based on this figure, because I did not have the opportunity to examine the Canadian specimen. The exact homologies of the two posterior molars are difficult to determine unless we assume that *Thylacaelurus* is a eutherian. On this assumption, it is quite likely that the enlarged, unusually shaped premolar is P^4 , and apparently the two following teeth are M^1 and M^2 , respectively. Judged from the relative size of M^2 , as compared with M^1 , M^3 may or may not have been present: if present, it was probably relatively very small.

The presumed P^4 , completely premolariform and also specialized, does not resemble its homologue either in the plagiomenids or in the galeopithecids. The presumed degree of reduction of M^3 in *Thylacaelurus* is not seen in either of the latter two families. The base of the zygomatic arch is exceptionally strong in the two known genera of plagiomenids and in the Recent colugos, but this structure is quite slender in *Thylacaelurus*. The only similarity to plagiomenids that may be meaningful is restricted to the presence of similarly situated stylar cusps on the molars. On M^1 there appears to be a small hypocone, a cusp that is completely absent from all known specimens of plagiomenids. In the Recent talpid *Desmana* and in the fossil dimylids, these stylar cusps are also present in the position seen in *Thylacaelurus*. In dimylids the fourth premolar is premolariform, bulky and could be said to be somewhat enlarged. Although not known in dimylids, in *Desmana* the base of the zygoma is quite slender. Although M^3 is present in *Desmana*, dimylids show a pronounced trend for either extreme reduction or loss of the third molar (see figures of dimylids in Hürzeler, 1944). I neither suggest close affinities of the Kishenehn genus to talpids like *Desmana* nor believe that *Thylacaelurus* is a dimylid; the most probable affinity that I favor on presently available evidence is with insectivores close to the dimylid stem.

Simpson (1936, p. 16), in his first major discussion of the mixodectids (*sensu lato*), noted that *Elpidophorus* tended to bridge the structural gap between plagiomenids and mixodectids (*sensu lato*). In 1937 (pp. 130-131) he thoroughly discussed the possibility that

Paleocene *Planetetherium*. A.M.N.H. No. 22229, comprised of two partial palates, shows the upper molars with very little apical wear and considerable prevallid-postvallum shear. C.M. No. 11671, on the other hand, shows almost exclusively apical wear, without any evidence of shear between the upper and lower teeth. Both specimens are clearly of the same species. (See pl. 29, figs. 3-6, 13-15).

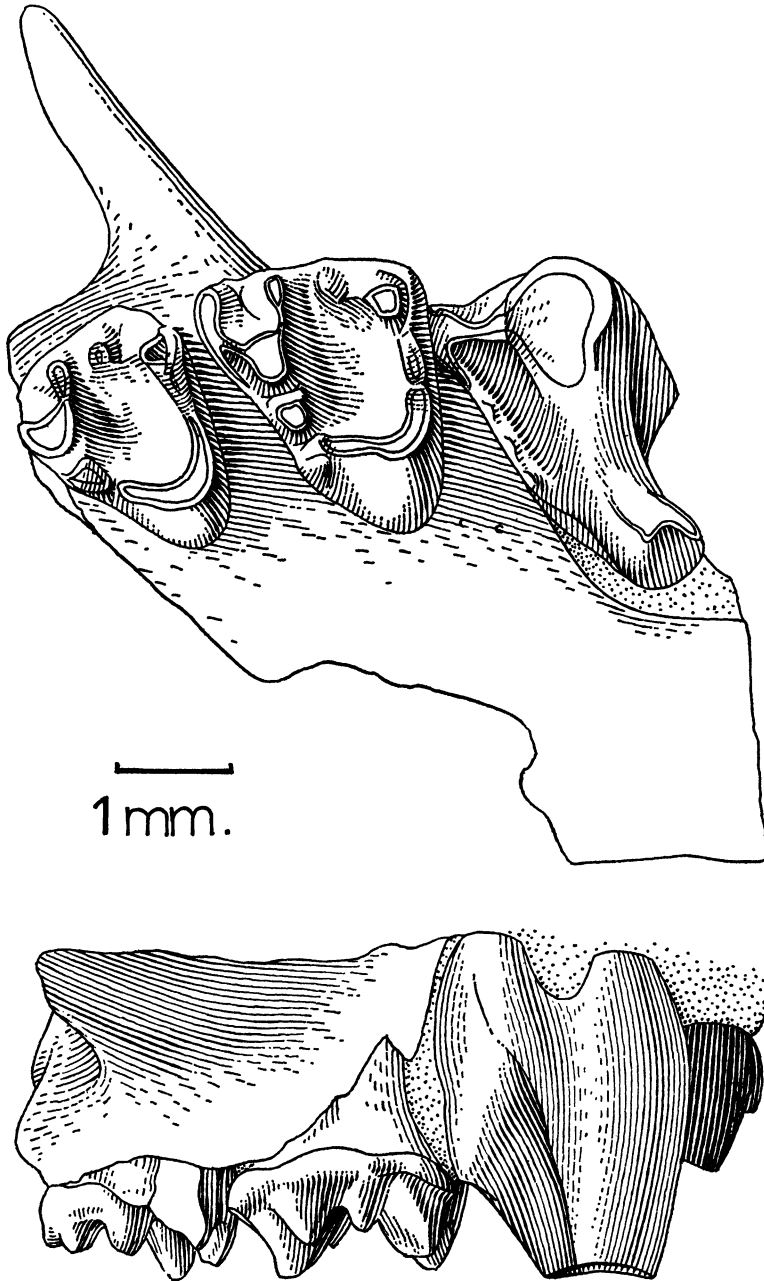


FIG. 8. *Thylacaelurus montanus*, fragment of right maxilla with P^4-M^2 , N.M.C. No. 8910, from the Kishenehn Formation, Canada. Above: Occlusal view. Below: Lateral view. $\times 15$.

mixodectids, *Elpidophorus* in particular, were related to the plagiomenids, but in conclusion he listed the following features of plagiomenids that bar the recognition of a close affinity (p. 131): "Rather than a single mesostyle developed as a fold of the ectoloph, the

plagiomenids have two independently median cusps on the outer shelf of the upper molars.

"The anterior incisors (in the lower jaw, at least) are not reduced in number and none is markedly enlarged.

"The hypoconulid does not have the char-

acteristic mixodectid displacement toward the entoconid.

"The cheek teeth are all deeply furrowed and tend to proliferate cuspules."

The upper dentition of *Plagiomene* described above substantiates the observation that there was no enlargement of the incisors in plagiomenids, in contrast to the situation in mixodectids.

During the 30 years that have elapsed between Simpson's evaluation and the present study, no more conclusive evidence for a plagiomenid-mixodectid affinity has appeared. If anything, the detailed study of mixodectids and *Elpidophorus* in particular does not bear out any special affinity between the two groups.

Van Valen (1967), however, took the formal step of including the Mixodectidae in the suborder Dermoptera. This can be regarded,

at best, as an opinion, since Van Valen presented no evidence nor discussed his conclusion as being based on evidence available in print elsewhere. As an expression of an opinion, the pointing out of similarities between mixodectids and plagiomenids can be stimulating and highly useful. The formal placing of the Mixodectoidea in the Dermoptera, however, is unwarranted on the basis of available evidence.

Once formalized, a classification tends to serve as a guide of high probability to workers not familiar with these groups. The continued practice of formal grouping of major categories in cases in which the evidence is inconclusive, instead of expressing this uncertainty in correct taxonomic methodology, such as the use of question marks or *incertae sedis*, results in greatly diminished stability.

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE OF THE MICROSYOPIDAE

THERE ARE NO UNDOUBTED microsyopids reported that antedate the European Sparnacian and the North American Wasatchian, and the last occurrence of a microsyopid is reported from the Uintan of the Sespe Formation of California. In spite of the probable Tiffanian microsyopid *Navajovius*, the family may be considered as predominantly Eocene.

For the same reasons as those given above on the stratigraphic and geographic occurrence of mixodectids (p. 210), Eocene stratigraphy is not considered in detail. Of the numerous publications of importance to the North American continental early Eocene correlation, the most pertinent are those of Gazin (1952, 1959a, 1962), Guthrie (MS), McKenna (1960), Robinson (1966), Simpson (1948), and Van Houten (1945). These works are concerned mainly with regional early Eocene correlation, as well as discussions of the important mammal faunas of Wasatchian or slightly younger age.

The published literature on the detailed stratigraphy of the Bridger Formation, a middle Eocene rock unit pertinent to the present work, is rather unsatisfactory. Errors and inaccuracies mar the fine pioneering works of Wortman (1901), Matthew (1909a), and Osborn (1929). The brief discussions relating to the stratigraphy that are found in H. E. Wood, 2nd (1934), Kitts (1957), Robinson (1957), and Wheeler (1961) are the best available guides to Bridger stratigraphic and faunal relationships. Recent geological work by Bradley (1964) offered a valuable map on which detailed future work can be based. A recent paper by Koenig (1960) treated the geology of the Bridger Formation in a summary fashion.

It is fairly certain that two distinct faunas are present (Wortman, 1901), the earlier one having been collected from beds (A and B beds of Matthew, 1909a) stratigraphically below the Sage Creek White layer, and the later fauna in the beds above the Sage Creek White layer (C, D, and E beds of Matthew, 1909a). The stratigraphy of the important Sage Creek White layer was carefully studied and documented by Bradley

(1964, pp. 51–53). Bradley's information has been confirmed by original field work by C. L. Gazin (personal communication) on the same (and an even more extensive) geographic area.

Navajovius kohlhaasae, considered to be a probable microsyopid in the present paper, is a Tiffanian species from the Mason Pocket, Tiffany Formation, San Juan Basin of Colorado. A smaller species of probably the same genus, *Navajovius? mckennai*, new species, from the Almagre facies of the San José Formation, San Juan Basin of New Mexico, is of Wasatchian age.

The earliest and most primitive sample of *Microsyops* is *M. wilsoni*, new species. It occurs both at the base of the Gray Bull of the Willwood Formation of the Big Horn Basin, Wyoming, and in the East Alheit Pocket Quarry of the Hiawatha Member of the Wasatch Formation in the eastern Sand Wash Basin, Colorado. Although the two areas are separated by more than 300 miles, the samples probably represent the same species.

The size range and morphology of *M. alfi* and *M. angustidens*, as known at present, are virtually the same, and the degree of variation in the fourth premolars of these species is poorly known. An accurate species allocation, therefore, is difficult to make of specimens from the Gray Bull beds of the Willwood Formation, from the Four Mile Fauna localities (except for Alheit Pocket), and from the lower part of the Knight Member in the Bridger Basin, Wyoming.

Microsyops latidens is known from the middle Wasatchian Lysite beds of the Big Horn and Wind River basins in Wyoming and from a slightly larger but morphologically indistinguishable sample from the La Barge local fauna of the Knight Member of the Wasatch Formation, Bridger Basin, Wyoming. This, or a very similar species, is also known from the Huerfano Fauna (see Robinson, 1966, and the present paper).

The late Wasatchian *Microsyops scottianus* is known from the Lost Cabin beds of the Wind River Basin, and it has also been reported by Gazin (1952) from the New Fork

TABLE 7
DISTRIBUTION OF SPECIES OF MICROSYOPS IN VARIOUS BASINS OF DEPOSITION AND IN TIME

	Big Horn Basin, Wyoming	Wind River Basin, Wyoming	Bridger and Green River Basin, Wyoming	Washakie and Sand Wash Basins, Wyoming and Colorado	Huerfano Basin, Colorado	California
Uintan						<i>Craseops sylvestris</i> <i>M. kratos</i>
Bridgerian	<i>Microsyops</i> sp.		<i>M. annectens</i> <i>M. elegans</i>			
Wasatchian	<i>M. latidens</i> <i>M. angustidens</i> <i>M. wilsoni</i>	<i>M. lundeliusi</i> <i>M. scottianus</i> <i>M. latidens</i>	<i>M. scottianus</i> <i>M. latidens</i> <i>M. angustidens</i>		<i>Cf. M. latidens</i> <i>Cf. M. scottianus</i> <i>Cf. M. lundeliusi</i>	

Tongue of the Wasatch Formation of the Bridger Basin, Wyoming.

As is *M. latidens*, *M. scottianus* is almost certainly represented in the Huerfano Fauna, although reliable samples of one cannot be separated from those of the other species.

The Lost Cabin beds in the Wind River Basin, Boysen Reservoir area, Wyoming, yielded the type specimen of *Microsyops lundeliusi*. Either the latter or a closely related "species" (see the discussion under *M. lundeliusi*) is well represented in the Huerfano Formation of Colorado.

It appears that *M. lundeliusi*, as well as *M. scottianus*, is late Wasatchian in age.

The two distinct species from the lower (A-B) and upper (C-D) beds, *M. elegans* and *M. annectens*, respectively, are known only from the Bridger Formation of the Bridger Basin, Wyoming.

Microsyops sp. from the Carter Mountain locality 3 of Yale University in the Big Horn Basin, Wyoming, is approximately intermediate in size between the smaller and larger Bridger species.

The poorly known *M. kratos* and *Craseops sylvestris* from the Poway Formation and the Sespe Formation, respectively, are known from the late Eocene of California. The early Uintan *M. kratos* is the youngest species of *Microsyops*, and the late Uintan *Craseops* marks the latest known occurrence of the Microsyopidae.

Following the work of Wortman (1901), Matthew (1909a), and Osborn (1929), Gazin (on the basis of the species of *Hyopsodus*; personal communication), and I (on the basis of the occurrence of the two distinct species of *Microsyops*) confirm the fact that the Bridger Formation represents two time intervals. I follow Gazin (1958) and others in referring to those rock units separated by the Sage Creek White layer as lower and upper Bridger and designate the age of the two distinct faunas as early and late Bridgerian.

I do not accept the "substages" "Blacksforkian" (=early Bridgerian) and "Twinbuttesian" (=late Bridgerian) proposed by Robinson (1966). At the present stage of our knowledge, I find "early" and "late" designations for the Bridgerian satisfactory; the unnecessary burden of new names is also

avoided. Robinson (1966) also proposed the "Gardnerbuttean," a biochronological unit supposedly younger than the "Lostcabinian." The former biochronological unit may represent an ecologically different but chronologically late Wasatchian ("Lostcabinian") assemblage, and because Robinson does not prove this to be incorrect, the supposed "Gardnerbuttean" cannot be accepted. Also because the North American Land-Mammal Ages do not conform to the time-rock unit, the stage (see Evernden, Savage, Curtis, and James, 1964), it is meaningless to propose new "substages."

Black and Dawson (1966) have provided an up-to-date summary of faunal correlation of the late Eocene.

ORDER ?PRIMATES LINNAEUS, 1758

SUBORDER UNCERTAIN

FAMILY MICROSYOPIDAE OSBORN AND WORTMAN, 1892

Microsyopidae OSBORN AND WORTMAN, 1892, p. 101.

Microsyopinae MATTHEW, 1915, p. 467.

TYPE GENUS: *Microsyops* Leidy, 1872.

INCLUDED GENERA: The type genus and *Craseops*. The inclusion of *Navajovius* is queried.

KNOWN DISTRIBUTION: Unquestioned microsyopids range from the earliest Wasatchian to the late Uintan faunas of North America. *Navajovius* is known from the Tiffanian of Colorado and the Wasatchian of New Mexico.

DIAGNOSIS: Eutherian mammals, probably primates, with one pair of enlarged upper incisors and at least one pair of enlarged lower incisors. The range in size was probably from that of a rat to that of a beaver.

Microsyopids are characterized in primitive stages by the complete lack of a stylar shelf. This shelf develops, however, secondarily in the late Uintan *Craseops*. The cusps and conules are relatively low and bulbous; in no instance is the metaconid the highest cusp on the trigonid.

The differences between microsyopids and mixodectids are cited under the diagnosis of the latter family, and their ties to each other are also discussed in the section dealing with the affinities of the Mixodectidae.

Primitive microsyopids differ from Paleocene paromomyids in having the entoconid and hypoconulid distinct and in close proximity; in the latter group these two cusps are low and not very close to each other.

The major differences of microsyopids from the notharctines, adapines, and plesiadapids are in the structure of the basicranium, discussed in detail in the section on cranial morphology.

Microsyopids differ most noticeably from leptictids in having transversely narrower molars, less tall and more bulbous cusps, enlarged incisors, and a relatively shorter and broader skull.

MICROSYPIDS LEIDY, 1872

Limnotherium: MARSH, 1871, p. 45.

Microsyops LEIDY, 1872, p. 373.

Hyopsodus: LEIDY, 1872, p. 373.

Bathrodon: MARSH, 1872, p. 211.

Mesacodon: MARSH, 1872, p. 212.

Palaeacodon: LEIDY, 1872, p. 373.

Pantolestes: COPE, 1882, p. 150.

Cynodontomys COPE, 1882, p. 151.

Pelycodus: COPE, 1882, p. 151.

Notharctus: LOOMIS, 1906, p. 284.

Diacodexis: GAZIN, 1952, p. 71.

TYPE SPECIES: *Microsyops elegans* (Marsh, 1871) Leidy, 1872.

INCLUDED SPECIES: The type species; *Microsyops wilsoni*, new species; *M. alfi*; *M. angustidens*; *M. latidens*; *M. scottianus*; *M. annectens*; *M. lundeliusi*; and *M. kratos*.

KNOWN DISTRIBUTION: From the earliest Wasatchian to early Uintan (early to late Eocene) of western North America.

GENERIC DIAGNOSIS: Rat- to beaver-sized mammals with a single pair of enlarged upper and lower incisors and reduced lower incisors, canine, and first premolar; from the upper dentition only the non-enlarged incisors are absent. Known cranial features show that the skull had a relatively short muzzle and laterally extending zygomata which give the cranium a rounded appearance in dorsal view. Almost all the features cited in the diagnosis of the family apply equally to *Microsyops*.

The earliest and most primitive species of *Microsyops* that bear a strong resemblance to *Navajovius* are compared in detail in the discussion of *Navajovius*. The latter genus appears to have an additional, slightly

enlarged anterior lower tooth, probably an incisor, and a less distinct and less closely twinned entoconid and hypoconulid.

Craseops differs from *Microsyops* in the greater development of the mesostyle and the reduction of the metaconule and hypocone.

DISCUSSION: Nowhere in the literature is there an adequate diagnosis or a discussion which justifies either a generic separation or lumping of the genera *Microsyops* and *Cynodontomys*. The latter genus is considered here as a synonym of *Microsyops*. Under the detailed treatment of the species allocated to *Microsyops* it is shown that the generic separation of the early and middle Eocene species cannot be justified on morphological grounds. The known series of specimens of the various early, middle, and late Eocene species clearly document the fact that the changes in the *Microsyops* lineages involved minor changes in size, a very gradual molarization of the fourth premolars, and the equally slow development of a molar mesostyle. Most of the discussion about evolutionary trends observed in the Microsyopidae is closely pertinent to the taxonomy of the genus. The discussions of *Microsyops wilsoni* and *Microsyops alfi* attempt to justify my taxonomic delineation of the known samples of *Microsyops*.

The lack of adequate generic distinction between *Cynodontomys* and *Microsyops* is not a new discovery. Matthew (1915, p. 468) recognized an unusually arbitrary generic boundary between them. He seemed to have preferred the generic separation of *Cynodontomys* from the earlier described *Microsyops* on a stratigraphic but not a systematic basis. His views on this matter are quoted here: "The Bridger species are all distinguished by equal height of the two outer cusps (protocone and deutocone) of P⁴, and the two trigonid cusps, protoconid and deutoconid, of P₄. These, with the broader and more distinctly bicuspid basined heel of P₄, and presence of a strong curved crest on the same tooth in the position of the paraconid of the true molars, are the only generic distinctions which I can make from *Cynodontomys*. But *M. scottianus* of the Wind River agrees with *Cynodontomys* in all except the broader heel of P₄, and even this is not so distinctly bicus-

pid as in the Bridger species. It should be transferred to *Cynodontomys*. This leaves *Microsyops* as an exclusively Middle Eocene genus" (Matthew, 1915, p. 468).

Leidy (1872) described *Microsyops gracilis* and referred to the specimens on which he based his notes as "several jaw fragments"—uncatalogued specimens that have since vanished. Leidy (p. 363) referred to *Hyopsodus gracilis* of Marsh (1871) as being the same as *Microsyops gracilis*. As Leidy stated it: "Prof. Marsh has described some remains from Grizzly Buttes, which he refers to a species with the name of *Hyopsodus gracilis*. These I suspect belong to the same animal." In other words, Leidy, as far as he was aware, based *Microsyops* on Marsh's *Hyopsodus gracilis*. Leidy later (1873) in his major work, "Contributions to the extinct vertebrate fauna of the Western Territories," treated *Microsyops* in greater detail. He gave a succinct history of the origins of the generic nomenclature of the genus (1873, p. 84): "The specific name of *M. gracilis* was originally given under the impression that the remains referred by Professor Marsh to *Hyopsodus gracilis* pertained to the same animal. A specimen exhibited to the writer by Professor Marsh would indicate that *M. gracilis* is the same as the animal named by him *Limnotherium elegans*. As *Microsyops* is generically distinct from *Limnotherium*, as characterized from the typical species *L. tyrannus*, the specific name of the former would be *Microsyops elegans*." Leidy quite clearly said that *M. gracilis* was a synonym of *M. elegans*. Nevertheless, Wortman (1903, p. 208) revived the species *M. gracilis*, claiming that the type of "*Bathrodon typus*" Marsh, a lower jaw fragment from the lower Bridger beds (clearly a specimen of *M. elegans*) and additional upper teeth from the "type locality" (possibly a reference to the type locality of *Bathrodon typus*) closely agreed with Leidy's figures of *M. gracilis* and were specifically different from *M. elegans*. There is no doubt that Leidy was correct.

When the generic distinction of *Microsyops elegans* was noted by Leidy, no upper molars were known. Leidy (1873, p. 85, figs. 19, 20, pl. 27) stated, of an upper molar which he questioningly referred to *Microsyops*: "The only specimen of an upper tooth

which may, with any probability, be supposed to belong to *Microsyops*, is contained in a small fragment of the jaw, found by Dr. Carter on Dry Creek." If Leidy's figures are even approximately accurate, the tooth illustrated represents either the first or second molar of *Hemiacodon gracilis*.

Microsyops wilsoni, new species

Plate 30, figures 1-7, plate 32; text figures 9-13

ETYMOLOGY: The new species is named for Dr. Robert W. Wilson, the collector of the holotype.

TYPE: U.K.M.N.H. No. 8520, fragmentary left mandible with P₄-M₂, collected in lower Gray Bull beds of the Willwood Formation, at locality 32 of the University of Kansas Museum of Natural History, in Big Horn County, Wyoming. The exact position of locality 32 is as follows: South Fork of Elk Creek, SW. $\frac{1}{4}$, sect. 28, T. 50 N., R. 93 W. (south of Wyoming state highway 31). For more details, Wilson's field notes in the University of Kansas Museum of Natural History should be examined.

HYPODIGM: U.K.M.N.H. Nos. 8520 and 8600; A.M.N.H. Nos. 6849, 15083, and 16234 and numerous isolated upper and lower molars in the collection of the American Museum of Natural History. The type and the other University of Kansas specimens are from the Gray Bull beds of the Willwood Formation. The isolated teeth, the sample used for the statistical studies of this species, are from the lowest beds of the Wasatch Formation, from East Alheit Pocket Quarry (localities V-5357B and V-5357C of the University of California Museum of Paleontology), eastern Sand Wash Basin, Colorado, from which McKenna made a large collection for the American Museum of Natural History in 1961.

SPECIFIC DIAGNOSIS: *Microsyops wilsoni* is the smallest and the most primitive known species of *Microsyops*, and it is also probably the oldest. It differs from the other species allocated to the genus in having a completely premolariform P₄, without any traces of a metaconid, and also in being the smallest member of the genus.

DESCRIPTION: *Microsyops wilsoni* is known mostly from teeth. Although enlarged lower incisors from East Alheit Pocket have been

TABLE 8

MEASUREMENTS OF SPECIMENS OF *Microsyops wilsoni*, NEW SPECIES, FROM THE GRAY BULL BEDS OF THE WILLWOOD FORMATION, BIG HORN COUNTY, WYOMING

	P ₄	M ₁	M ₂	M ₃
U.K.M.N.H. No. 8520 (type)				
L	2.70	2.90	2.82	—
PW	1.51	2.00	2.10	—
AW	1.51	2.00	2.10	—
U.K.M.N.H. No. 8521				
PW	—	—	—	2.00
U.K.M.N.H. No. 8600				
L	2.70	2.82	—	—
PW	1.70	1.80	—	—
AW	1.70	2.10	—	—

referred to the species by me (virtually identical to those referred to *M. alfi* from the Timberlake, Sand, and Despair quarries) it is possible (but not probable) that these incisors may have belonged to another mammal.

The dentition anterior to the fourth premolar is not known. P₄ is premolariform, with only the protoconid present, and lacks any recognizable cusps on the incipient talonid. The lower molars have low trigonids with rather low and bulbous, blunt cusps; the trigonid is relatively narrower transversely than the talonid. The trigonid notch is a very wide V. The paracristid is angulate and is longest on M₁ and shortest on M₃. There is no precingulid. A very short buccal cingulid closes off a small hypoflexid. There is a small postcingulid. The cristid obliqua joins the base of the protolophid at the buccal base of the protoconid. Rather distinct sulci run into the deepest point of the talonid basin, separating the mesoconid from the hypoconid, the hypoconid from the hypoconulid, and the hypoconulid from the entoconid. The talonid notch is V-shaped.

The P₄ appears very wide transversely only because it is relatively shorter than the molars following it. Buccally the paracone is the only cusp on this tooth. The protocone is large and distinct; there are no conules. The ectocingulum and the precingulum are faint, but the postcingulum is strong and distinct. The preprotocrista runs directly anterobuccally from the protocone, but the postparacrista turns first posteriorly and then posterobuccally.

On the molars there is virtually no stylar shelf, only a strong ectocingulum. There is no trace of a mesostyle. A parastyle is continuous with the ectocingulum, and the precingulum and postcingulum are strong and distinct. The slightly more buccal paracone is somewhat larger than the metacone, and the buccal wall of the former is more vertical in relation to the base of the tooth than that of the metacone. There is a characteristic and distinct metastyle at the posterobuccal corner of the molars, on the posterior portion of the postmetacrista. The paraconule and metaconule are quite strong and about equal in size. The hypocone on the postcingulum is invariably small, but it is cusped.

M¹ of this and other species of *Microsyops* appears to be relatively longer and transversely narrower than M². The third molar is easy to distinguish; it is slightly rounded off posterobuccally, and it lacks a hypocone.

DISCUSSION: The following argument is presented for the specific separation of *Microsyops wilsoni* from *Microsyops alfi*. The size ranges of both upper and lower molars from East Alheit Quarry are separable from those found in the other Four Mile localities of McKenna (1960). The East Alheit, on one hand, and the remaining Four Mile localities taken together, on the other hand, have characteristic length/width scatters (see text figs, 9–11) easily distinguishable from one another. Although the overlap between the two samples treated as two species is negligible, it does not constitute proof of specific distinctness. It can be argued that the Four Mile

Microsyops material represents either sexual dimorphism or an example of disruptive selection on the same population. It must be kept in mind, however, that East Alheit Quarry is at a maximum distance of 6 miles from Kent Quarry, the farthest quarry from East Alheit that yielded *Microsyops*. Both Timberlake and Sand quarries are only about 3 to 4 miles from East Alheit Quarry, and both of these have yielded abundant specimens of *Microsyops* which are referred to *Microsyops alfi*. When the close proximity of the East Alheit Pocket to the other Four Mile localities is considered, it appears improbable to me that the observed quantitative differences between specimens of the former and those of the latter localities are

due to contemporaneous subspecific differences. Although the type specimen of *Microsyops wilsoni* is from the Gray Bull beds of the Willwood Formation in the Big Horn Basin, a distance well over 300 miles from East Alheit Quarry, the type and the additional two specimens from the type beds clearly fall into the range of measurements of East Alheit Quarry specimens and the P_4 morphology of the sample. The absence of a metaconid from P_4 of the specimens of *M. wilsoni* from the Willwood Formation and from East Alheit Quarry, as opposed to its presence on specimens of P_4 from the remaining Four Mile localities, strongly suggests that the two former samples taken together merit specific distinctness from the samples

TABLE 9

NUMERICAL DATA FOR SPECIMENS OF *Microsyops wilsoni* FROM EAST ALHEIT POCKET QUARRY OF THE HIAWATHA MEMBER OF THE WASATCH FORMATION, COLORADO*

	N	OR	\bar{X}	S ²	S	V
P_4						
L	12	2.4-2.7	2.56	.008	.090	3.51
PW	12	1.3-1.7	1.57	.015	.122	7.77
M_1						
L	30	2.5-3.0	2.76	.015	.123	4.45
PW	30	1.8-2.2	2.02	.015	.122	6.03
AW	27	1.6-2.0	1.82	.023	.152	8.35
M_2						
L	23	2.6-3.15	2.87	.015	.122	4.25
PW	24	1.9-2.3	2.16	.012	.107	4.95
AW	24	1.7-2.15	2.00	.010	.101	5.05
M_3						
L	35	2.8-3.2	3.05	.016	.126	4.13
PW	35	1.7-2.0	1.88	.008	.087	4.62
AW	34	1.6-1.9	1.75	.012	.110	6.28
P^4						
L	15	1.65-2.3	2.04	.031	.176	8.62
AW	15	2.7-3.4	2.95	.028	.167	5.66
M^1						
L	29	2.5-2.9	2.78	.013	.113	4.06
AW	29	2.85-3.9	3.38	.038	.194	5.73
M^2						
L	39	2.5-3.0	2.80	.015	.121	4.32
AW	39	3.2-3.9	3.65	.028	.167	4.57
M^3						
L	29	2.25-2.7	2.51	.018	.134	5.33
AW	29	2.7-3.4	3.05	.033	.182	5.96

* The data obtained from the type and additional specimens from the Willwood Formation, Big Horn Basin, Wyoming, although well within the sample from the East Alheit Pocket Quarry, are not included but are given separately in table 8.

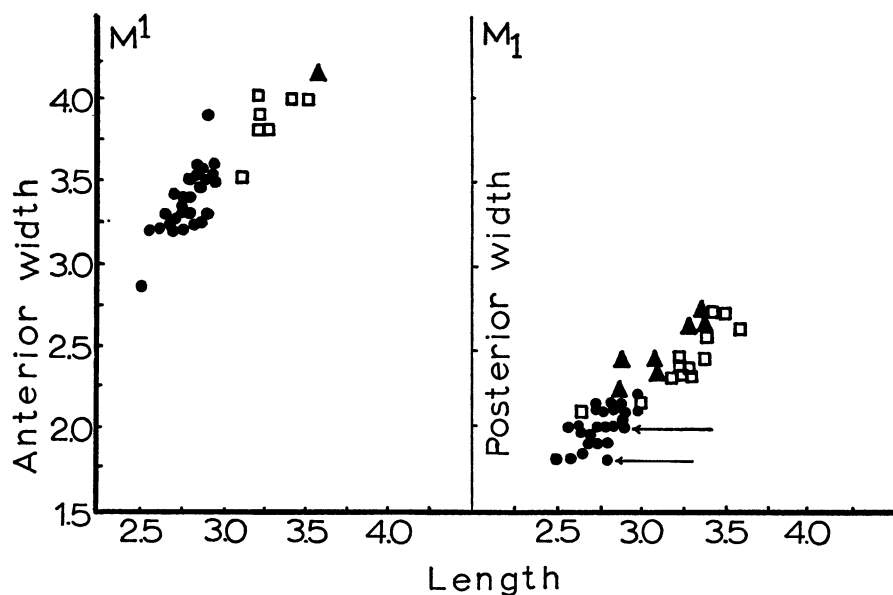


FIG. 9. Scatter diagrams of the anterior width/length and posterior width/length of the first upper and lower molars of *Microsyops wilsoni* (black dots), *M. alfi* (light squares), and *M. angustidens* (black triangles). The plotted sample of *Microsyops wilsoni* is from the East Alheit Quarry of the Wasatch beds in Colorado and from the lower Gray Bull beds of the Willwood Formation in the Big Horn Basin, Wyoming; the *M. alfi* sample is from various Four Mile localities other than the East Alheit Quarry; the sample referred to *M. angustidens* was collected at various Gray Bull localities. The arrows show the two specimens of *M. wilsoni* (one of them is the type) from the Willwood Formation.

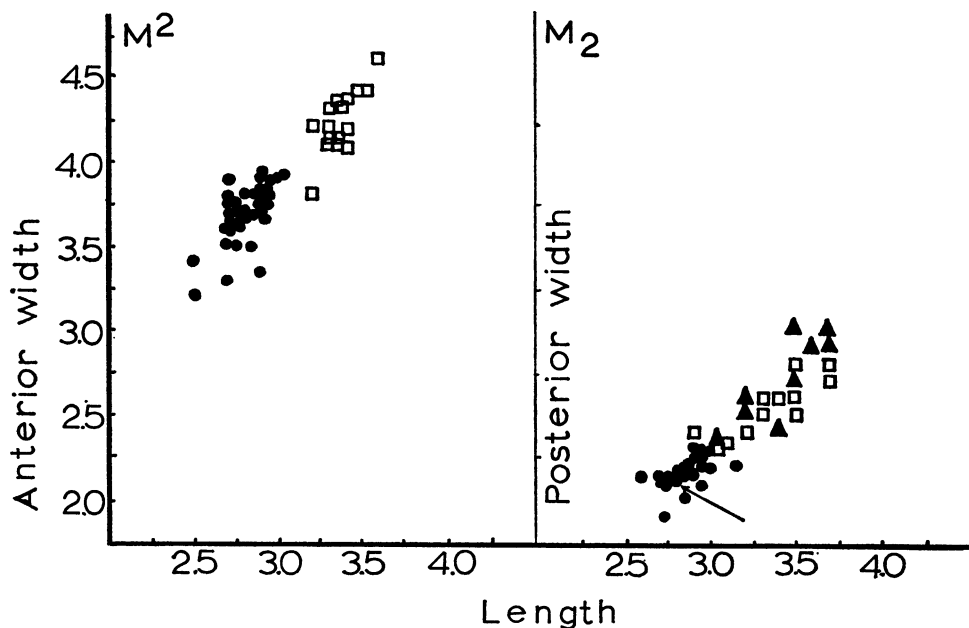


FIG. 10. Scatter diagrams of the anterior width/length and posterior width/length of the second upper and lower molars of *Microsyops wilsoni* (black dots), *M. alfi* (light squares), and *M. angustidens* (black triangles). The plotted sample of *Microsyops wilsoni* is from the East Alheit Quarry of the Wasatch beds in Colorado and from the lower Gray Bull beds of the Willwood Formation in the Big Horn Basin, Wyoming; the *M. alfi* sample is from various Four Mile localities other than the East Alheit Quarry; the sample referred to *M. angustidens* was collected at various Gray Bull localities. The arrow shows a specimen of *M. wilsoni* from the Willwood Formation.

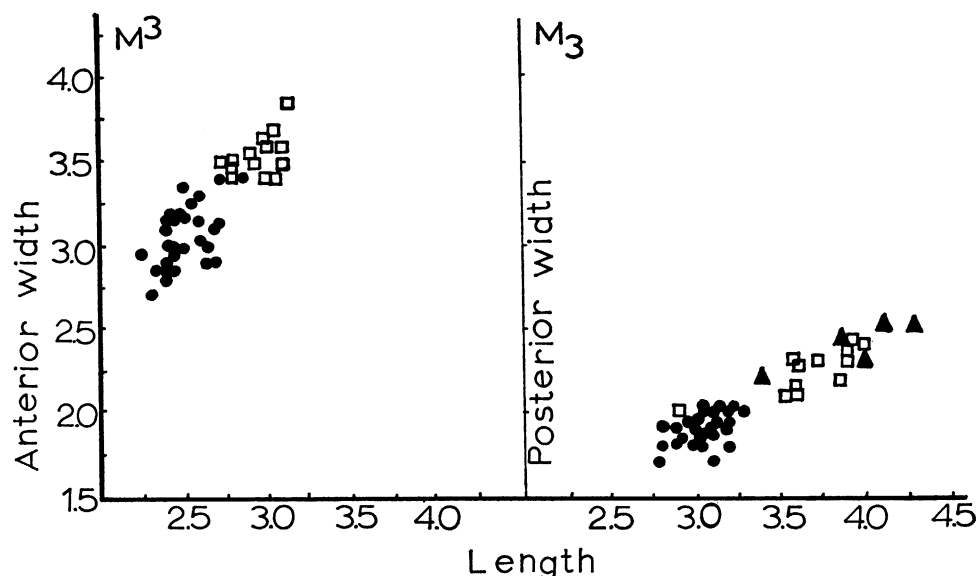


FIG. 11. Scatter diagrams of the anterior width/length and posterior width/length of the third upper and lower molars of *Microsyops wilsoni* (black dots), *M. alfi* (light squares), and *M. angustidens* (black triangles). The plotted sample of *Microsyops wilsoni* is from the East Alheit Quarry of the Wasatch beds in Colorado and from the lower Gray Bull beds of the Willwood Formation in the Big Horn Basin, Wyoming; the *M. alfi* sample is from various Four Mile localities other than the East Alheit Quarry; the sample referred to *M. angustidens* was collected at various Gray Bull localities.

of the latter localities. The justification for the specific separation of *M. wilsoni* from *M. alfi* lies in the consideration of the entire *Microsyops* lineage. If the East Alheit and the Willwood sample were not to be delineated from *M. alfi*, the distinctness of the latter species from *M. angustidens* could not be justified, and so on through the samples of *M. latidens* and *M. scottianus*. Similarly, were it not for the stratigraphic separation of the Lost Cabin beds from Bridger strata, *M. scottianus* could hardly be called a distinct species from *M. elegans*. Considering *M. wilsoni* a distinct species, however (in spite of the biologically tenuous nature of this designation, since the East Alheit sample, if stratigraphically different and temporally earlier, is probably ancestral to the *M. alfi* sample), greatly facilitates and clarifies discourse on the evolution of the entire *Microsyops* lineage.

Although the evidence is only the different P_4 (a difference that may very well disappear when a larger number of premolars is known) and the statistical difference (which is very

probably correct, since the number of specimens used was rather large) between the respective samples, I nevertheless suspect that East Alheit Quarry may be stratigraphically lower than the remaining Four Mile quarries which (taken together) are probably of exactly the same age. The difference between the East Alheit Pocket sample on the one hand and the samples of *Microsyops* from Timberlake, Sand, Kent, and Despair quarries, on the other, seems to indicate a period of time long enough to be detectable in a quantitative treatment of the samples. As stated above, the *M. wilsoni* sample is probably older and directly ancestral to the samples referred to *M. alfi* of the same geographic area. An obvious argument against this interpretation is the alternative, not favored here, that the specimens referred to *M. wilsoni* and *M. alfi*, respectively, represent synchronous subspecies of very sharply changing habitats. I believe, however, that the gradual size increase and the slow but rather steady molari- zation of the fourth premolar, seen in the over-all perspective of the *Microsyops* lin-

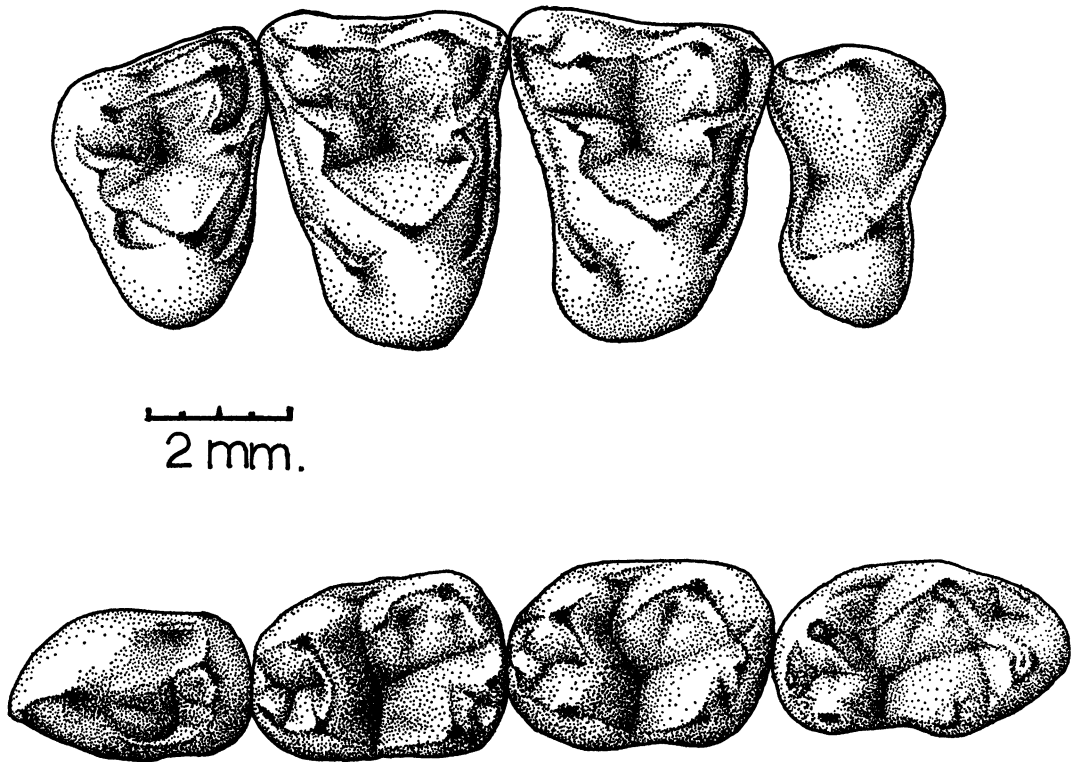


FIG. 12. *Microsypops wilsoni*, composite upper and lower fourth premolars and molars, A.M.N.H. No. 80965, from East Alheit Quarry.

eage, support a probably older age and slightly more primitive character for the *M. wilsoni* sample than for the *M. alfi* one. As far as can be judged from the available evidence, it does not seem possible that there was collecting bias involved in the quarrying of the East Alheit Pocket locality, nor do the faunal lists of the various quarries reported by McKenna (1960) indicate a biased thanatocenose in East Alheit Quarry, favoring smaller individuals.

The assumption that East Alheit Quarry is older than, and hence probably different stratigraphically from, the other known Four Mile localities is certainly not proved. McKenna is thoroughly acquainted with the geology of the area in question, and he cannot suggest any geological evidence for or against a stratigraphic difference among the Four Mile localities. Furthermore, even if the temporal distinctness could be proved, it would have to be confirmed on stratigraphic evidence. Additional statistical analyses of species in addition to those of *Microsypops*,

e.g., the abundant artiodactyl *Diacodexis* or the condylarth *Hyopsodus*, or the stem perissodactyl *Hyracotherium* which occur in most of the Four Mile localities, would add weight to any further confirmation or refutation of the proposed age difference of the quarries in question. If it can be proved that there was a time difference between the deposition of the rocks in East Alheit Pocket and in the remaining localities, then the well-collected, well-known Four Mile fauna may serve as a unique basis for studies of comparative size and morphological evolutionary rates among many well-sampled early Eocene mammal lineages.

***Microsypops alfi* (McKenna, 1960),
new combination**

Plate 33; text figures 9–11

Cynodontomys alfi McKenna, 1960, p. 79.

TYPE: U.C.M.P. No. 44777, fragmentary right maxilla with M^1 – 3 , collected from Timberlake Quarry of the Wasatch Formation of

TABLE 10

NUMERICAL DATA FOR SPECIMENS OF *Microsyps alfi* FROM TIMBERLAKE, DESPAIR, WEST DESPAIR, AND SAND QUARRIES OF THE HIAWATHA MEMBER OF THE WASATCH FORMATION, COLORADO

	N	OR	\bar{X}	S ²	S	V
P ₄						
L	1	—	3.10	—	—	—
PW	1	—	1.90	—	—	—
M ₁						
L	11	3.0–3.6	3.35	.026	.159	4.74
PW	10	2.15–2.7	2.44	.035	.186	7.62
AW	12	1.9–2.4	2.20	.025	.156	7.09
M ₂						
L	12	3.05–3.7	3.39	.043	.207	6.10
PW	11	2.3–2.8	2.57	.028	.166	6.45
AW	12	2.2–2.8	2.42	.024	.153	6.32
M ₃						
L	11	3.55–4.0	3.75	.200	.440	11.73
PW	11	2.1–2.4	2.23	.010	.097	4.34
AW	11	1.9–2.3	2.11	.012	.109	5.16
P ₄						
L	3	2.65–3.05	2.86	.040	.202	7.06
AW	3	3.3–3.75	3.55	.053	.229	6.45
M ₁						
L	6	3.2–3.5	3.27	.022	.147	4.49
AW	6	3.5–4.0	3.80	.035	.186	4.89
M ₂						
L	13	3.2–3.6	3.38	.012	.107	3.16
AW	13	4.1–4.6	4.25	.024	.154	3.62
M ₃						
L	14	2.75–3.15	2.96	.017	.130	4.39
AW	14	3.4–3.85	3.50	.016	.125	3.57

northern Colorado. See McKenna (1960) for the pertinent geographic and stratigraphic data.

HYPODIGM: The type U.C.M.P. Nos. 44062, 44063, 44145, 44776A–44776E, 44866, and numerous isolated, uncatalogued teeth in the collection of the American Museum. The hypodigm is from Anthill, Despair, Kent, Sand, and Timberlake quarries of McKenna (1960) which are in close proximity geographically and presumably are stratigraphically identical with the type locality.

SPECIFIC DIAGNOSIS: The observable differences of this species from *M. wilsoni* are the distinctly larger size of *M. alfi* and, as far as known from the available sample, the more molariform P₄, with a metaconid, of *M. alfi*.

DISCUSSION: See the discussion under *Microsyps wilsoni*. It pertains closely to the present species also.

Almost nothing is known of the morphological variation of the upper fourth premolar of *M. angustidens*. It may, when known, confirm or eradicate the specific distinctness of *M. alfi*.

Microsyps angustidens (Matthew, 1915),
new combination

Plate 35, figures 3–6, plate 39, figures 5, 6;
text figures 9–11

Cynodontomys angustidens MATTHEW, 1915,
p. 477.

Pantolestes nuptus COPE, 1882, p. 150.

Diacodexis nuptus: GAZIN, 1952, p. 71.

TYPE: A.M.N.H. No. 15073, fragmentary left mandible with P₃–M₃ and fragment of right mandible with P₄–M₂, collected from Gray Bull beds of the Wasatch Formation in the Big Horn Basin, Wyoming, 5 miles south

of the town of Otto. More precise information on the type locality is lacking.

HYPODIGM: The type and A.M.N.H. Nos. 8243, 8244, 15690, 15080-15082, 15691, 16235, 16834, 16836, 16875. The hypodigm is known from various geographical localities in the Gray Bull beds of the Big Horn Basin, Wyoming.

SPECIFIC DIAGNOSIS: Differs from *Microsyops alfi* in having a small but distinct metacone on P^4 and a slightly more molariform talonid on P_4 . The species can be distinguished from *M. latidens* by the lack of a mesostyle on the upper molars. Such a mesostyle first appears in species of *Microsyops* found in Lysite beds. The talonid of P_4 of *M. angustidens* is less molariform than that of *M. latidens*.

DESCRIPTION: P_3 in the type of this species has a distinct paracristid which sharply turns lingually at its base. The small talonid bears a small, cone-shaped cusp. Compared with P_4 of *Microsyops alfi*, P_4 of *M. angustidens* is slightly more molarized on the talonid.

The morphology of the lower molars is identical to that of *M. wilsoni* and *M. alfi*. These teeth display the same approximate size range as those of *M. alfi*.

The upper teeth are very poorly known. There is only one maxilla fragment with P^4 - M^1 , A.M.N.H. no. 16875 (pl. 35, figs. 3, 4), from undisputed upper Gray Bull beds. P^4 bears a small but distinct metacone which results in a relatively longer tooth than that of *M. alfi* or of *M. wilsoni*. The upper molar is completely similar to its homologous counterparts in *M. wilsoni* and *M. alfi*. U.S.N.M. No. 22121 reported by Gazin (1962, p. 40, pl. 1, fig. 6) from the lower part of the Knight Member near Bitter Creek Station is a maxilla with M^{1-2} correctly referred to *M. angustidens* by Gazin. The upper molars completely lack a mesostyle.

DISCUSSION: Kelly and Wood (1954, pp. 339-340) suggested that *M. angustidens* and *M. latidens* of the Lysite beds should be considered conspecific. They found that there was an overlap in all dental characters studied of the specimens in the Amherst Museum. Valid as this suggestion may be, it would jeopardize the taxonomy of all species of early and middle Eocene *Microsyops*. It appears to me, however, that the absence of a

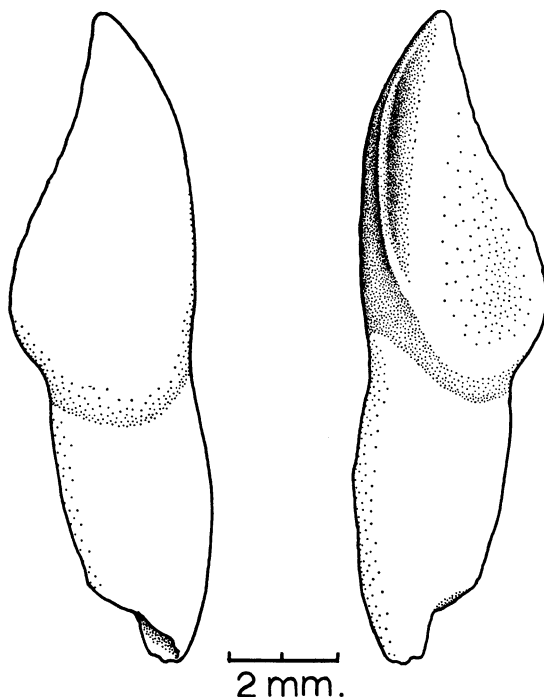


FIG. 13. ?*Microsyops wilsoni*, enlarged right lower incisor, A.M.N.H. No. 80964, from East Alheit Quarry. Left: Buccal view. Right: Lingual view.

mesostyle from the upper molars of the middle and upper Gray Bull *Microsyops* is a noticeable morphological break to warrant the specific distinction of *M. angustidens*. It cannot be doubted, however, that similar individuals are probably abundantly represented in both the later Lysite and earlier Gray Bull samples. Both McKenna (1960) and Guthrie (MS) maintained that *M. angustidens* should be separated from *M. latidens*. I agree with them in maintaining the specific distinction of the middle and upper Gray Bull *Microsyops* from material found in Lysite beds. As tenuous as this distinction may appear, it seems practical at the present to maintain it.

A peculiar specimen of *Microsyops*, A.M.N.H. No. 4699, probably a specimen of the *M. angustidens* section of the lineage, deserves a special and detailed discussion. The taxonomic history of this specimen is chaotic, as are many nomenclatorial problems stemming from the descriptions of Cope and Marsh. In 1882 Cope described a species,

Pantolestes nuptus, based on the specimen. Although he did not refer to it by number, his measurements and over-all description clearly refer to A.M.N.H. No. 4699. The specimen, which falls into the size range of *Microsyops angustidens*, has a premolariform P_4 , although there is an enamel fold at the point where the metaconid usually appears in other specimens. Unfortunately, the locality data simply refer to the provenance of the specimen as *Coryphodon* beds, Wasatch Formation, from the Big Horn Basin. It is fairly certain that the allocation of the specimen to *M. angustidens* is correct, in spite of features of P_4 more primitive than those observed in other specimens of this species. At the stage of evolution of the *Microsyops* lineage that *M. angustidens* displays, I consider a great variation, or rather a primitive retention, in the structure of P_4 that had proved very plastic during the history of the lineage much more probable than a gross deviation

in size from the earlier species which have premolariform P_4 's. It is possible, of course, that the specimen represents a large individual of *M. alfi*. That the type of "*Pantolestes nuptus*" represents a new species of *Microsyops* is improbable. The type specimen of *M. angustidens* differs from the former specimen only in the presence of a very small metaconid on the fourth premolar. Both specimens apparently are covered with the same type of matrix. In the records of the American Museum of Natural History, A.M.N.H. No. 4699 is listed as the type of *Trigonolestes nuptus*, and, as the original reference, Cope's 1882 description of *Pantolestes nuptus* is given. The generic reference to *Trigonolestes* is obviously derived from Cope's undiagnosed genus *Trigonolestes* (a junior synonym of *Diacodexis*), which he buried in the text, basing it on "*Pantolestes brachystomus*" in his 1894 critical review of Marsh's Tertiary Artiodactyla.

TABLE 11
NUMERICAL DATA FOR SPECIMENS OF *Microsyops angustidens* FROM THE GRAY BULL BEDS
OF THE BIG HORN BASIN, WYOMING

	N	OR	\bar{X}	S ²	S	V
P_3						
L	1	—	2.20	—	—	—
PW	1	—	1.30	—	—	—
P_4						
L	7	2.7–3.3	3.03	.066	.256	8.44
PW	9	1.9–2.2	2.04	.018	.133	6.51
AW	9	1.9–2.2	2.10	.010	.100	4.76
M_1						
L	10	2.9–3.4	3.17	.033	.182	5.74
PW	9	2.2–2.7	2.47	.035	.187	7.57
AW	10	1.9–2.3	2.16	.023	.150	6.94
M_2						
L	11	3.1–3.7	3.40	.050	.223	6.55
PW	9	2.3–3.0	2.70	.070	.264	9.77
AW	8	2.0–2.5	2.30	.029	.151	6.56
M_3						
L	5	3.4–4.3	3.94	.113	.331	8.40
PW	5	2.2–2.5	2.38	.017	.130	5.46
AW	5	1.9–2.2	2.10	.015	.122	5.80
P^4						
L	1	—	3.20	—	—	—
PW	1	—	3.70	—	—	—
M^1						
L	1	—	3.60	—	—	—
PW	1	—	4.20	—	—	—
AW	1	—	4.20	—	—	—

This specimen¹ complicates the species taxonomy of *Microsyops*. The name *Pantolestes nuptus*, however, is obviously a *nomen oblitum*. The specimen can be referred to the well-known taxon *M. angustidens*, although I prefer not to make it part of the hypodigm. The name "*P. nuptus*" has not been in use in the literature pertaining to *Pantolestes*, *Diacodexis*, or *Microsyops* (including *Cynodontomys*) for approximately 80 years. Gazin (1952, p. 71), in discussing *Diacodexis*, wrote: "*Diacodexis nuptus* (Cope) and *Diacodexis secans* (Cope) are described from the Wind River beds, hence according to Simpson (1933, pp. 115–116), are from the Lost Cabin horizon. *D. nuptus* is exceedingly small in comparison with Gray Bull materials, and the paraconid in the preserved lower molar is rather well forward in position and slightly less lingual than observed in the Gray Bull species." The specimen represents *Microsyops*, and it is within the size range of *M. angustidens* from the middle and upper Gray Bull beds, as discussed above.

Jepsen (1963) reported *Microsyops* cf. *M. angustidens* from the Golden Valley Formation of western North Dakota.

***Microsyops latidens* (Cope, 1882),
new combination**

Plate 34, figures 1–9, plate 35, figures 1, 2, 7, 8,
plate 36, plate 37, figures 3–7, plate 40,
figures 3–5; text figures 14, 15

Cynodontomys latidens COPE, 1882, p. 151.

Pelycodus angulatus COPE, 1882, p. 151.

Notharctus palmeri LOOMIS, 1906, p. 283.

Notharctus cingulatus LOOMIS, 1906, p. 284.

Cynodontomys knightensis GAZIN, 1952, p. 20.

TYPE: A.M.N.H. No. 4195, fragmentary lower jaw with left P₄ and right M₁₋₂. The records of the type specimen indicate merely that it was collected from Lysite beds in the Big Horn Basin.

HYPODIGM: The type and A.M.N.H. Nos. 4184, 4195, 8226, 8234–8239, 8241, 8242, 12742–12747, 12750, 12753–12755, 14694, 14695, 14701, 15629, 15630, 12748, 12749; Y.P.M. Nos. 17464, 17466, 17468, 17470, 17472, 17474, 17480, 17481, 17500–17507, 17509, 17511, 17516–17518, 17570, 17594,

¹ I thank Dr. D. A. Guthrie, who brought the specimen to my attention. It was labeled *Diacodexes nuptus*, but he recognized it as being a microsyopid.

18586, 18587, 18589, 18608, 18700–18706, 18708, 18709, 19024, 19026, 21385–21388; U.S.N.M. Nos. 19311–19319, 19322–19324, 22106–22108, 22110–22116, 22441–22442. The part of the hypodigm from the Lysite beds is from the Big Horn and Wind River basins, without adequate locality data. The United States National Museum specimens, with the exception of U.S.N.M. Nos. 19314 and 19323, were collected from beds of the Knight Member of the Wasatch Formation, at the Muddy Creek locality, 12 miles north of Big Piney, Bridger Basin, in Sublette County, Wyoming. For details of the locality and age of the associated fauna, Gazin (1952) should be consulted.

Specimens of *M. latidens*, although not included in the hypodigm, are clearly represented in various localities of the late Wasatchian Huerfano Formation (see the discussion of "*Microsyops* from the Huerfano Formation," below).

SPECIFIC DIAGNOSIS: *Microsyops latidens* differs from *M. angustidens* in having a more molariform fourth premolar, and a molar mesostyle. For the diagnostic differences of *M. latidens* from *M. scottianus*, see the specific diagnosis of the latter species.

DESCRIPTION: In spite of the more advanced fourth premolars, the presence of a molar mesostyle, and its slightly larger size, *M. latidens* is similar to *M. angustidens*. In *M. latidens* specimens are available that show the dentition anterior to the fourth premolars. The lower incisor, which is better known in *M. scottianus* and *M. lundeliusi*, is described in conjunction with the latter species, since there are no discernible differences in the morphology of the tooth between these species.

The lower antemolar dentition consists of the enlarged incisor, followed by the second, third, and fourth premolars. P₂ is single-rooted, but several specimens clearly show traces of fusion of two separate roots, strongly suggesting that the postincisor tooth is a premolar and not a canine. The crown of this tooth is not well known in this species.

P₃ is double-rooted, premolariform, very much like P₄ of *M. wilsoni*, although P₃ of *M. latidens* has a relatively smaller, incipient talonid.

The enlarged upper incisor is known in

TABLE 12

NUMERICAL DATA FOR SPECIMENS OF *Microsyops latidens* FROM THE LYSITE BEDS OF WYOMING

	N	OR	\bar{X}	S ²	S	V
P ₂						
L	1	—	2.00	—	—	—
PW	1	—	1.10	—	—	—
P ₃						
L	6	2.0–2.7	2.37	.059	.242	10.21
PW	6	1.3–1.6	1.53	.015	.121	7.90
P ₄						
L	22	3.0–3.6	3.30	.035	.187	5.66
PW	23	1.8–2.7	2.23	.038	.194	8.70
AW	20	1.8–2.4	2.18	.041	.202	9.26
M ₁						
L	29	3.0–3.7	3.30	.030	.172	5.21
PW	30	2.3–2.8	2.54	.021	.146	5.74
AW	28	2.0–2.5	2.20	.060	.244	11.09
M ₂						
L	23	3.2–4.0	3.60	.077	.276	7.66
PW	22	2.4–3.3	2.74	.031	.176	6.42
AW	26	2.2–2.7	2.43	.016	.126	5.19
M ₃						
L	16	3.4–4.5	4.07	.103	.320	7.86
PW	19	2.1–2.7	2.43	.027	.163	6.70
AW	22	1.8–2.5	2.21	.035	.187	8.46
P ³						
L	2	2.5–3.0	2.75	—	—	—
PW	2	2.5–2.9	2.70	—	—	—
P ⁴						
L	4	3.1–3.5	3.37	.036	.189	5.60
PW	4	3.5–4.0	3.70	.047	.215	5.81
M ¹						
L	6	3.2–3.8	3.42	.046	.213	6.22
PW	7	3.7–4.4	3.97	.062	.249	6.27
AW	8	3.7–4.6	4.06	.094	.306	7.53
M ²						
L	7	3.3–3.8	3.58	.048	.219	6.11
PW	7	3.8–4.4	4.11	.088	.296	7.20
AW	7	3.8–4.8	4.38	.135	.360	8.21
M ³						
L	5	3.0–3.8	3.42	.082	.286	8.36
PW	6	3.4–4.3	3.90	.104	.321	8.23

U.S.N.M. No. 19319, a specimen from the La Barge local fauna. It is the only specimen of an upper incisor of *Microsyops*, in addition to the one known in the type of *M. lundeliusi* and A.M.N.H. No. 55284, a Huerfano specimen of *M. lundeliusi*. Various figures on plates 33, 48, and 50 illustrate these specimens, and under *M. lundeliusi* certain aspects of the morphology of this characteristic tooth are discussed, in addition to the description given here. The enlarged upper incisor, if it

be imagined in its alveolus, had the apex pointing downward and slightly posteriorly. The robust, long, and wide root (longer and wider than the longest or widest portion of the crown) is transversely slightly flattened. The limits of the enamel are well defined. The crown is somewhat transversely flattened, like the root. The posterolingual surface of the crown is more concave than any other area of the crown, owing mainly to the natural condition of the tooth as well as to some

wear by the enlarged lower incisor. There is distinct wear on the anterior convex arc of the crown. It is not an occlusal wear surface but probably due to objects either gnawed or grasped by the incisors.

In A.M.N.H. No. 55284, a skull of *M. lundeliusi*, an upper canine and a full complement of premolars followed the upper incisor. The canine and the first upper premolars are not known in this species. P² is known in U.S.N.M. No. 12140 (pl. 34, figs. 7, 9), a specimen from the La Barge local fauna assigned to *M. latidens*. The second upper premolar is slightly oblong in shape, and it has a crown higher than in any of the teeth following it.

The third upper premolar is known from several specimens (see pl. 34). The extent to which a metacone may develop is quite variable on the tooth, which is slightly wider than long.

The morphology of P⁴ is rather decisive in the taxonomy of the samples involved. Although the metaconule is present on P⁴ of U.S.N.M. No. 12140, that cusp is clearly absent from two specimens, U.S.N.M. Nos. 12138 and 22108, from the same locality. From the few specimens of *Microsyops* from the Lysite beds the metaconule is absent. In spite of the sporadic occurrence of a specimen with a definite metaconule in the La Barge local fauna, it is quite apparent that the degree of molarization of the fourth premolars did not advance beyond the condition seen in the Lysite specimens. The latter factor and the same general size range of the dental elements of the Lysite and La Barge samples alter the idea that "*Cynodontomys knightensis*" is distinct from *M. latidens*, a view that is discussed below.

The molars of *M. latidens* invariably bear a small mesostyle.

DISCUSSION: Gazin (1952, p. 20), in describing his new species "*Cynodontomys knightensis*" from the La Barge local fauna stated: "... Size close to that of *Cynodontomys latidens* Cope (1882a, pp. 151-152), much smaller than more nearly contemporaneous *Cynodontomys scottianus* (Cope) (1881a, pp. 188-189). P⁴ with paraconid distinct and low, and with metaconid almost as large as protoconid and well separated from it though not so much so as in *Microsyops*. Talonid of P⁴

broad and fully molariform, though slightly narrower than the molars, with protoconid, entoconid and hypoconulid sharp and well defined. P⁴ distinctly more progressive than illustrated (Matthew, 1915c, figs. 45, 46) for *Cynodontomys latidens* Cope."

Similarities between *M. angustidens* and *M. latidens* and the consequent taxonomic problems are discussed above under *M. angustidens*.

There is no significant size difference between the Lysite and La Barge samples. The means of the various parameters of the La Barge sample are only very slightly higher than those of the Lysite ones (see tables 12 and 13). The characters of P⁴ listed by Gazin (1962, p. 41) are not consistently different from those of *M. latidens* of the Lysite beds. A.M.N.H. No. 14695, a right mandible from the Lysite beds of the Wind River Basin illustrated by Matthew (1915, fig. 45; see pl. 36, fig. 1, of the present paper), is on the least molariform end of the sample for P⁴ from the Lysite beds. In addition to citing this specimen, Gazin referred to A.M.N.H. No. 15691 (or rather to Matthew's figure) as an illustration of *M. latidens*. In the latter specimen, P⁴ is less molariform than in any other undoubted Lysite specimen. Matthew (1915, fig. 46), however, clearly queried his own allocation of that specimen, which was collected from upper Gray Bull beds of the Big Horn Basin. To stress this point, the type of *M. latidens*, A.M.N.H. No. 4195, from the Lysite beds of the Big Horn Basin easily fits into the known spectrum of the degree of molarization of the *Microsyops* P⁴'s from the La Barge local fauna. Similarly, there is hardly any (if any) more influence of the field of molarization on the upper fourth premolars of the La Barge sample than is seen in the variation of the Lysite specimens. Specific references to important specimens are given above in descriptions of P⁴ of *M. latidens*.

Gazin (1952, p. 20) stated that P⁴ of *Microsyops* specimens of the La Barge local fauna is as molariform as P⁴ in *M. scottianus*. There are no significant differences in the degree of molarization of this tooth among *Microsyops* specimens from the Lysite, Knight Member (the provenance of the La Barge local fauna), or Lost Cabin. To determine the relative

TABLE 13

NUMERICAL DATA FOR SPECIMENS OF *Microsyops latidens* FROM THE LA BARGE LOCAL FAUNA OF THE KNIGHT MEMBER OF WASATCH FORMATION OF THE GREEN RIVER BASIN, WYOMING

	N	OR	\bar{X}	S ²	S	V
P ₃						
L	1	—	2.30	—	—	—
PW	1	—	1.70	—	—	—
P ₄						
L	7	3.3–3.6	3.40	.017	.129	3.79
PW	7	2.1–2.5	2.33	.019	.137	5.87
AW	6	2.2–2.5	2.33	.015	.121	5.19
M ₁						
L	13	3.3–3.7	3.48	.010	.101	2.90
PW	13	2.4–2.7	2.62	.012	.110	4.19
AW	13	2.1–2.5	2.37	.017	.130	5.48
M ₂						
L	12	3.7–4.2	3.86	.029	.169	4.37
PW	12	2.8–3.1	3.01	.014	.116	3.85
AW	12	2.5–2.8	2.65	.014	.116	4.37
M ₃						
L	5	4.2–4.7	4.46	.033	.181	4.05
PW	5	2.6–2.9	2.77	.020	.139	5.01
AW	5	2.2–2.8	2.54	.053	.230	9.05
P ₄						
L	3	3.3	3.30	—	—	—
PW	3	3.7–4.0	3.90	.030	.173	4.43
M ¹						
L	4	3.5–3.6	3.52	.003	.050	1.42
PW	4	4.0–4.4	4.22	.029	.170	4.02
AW	4	4.0–4.3	4.20	.020	.141	3.35
M ²						
L	3	3.5–3.7	3.63	.012	.107	2.94
PW	3	4.3–4.4	4.37	.003	.574	3.13
AW	3	4.5–4.8	4.63	.023	.152	3.28
M ³						
L	4	3.3–3.5	3.42	.009	.095	2.77
PW	4	3.5–4.1	3.92	.083	.287	7.32

degree of molarization of the upper fourth premolar of *M. scottianus* is impossible, because about two specimens are known. On these the metaconule is present, and this tooth appears to be less triangular and more squared off than any of the homologous teeth of the Lysite and La Barge samples. *Microsyops scottianus*, of course, is slightly larger than the specimens referred to *M. latidens*.

In spite of the presence of *Microsyops latidens*, I follow Gazin in believing that the La Barge local fauna is a probable age equivalent of the assemblage from the Lost Cabin beds.

Although it is clear that there was a progressive over-all trend during the early and

middle Eocene toward molarization of the lower and upper fourth premolar, it is equally clear that the same trend did not involve all populations of some species—*M. latidens*, for example. At least one lineage (the La Barge sample) or probably two (the cf. *M. latidens* specimens of the Huerfano Formation discussed below) lineages retained the dental morphology of *M. latidens*, whereas the phyletic evolution of other unknown populations of *M. latidens* resulted in discernible morphological and size changes of later forms such as *M. scottianus* and *M. lundeliusi*. The synchronous occurrence of *M. scottianus* and *M. lundeliusi* in the same strata would tend to

preclude the origin of *M. lundeliusi* from *M. scottianus*. Guthrie (MS) noted that *M. latidens* was the most common species of primates from the Lysite fauna, a strong indicator of the success of this species.

Gazin (1952) has suggested that the difference of the La Barge *Microsyops* from *M. scottianus* was due probably to ecological causes, but Guthrie (MS) attributed the difference to chronological rather than ecological causes. The fact that *M. latidens* occurs in the Huerfano Formation roughly synchronously with *M. lundeliusi* and *M. scottianus* appears to support Gazin. Both Guthrie (MS) and Robinson (1966) either critically accepted or followed Gazin's specific distinction of

the La Barge *Microsyops* from *M. latidens*. Robinson referred several Huerfano specimens to Gazin's "*C. knightensis*."

***Microsyops scottianus* Cope, 1881**

Plate 38, plate 39, figures 1-4, plate 44;
text figures 14, 15

Microsyops scottianus COPE, 1881, p. 188.

Microsyops? scottianus: OSBORN, 1902, p. 210.

Cynodontomys scottianus: MATTHEW, 1915, p. 468.

TYPE: A.M.N.H. no. 4748, fragmentary left mandible with P₄, from the Lost Cabin beds of the Wind River Basin; no exact locality data are available.

HYPODIGM: The type and A.M.N.H. Nos.

TABLE 14
NUMERICAL DATA OF SPECIMENS OF *Microsyops scottianus* FROM THE
LOST CABIN BEDS OF WIND RIVER BASIN, WYOMING

	N	OR	\bar{X}	S ²	S	V
P ₂						
L	1	—	2.20	—	—	—
PW	1	—	1.30	—	—	—
P ₃						
L	2	2.8-2.9	2.85	—	—	—
PW	2	1.8-2.2	2.00	—	—	—
P ₄						
L	13	3.4-4.2	3.87	.045	.212	5.47
PW	12	2.4-3.0	2.73	.030	.175	6.41
AW	11	2.3-2.9	2.63	.042	.205	7.79
M ₁						
L	16	3.8-4.1	3.91	.017	.128	3.27
PW	17	2.8-3.2	3.10	.029	.171	5.51
AW	16	2.4-3.0	2.71	.020	.143	5.27
M ₂						
L	15	3.8-4.5	4.11	.037	.192	4.67
PW	17	3.0-3.7	3.35	.029	.169	5.04
AW	13	2.6-3.1	2.90	.020	.141	4.86
M ₃						
L	11	4.5-5.4	4.84	.077	.276	5.70
PW	12	2.8-3.2	3.02	.022	.146	4.83
AW	13	2.5-2.9	2.71	.017	.132	4.87
P ₄						
L	1	—	3.60	—	—	—
PW	1	—	4.30	—	—	—
M ¹						
L	1	—	3.10	—	—	—
PW	1	—	4.30	—	—	—
AW	1	—	4.50	—	—	—
M ²						
L	1	—	4.20	—	—	—
PW	1	—	4.20	—	—	—
AW	1	—	4.80	—	—	—

2969, 4191, 4743, 4744, 4746, 6838, 6839, 6842, 6844, 6845, 8245, 12751, 14685-14693, 14696-14699, 14969, 14700, 14702, 14703, 14706; U.S.N.M. Nos. 22117-22120. In addition to the type, all the American Museum specimens were collected from Lost Cabin beds of the Wind River Basin. The United States National Museum specimens were collected from New Fork beds, east of Big Piney, Bridger Basin, Wyoming (see Gazin, 1962, for exact details of the locality).

SPECIFIC DIAGNOSIS: *Microsyops scottianus* is larger than *M. latidens*. The metaconid on P_4 is large, and the talonid is distinctly molariform. There is no adequate sample of the upper fourth premolar, although it appears that this tooth of *M. scottianus* is less triangular and more square than that of *M. latidens*. On P^4 of *M. scottianus* the metaconule is present, although the premetaconule crista is lacking.

DESCRIPTION: Nothing of value can be added to the descriptions of the dental characters of the species that are described above. Except for the somewhat characteristic feature of the fourth premolars and the noticeable difference in size, which are noted under the specific diagnosis, the morphological similarities of this species to the ones described above are close.

A fragmentary mandible, U.S.N.M. No. 22118, from the New Fork Member of the Wasatch Formation contains P_3 in the same transversely oriented position as seen in *M. lundeliusi* and in the Bridger *Microsyops*. This minor but noticeable feature is present consistently in the later Huerfano and Bridger individuals of *Microsyops*, but apparently occurs sporadically in specimens referable to *M. scottianus*.

DISCUSSION: This species was originally allocated to *Microsyops* by Cope, until Matthew (1915) transferred it to *Cynodontomys*. Under the discussion of *Microsyops*, the lack of sufficient generic distinction between this species and the lower Bridger *Microsyops* is discussed.

Microsyops lundeliusi (White, 1952)
McKenna, 1966

Plate 41, figures 4, 5, plate 45, figures 3, 4,
plates 48-52; text figures 17, 18

Cynodontomys lundeliusi WHITE, 1952, p. 191.
Microsyops lundeliusi: MCKENNA, 1966, p. 18.

TYPE: U.S.N.M. No. 18371, almost complete right mandible with M_2 and posterior halves of M_1 and M_3 ; fragment of left mandible with the mandibular condyle; left upper incisor. The type is from the Lost Cabin beds, according to White (1952, p. 191), NW. $\frac{1}{4}$, SW. $\frac{1}{4}$, sect. 5, T. 4 N., R. 6 E. south side of Cottonwood (Dry Muddy) Creek, 11 miles (airline) north-northwest of Shoshoni, Boysen Reservoir area, Wind River Basin, Fremont County, Wyoming.

The measurements of the type mandible and teeth are: alveolar length, P_2 , 4.0; alveolar length, P_3 , 3.8; alveolar length, P_4 , 5.1; length, M_2 , 5.8; posterior width, M_2 , 4.4; anterior width, M_2 , 4.4; posterior width, M_3 , 4.0.

HYPODIGM: The type and A.M.N.H. Nos. 6846, 6847, 17463-17469, 55169-55179, 55208, 55212-55214, 55283-55285; Y.P.M. No. 16456; U.C.M. Nos. 20806-20808, 23479, 24692, 26544. With the exception of the type, the hypodigm was collected at various localities from the Huerfano Formation, Colorado.

SPECIFIC DIAGNOSIS: *Microsyops lundeliusi* is recognizably larger than any of the other early and middle Eocene species of *Microsyops*.

DESCRIPTION: The anterior dentition of this species is more thoroughly known than in any other species. The molars are characterized briefly, since they closely resemble those of other species of the genus. *Microsyops lundeliusi*, although the best-known species of *Microsyops*, has not previously been fully described.

The enlarged incisor is not excessively large in relation to the cheek teeth. The tooth is massive, and *in situ* in the mandible it forms an angle of approximately 130 degrees with the horizontal plane of the ramus. The anteroposterior broadest dimension of this incisor is approximately 5 mm. above the beginning of the enamel line, although in the live animal this broadest portion of the tooth was probably the limit to which the gum extended. The incisor is convex buccally, and the sharp crest that forms the most dorsal extent of the tooth is directed in an anterolingual (or posterobuccal) direction. It is unique and remarkable in that this sharp and serrate knife edge of the enlarged lower incisor is not or only slightly worn, even in senile individuals. Although the crista running posteriorly

from the apex of the tooth is rarely or never worn, there is usually a distinct wear facet posterobuccal to the apex of the incisor. Anterolingually, from the apex downward, a crista runs ventrally on the anterior border of the tooth about three-fifths of the way down, where it gradually turns posteriad. This crest is invariably worn down smoothly on the vertical plane of the symphysis. It appears to indicate that the mandibular symphysis of *Microsyops* was mobile. Incidental to the masticatory function of the mobile symphysis, the motion of the independently moving rami resulted in smooth wear on the anterolingual cristae of the juxtaposed lower incisors. Posterior to the anterolingual cristae there is a groove, similar to that of ordinary pocket knives for holding the blade.

Dorsal to the groove noted above there is a broad, rounded ridge which runs from the apex of the incisor crown to the posterior limit of the crown. This ridge separates the lingual surface from the slightly concave, posteromedially facing dorsal surface of the incisor.

The cheek teeth of *M. lundeliusi* tend to have a continuous buccal cingulum, of varying strength on different specimens.

There is a very short diastema between the enlarged incisor and P_2 . The latter tooth is simple-crowned; it is poorly known because it is either shattered or broken out of the known mandibles. P_3 is premolariform, thickened transversely, and bears a small talonid. This tooth is rotated anterobuccally in comparison with the P_4 behind it. On P_4 the protoconid and the metaconid are subequal, and the paraconid is only a nubbin. The talonid is completely molariform.

The enlarged upper incisor of the type specimen from the Boysen Reservoir area is very low-crowned and blunt, with a wide, massive root (see pl. 48). In contrast, A.M.N.H. No. 55284, from the upper Huerfano beds, the only known skull of this species, has a very caniniform upper incisor. This tooth of the Huerfano specimen is slightly curved in a posterior direction, has a high crown which tapers gradually, and, as does the type, has a massive root.

The upper canine, although it persisted in Huerfano specimens, is poorly known; it was relatively rounder, judged from its alveolus,

than either the incisor or P^1 , and strikingly smaller than the incisor. P^1 is caniniform, but transversely flattened, and its two roots are fused. Sharp anterior and posterior cristae originate from the apex of the tooth. P^2 is virtually identical to the preceding P^1 . P^3 has a distinct, small protocone and a metastyle.

On P^4 the metacone is slightly smaller than the paracone, and there is no evidence of a mesostyle. The paraconule is invariably present, but from half of the specimens the metaconule is absent. The lingual half of P^4 is relatively narrower than the buccal half. In some specimens, A.M.N.H. No. 55212, for example, there is a distinct hypocone.

A.M.N.H. No. 55208 (pl. 51, figs. 1-4) from the upper Huerfano Formation is the maxillary fragment of a young individual of *M. lundeliusi* with DP^{3-4} and M^1 . DP^{3-4} are excellently preserved, and M^1 , although badly shattered, is recognizable. Both of the deciduous teeth are relatively more elongate than their replacement homologues. DP^3 bears a distinct metacone, and the completely molariform DP^4 has had a mesostyle and a hypocone—two features that are missing from most of the permanent P^4 's (some have a hypocone as cited above but none shows a mesostyle).

It is rather curious that, although the replacement P^3 of this species has a relatively large protocone and bears no trace of a metacone, the deciduous P^3 noted here has a metacone (as expected from a tooth influenced to a greater degree by the field of molarization than the replacement P^3) but has only a barely discernible tiny protocone. It is, of course, possible that the teeth I identify as DP^3 and DP^4 are actually DP^2 and DP^3 , but I have no confidence in such an interpretation.

DP^3 has a distinct but incipient metastyle. On DP^4 the parastyle is very large, and the metastyle is distinct. Both deciduous teeth have a strong postcingulum and precingulum but a weak and intermittent ectocingulum.

DISCUSSION: Because of the discrepancy between the morphology of the incisors of the type from the Lost Cabin beds of the Boysen Reservoir area and that of A.M.N.H. No. 55284 from the upper Huerfano Formation in Colorado, it is quite likely that the

TABLE 15
NUMERICAL DATA FOR SPECIMENS OF *Microsyops lundeliusi*
FROM THE HUERFANO FORMATION OF COLORADO^a

	N	OR	\bar{X}	S ²	S	V
P ₃						
L	4	4.0-4.8	4.32	.116	.338	7.82
PW	4	2.6-3.3	3.10	.113	.333	10.74
P ₄						
L	11	5.1-6.5	5.71	.225	.472	8.26
PW	11	3.7-4.5	4.05	.095	.307	7.58
AW	11	3.3-4.3	3.89	.085	.291	7.48
M ₁						
L	15	4.9-6.2	5.55	.111	.332	5.98
PW	12	3.9-4.5	4.24	.039	.197	4.64
AW	15	3.3-4.0	3.73	.036	.190	5.09
M ₂						
L	18	5.2-6.5	5.90	.138	.370	6.27
PW	18	4.2-4.8	4.58	.029	.168	3.66
AW	18	3.6-4.6	4.09	.073	.270	6.60
M ₃						
L	8	5.9-8.4	6.84	.580	.761	11.04
PW	9	3.8-4.5	4.20	.065	.255	6.07
AW	10	3.3-4.2	3.75	.850	.290	7.73
I ^u						
L	2	4.7	4.7	—	—	—
W	2	2.0-2.2	2.1	—	—	—
C ^u						
L	1	3.3	—	—	—	—
W	1	3.0	—	—	—	—
P ¹						
L	2	2.9-3.1	3.0	—	—	—
W	2	2.0-2.2	2.1	—	—	—
P ²						
L	3	3.3-3.7	3.5	—	—	—
W	2	2.0-2.2	2.1	—	—	—
P ³						
L	4	4.2-5.0	4.8	—	—	—
W	3	5.0-5.3	5.15	—	—	—
P ⁴						
L	6	4.6-5.8	5.21	.290	.538	10.32
PW	4	5.4-6.8	6.12	.609	.780	12.74
AW	3	4.9-5.4	5.20	.070	.264	7.07
M ¹						
L	5	5.2-6.2	5.82	.202	.450	7.73
PW	5	6.3-7.1	6.38	.597	.771	12.08
AW	5	5.6-7.2	6.58	.392	.628	9.54
M ²						
L	4	5.4-6.3	6.02	.176	.418	6.94
PW	5	5.9-7.0	6.44	.233	.483	7.50
AW	5	6.6-7.4	7.06	.118	.344	4.87
M ³						
L	5	5.2-5.6	5.40	.040	.200	3.70
PW	4	5.0-6.3	5.77	.329	.573	9.93

^a Data obtained from the type specimen, which was collected from Lost Cabin beds of the Wind River Basin, Wyoming, are not included.

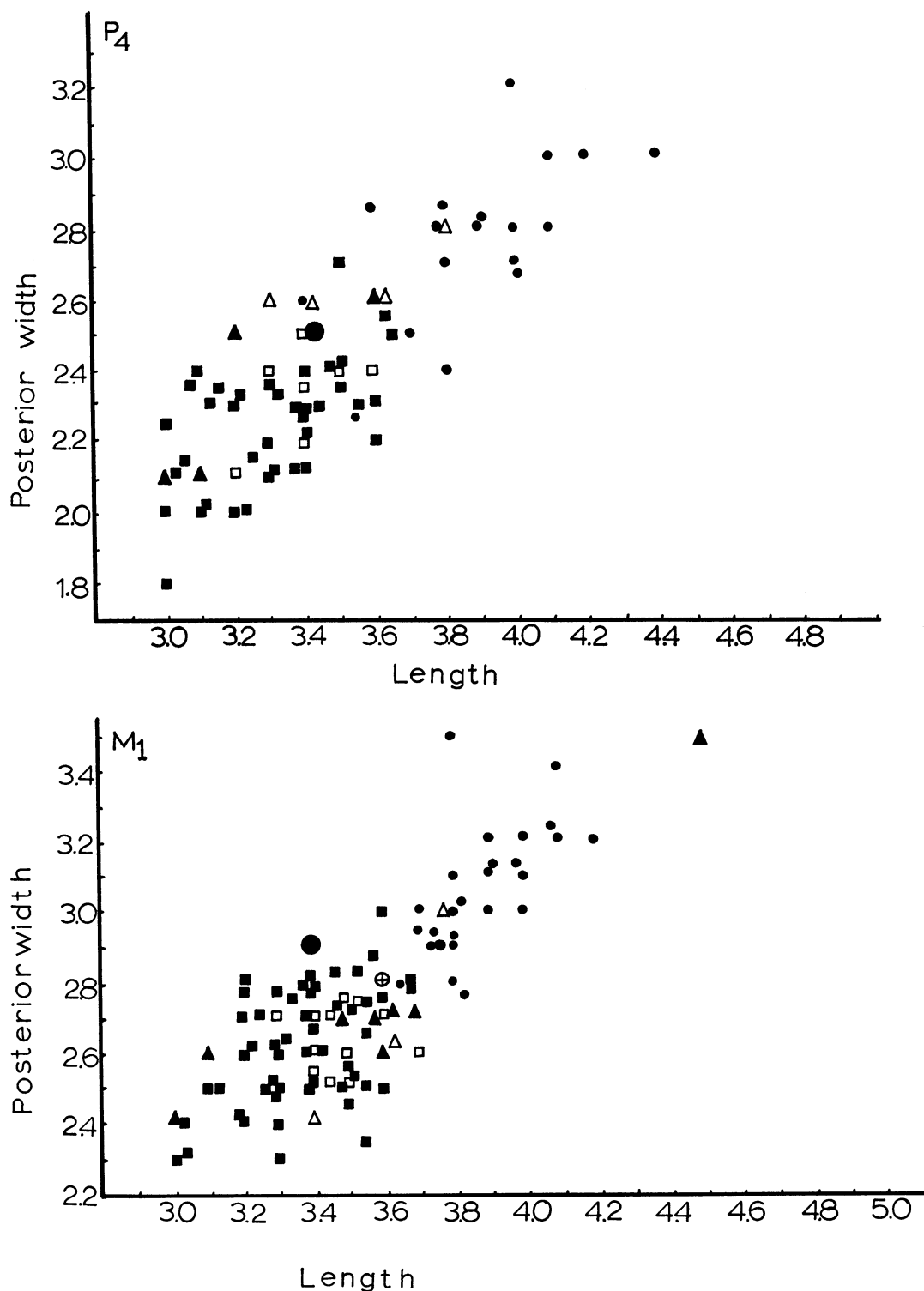


FIG. 14. Scatter diagrams of length/posterior width of fourth lower premolar and first molar of the Lysite and La Barge samples of *Microsyops latidens*, the Lost Cabin *Microsyops scottianus*, and all other species of *Microsyops* (except *M. lundeliusi*) from the Huerfano Formation of Colorado.

Symbols: Open triangles, specimens collected during the 1916 and 1918 Huerfano expeditions that lack locality data; black triangles, specimens from A.M.N.H. locality II; large black dot, specimens from A.M.N.H. locality III; circle with plus symbol, specimens from A.M.N.H. locality VI; solid square, specimens from Lysite beds; open square, specimens from the La Barge local fauna; solid black dot, specimens from the Lost Cabin beds.

Huerfano sample may have been specifically different from the sample that the type from Wyoming represents. Neither the author of *M. lundeliusi*, White (1952), nor Robinson (1966), who treated the Huerfano sample in detail, reported that the type of *M. lundeliusi* contained an upper incisor as well as the posterior portion of the mandible in addition to the horizontal ramus noted. The upper incisor of the type is broad, low-crowned, and rather blunt, as described above, whereas the homologous tooth from the Huerfano skull is distinctly more slender, higher-crowned, and was more pointed, previous to wear.

The difference between the upper incisors is the only clue to the possible specific distinction of the two samples. On the basis of the available evidence, however, I prefer to avoid any formal taxonomic statement concerning this possibility. There is an overriding similarity, as opposed to the only detectable difference based on single specimens of each sample, between the general morphology of the known features of the Boysen Reservoir *Microsyops* and that of the sample from the Huerfano Formation. Before anything more conclusive can be said, additional specimens are needed from the Boysen Reservoir area.

Robinson (1966, p. 41), from the frequency distribution of the widths of P_3 and P_4 , has suggested that sexual dimorphism may have existed in *M. lundeliusi*, the males having the larger, and the females the smaller, premolars. On the basis of four P_3 's, 11 P_4 's, and 10 to 20 M_1 's, M_2 's, and M_3 's, I cannot agree with his conclusions. The sample is rather small and the plotted scatter of my measurements (I have used length/posterior width ratios) do not warrant a postulation of sexual dimorphism.

The most probable ancestor of *M. lundeliusi* is *M. latidens*.

Microsyops FROM THE HUERFANO FORMATION

Plate 37, figures 1, 2, plate 40, figures 1, 2, 6, 7, plate 41, figures 1-3, plate 42; text figures 14, 15

Many specimens of *Microsyops*, referable to at least three of the previously reviewed species, have been collected by expeditions of the American Museum of Natural History during the years 1916, 1918, and 1952. The taxonomic problems that these specimens

present are virtually insoluble on the basis of the dental remains alone.

The Huerfano localities were arranged by Robinson (1966) in the following relative position as found in the Huerfano facies: localities I, II, III, and V are the youngest; localities VI, VII, VIII, VIIIa, and IX, the oldest. In the Farasita facies, locality IV is the oldest. Robinson believes that locality X is probably of the upper faunal level.

The following localities yielded species of *Microsyops* other than *M. lundeliusi*: I, II, III, IV, VI, VIII, VIIIa. Robinson allocated the *Microsyops* specimens other than *M. lundeliusi* from the various localities as follows: "*Cynodontomys knightensis*," from localities I, II, III, VI, VIII, VIIIa, and X; "*Cynodontomys scottianus*," from locality IV; both "*C. knightensis* and *C. scottianus*," from locality VI, although the only specimen of "*C. scottianus*" was queried by Robinson.

An examination of text figures 14 and 15, attempts to plot the specimens under discussion, may help the reader to appraise and evaluate this minor but very difficult taxonomic problem. With the exception of A.M.-N.H. Nos. 55225 from locality II (see pl. 40, figs. 1, 2), a specimen with measurements that fall on the lower end of the range in size of *M. latidens*, the proper evaluation of specimens other than *M. lundeliusi* is rather hopeless on the basis of the available material.

Specimens from locality II and III seem to belong to *M. latidens*, but locality VIII yielded specimens with measurements that fall in the size range of *M. scottianus* and not "*C. knightensis*" as implied by Robinson. The individual small samples from the various Huerfano localities, the differences that may have been due to depositional sampling biases, and the minor habitat differences that may have been involved add up to a vexing and insoluble taxonomic difficulty. The total variation of the length/posterior width of all Huerfano *Microsyops* specimens, exclusive of *M. lundeliusi*, extends from the known lower limits of *M. latidens* to the known upper limits of *M. scottianus* of these parameters. It seems quite certain that there were at least two species of *Microsyops* in addition to *M. lundeliusi* in the upper Huerfano and Farasita facies. Allocation of each specimen to either *M. latidens* or *M. scottianus*

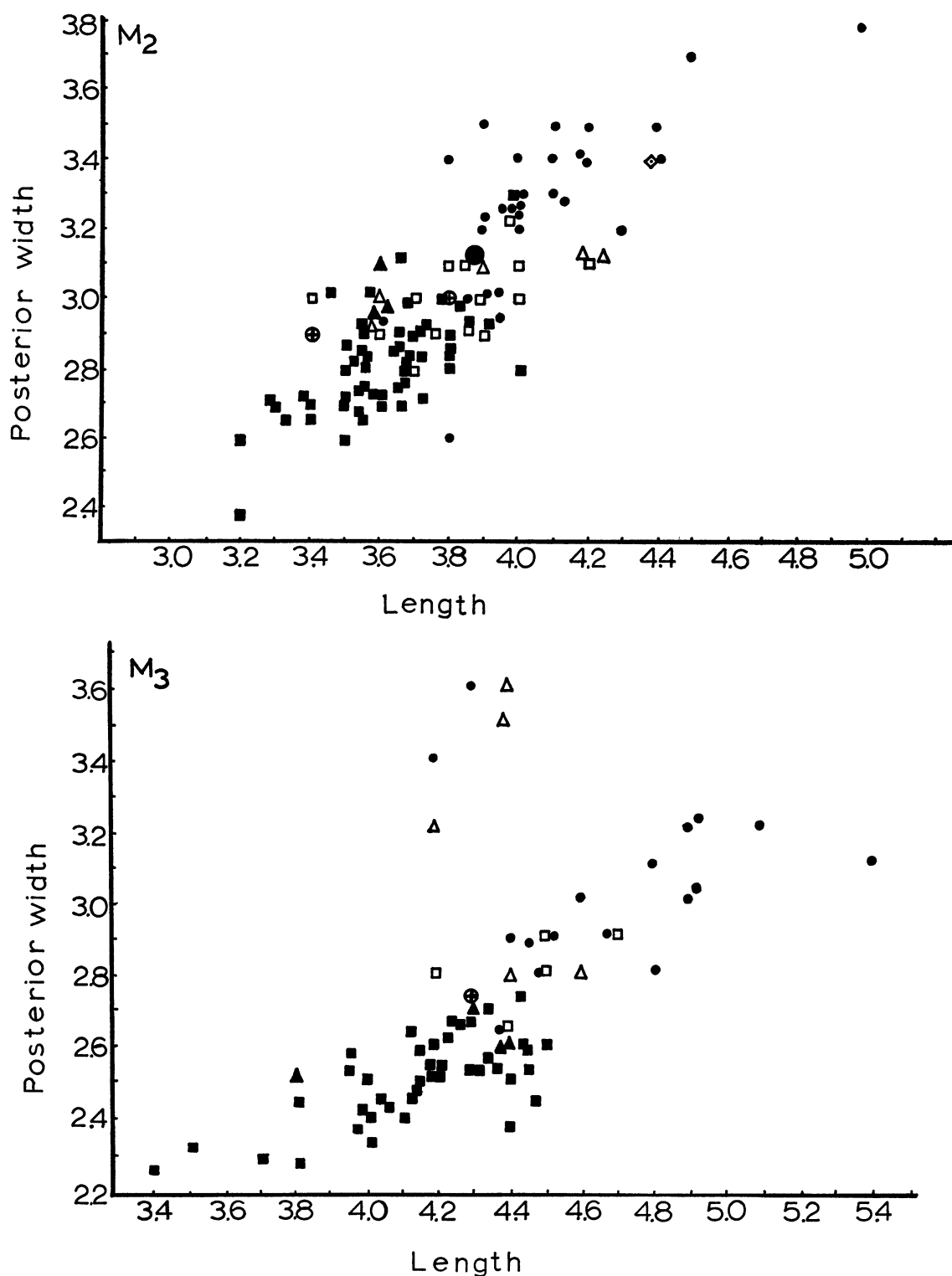


FIG. 15. Scatter diagrams of length/posterior width of second and third lower molars of the Lysite and La Barge samples of *Microsyops latidens*, the Lost Cabin *Microsyops scottianus*, and all other *Microsyops* (except *M. lundeliusi*) from the Huerfano Formation of Colorado.

Symbols: Open triangles, specimens collected during the 1916 and 1918 Huerfano expeditions that lack locality data; black triangles, specimens from A.M.N.H. locality II; large black dot, specimens from A.H.N.H. locality III; circle with plus symbol, specimens from A.M.N.H. locality VI; tilted square with small dot, specimens from A.M.N.H. locality VIII; solid square, specimens collected from Lysite beds; open square, specimens from the La Barge local fauna; solid black dot, specimens from the Lost Cabin beds.

is, however, impossible at present. The variability of Huerfano *Microsyops* is not necessarily proof for the contention that two species are represented in addition to *M. lundeliusi*. It may be speculated that *M. latidens* and *M. scottianus* were hybridizing after a long period of pursuing independent phyletic evolution.

***Microsyops elegans* (Marsh, 1871)
Leidy, 1872**

Plate 39, figures 7, 8, plate 45, figures 1, 2,
plates 46, 47

Limnotherium elegans MARSH, 1871, p. 45.

Hyopsodus gracilis LEIDY, 1872, p. 373.

Microsyops gracilis: LEIDY, 1872, p. 373.

Palaeacodon verus LEIDY, 1872, p. 373.

Bathrodon typus MARSH, 1872, p. 211.

Mesacodon speciosus MARSH, 1872, p. 212.

?*Microsyops typus*: OSBORN, 1902, p. 173.

Microsyops verus: OSBORN, 1902, p. 172.

TYPE: Y.P.M. No. 11794, fragment of left ramus with P₄-M₂, collected from lower Bridger beds; no adequate type locality data are available.

HYPODIGM: The type and Y.P.M. Nos. 1072, 11790, 11794, 12594, 12992, 13251, 13255, 13256, 13259, 13260, 13263, 13265, 13268-13270, 16273, 16274; A.M.N.H. Nos. 1773, 1775, 1776, 11431, 11433, 11434, 11437, 11439, 11444, 11445, 12590-12592, 12597, 13040, 14569, 19197; U.S.N.M. Nos. 12138, 12140, 13283, 13284, 13440, 17802-17810, 17812, 17814-17816, 17818, 18015, 18016, 18018-18021. The entire hypodigm was collected at various localities in southwestern Wyoming from either Bridger A or Bridger B beds.

SPECIFIC DIAGNOSIS: The observable morphological differences that differentiate this species from other closely similar species of *Microsyops* are few. Both the upper and fourth premolars are completely molariform, although P₄ still lacks a hypocone and a mesostyle. The conules are strong and distinct on all the known P₄'s. The paraconid on P₄ is very small as in the older species of the genus. P₃ in all the specimens is quite wide transversely in the mandible, unlike P₃ of the older species, but occasional specimens of *M. scottianus* also show this trait.

The size ranges and the means of *M. scot-*

tianus and *M. elegans* are somewhat similar, although *M. elegans* on the average is smaller than *M. scottianus*. Future collecting may very well result in the finding of new localities from which new samples may prove *M. scottianus* to be a synonym of *M. elegans*. At present, the descent of *M. elegans* from *M. latidens* seems most probable.

The main difference of *M. elegans* from *M. annectens* is the smaller size of the former.

DESCRIPTION: In addition to the minor changes in the premolars, noted above in the specific diagnosis, no meaningful change can be recorded from the morphology seen in the older species of the genus.

DISCUSSION: *Microsyops elegans* is the only species of *Microsyops* known from the lower (A and B) Bridger beds of Wyoming.

Wortman (1903) reviewed the various proposed species of *Microsyops* and greatly improved the situation. He still maintained, however, that *M. elegans* and *M. gracilis* were distinct species, an opinion that he based on exaggerated differences of individual specimens of *M. elegans* (Wortman, 1903, vol. 16, pp. 358-359). These "differences" concerned tooth size, mandible depth, and the relative flattening and the crescent nature of various cusps, all valid individual differences but accountable for by infraspecific variation.

With the exception of the *Microsyops* collection in the United States National Museum from the Bridger Formation, collected by C. L. Gazin, all other Bridger collections lack accurate stratigraphic information. From the fine United States National Museum collection, which has excellent locality data, as the core of the hypodigm, and with due consideration of the numerous "types" of "species" of *Microsyops* from the Bridger beds, it appears clear that *Microsyops elegans* is the only valid species of the genus from the lower level of the Bridger Formation (beds A and B, which are below the Sage Creek White Layer).

The lingual half of P₄ of *M. elegans* is rather constricted relative to the buccal half of the tooth. This condition is very similar to that seen in *M. latidens* and unlike the lingually broad fourth upper premolar of *M. scottianus* and *M. lundeliusi*. From this inconclusive but suggestive bit of evidence, I suspect *M. elegans* evolved from *M. latidens*.

TABLE 16

NUMERICAL DATA FOR SPECIMENS OF *Microsyops elegans* FROM BRIDGER A-B BEDS,
STRATIGRAPHICALLY BELOW THE SAGE CREEK WHITE LAYER,
BRIDGER BASIN, WYOMING

	N	OR	X	S ²	S	V
P ₂						
L	2	1.6-1.8	1.70	—	—	—
PW	2	1.1-1.4	1.25	—	—	—
P ₃						
L	2	2.7-3.2	2.95	—	—	—
PW	2	1.75-1.85	1.80	—	—	—
P ₄						
L	12	3.2-4.2	3.87	.082	.286	7.39
PW	12	2.1-3.0	2.77	.070	.263	9.49
AW	12	1.7-3.0	2.65	.114	.340	12.83
M ₁						
L	18	3.5-4.2	3.80	.039	.196	5.17
PW	18	2.5-3.1	2.81	.026	.161	5.73
AW	17	2.3-2.7	2.49	.011	.105	4.21
M ₂						
L	22	3.8-4.5	4.07	.026	.161	3.95
PW	19	3.1-3.5	3.22	.016	.126	3.91
AW	20	2.55-3.0	2.80	.016	.128	4.57
M ₃						
L	10	4.5-5.0	4.72	.037	.192	4.06
PW	9	2.9-3.2	3.02	.014	.120	3.97
AW	8	2.4-2.8	2.59	.016	.124	4.78
P ₂						
L	1	—	2.60	—	—	—
PW	1	—	1.80	—	—	—
P ₃						
L	3	2.9-3.1	3.00	.010	.100	3.33
PW	3	3.0-3.75	3.12	.016	.125	4.00
P ₄						
L	4	3.4-4.0	3.70	.067	.258	6.97
PW	4	3.85-4.6	4.21	.017	.131	3.11
M ₁						
L	5	3.6-4.9	4.10	.250	.500	12.19
PW	5	4.2-4.8	4.38	.057	.238	5.43
AW	5	4.2-5.0	4.42	.112	.335	7.57
M ₂						
L	9	3.6-4.3	4.10	.063	.250	6.09
PW	9	4.2-5.0	4.59	.084	.289	6.29
AW	9	4.3-5.5	5.01	.156	.390	7.78
M ₃						
L	5	3.65-4.0	3.89	.255	.505	12.98
PW	5	3.8-4.7	4.32	.112	.335	7.75

rather than from *M. scottianus*. Robinson (1966) also suggested that the likely ancestor of the lower Bridger *Microsyops* was the Huerfano sample he referred to "*Cynodontomys knightensis*."

Microsyops annectens (Marsh, 1872)
Osborn, 1902

Plate 39, figures 9, 10, plates 53, 54

Bathrodon annectens MARSH, 1872, p. 212.

Microsyops annectens: OSBORN, 1902, p. 173.

Microsyops schlosseri WORTMAN, 1903, vol. 16, p. 361.

TYPE: Y.P.M. No. 11791, left M_3 in mandible fragment, collected at the classic Henry's Fork locality of the Bridger Basin, Wyoming.

HYPODIGM: The type and Y.P.M. Nos. 11791, 13242-13244, 13246, 13248, 13249, 13253 (1), 13254, 13258, 13279, 13280; A.M. N.H. Nos. 1732, 11436, 12049, 12050, 12595; U.S.N.M. Nos. 13286, 17798-17801, 17817. The hypodigm was collected from various localities from Bridger beds C, D, and E.

SPECIFIC DIAGNOSIS: *Microsyops annectens* is one of the most bunodont species of *Microsyops* (or at least as much so as *M. lundeliusi*). The cusps are bulbous, blunt, and low, although the centrocrista is slightly V-shaped

and forms an important shearing crest. In some specimens of this species extensive wrinkling of the enamel occurs, a feature not known in any other species of the genus.

Microsyops annectens is larger than *M. elegans*, but it is slightly smaller than *M. lundeliusi*. The anterior lower premolars of *M. annectens* are relatively less robust and smaller than those of *M. lundeliusi*.

DESCRIPTION: One of the outstanding features of *M. annectens* is the relatively more bunodont nature of the molars. In addition, in some of the known specimens (see pls. 53 and 54) the centrocrista (a portion of the ectoloph, which, in perissodactyls, for example, is usually meant to include the paracone and metacone) is functionally and morphologically very "ectoloph"-like, that

TABLE 17
NUMERICAL DATA FOR SPECIMENS OF *Microsyops annectens* FROM BRIDGER C-D BEDS,
STRATIGRAPHICALLY ABOVE THE SAGE CREEK WHITE LAYER,
BRIDGER BASIN, WYOMING

	N	OR	\bar{X}	S ²	S	V
P ₂						
L	1	—	3.10	—	—	—
PW	1	—	1.60	—	—	—
P ₃						
L	2	—	4.00	—	—	—
PW	1	—	2.30	—	—	—
P ₄						
L	7	4.5-5.1	4.71	.048	.219	6.65
PW	7	3.2-3.5	3.39	.026	.160	4.71
AW	6	2.8-3.3	3.13	.031	.175	5.59
M ₁						
L	6	4.5-4.9	4.68	.018	.133	2.84
PW	6	3.3-4.0	3.58	.054	.231	6.45
AW	6	3.0-3.5	3.18	.030	.172	5.40
M ₂						
L	6	4.5-5.1	4.85	.075	.273	5.62
PW	7	3.3-4.3	3.87	.096	.309	7.98
AW	7	2.9-3.8	3.44	.083	.287	8.34
M ₃						
L	6	5.6-5.9	5.73	.023	.150	2.61
PW	6	3.5-3.8	3.66	.023	.150	4.09
AW	6	2.8-3.4	3.17	.043	.206	6.49
M ²						
L	1	—	5.20	—	—	—
PW	1	—	5.60	—	—	—
AW	1	—	6.10	—	—	—
M ³						
L	1	—	5.10	—	—	—
PW	1	—	5.55	—	—	—

is, this structure is anteroposteriorly more elongated than in other species of the genus, and it appears to play a more important role on the tooth than on that of previous species.

DISCUSSION: The specimen on which "*Microsyops schlosseri*" was based is larger than the type of *M. elegans*. Both specimens were collected at the same locality, at Henry's Fork, about one year apart. The range of the known specimens from this locality and other upper Bridger beds, however, completely bridges the size gap between the two individuals.

The wrinkled enamel of Y.P.M. No. 11791, the type of "*M. schlosseri*" (see pl. 53, figs. 3-6), does not seem to warrant specific distinction from specimens of similar size and identical morphology from the upper Bridger beds, which are clearly referable to *M. annectens*. It cannot be denied, however, that the type of "*M. schlosseri*" may represent a species different from *M. annectens*. There are no adequate upper Bridger collections from controlled localities with enough specimens to resolve this taxonomic problem

about *M. annectens* as presently understood. I cannot justify the retention of a proposed taxon, most likely a synonym of *M. annectens*, based on wrinkled enamel on a single specimen.

Microsyops sp.

Plate 41, figures 6-17

Under Y.P.M. Nos. 19892 and 19893 are catalogued 24 isolated teeth from the Yale locality 3 of the Carter Mountain local fauna from the Big Horn Basin, Wyoming.

The only known P⁴ of this sample shows the same degree of molarization as that of *M. elegans* or *M. annectens*. The size ranges of the lower and upper teeth measured are very nearly intermediate between those of the latter two species. The morphology of the Carter Mountain *Microsyops* is very similar to *Microsyops* with the small mesostyle of *M. scottianus* or *M. elegans*, and with the characteristic length/posterior width ratios of all the other known *Microsyops* lower molars.

If one considers the rather steady, pro-

TABLE 18

NUMERICAL DATA FOR SPECIMENS OF *Microsyops* SP., Y.P.M. Nos. 19892, 19893, FROM CARTER MOUNTAIN LOCALITY 3 OF PEABODY MUSEUM OF NATURAL HISTORY, YALE UNIVERSITY, BIG HORN BASIN, WYOMING

							\bar{X}
P ₄							
L	4.4	—	—	—	—	—	—
PW	2.9	—	—	—	—	—	—
AW	2.7	—	—	—	—	—	—
M ₁ or M ₂							
L	4.5 ^a	4.5 ^b	—	—	—	—	—
PW	3.7 ^a	3.65 ^b	—	—	—	—	—
M ₃							
AW	3.1 ^a	2.9 ^b	—	—	—	—	—
M ₃							
L	5.2	5.55	—	—	—	—	—
PW	3.25	3.35	—	—	—	—	—
AW	2.85	2.9	—	—	—	—	—
M ¹ or M ²							
L	4.75	4.55	4.7	4.55	4.65	4.64	
PW	4.5	4.8	5.15	4.55	—	4.75	
AW	5.45	5.35	5.5	5.45	5.6	5.47	
M ³							
L	4.5	—	—	—	—	—	—
AW	5.3	—	—	—	—	—	—

^a ?M₁.

^b ?M₂.

gressive increase in size in the dentition of *Microsyops* from the earliest Wasatchian to the latest Bridgerian, one may conclude that the Carter Mountain local fauna from locality 3 may be middle Bridgerian in age. This conclusion, based on one species, particularly a small mammal, is an extremely tenuous one, although it is suggestive. Radinsky (1963, p. 51) assigned a late "Lostcabinian" or early Bridgerian age to the *Helalestes* sp. from the Carter Mountain local fauna, in spite of his statement that this form resembles the late Bridgerian *Helalestes intermedius* "... in the large size and some of the more molariform premolars." Radinsky's age determination of the Carter Mountain local fauna is based as follows (p. 51): "However, affinities to *H. nannus* are suggested by the early age (not later than early Bridgerian), some of the less molariform premolars, and perhaps the slightly convex upper molar metacones." The most important criterion, the early age, cited by Radinsky seems to be established *a priori* in the statement and hence it is not meaningful in an attempt to determine the relative age of the Carter Mountain assemblage.

***Microsyops kratos* Stock, 1938**

Plate 55

Microsyops kratos STOCK, 1938, p. 299.

TYPE: L.A.C.M. No. CIT2232, left mandible with dP_3 and P_4-M_3 . The type was collected at the former locality No. 249 of the California Institute of Technology, early Uintan Poway sandstones and conglomerates, San Diego County, California. These records are now part of the Los Angeles County Museum field records.

HYPODGM: Type only.

SPECIFIC DIAGNOSIS: Since the type is the only known specimen, a meaningful distinction from species of similar size such as *M. lundeliusi* or *M. annectens* cannot be given. The size of the teeth of these three species are rather similar.

The following measurements characterize the type of *M. kratos*: length of dP_3 , 4.0; length of P_4 , 6.4¹; length of M_1 , 5.4; length

¹ P_4 is split transversely; the pieces are glued together with matrix wedged between the anterior and posterior halves. This condition accounts for the excessive length of the tooth.

of M_2 , 5.8; length of M_3 , 6.1; posterior width of dP_3 , 2.4; posterior width of P_4 , 4.0; posterior width of M_1 , 3.9; posterior width of M_2 , 4.2; posterior width of M_3 , 3.9; anterior width of P_4 , 3.9; anterior width of M_1 , 3.6; anterior width of M_2 , 4.0; anterior width of M_3 , 3.8.

DESCRIPTION: DP_3 of *Microsyops* is known only in *M. kratos*. There is a nubbin anterolingually on this tooth which corresponds to the paraconid. A crest on the posterior slope of the protoconid is a homologue of the cristid obliqua. There is also a discernible equivalent of the talonid basin.

On the robust P_4 there is no paraconid; the metaconid is pronouncedly less tall and less robust than the protoconid. The talonid basin is molariform, and there is an apparent accessory cusplule on the postcristid immediately posterolingual to the hypoconid; the hypoconulid is tiny, barely noticeable.

There are a postcingulid and an ectocingulid on the molars. The trigonids of the molars show an interesting feature, noted above in the preceding species—the gradual reduction of the paraconid from the first to the third molar. There is a noticeable increase in the distance between the apices of the metaconid and protoconid from the first to the last molar. The talonid notch of the molars is V-shaped as in the other species of *Microsyops*.

M_3 of the type is slightly damaged; the posterolingual portion, including the hypoconid, is broken off.

DISCUSSION: On the basis of the presently available meager evidence, *Microsyops kratos* unquestionably belongs to *Microsyops*.

Stock's (1938) comparisons of *M. kratos* to *M. elegans* and *M. annectens* are almost without significance, because he used isolated specimens of the Bridger species. For the same reason a comparison of *M. kratos*, known from one specimen, to the Bridger or Huerfano species of the genus would be of little value. The differences among most of the recognized species of the genus, discussed under the preceding species, are largely statistical in nature. The ranges in size of teeth are considered important, since the morphology of the molar teeth is confusingly similar. Whatever differences can be noted of the type of *M. kratos* from many specimens of *M.*

lundeliusi or *M. annectens* can also be observed in the infraspecific variations of the latter two species. This observation, however, clearly does not mean that the poorly known *M. kratos*, geographically and stratigraphically widely separated from the middle Eocene species of *Microsyops*, is conspecific with any of these species of similar size. It is very probable that additional specimens of the Poway species will clearly prove its specific distinction from the species apparently most similar to it.

CRASEOPS STOCK, 1934

Craseops STOCK, 1934, p. 349.

TYPE SPECIES: *Craseops sylvestris* Stock, 1934.

KNOWN DISTRIBUTION: Late Uintan of California.

GENERIC DIAGNOSIS: Microsyopids with low-crowned teeth, with exceptionally large and bulging mesostyle, vestigial metaconule, and very small or absent hypocone. *Craseops* clearly differs from *Microsyops* in having a virtually dilambdodont ectoloph, a vestigial to absent metaconule on the upper molars, and a U-shaped talonid notch, in contrast to the V-shaped one in *Microsyops*.

DISCUSSION: *Craseops* is a poorly known genus, almost certainly derived from *Microsyops*, although actual confirmation of such derivation from the anterior dentition is still lacking. The genus is the latest one of the family. The upper molars are very distinct from those of any species of *Microsyops*, but the lower molars by themselves are not so different. If it were not for the distinctive U-shaped talonid notch of *Craseops*, the lower molars alone could not be justifiably allocated to any other genus than *Microsyops*.

Quite likely either the Poway *M. kratos* or the upper Bridger *M. annectens* was ancestral to *Craseops*, but, as discussed above under *M. kratos*, the exact specific status of the latter species is uncertain.

If it is assumed that *Craseops* is certainly a derivative of *Microsyops*, which appears unquestionable at present, several interesting morphological changes occurred from one genus to the other. The metaconule, which was as equally strong as the paraconule in the known species of *Microsyops*, is virtually lost in *Craseops*. Although in *Microsyops* the paracrista, metacrista, and centrocrista are

relatively independent functional units, in *Craseops* the three structures form a more closely knit functional unit, an ectoloph, the latter term being a convenient, one-word expression for the three structures. It is striking that the molars of *Craseops* acquired a secondary styler shelf. From the earliest known undoubted microsyopid, *Microsyops wilsoni*, and from the even earlier *Navajovius kohlhaasae*, the styler shelf was completely absent. The combined effects of a highly developed and buccally bulging mesostyle and the accentuated crestlike ectocingulum resulted in the well-defined, broad, secondarily developed styler shelf in the *Sespe* genus.

If the *Microsyops*-*Craseops* phylogeny is correct, it is clear that a great reduction of the hypocone took place. Although the hypocone is not very strong in *Microsyops*, it is invariable present. In *Craseops*, however, with the exception of a very small hypocone on M^1 , this cusp is not present on M^2 or M^3 of the type specimen. It must be remembered that the three upper molars probably represent a single individual, which greatly lessens the comparative value of the conclusion.

Craseops sylvestris Stock, 1934

Plate 56

Craseops sylvestris STOCK, 1934, p. 349.

TYPE: L.A.C.M. No. CIT1580, associated M^1 , M^2 , and M^3 . The type and the only additional specimen known were collected at locality 180 of the California Institute of Technology, at Tapo Ranch, Sespe Formation, north of Simi Valley, California.

HYPODGM: The type and L.A.C.M. No. 1399, a fragment of right mandible with M_{2-3} , both collected at the type locality.

SPECIFIC DIAGNOSIS: Only known species of the genus. The following measurements are of the known specimens: length of M^1 , 6.3; length of M^2 , 6.8; length of M^3 , 5.6; posterior width of M^1 , 6.2; posterior width of M^2 , 7.5; posterior width of M^3 , 5.6; length of M_2 , 5.8; length of M_3 , 6.95; posterior width of M_2 , 4.6; posterior width of M_3 , 4.55; anterior width of M_2 , 4.45; anterior width of M_3 , 4.3

DESCRIPTION: On the upper molars the anterior segment of the ectocingulum and the portion of the latter structure posterior to the mesostyle form a relatively tall and sharp crest. A portion of the cingulum immediately

anterior to the mesostyle is missing. The mesostyle is exceptionally large and bulges buccally; the parastyle is prominent, but the metastyle is tiny. The ectoloph forms a pattern which is slightly dilambdodont.

The paracone and the metacone are about equal in size. There is a small basin formed by the crestlike ectocingulum posterior to the mesostyle and the buccal wall of the metacone. On all three known upper molars the metaconule is represented by a nubbin on the postprotocone crista; there is no trace of a premetaconule crista. The paraconule is distinct, although the postparaconule crista is very ill defined. The protocone is of about the same height as the paracone and metacone. On the three specimens of upper molars the precingula and postcingula tend to be confluent lingually. The very small hypocone can be considered a distinct cusp on M^1 of the type; on the remaining upper teeth it is hardly distinguishable from the postcingulum. The enamel on the upper molars is considerably wrinkled, although this feature is not characteristic of the known lower teeth.

Of the lower dentition only M_2 and M_3 are known, and in one specimen only. The paraconid is lost on both of the teeth, and there is a rather broad shelf on the anterior part of the trigonid, forming a slope in a posterobuccal direction. The protoconid and metaconid are about equal in height. The mesoconid and the hypoconid are strong; the entoconid is considerably taller and stronger on M_2 than on M_3 . About half of the entoconid is broken off from the last molar, and the talonid basin of the lower molars is very shallow. The talonid notch is much more the shape of a U than of a V; the bottom of this notch is completely rounded. A faint ectocingulid and a faint postcingulid are present on the lower molars.

The mandible fragment of the young adult represented by L.A.C.M. No. CIT1399 is rather strong and robust.

ORDER PRIMATES LINNAEUS, 1758

SUBORDER UNCERTAIN

FAMILY ?MICROSYOPIDAE OSBORN AND WORTMAN, 1892

NAVAJOVIUS MATTHEW AND GRANGER, 1921

TYPE SPECIES: *Navajovius kohlhaasae* Matthew and Granger, 1921.

INCLUDED SPECIES: The type species

and *Navajovius? mckennai*, new species.

DISTRIBUTION: The Tiffanian of Colorado and probably the early Wasatchian of New Mexico.

GENERIC DIAGNOSIS: Very small to minute primates with enlarged upper and lower incisors and trenchant, double-rooted P^1 , P^2 , and P^3 . P^4 is premolariform to semimolariform; metastyle present on P^4 and M^{1-2} ; the third molar is reduced in size.

Although the generalized tritubercular upper teeth, the enlarged lower incisors, and the general construction of the upper premolars of primitive *Microsyops* and of *Navajovius* are quite similar, there are also important differences between the primitive species of *Microsyops* (including *Cynodontomys*) and the species of *Navajovius*. The characteristically close and distinct entoconid and hypoconulid in *Microsyops* are not very similar to those in *Navajovius*, although these cusps are rather close to each other in the latter genus. The talonid of M_3 of *Microsyops* is more elongated than that of *Navajovius*. Additional minor diagnostic details from other possibly related genera are noted below.

DISCUSSION: *Navajovius* is probably the most disputed and enigmatic genus among the known Paleocene and Eocene primates. The authors of the genus, Matthew and Granger (1921), implied relationship to the Eocene anaptomorphids (*sensu lato*) by allocating *Navajovius* to the Tarsiidae. Simpson (1935a) thought this relationship to be quite probable and stated his belief in a close resemblance of the fourth upper premolar and the molars to those of *Omomys*. Simpson (1940, pp. 197–198) included *Navajovius* in the Omomyinae of the Anaptomorphidae, with *Omomys*, *Teilhardina*, *Loveina*, *Dyseolemur*, *Washakius*, *Shoshonius*, *Hemiaecodon*, and *Chumashius*. He noted that *Palenochtha* was near the above group, but, because he believed the latter genus to be closer to *Paromomys* (correctly, I believe), his Paromomyinae consisted of *Paromomys*, with *Plesiolestes*, *Palaechthon*, and *Palenochtha*. In his 1937 and 1955 papers on the fauna of the Crazy Mountain Field and on the Phenacolemuridae, respectively, Simpson made no reference to *Navajovius*, although he extensively discussed most Paleocene primates.

Gazin (1958, p. 11) has remarked that *Navajovius* is possibly an anaptomorphid. He thought (p. 94) that Simpson's (1940) inclusion of the genus in the Omomyidae was untenable because of the supposed absence of a lower canine and the presence of only one lower incisor and the large P_2 . This reduced dental formula, according to Gazin, "... precludes derivation from it of any of the better known omomyids" (p. 95). Nevertheless, in his phylogenetic arrangement of the North American early Tertiary primates (chart 1 of his paper) he derived *Omomys* from a source closer to *Navajovius* than any other Paleocene primate known at that time.

McKenna (1960, p. 64), in commenting on *Niptomomys*, referred to *Navajovius* as "... the peculiar tupaiid- and amphilemurid-like ... genus."

Simons (1963), in reviewing the Tertiary primate record, included *Navajovius* in the subfamily Paromomyinae of Simpson's (1955) controversial Phenacolemuridae, with *Paromomys*, *Palaechthon*, *Palenochtha*, and *Plesiolestes*. He placed *Phenacolemur* in a monotypic subfamily, the Phenacolemurinae. He also noted that further investigation of *Navajovius* may show that it belongs to the Anaptomorphidae, as Gazin (1958) suggested.

Van Valen (1965b, p. 436) noted of *Navajovius* that it and "*Mckennatherium*" (see footnote on p. 313 on this taxon) are "... in most of their known characters, the most primitive primates as determined by comparison with possible near ancestors in the Insectivora."

When describing the genus *Purgatorius*, Van Valen and Sloan (1965) arranged all the known paromomyid genera in the Paleocene into two subfamilies, the Paromomyinae and the Purgatoriinae. There was no mention of *Navajovius*, implying an exclusion from the Paromomyidae.

Recently, McKenna (1966, p. 4) has briefly discussed the affinities of Paleocene primates. He noted that the Eocene anaptomorphids, omomyids, and notharctids cannot be derived from known Paleocene genera, although *Navajovius* and *Berruvius* may be closer to the ancestry of these families than the other known Paleocene primate genera.

Navajovius has never been compared with

microsyopids. The main reason is probably the fact that two of the most primitive species of *Microsyops* (*Microsyops alfi* and *M. wilsoni*, new species) have not been studied in considerable detail until the present report. This revision of the microsyopids has revealed features in the earliest known *Microsyops* and the Tiffanian *Navajovius* that appear to indicate a possibly close, non-convergent similarity between the two genera.

Although the earliest, undoubtedly associated, enlarged lower incisors of *Microsyops* are known only in the Lysite *M. latidens*, the general shape and character of this incisor in *Navajovius* and *Microsyops* are strikingly similar. Based on better-known although later species of *Microsyops*, the lower dentition of the latter is more reduced than that of *Navajovius*. The Tiffanian genus has either a first lower premolar or a lower canine, whereas in the better-known *Microsyops* the postincisor tooth row begins with P_2 . The very important facts of the antemolar dentition of the most primitive species of *Microsyops* are not known, so speculation on the comparative aspects of teeth between the enlarged incisor and P_2 of the two genera is not meaningful. P_2 of *Navajovius* is a relatively very tall and anteroposteriorly short tooth, its roots having been fused together. P_3 , as described and illustrated by Simpson (1935a, p. 13), was a double-rooted small tooth wedged between P_2 and P_4 . This tooth was known only in the type, and as noted under the species description, it could not be re-studied because it was lost between 1935 and 1963.

P_2 and P_3 are not known in the two most primitive species of *Microsyops*, but in *M. angustidens* and *M. latidens* these two teeth are premolariform, double-rooted, P_3 being slightly stronger than P_2 . P_4 of primitive *Microsyops* and *Navajovius* are very much alike.

Both the upper and lower molars of the two genera are constructed on a very similar plan. One noticeable difference is that the entoconid and hypoconulid are less clearly separated in *Navajovius* than in *Microsyops*; in the latter these two cusps, although characteristically close to each other, are separated by a deep groove. That the fourth upper premolar is different from that of the

primitive (or advanced) *Microsyops* is a warning against unconditional allocation of *Navajovius* to the Microsyopidae. In the only certainly referred species of the genus, the genotype from Mason Pocket in the Tiffany beds, P⁴ is buccally more elongated in an anteroposterior direction than in *Microsyops*. From the apex of the paracone to the posterobuccal border of P⁴ of *Navajovius*, a continuous crista is formed by the centrocrista and the metacrista; the lingual aspect of this crest forms a posterobuccally oriented shearing surface. In its general aspect, this fourth premolar is similar to P⁴ of *Palaechthon* and to the P⁴ which is thought to belong to *Purgatorius* (see pl. 57). P⁴ of *Navajovius* differs from the fourth upper premolars of the latter two genera in having a more pronounced paracrista and a consequently relatively more elongate buccal half of the tooth.

It is probable that in general the extent of molarization or lack of it on the fourth premolar, depending on the primitive condition, may be correlated with the reduction of the antemolar dentition. There may have been a correlation also between the enlargement of the incisors and the reduction of the antemolar dentition in the primitive prosimians, and also in the insectivore apatemyids and mixodectids. For this reason the structure of the fourth premolar cannot be given great weight in taxonomic decisions involving categories above the species level. The rather dissimilar fourth premolars in the various genera within the Paromomyidae and Mixodectidae are highly instructive in this respect.

P¹ and P² of *Navajovius* and *Microsyops* are double-rooted, very elongate, and are considerably constricted transversely. Although such is the condition of the two teeth in the San José *Phenacolemur jepseni* (Simpson, 1955, pl. 30) from the Almagre facies, the more meaningful confirmation of a *Navajovius*-paromomyid similarity in this respect is lacking; the condition of the upper anterior premolars is not known in primitive paromomyids such as *Palaechthon*, *Plesiolestes*, or *Palenochtha*. P³ of *Navajovius* is less triangular than this tooth of *Palaechthon* or that of *Paromomys*, which are very similar to the homologous tooth of late early Eocene *Microsyops*. P³ of Gray Bull *Microsyops* is unfortunately not known.

As described under *Navajovius kohlhaasae*, A.M.N.H. No. 17399, maxilla and partial upper dentition, shows a large, flattened, upper tooth between the tooth rows of the anterior upper dentition. This tooth is almost certainly the enlarged upper tooth of *Navajovius*. Although this tooth bears general similarity to incisors of late early Eocene *Microsyops*, the fact is not very meaningful because the tooth is poorly preserved, and the Gray Bull homologues of *Microsyops* are not known. Also, important and highly pertinent information about the upper incisors of paromomyids, with the exception of *Phenacolemur*, is completely lacking. At present, it appears that *Navajovius* is closer to the earliest Wasatchian *Microsyops* than to any other genus, particularly any of the primitive paromomyids of the North American Paleocene. Since multiple hypotheses are necessary in all objective phylogenetic conclusions, it is important to point out that the *Navajovius*-*Microsyops* and *Navajovius*-paromomyid similarities also indicate a possibly close origin for the paromomyids and microsyopids. Tempting as this type of speculation may be, it has only suggestive value until more is known of the cranial morphology of primitive paromomyids, microsyopids, and *Navajovius*. At the present state of knowledge the deceptive results of convergence of simple, uncomplicated tritubercular (not tribosphenic) teeth, such as those of *Navajovius* and the primitive species of *Microsyops*, would probably be impossible to differentiate from true similarities rooted in common ancestry.

In describing the Thanetian *Berruvius*, D. E. Russell (1964, p. 125) stated that he considered that genus very close to *Navajovius*. I cannot agree with Russell on this supposed similarity. The relatively broader talonid, the weaker paracristid, and the distinguishing buccal and lingual profiles of *Berruvius* sharply separate that genus (M₁₋₂, one specimen) from the relatively well-known *Navajovius*. It is possible, however, that both *Navajovius* and *Berruvius* have close ties with the primitive omomyids. I believe, as Russell does, that *Berruvius* is a primate, regardless of my ignorance of its more immediate affinities among the prosimians.

D. E. Russell (1964, p. 126, pl. 16, fig. 3d) described and figured a probably primate

lower molar and noted its closeness to that of *Berruvius* and *Navajovius*. In my opinion, the tooth is closest to that of omomyids chiefly because of the transversely very wide (relatively) talonid and the strong, triangular, lingually rather open trigonid. Although the tooth in question is very likely M_1 , as was noted by Russell, the trigonid is considerably more elongated than that on M_2 and M_3 of *Berruvius* and slightly more so than that of M_1 of *Navajovius*.

***Navajovius kohlhaasae* Matthew
and Granger, 1921**

Plate 30, figures 8, 9, plate 31, figures 1-6

Navajovius kohlhaasae MATTHEW AND GRANGER, 1921, p. 5.

TYPE: A.M.N.H. No. 17390, left P^4-M^3 , right P^2-4 , left mandible with broken P_1 , P_2 , P_4-M_3 (P_3 is now missing but was present when originally described), associated enlarged anterior incisor, fragmentary right mandible with M_2-3 and part of the posterior portion of the mandible, collected from the Tiffany beds, Mason Pocket, San Juan Basin, Colorado.

HYPODIGM: The type and A.M.N.H. Nos. 17399, 17406. All the known specimens of this species were collected at the Tiffanian type locality in Colorado.

SPECIFIC DIAGNOSIS: Larger of the two known species. P^3 is narrower transversely than that of *N. ? mckennai*.

DESCRIPTION: The enlarged anterior lower incisor of this species is known in the type specimen. The crown of this tooth is spatulate and mediolaterally flattened; the tooth is broadest at a point somewhat above the ventral limit of the enamel. The crown gradually tapers from its longest anteroposterior dimension presumably into an apex, although the tip of the only known specimen is broken off. The canine is probably lost in this species, although such cannot be ascertained beyond doubt from the only known complete lower dentition. The crown of the single-rooted, procumbent P_1 of the type is broken off. It is possible that the tooth called P_1 in this paper may be either the canine or a second enlarged incisor. There is a considerable diastema between the latter tooth (interpreted as P_1) and P_2 . A small sliver of bone in the mandible may

be the root of a small tooth, which would mean that the tooth held here to be P_1 is either an incisor or the canine, and the sliver of bone is a remnant of P_1 in the damaged specimen. The single-rooted P_2 is the tallest of the cheek teeth (the incisor is taller) with a slim, tall protoconid and a notch that represents the incipient talonid. This tooth is shown on figure 9 of plate 30 and on figure 6, but not figures 4 and 5, of plate 31. During the interval when the two sets of photographs were taken, the crown of P_2 was broken off and lost. Fortunately, another specimen of this tooth is present in A.M.N.H. No. 17390. P_3 was lost from the type after 1935,¹ following a description by Simpson (1935a, p. 13), " P_3 has two roots and it is similar to the preceding tooth save for being much smaller." Simpson also showed this tooth on the figure of the left mandible of the type.

P_4 is slightly taller than M_1 ; the former has a large protoconid and no trace of a paraconid, but a posterolingual bump on the protoconid may indicate an incipient metaconid. P_4 , in contrast to the molars posterior to it, has a large hypoflexid. The talonid is small and has three tiny cusps which are probably the homologues of the three talonid cusps.

The molars have a low trigonid, a protoconid and metaconid which are about equal in size, and a small paraconid. The paracristid is very characteristic; it "... is angulate at the anteroexternal corner of the crown (as in many early primates)," as Simpson (1935a, p. 13) pointed out. There are faint indications of a buccal cingulid. The hypoconulid is close to the completely lingual entoconid, but, contrary to Simpson's (1935a) observation, I see no evidence of the twinning of the entoconid. There is a mesoconid on the cristid obliqua in the usual position for this cusp. Of the lower molars M_2 is the largest and is relatively wider transversely than either M_1 or M_3 . M_3 is reduced in size, and its hypoconulid lobe is strong and placed close to the equally strong entoconid lobe.

The upper incisor is known only in A.M.N.H. No. 17399, in which it is quite broken

¹ Judged from photographs taken of the type in 1963 (pl. 31, figs. 4, 5), the time of loss cannot be narrowed more closely than between 1935 and 1963.

up (see pl. 31, figs. 1-3). The association of this tooth with the rest of the upper dentition of the specimen seems to be fairly certain, since they were collected in the small slab of rock in which they are at present. This tooth is relatively large compared to the cheek teeth, and apparently it was flattened slightly after burial. The exact limits of the enamel cannot be determined, but it appears that the root continues to widen probably past the upper limit of the enamel. The tooth is too shattered and flattened to yield more information.

P¹⁻³ are strongly flattened transversely, which results in the combined bladeliike effect of these three premolars. P¹ is larger than P², and the latter is larger than P³. P³ is wider transversely than the premolars preceding it, and in turn P² is wider transversely than P¹.

P⁴ is as long and almost as wide transversely as M¹; the tooth may be called premolariform to semimolariform. The paracone of the fourth premolar is the tallest and most robust cusp of the cheek teeth. The buccal wall of this cusp on P⁴ is vertical; there are a tiny parastyle and a small metacone and metastyle. The protocone is directly lingual to the paracone; the preprotocrista leads directly anterobuccally from the apex of the protocone to the parastyle, whereas the postprotocrista first runs directly posteriorly from the apex of the protocone and then turns buccally at almost 90 degrees at the posterior border of P⁴. The small homologue of the trigon basin is formed on the posterolingual region of the tooth. The conules are not developed, but a faint ectocingulum is present.

The paracone and metacone are of about equal height on the molars. The apex of the paracone is invariably more buccal than that of the metacone. The ectocingulum is strong, the parastyle is distinct, the metastyle is present, and the stylar shelf is virtually absent. There is a slight ectoflexus on the buccal border of the molars. The paraconule and metaconule are about halfway between the buccal and lingual borders of the molars. The precingulum and postcingulum are present; the hypocone is relatively larger on M¹ than on M². M³ is greatly reduced in size,

particularly the posterior half of the tooth.

DISCUSSION: Simpson (1935a, p. 14) implied that the fourth tooth anterior to the

TABLE 19

NUMERICAL DATA OF THE THREE KNOWN SPECIMENS OF *Navajovius kohlaasae* FROM THE TIFFANY BEDS OF MASON POCKET, COLORADO

	A.M.N.H. No. 17390 ^a	A.M.N.H. No. 17406	A.M.N.H. No. 17399 ^b
P ₂			
L	0.85	—	—
P ₄			
L	1.6	—	—
PW	0.9	—	—
AW	0.9	—	—
M ₁			
L	1.55	—	—
PW	1.2	—	—
AW	1.1	—	—
M ₂			
L	1.6 (1.65)	1.45	—
PW	1.2 (1.3)	1.25	—
AW	1.1 (1.2)	1.2	—
M ₃			
L	1.65 (1.5)	1.5	—
PW	1.0 (0.95)	—	—
AW	1.0 (1.0)	1.0	—
P ¹			
L	—	—	1.1
PW	—	—	0.45
P ²			
L	—	—	1.0 (1.0)
PW	0.45	—	0.5 (0.45)
P ³			
L	0.8	—	0.8 (0.8)
PW	0.5	—	0.5 (0.5)
P ⁴			
L	1.7	—	1.65 (1.65)
AW	1.55	—	—
M ¹			
L	1.6	—	1.6 (1.5)
AW	1.75	—	2.0 (1.95)
M ²			
L	1.5	—	1.45
AW	1.95	—	2.1
M ³			
L	1.2	—	1.05
AW	1.4	—	—

^a The parameters of right M₂₋₃ are given in parentheses.

^b Measurements from the left side are given in parentheses.

first molar is probably a two-rooted canine and not P^1 as suggested in the present paper. He further stated that "it is not absolutely impossible but is in the highest degree improbable that there was another more anterior in the maxilla." Simpson's reference is to A.M.N.H. No. 17399. As described above, this specimen contains a badly shattered and crushed enlarged anterior tooth which I interpreted to be the enlarged incisor. Although this tooth may be a large canine, I am more inclined to believe that it is an enlarged incisor, probably homologous to that of *Microsyops*. There is of course, no absolute proof for this homology. The tooth that almost certainly occluded with and functioned in unison with the enlarged lower tooth was the enlarged upper tooth that I call the incisor. The question immediately arises: Was there an additional tooth between the enlarged upper tooth (interpreted by me as the enlarged incisor) and the tooth that is called here P^1 (the canine of Simpson, 1935a)? Simpson (1935a, p. 14) wrote of this P^1 : "From its being two-rooted, one would suppose this to be a premolar, but two-rooted canines do occur among primitive mammals; and from its enlargement and general function, its forward position and occlusion apparently even anterior to the caniniform tooth of the lower jaw, and the fact that in the apparently most nearly related animals a premolar is almost invariably lost and the upper canine almost invariably retained it seems more likely to be a canine." Simpson's reference to the "most nearly related animals" pertained to tarsionids. In *Microsyops* the blade-like, two-rooted first premolar, as in *Navajovius*, is larger than the following P^2 . The peg-like canine of *Microsyops* is greatly reduced, and the incisor is greatly enlarged, more or less at the expense of the reduced canine. Although, owing to the imperfect nature of the *Navajovius* specimens, evidence is completely lacking on this point, the possibility exists that in the latter genus as in *Microsyops*, there was a small reduced canine between the trenchant P^1 and the enlarged anterior incisor.

Pertinent comparisons and remarks concerning the affinities of *Navajovius* are treated under the generic discussion.

***Navajovius? mckennai*, new species**

Plate 30, figures 10, 11

ETYMOLOGY: For Dr. Malcolm C. McKenna, who brought the type specimen to my attention.

TYPE: A.M.N.H. No. 48612, left maxilla fragment with P^3 - M^1 . The specimen was collected from the San José Formation, at Regina, New Mexico, from Quarry 58 of the American Museum of Natural History. The detailed geographic and geologic description of Quarry 58 in the early Eocene Almagre facies was given by Simpson (1948).

HYPODIGM: The type only.

SPECIFIC DIAGNOSIS: The proposed new species is smaller than *N. kohlhaasae*, its P^4 is relatively less elongated, and its P^3 is wider transversely, than the teeth in that species. The dimensions of the type specimen are: length of P^3 , 0.5; length of P^4 , 0.95; length of M^1 , 1.05; width of P^3 , 0.45; anterior width of P^4 , 1.2; anterior width of M^1 , 1.2.

DESCRIPTION: One of the few noticeable differences from *N. kohlhaasae*, besides the clearly smaller size of the Almagre species, is in the structure of P^3 . As the dimensions of this tooth indicate, P^3 is almost triangular in outline, whereas that of the Tiffany genoholotype is relatively more elongate (although it is relatively wider transversely than the P^2 preceding it). P^3 of *Navajovius? mckennai* is quite vertical buccally, but posterolingually it slopes rather gently from the apex of the paracone to the base of the crown. Although the bone is broken around P^3 of the type specimen, it is apparent that this tooth is implanted in a way similar to that in *N. kohlhaasae*. The long axis of P^3 is somewhat anterolingually oriented, and the posterior half of the tooth is lingual to the parastyle of P^4 . Viewed in terms of the entire tooth row, this condition causes a rather sharp break at P^3 , the point at which the transverse width of the dental battery drastically narrows.

P^4 is very similar to that of the genoholotype, although it is relatively shorter in relation to its transverse diameter.

The posterobuccal part of M^1 , including the entire metacone, has broken off and has since been reglued to the specimen. This "repair" has resulted in a considerable dis-

tortion in the *Gestalt* of the tooth. Several attempts to return the metacone to a more natural and accurate position have failed, mainly because the specimen is extremely small and the chip is, for all practical purposes, weightless. As the glue dries on the specimen, tensions within the coating lacquer are free to pull the tiny fragment in any direction. Any judgment based on the only specimen of an upper molar of this species must be regarded with caution, particularly considering its present condition. Tenuous as the observations and the conclusions that follow them may be, they must be made. The paracone is, as in to the genoholotype, rather close to the buccal border of the tooth, because the molar completely lacks a stylar shelf. The postmetaconule crista and the premetaconule crista appear to be completely absent from the only known molar of this species, although wear at these points on the tiny tooth may be responsible for this condition. The postprotocrista does not have the initial posterior turn after running down from the protocone, after which it turns posterobuccally as seen on the molars of the genoholotype. In *Navajovius? mckennai* the postprotocrista continues directly posterobuccally from the apex of the protocone. This feature may be correlated with the very small size of the species. The lingual border of the known single molar appears to be more rounded than the upper molars of *N. kohlhaasae*.

DISCUSSION: As the allocation indicates, although it is questioned, the species described above is more similar to the genoholotype of *Navajovius* than to other known species. The allocation is by no means certain, and the new species is too poorly known for a more accurate determination of its affinities. Additional specimens may result in our placing the species in a new genus, although any action to that effect on the basis of the presently available sample is strongly opposed.

SUPPOSED MICROSYOPIDS FROM EUROPE

Through the generosity of Drs. Donald E. Russell, P. Louis, and D. E. Savage, I was permitted to examine illustrations and des-

criptions of and their comments on an early Eocene specimen from Europe referred by them to the Microsyopidae.

The specimen (Louis-15C),¹ from the Cuisian, is a broken left lower molar. The posterobuccal part, approximately one-fourth of the tooth, is broken off, making comparison extremely difficult. The cristid obliqua, although most of it is broken, joins the protolophid at about the same point as in *Microsyops*, but more buccally than in *Alsaticopithecus*. The relative size and position of the paraconid strongly resemble the condition in the latter two genera.

In spite of the breakage, it appears that the lingual portion of the talonid is considerably lower than the trigonid in front of it, a feature very unlike the known morphology of *Microsyops* and *Alsaticopithecus* in this particular respect. Unfortunately, the line drawings do not allow any further comparisons. At present I question the microsyopid affinity of the Cuisian specimen in spite of the fact that the morphology known to me (which borders on the permissible minimum that may serve as the basis of a taxonomic opinion) could be said to be microsyopid-like.

Is *Alsaticopithecus* HÜRZELER (1947) A MICROSYOPID?

McKenna (1960, p. 79) made a revealing comparison between microsyopids and the Lutetian genus *Alsaticopithecus* Hürzeler (1947) from Alsace. Hürzeler suggested a possible close relationship between *Alsaticopithecus* and the Anthropeoidea. My present comments and comparisons are based on the excellent figures published by Hürzeler.

Alsaticopithecus leemanni was a relatively

¹ While the present paper was in press, "Primates of the French early Eocene" by D. E. Russell, P. Louis, and D. E. Savage (1967) was published. The specimen Louis-15C is discussed under the Microsyopidae, genus and species indet. Because of an unfortunate error in matching captions with figures, the broken Louis-15C is illustrated as figure 13c, d, and e, instead of figure 12a, b, and c, which carries the correct caption. The specimen M.N.H.N. Levé 29 Py, "a primate unlike any other in the collections . . ." (p. 43), is erroneously illustrated as figure 12a, b, and c, instead of figure 13a, b, and c. This molar is probably not from a primate, but most likely represents a primitive artiodactyl.

small primate; the measurements of the teeth indicate that this mammal was in the approximate size range of *Microsyops angustidens* (for the sake of an easy size comparison, a microsyopid treated in this paper is used). McKenna (1960) pointed out the differences between *M. alfi* and *Alsaticopithecus leemanni*, which were the presence of a strong mesostyle and a strong hypocone in the latter. A brief but more detailed comparison between the Alsatian species, primitive *Microsyops*, and some other primates is necessary before the relationship suggested by McKenna can be evaluated.

McKenna's (1960, p. 79) statement, "The simple P_4^4 are more generalized than in any other microsyopid," is partly incorrect. Both the upper and lower fourth premolars are similar to those seen in *Microsyops alfi*, although the talonid of P_4 in *Alsaticopithecus* is relatively wider transversely than that in either *M. wilsoni* or *M. alfi*. The trigonid of P_4 is at about the same stage of molarization as in *M. wilsoni*. The upper fourth premolar of *Alsaticopithecus* is virtually identical with that in *M. wilsoni* and *M. alfi*. The lower molars, with the exception of two differences which are noted below, are extraordinarily microsyopid-like in the relationship of the entoconid and hypoconulid, in having a wider talonid than trigonid, and in the relatively small paraconid. The latter two characters are, of course, characteristic primitive primate features.

There is a peculiar feature on the lingual profile of *Alsaticopithecus* in comparison with the lingual profile of any of the recognized species of microsyopids. In *Alsaticopithecus* a small cuspule on the entocristid anterior to the entoconid is analogous to the one in plagiomenids (the latter are illustrated in this paper). A similar feature is seen, although it is less pronounced, on the lingual profile of *Gesneropithecus*, a Ludian genus described by Hürzeler (1946).

M_3 of *Alsaticopithecus leemanni* is characteristically shorter and smaller than either M_1 or M_2 . In the North American species of microsyopids M_3 is invariably larger than any of the preceding molars.

The hypocone of *Alsaticopithecus* is larger than that of any undoubted microsyopid. If McKenna's suggestion that *Alsaticopithecus*

and *Microsyops* were derived from a common ancestor is correct, then, as he implied, the mesostyle developed independently in the two genera. In some specimens of *Microsyops* that have a fairly strong mesostyle the buccal border of the tooth tends to bulge slightly buccally at the base of the mesostyle. In *Alsaticopithecus*, which has a moderately strong mesostyle, the buccal extension of the base of the tooth is slightly posterior to the mesostyle. This latter feature is well illustrated in the figure of M^1 of *Alsaticopithecus* (see Hürzeler, 1947, fig. 1).

The antemolar dentition of *Alsaticopithecus* figured by Hürzeler (1947, figs. 2-4, 10-12) casts the most serious doubt on the microsyopid affinity of the genus. The three lower teeth figured by Hürzeler (figs. 10-12) as $?P_3$, $?P_4$, and $?C$ do not particularly resemble any antemolar element of the known microsyopid dentition. *Microsyops* has no lower canines, although the possibly microsyopid *Navajovius* may have had one. The protoconids, the only cusps on these antemolar teeth figured by Hürzeler, lean more anteriorly than those on the antemolar teeth of *Microsyops*. The general outline and form of the three figured specimens are quite similar to the anterior lower premolars of adapids. None of the lower premolars of the Alsatian genus described by Hürzeler bears resemblance to premolars of microsyopid.

Hürzeler (1947, figs. 2-4) illustrated four isolated upper teeth. On figure 2a, a " P^3 " (equivalent to the P^2 of the widely used system in North America and Europe) is illustrated only in occlusal view, which prohibits a valid comparison. Figures 2b, 3a, and 4a illustrate a tooth identified by Hürzeler as $?P^4$ (i.e., P^1). I cannot recognize any pertinent similarity between this tooth and any other element of microsyopids or adapids. Figures 2c, 3b, and 4b show a questioned upper canine which may be said to bear a general resemblance to an enlarged upper incisor, although certainly not to that of *Microsyops*. It is clear from the illustrations that the root of this tooth immediately above the enamel-bone interphase is distinctly narrower than the base of the crown. In all known enlarged upper incisors of *Microsyops* the root continues to be broader for a considerable distance above the crown. Although

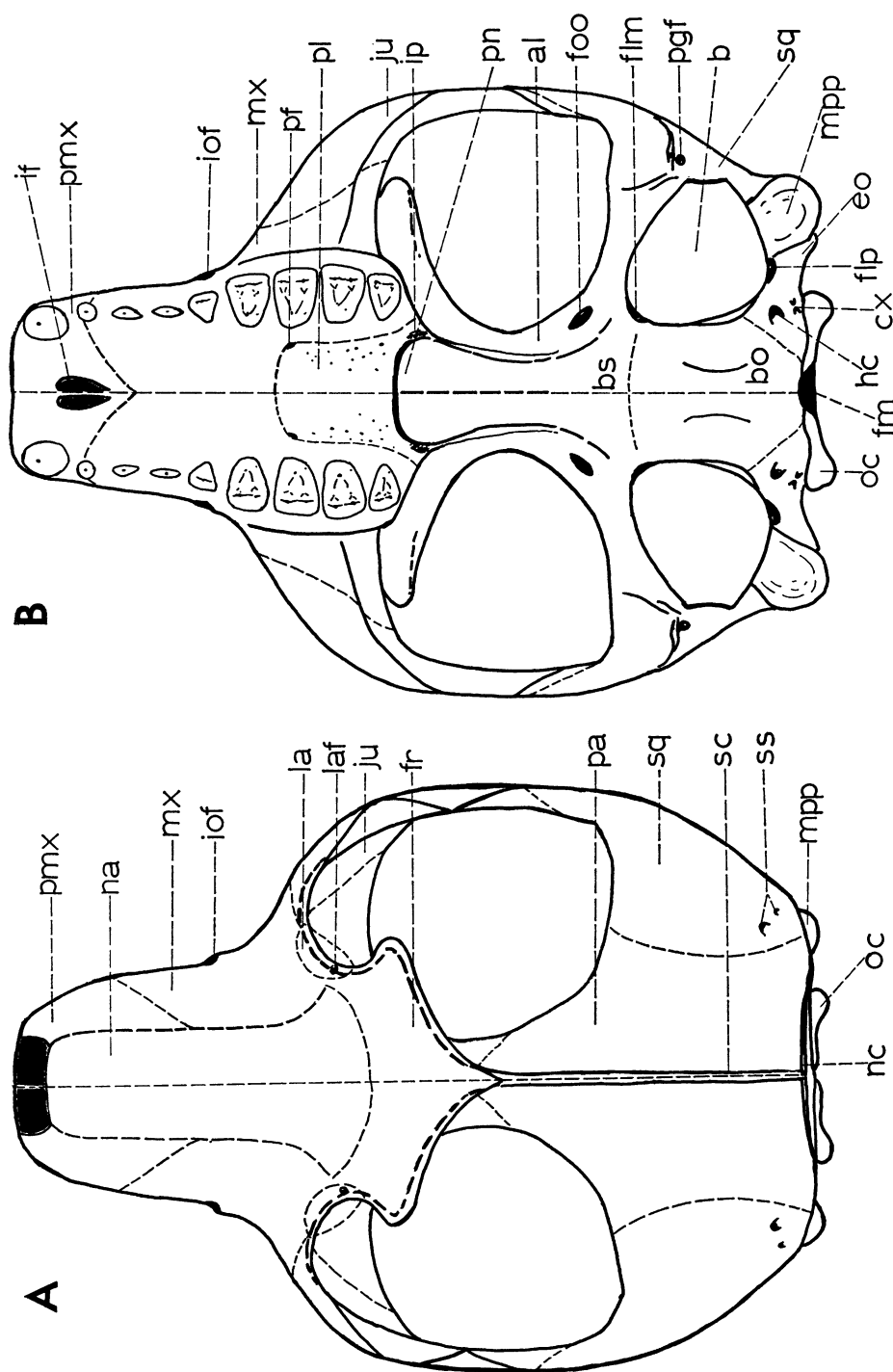


FIG. 16. Reconstructions of *Microsophs*, based primarily on A.M.N.H. No. 55284, a somewhat crushed skull of *Microsophs lundeliusi* from upper Huerfano Formation. Restoration of basicranium based on A.M.N.H. No. 55286, *Microsophs* cf. *M. latidens*, from same locality. Bulla not present on either specimen; only postulated on figures. A. Dorsal view. B. Ventral view.

Abbreviations: al, alisphenoid; b, bulla; bo, basioccipital; bs, basisphenoid; cx, canal x; eo, exoccipital; flm, foramen lacerum medius; flp, posterior lacerate foramen; fm, foramen magnum; foo, foramen ovale; fr, frontal; hc, hypoglossal canal; if, incisive foramen; ioof, infraorbital foramen; ip, palatine incisure; ju, jugal; la, lacrimal; laf, lacrimal foramen; mpp, mastoid process of petrosal; mx, maxilla; na, nasal; nc, nuchal crest; oc, occipital condyle; pa, parietal; pf, anterior palatine foramen; pgf, postglenoid foramen; pgp, postglenoid process; pl, palatine; pmx, premaxilla; pn, posterior nares; sc, sagittal crest; sq, squamosal; ss, canals for squamosal sinuses.

the morphological details of the microsyopid canine crown are not known, it is quite certain that the tooth was basically circular in cross section, unlike the specimen of *Alsaticopithecus* discussed here. The tooth in question bears a striking similarity to the canine of *Adapis*, and it is of particular importance in an assessment of the family affinities of the Lutetian genus.

Figures 2d and 3c of Hürzeler (1947) show an upper incisor. This tooth resembles the upper incisor of *Adapis* more than any other tooth I know. There is also a somewhat less striking similarity to the first and second upper premolars of *Microsyops*.

The above re-evaluation of *Alsaticopithecus*, although based solely on illustrations, requires some conclusions, tentative as they may be. On morphological grounds, the upper and lower fourth premolars and the molars, were the additional specimens of the antemolar dentition described by Hürzeler (1947) not known, could be assigned to the Microsyopidae with a fair degree of certainty. The antemolar dentition, however, if one accepts the fact that it is associated, strongly contradicts the conclusions based on the molars. Apparently the enlarged tooth of *Alsaticopithecus* was the canine, as in unspecialized mammals, which implies that there were no enlarged incisors in *Alsaticopithecus*. If the latter contention is correct, then I cannot justifiably allocate the latter genus to the Microsyopidae, if the family distinction of the latter group is to be maintained.

THE CRANIAL ANATOMY OF *MICROSYOPS*

The skull of *Microsyops* is known from three specimens: two skulls and one skull fragment, each belonging to a different species of the genus. The two skulls are described separately, because they depict different parts of the cranial anatomy.

THE SKULL OF *Microsyops lundeliusi*

The general shape of the entire cranium is not unlike that of *Plesiadapis* figured by D. E. Russell (1959, 1964). There are, however, important differences in the outline of the skulls of these two genera: in *Microsyops* there is an extensive, rather pronounced postorbital process from the frontals, which

is missing in *Plesiadapis*. In both *Plesiadapis* and *Microsyops* the cranium is constricted behind the posterior limit of the maxilla, showing the accentuated, undoubtedly primitive, separation of the facial and cerebral portions of the skull.

A.M.N.H. No. 55284 is a somewhat damaged skull of *Microsyops lundeliusi*. The entire ventral portion of the cerebral skull is fractured to pieces, although the dorsal part and the facial skull are relatively well preserved. The anterior half of the skull is much better preserved than the posterior one. Although the occiput and the ear regions are completely missing from A.M.N.H. No. 55284, the glenoid fossae and the major portions of the squamosal, with the rest of the skull roof, are fairly well preserved. The length of the skull is about two and one-fourth times that of the secondary palate. The absolute length of the skull is approximately 10.5 cm. The width at the estimated zygoma was approximately 6 cm. The maximum height of the skull, from the level of the palate to the very top of the sagittal crest, did not exceed 4 cm. It must be remembered that slight dorsoventral flattening of the skull tends to obscure the dimensions and the correct shape. The specimen is that of a very old individual, a fact that, in addition to rather bad fracturing, makes the interpretation of the correct location of sutures difficult.

DORSAL AND LATERAL VIEWS: The premaxillae are large and extensive bones and cover approximately one-third of the area laterally in front of the orbit. A pair of long, median nasals reach far up on the dorsal side of the skull, coming in contact with the frontals approximately 1 cm. in front of the posterior border of the postorbital process.

The maxillae are in contact with the premaxillae anteriorly, with the nasals and frontals dorsally. As far as can be seen from the damaged specimen, the maxilla does not enter the border of the orbit, but is in contact with the frontal, lacrimal, and jugal, three bones that make up the dorsal, anterior, and anteroventral borders of the orbit, respectively.

Dorsoventral crushing of the facial portion of the skull makes it very difficult to judge correctly the orientation of the orbits. I esti-

mate the angle between the longitudinal axis of the orbit (which, let us suppose, went through the lens of the eye at rest) and the longitudinal axis of the skull itself to be about 50 degrees.

The rim of the orbit is greatly thickened. This region of thick bone deposition, beginning on the jugal, is continuous at the rim of the orbits, on the edges of the superior post-orbital processes onto the sagittal crest. The

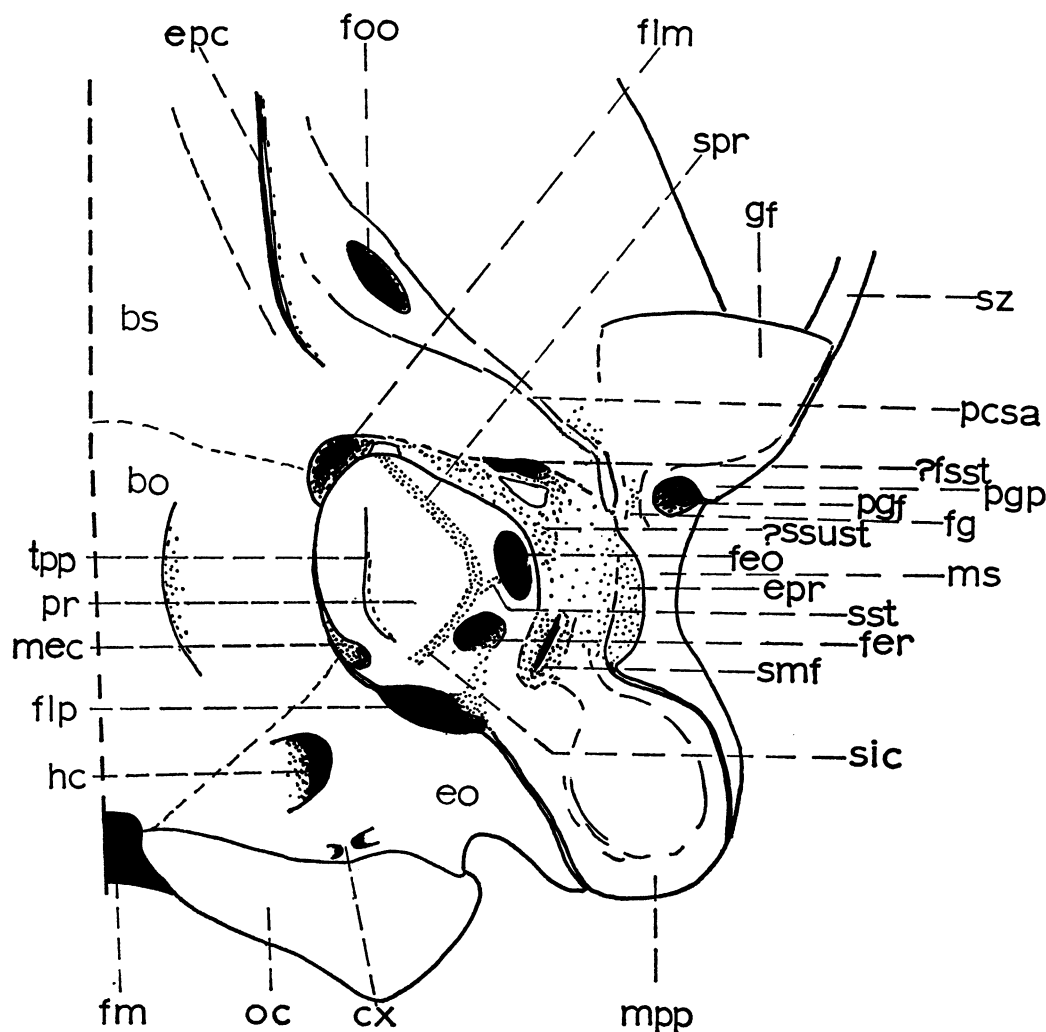


FIG. 17. Slightly restored left basicranial region of *Microsyops* cf. *M. latidens*, A.M.N.H. No. 55286, from the upper Huerfano Formation, A.M.N.H. locality II.

Abbreviations: bo, basioccipital; bs, basisphenoid; cx, canal x; eo, exoccipital; epc, entopterygoid crest; epr, epitympanic recess; feo, fenestra ovale; fer, fenestra rotunda; fg, fissura Glaseri; flm, foramen lacerate foramen; flp, posterior lacerate foramen; fm, foramen magnum; foo, foramen ovale; fsst, foramen for superior branch of stapedial artery; gf, glenoid fossa; hc, hypoglossal canal; mec, groove for the medial entocarotid artery and for the inferior petrosal sinus; mpp, mastoid process of petrosal; ms, meatal surface; pcsa, preotic crest of squamosal and alisphenoid; pgf, postglenoid foramen; pgp, postglenoid process; pr, promontorium; sic, sulcus for internal carotid; smf, stylomastoid foramen; spr, sulcus for promontory artery; sst, sulcus for stapedial artery; ssust, sulcus for either inferior or superior branch of stapedial artery; sz, squamosal portion of zygoma; tpp, tympanic process of petrosal.

area of contact of the different bones and the position of the foramina within the orbit are obscured by crushing and the consequent fracturing of the bone.

Frontal-parietal contact can be approximated: it is at the point of greatest constriction between the cerebral and facial crania. The sagittal crest, made up entirely of the parietals, is thick, strong, and unusually high.¹

The zygomatic arch is missing on both sides, but the base of this structure is present on the right side. This base of the zygoma is made up of the jugal and maxilla, forming a massive and broad structure on the skull of the animal.

VENTRAL VIEW: About two-thirds of the hard palate is formed by the maxilla, and one-third is made up of the palatine. The palatine is in contact with the maxilla at the level of the anterior border of the first molar. The maxilla-palatine suture turns posteriorly and remains very close to the lingual border of the molars. The posterior palatine torus is greatly thickened; the posterior extension of the palatine, with the presumably continuous pterygoid, is completely broken off.

The presphenoid (= ?basisphenoid) and the basisphenoid, posterior to the former, are present. These two are the only ventral elements posterior to the palatines that are preserved on A.M.N.H. No. 55284.

The glenoid fossae of the squamosals, particularly on the right-hand side, are well preserved. The articulating surface is virtually flat; it is about one and a half times wider transversely than long. A sturdy, anteroposteriorly flattened, peglike, postglenoid process is directly posterior to the articulating surface; more medially the articulating surface extends downward in a posteromedial direction and forms a medial boundary for the glenoid fossa. This is the preotic crest of the squamosal. There is a somewhat medially placed postglenoid foramen at the posterior base of the postglenoid process. There is no preglenoid process, and the articulating surface is completely unrestricted anteriorly. The posterolateral border of the glenoid fossa is broken, but it shows the area where the

zygomatic portion of the squamosal was attached.

In the large *Microsyops lundeliusi*, judged from the probably larger frontal sinuses, the facial skull may have grown at a different rate from the cranial skull than it did in the smaller *Microsyops annectens*.²

FORAMINA AND FENESTRAE ON THE SKULL: The infraorbital foramina are above the anterior border of P⁴. These foramina are similar to a laterally constricted tear in shape, with the rounded end ventral. On A.M.N.H. No. 55284 the infraorbital canal is approximately 1 cm. long.

The double entrance of the infraorbital canal is unusual. The two foramina (see text fig. 19) probably represent openings for the maxillary division of the trigeminal and for the infraorbital artery. There is only one exit for these, however, the large, tear-shaped, infraorbital foramen.

In *Plesiadapis* and later primates the lacrimal foramen is outside the orbit. In the Oligocene *Leptictis* (A.N.M.H. No. 9316) the lacrimal foramen is inside the orbit. Although the lacrimal area is badly crushed, it is clearly recognizable that there was a small lacrimal foramen outside the orbit on the lacrimal. The foramina on the alisphenoid and on the inside of the orbit are badly obliterated because of crushing.

The anterior palatine fenestrae run the length of the space between the anterior

¹ The individual under discussion, judged from its very heavily worn molars, was senile. The development of the sagittal crest is probably a maximum for this species.

² DuBrul (1965) has pointed out, in a study of the callithricid *Leontideus rosalia*, how phylogenetic size increase changes the proportions and the mechanics of the skull. As the skull increases in size, the facial skull grows at a more rapid rate than the neurocranium. The cause of this phenomenon is probably attributable to a special case of allometry. DuBrul (1965, p. 261) noted, concerning a heuristically arranged series of skulls of callithricids, cebids, cercopithecids, and hominoids (a phylogenetically meaningless grouping): "Smaller skulls have orbits closely pressed together, separated only by a simple bony septum. As skulls increase in size the orbits move apart to be separated, first by slight hollows in the skull base, then progressing to increasingly complicated air or marrow spaces." Unfortunately there is no well-documented primate sequence in the fossil record by which to verify such a contention. Furthermore, there is no series with a similar size range, or adequate cranial material for the different size stages. It must also be pointed out that not all cranial size increase necessarily entails changes in the growth rates of the two portions of the skull.

border of P^1 and the posterior border of the enlarged incisor.

SKULL FRAGMENT OF *Microsyops annectens*

Text figure 20

A.M.N.H. No. 12595 is part of a skull of *Microsyops annectens* from the upper Bridger beds of Wyoming. Close association with the mandibles (see pl. 54, figs. 5, 6) confirms the identification. This preserved part of the skull is the posterior dorsal segment of the facial cranium and the anterior portion of the cerebral cranium.

Viewed ventrally, there are four fossae on each frontal. The medial fossae of the opposite sides are separated by a ridge which is very likely the remnant of the medial nasal septum. At present, there is no reason to doubt that this partition was the medial plate of the frontal. I interpret the four fossae on each side as housing the ethmoid scrolls. They are here referred to simply as fossae 1, 2, 3, and 4, beginning in the middle of the skull fragment and going in a lateral direction. Fossae 1 and 2 can be called the inner ethmoid scrolls, and fossae 3 and 4 can be called the outer ones. The first and second fossae are much more constricted than the outer ones.

Posterior to the fossae, there are two somewhat triangular depressions. I interpret them to be the roof of the cavity in which the olfactory lobes of the cerebrum were situated.

The cribriform plate was probably on the anterior border of the olfactory fossa.¹

Superior to the olfactory fossa and the anterior portion of the cerebral fossa, there is just barely sufficient space for one (or several) frontal sinuses. I did not explore the presence (or absence) of sinuses, because to have done so would have damaged the specimen.

A.M.N.H. No. 12595 has both left and right postorbital processes intact. This extension of the frontal, as in *Microsyops lundeliusi*, is very broad at its base, very thickened at its edges, and its posterior border is much thicker than the anterior border. On the top of this skull fragment, the superior temporal lines, which are simply a linearly pronounced aggregation of bone for the attachment of the temporalis muscle, are a direct continuation of the thickened posterior edge of the postorbital process. The superior temporal lines are the beginnings of the sagittal crest.

¹ It occurred to me that what is called here the olfactory fossa may have been in reality the frontal sinus. Such an interpretation may seem reasonable at first, because the cerebral cavity in the better-known *Microsyops lundeliusi* is relatively farther from the roof of the skull than it is in A.M.N.H. No. 12595. It is well known, however, that, in two closely related species, the larger often develops relatively larger air sinuses above the olfactory region of the brain. Such an explanation would account for the fact that in *M. lundeliusi* the brain is relatively distant from the top of the cranium. Furthermore, sinus cavities as a rule are crisscrossed by an irregularly spaced network of thin-sheated bony lamellae. There are no signs of this on the smooth surface of the cavity under discussion.

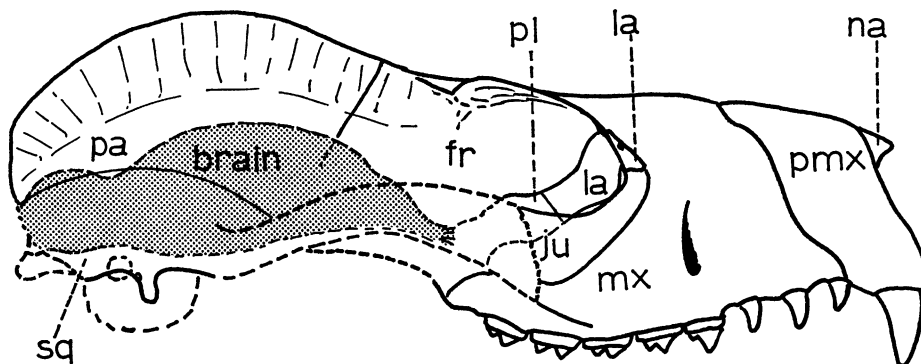


FIG. 18. Lateral view of reconstructed cranium of *Microsyops lundeliusi*, to show the size of the brain (stippled area) in relation to the skull.

Abbreviations: fr, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pl, palatine; pmx, premaxilla; sq, squamosal.

THE SKULL OF *Microsyops latidens*

A.M.N.H. No 55286 is a very crushed but relatively well-preserved skull of *Microsyops latidens* from locality II of an expedition in 1954 of the Department of Vertebrate Paleontology of the American Museum of Natural History. The skull is crushed dorsoventrally, but most of the details on both dorsal and ventral surfaces are relatively well preserved. Anterior to the alveoli of P⁴ the muzzle is missing, and only part of the ventral surface of the facial cranium is preserved, with unworn M²⁻³ on the left side. Slight anteroposterior crushing of the specimen resulted in the unfortunate telescoping of the cerebral cranium onto the facial one, and this further resulted in the obliteration of the orbits and the zygomatic arches. Also, because of this crushing, many important details of the middle of the skull have disappeared. I estimate that the uncrushed, un mutilated skull was approximately 5 cm. in length and about 3.5 cm. wide between the most lateral points of the zygomata. The maximum height of the skull, from the plane of the secondary palate to the top of the sagittal crest, must have been 2 cm.

DORSAL ASPECT: Approximately 6 mm. from the nuchal crest, there is a rather large foramen on each parietal, about 5 mm. from the sagittal crest. I interpret these foramina to be an outlet for one of the many venous sinuses, probably the superior petrosal sinus, from the corresponding region of the cranium. The sagittal crest is rather low, probably because the specimen represents a young individual. Immediately left and right of the sagittal crest, the superior temporal lines can be seen.¹

¹ Seth (1964), in a paper on the relation of the sagittal crest to the nuchal crest in *Nycticebus coucang* (Indian slow loris), illustrated a series of skulls of various ages of both sexes. The photographs clearly show the great variation in the approach to the midline of the skull by the temporal lines. This author referred to the superior temporal lines as "waves of living bone," implying the dynamic feature of this cranial character. In juveniles of both sexes of the Indian slow loris the temporal lines are weak, but, as the animal matures, these lines show a tendency to coalesce on the skull. As on adult males, on adult females these lines may also form a sagittal crest, and, on the other hand, on adult males the two bony crests may remain distinct without the formation of a sagittal crest. As a rule, all old individuals have a well-developed sagittal crest.

The squamosals are slightly pushed onto the lateral borders of the parietals. The anteriorly exposed portion of the endocranial cast on the right side of the specimen is not very informative. The brain cast of *Microsyops*, as revealed by the cast taken from A.M.N.H. No. 55284, is discussed below.

POSTERIOR ASPECT: The occiput appears to have been vertical. The transverse nuchal crest is relatively high and well defined. The mastoid part of the petrosal is exposed as a ventrolateral segment of the occiput. The petromastoid is discussed further in the section dealing with the ear region.

On the left side of the occiput of A.M.N.H. No. 55286 at least two supramastoid foramina are visible.

The two well-preserved occipital condyles almost completely surround the foramen magnum. There is no indication that the condyles were ventrally oriented as in some of the living prosimians. Each of the two condyles is broken into three parts; the breaks occurred on both sides symmetrically, indicating a probably structural weakness (perhaps due to embryonic or early postnatal contacts of the components of the condyles) at these areas. The dorsal atlantal facet is large, thickened, and appears to have been a functional part of the condyle. A small foramen is visible at the dorsomedial extremity of the dorsal atlantal facet.

The dorsal lobe of the occipital condyles (which is really less dorsal than the dorsal atlantal facet) is the most prominent part of the condyles. The articular surface of the dorsal lobe curves from a dorsomedial ex-

The relative development of the sagittal crest is a very poor taxonomic character, which is not to say that the degree of development is not or cannot be sex-linked or sex-influenced genetically, or that it cannot serve in a diagnosis of a species, a genus, or an even higher category. Before such a character is relied on, however, particularly among primates and other herbivores, great care should be taken to determine the relative age of the animal. Whether the strong or weak development of the sagittal crest is rigidly fixed genetically, or plastic to the individual needs of the animal, is a question to be answered for every taxon. As a general "rule," although a large sagittal crest may be rigidly fixed and diagnostic of certain carnivorous mammals, it may be more plastic among herbivores and may develop to a lesser or greater extent depending on individual requirements.

tremity to a ventrolateral surface at the ventral end.

At the point of two symmetrical breaks in the ventrolateral quarter of the ventral surface of the condyles, the dorsal lobes are slightly slipped onto the ventral lobes.

LATERAL ASPECT: The details of orbital construction are completely obliterated by crushing. A transversely wide, but anteroposteriorly also extensive, orbital shelf is preserved on the left side. The details of the construction of this area cannot be determined. The broad shelf seems to be made up entirely of the maxilla and occupies the area immediately dorsal to M^{2-3} .

The entire jugal is relatively well preserved on the left side. This bone is very stout; at one point it has a maximum height of 5 mm., which is relatively thick for a skull of this size. One can estimate the relative robustness of the squamosal part of the zygoma solely from its posterior remnant on the right side, immediately behind and above the glenoid fossa. It seems to be at least 2 mm. less stout than the average height of the jugal. The maxilla contributes a rather broad and strong flange to the anterior base of the zygoma. This base has its origin at the level of M^2 .

The flat, broad, somewhat triangular glenoid fossa extends laterally from the middle of the cerebral cranium. There is a rather stout postglenoid process posterolateral to the fossa. A relatively enormous postglenoid foramen is situated on the medial half of the base of the postglenoid process. The preotic crest of the squamosal bounds the glenoid fossa medially. This bony projection runs approximately 100 degrees to the transverse plane of the postglenoid process. The fissura Glaseri is clearly visible, running between the posterior edge of the preotic crest of the squamosal and the medial edge of the postglenoid process.

THE BASICRANIAL REGION: The basicranial region (see text fig. 17 and pl. 42), particularly on the left side, is excellently preserved. In spite of the fine preservation of the whole region, the left petrosal is slightly depressed ventrally. The extent of this slight distortion cannot be determined, but it does not obscure details of the anatomy of the ear region.

It is important that the external auditory

meatus was situated closely posterior to the postglenoid foramen. The meatal surface at that point is slightly concave. There seem to be no broken surfaces on the squamosal, basisphenoid, basioccipital, or alisphenoid that would indicate that a bulla was formed by any one of these bones. It is very likely, however, that the large promontorium was protected by an ossified entotympanic (?) bulla. Some of the indirect evidence for this assumption is given below.

The promontorium of the petrosal is roughly tear-shaped and bulges ventrally. Its natural orientation is probably not shown on either side of the specimen because of the distortion that the whole skull suffered. Medially, on the ventral surface of the promontorium, there is a prominent crest. It extends most ventrally on the posterior portion of the promontorium and decreases in height in an anterolateral direction. A probably homologous crest of *Ictops* (= *Leptictis*, Van Valen, 1967) has been referred to as the tympanic process of the petrosal. This crest obviously did not contribute to the auditory bulla in *Microsyops* or in *Leptictis*, but it very probably served as a medial attachment for the bulla.

There are two clearly defined fenestrae on the promontorium. The fenestra ovale is directly lateral, whereas the fenestra rotunda is posterolateral. Posterior to the promontorium, on the contact of the petrosal and the exoccipital, the posterior lacerate foramen (jugular foramen) is very large.

Anterior to the ventral lobe of the occipital condyle, there is a curious canal labeled canal X (see text fig. 17). Were this foramen on the inner surface of the condyle, it would undoubtedly be called a condyloid canal. Considering the location of the canal, however, I cannot offer any suggestion as to its homology at present.

On the medial surface of the petrosal a clearly defined groove runs almost the entire length of the petrosal. This groove may be interpreted in several ways. The most likely interpretation appears to be that a large sinus ran along it. Butler (1956b) interpreted the homologous structure of *Leptictis* as the groove for the inferior petrosal vein. I am inclined to believe that, in addition to the inferior petrosal sinus, the medial entocarotid

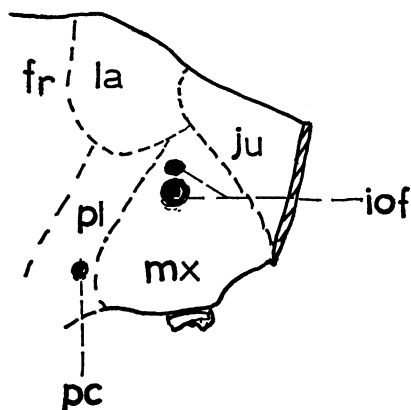


FIG. 19. Orbit of *Microsyops lundeliusi*, A.M.N.H. No. 55284, posterolateral view, showing diagrammatically the interrelationships of bones.

Abbreviations: fr, frontal; iof, infraorbital foramen; ju, jugal; la, lacrimal; mx, maxilla; pc, posterior palatine canal; pl, palatine.

was also present in this groove. Somewhat anterior to the groove under discussion, anteromedial to the promontorium, a large foramen is present on the basisphenoid. This opening into the skull probably represents two separate structures indistinguishable from each other because of poor preservation. The posterior, poorly exposed portion of the large opening probably represents a foramen for the entry of the medial entocarotid which at that point probably entered the circle of Willis. The more anterior and much better exposed part may be safely referred to as the median lacerate foramen for the outlet of the inferior petrosal sinus and the inferior jugular vein.

Posterolateral to the foramen ovale is a deep, rather long fissure running anteroposteriorly and slightly mediolaterally. It is possibly an area of exit for part of the seventh nerve.

There are unmistakable sulci on the ventral surface of the promontorium for the internal carotid, the promontory, and the stapedia arteries. The internal carotid (as inferred from the groove patterns) divided into a medial large branch (medial entocarotid artery), the promontory artery, that continued in an anteromedial direction on the surface of the promontorium, and a smaller stapedia artery that presumably passed through the crura of the stapes. The latter bone, like the other auditory ossicles, is

not preserved. There is a faint and short sulcus leading to the rear from the posterolateral border of the fenestra rotunda. It is probably a groove for the posterior ramus of the stapedia artery.

The mastoid part of the petrosal is roughly tongue-shaped and extends posterolaterally from the promontorium. The peculiarly concave surface of the ventral aspect of the petromastoid is striking. Since there is no paroccipital process, it is reasonable to assume that the digastric muscle originated medial to the petromastoid.

Anterolateral and lateral to the promontorium there is a large continuous cavity. It is posteriorly bordered by the facial canal mentioned above and the more lateral portion of the petromastoid. The tegmen tympani forms the lateral, and the alisphenoid forms the anterior border of this large cavity. The latter is partly the fossa muscularis major and the middle ear cavity combined, without any clear signs of demarcation between them. Immediately lateral and dorsal to the promontorium there appear to be faint traces of grooves. These may be interpreted as sulci for the superior and inferior rami of the stapedia artery. There is also a suggestion in this area of a foramen for the superior branch of the stapedia artery. The epitympanic recess is clearly defined posterior and dorsomedial to the postglenoid process and foramen. The recess is exposed by a broken segment of the posttympanic process of the squamosal. The tegmen tympani, a ventrally projecting wing of the petrosal, separates the recess medially from the tympanic cavity.

The entire tympanic cavity and the promontorium are bordered by the squamosal, the alisphenoid, the basioccipital, and the exoccipital bones. Whether or not the basisphenoid is in contact with the median lacerate foramen cannot be determined at present from the only known specimen that shows the basicranium.

MANDIBLE

In spite of the remarkable abundance of microsyopid teeth and broken jaw fragments, complete undamaged jaws are extremely scarce. Although the horizontal ramus is preserved often enough, as in most rather

common fossil mammals, the ascending ramus is very rarely preserved. Even in the best-preserved and only complete mandible, A.M.N.H. No. 55285, the area of the angle is missing. The angle on the mandible of *Microsyops lundeliusi*, a relatively late species of the genus, shows a much less delicate structure than that of *Navajovius*. We do not know, however, how the mandible appeared in the early Wasatchian species of *Microsyops*.

The symphysis is invariably unfused in *Microsyops*, indicating that the mandibles were probably movable during mastication, an inference made from wear facets on the medial surface (not lingual) of the enlarged lower incisor. One mental foramen is usually present under P_3 . On the only known mandible of *Microsyops kratos*, L.A.C.M. No. CIT2032, there are two foramina under dP_3 .

On the medial side at the anterior base of the coronoid process there is a triangular muscle scar for the insertion of a portion of the temporalis.

On U.S.N.M. No. 17813, a specimen of *M. elegans*, and on A.M.N.H. No. 55285, a mandible of *M. lundeliusi*, the articular condyle is above the level of the tooth row. The articular facet is flat and slopes slightly posteromedially. Medially the articular facet is broader lengthwise than it is laterally.

The mandible of *Microsyops* is relatively very high (the height of the ascending ramus is about five-eighths of the entire length of the mandible). The tooth-bearing portion of the mandible is also deep and heavy.

The large dental foramen opens posterodorsally; it is slightly below the tooth-row level on the anterior half of the ascending ramus. The mandible of the possible microsyopid *Navajovius* is reasonably, but not well, known. The two mandibles of A.M.N.H. No. 17390 show part of the lateral aspect of the horizontal ramus and the medial aspect of the posterior half of the mandible (see pl. 30, figs. 8, 9). The horizontal ramus is not deep. The outline of the posterior part indicates a not very steeply ascending coronoid process, an articular condyle high above the level of the tooth row, and a distinct, slim, posteriorly extended angle. The neck of the articular condyle is rather long; its longitudinal axis forms an angle of about 45 de-

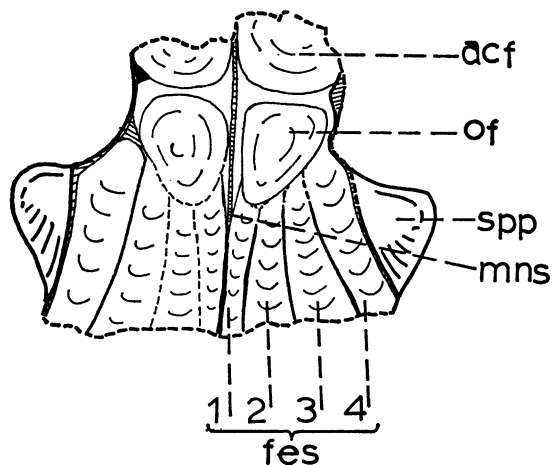


FIG. 20. Ventral view of skull fragment of *Microsyops annectens*, A.M.N.H. No. 12595, from lower Bridger beds. The broken lines and hatched areas represent broken outlines and broken surfaces, respectively.

Abbreviations: acf, anterior cerebral fossae; fes, fossae for ethmoid scroll; mns, medial nasal septum; of, olfactory fossa; spp, superior post-orbital process.

grees with the longitudinal axis of the horizontal ramus. As well as can be determined from the type, the masseteric fossa is rather well delineated.

THE ENDOCRANIAL CAST OF *Microsyops*

MATERIAL AND GENERAL ASPECT: The endocranial cavity is relatively well preserved in the only known skull of *Microsyops lundeliusi* (A.M.N.H. No. 55284), and consequently it was possible to prepare an adequate cast (see pl. 41, figs. 4, 5, and text fig. 24). This endocast shows only the dorsal surface of the endocranial cavity; the cavity occupied by the olfactory lobes of the brain could not be included because the olfactory chambers are obliterated on the skull. The left part of the dorsal cover of the endocranial cavity is better preserved than the right, which is reflected on the endocast itself. A.M.N.H. No. 12595, a fragment of the dorsal portion of the skull of *Microsyops annectens* with the ventral surface beautifully preserved, showing the dorsal part of the olfactory cavity and the arrangement of the ethmoidal scrolls, enabled the completion of an outline drawing of the general shape of the endocranial cast (see text fig. 24).

The fractured, broken surface of the endocranial cavity, and consequently of the cast itself, does not permit so many accurate interpretations as can usually be made from some endocasts reported [see, for example, Gazin's (1965) recent and detailed fine account of the endocast of *Smilodectes gracilis*].

The most striking features of the general aspect of the endocast is the relatively broad posterior part of the cerebrum and the exposed midbrain, or tectum mesencephali. The cerebral part of the cast is considerably higher than the cerebellar portion. The approximate length of the endocranial cavity in A.M.N.H. No. 55284, including an estimate of the olfactory chambers, is about 4.6 cm., and its width at the posterior one-fourth of the cerebral hemispheres is roughly 3.4 cm.

OLFACTORY BULBS: As noted above, the shape of the olfactory bulbs has been derived from the beautifully preserved inner surface of the Bridgerian skull fragment of *Microsyops annectens*, A.M.N.H. No. 12595 (see text fig. 20). Judged from the shape of the dorsal aspect of the cavity (the only part known), each of the olfactory chambers, which come to a blunt point anteromedially, is concave laterally, and probably fairly straight medially.

NEOPALLIUM: Only one sulcus is indicated definitely on the endocast. The impression of this sulcus is faint, not well defined, and is indicated only by a slight concave channel or depression. This depression extends almost all the way of the posterior part of the neopallium, about halfway from either the lateral or the medial borders of the cerebrum, gradually turning medially. Approximately at the posterior one-third of the cerebrum it becomes straight and runs forward, presumably almost the whole length of the neopallium. I tentatively interpret this sulcus as the sulcus lateralis. Of the most recent workers on fossil endocranial casts, Gazin (1965) and Russell and Sigogneau (1965) interpreted a topographically similar sulcus as the sulcus lateralis in the Bridgerian primate *Smilodectes* and in the Thanetian condylarths *Arctocyon* and *Arctocyonides*, respectively. As Gazin (1965, p. 4) noted, this sulcus "... is described as one of the more stable and earlier to appear in the various Mammalia."

MIDBRAIN AREA: This area is meant here to include the space between the posterior limits of the neopallium and the anterior border of the cerebellum. As described in the section dealing with blood vessels, the transverse venous sinus of the dura mater covers a large part of the midbrain area. Posterior to the transverse venous sinus, however, a large concave depression undoubtedly reveals the broadly exposed tectum mesencephali of *Microsyops*. It seems very probable that the area covered by the transverse venous sinus is also the area where the midbrain was clearly exposed ("covered" by the sinus) in the usual sense of the word, meaning that is not covered by any other part of the brain itself. Being roofed by a large sinus is quite distinct from being covered by a posteriorly expanded neocortex.

A slight but nonetheless distinct V-shaped depression on the cast anterior to the antero-medial limit of the transverse sinus may be interpreted as the confluens sinum.

CEREBELLUM: The vermis cerebelli and the lateral lobes of the cerebellum can be easily recognized. The three morphological entities are of about equal size; the vermis, however, is slightly more elevated than the two lateral lobes. The slight separation between the vermis and the lateral lobes, particularly pronounced on the posterior part of the cerebellum as two notches is interpreted as the paramedian fissure; this fissure is poorly developed in *Microsyops*.

The top of the cast of the cerebellum is approximately 7 mm. lower than the top of the cast of the neocortex. This is a striking feature, probably primitive in comparison to the slightly elevated condition of the cerebellum, relative to the cerebrum, as seen in *Smilodectes* (see Gazin, 1965, pls. 1, 2).

BLOOD VESSELS: There appears to be no trace of the longitudinal (or sagittal) sinus that is usually situated in mammal endocasts at the junction of the two neopallial halves on the surface of the endocast.

A convex, V-shaped thickening which runs posterolaterally, traversing over the anterolateral tip of the lateral lobes of the cerebellum, is very probably the transverse venous sinus in the dura mater. A few structures on the endocast can be interpreted as casts of veins draining into the transverse sinus.

On the left lateral side of the cerebral part of the cast there is the distinct impression of a vascular canal, probably representing the cast of a large, lateral venous sinus, although the homology of this vessel is quite uncertain. Gazin (1965) reported a blood vessel in the identical position of the endocast of *Smilodectes*.

COMPARISONS AND REMARKS: Published information on endocasts of Oligocene or older insectivores is extremely meager, and nothing has appeared on Paleocene prosimians. Much that is published needs a more accurate and critical restudy. Moodie's (1922) figures of the endocast of *Leptictis*(=*Ictops*), for example, are vague, and the specimens studied by him did not show the crucial details of the midbrain and the cerebellum. Except for the meager information published on the latter genus, endocasts of other early Tertiary insectivore have not been described or commented on in any detail.

In *Leptictis* the olfactory bulbs are short, broad, and very large (Moodie, 1922, p. 349). The condition of these structures cannot be judged with sufficient accuracy in *Microsyops*, but they appear to be relatively smaller than those of *Leptictis*. These structures of the notharctine *Smilodectes*, recently described by Gazin (1965), were not preserved in the specimen he studied.

Both the figures of *Smilodectes* by Gazin and the figure of *Leptictis* by Moodie indicate a relatively smooth cerebral endocast, similar to the condition seen in *Microsyops*. The lack of proliferation of sulci on the neopallium in all probability is the primitive therian condition. The endocasts of *Microsyops* and *Smilodectes* appear to show the same degree of development for the sulcus lateralis; it is not well developed in either endocast.

Some differences between the relative height of the neopallium and that of the cerebellum are apparent between *Leptictis* and *Microsyops* on the one hand, and *Smilodectes* on the other. In *Leptictis* and *Microsyops* the cast of the neocortex is higher than that of the cerebellum, but in *Smilodectes*, as Gazin (1965, p.5) noted, "The vermis cerebelli extended prominently above the general level of the posterior lobes of the cerebrum."

Moodie's (1922) illustration of the midbrain area of the endocast of *Leptictis* is unclear. Some uncatalogued and unprepared *Leptictis* material in the American Museum of Natural History indicates that there may have been midbrain exposure in that genus. Russell and Sigogneau (1965, p. 26), in discussing the major characters that they considered to be primitive in the insectivore brain macrostructure, stated as well as repeatedly implied the generally held view that a largely exposed midbrain is primitive in mammals (presumably meaning the Theria).

There is no information of any sort on the features of the brain of Paleocene primates. The known Eocene endocasts shed no light on the structure of the midbrain region in the primitive members of the order. On the condition of the midbrain in *Smilodectes*, Gazin (1965, p.3) stated, "The posterior poles (i.e., of the cerebrum) extended well over the mesencephalon, nearly or quite to the cerebellar portion, but as in *Lemur* the vermis and lateral lobes were not overlapped by the cerebrum." It must be added, as Gazin pointed out, that *Smilodectes* shows an extraordinarily well-developed cerebral cortex for a middle Eocene mammal.

In *Microsyops*, the midbrain is broadly exposed. If my suggestion that microsyopids are primates is correct, then the exposed midbrain was evidently present in the earliest Primates. Any further speculation on this point is completely futile, since the crucial late Cretaceous and the Paleocene evidence is unknown.

There is an apparent contradiction in Edinger's (1964) paper devoted to midbrain exposure and overlap in mammals concerning what is primitive in eutherian or therian brains (or endocasts). Edinger argued that the exposure of the midbrain in a mammal does not mean that the animal has a primitive brain, and she implied throughout her paper that midbrain exposure is not primitive. It must be noted that the hypothesis suggesting that midbrain exposure is not primitive in mammals (?) is distinct from the notion that midbrain exposure can be secondary, without implying a primitive brain. In consideration of the fluid nature of what different workers have recognized as a "mammal" (see references in Olson, 1959;

Simpson, 1959b, 1960; Van Valen, 1960; Mac Intyre, 1966; and others), it is of the utmost importance that the taxonomic level at which one refers to what is or is not considered primitive for any particular taxon be clearly stated. What may generally be primitive in the Theria may not be in the Prototheria, Allotheria, and other groups of uncertain relationships. At the present time, meaningful phylogenetic ties can be established only for the Theria; within this major group the symmetrodonts, pantotheres, metatherians, and eutherians have undoubted affinities.

Some of the fossil evidence and some of the arguments based on it that Edinger cited in support of her thesis are questionable. Although far from knowing the correct answers, I consider it important for the present discussion to question some of the evidence presented in that paper. Edinger's derivation of the chiropteran brain¹ from the brain of the "lower Paleocene *Apternodus*" (*Apternodus* is an Oligocene genus of tenrecoid insectivores), which lacks midbrain exposures, is inexplicable. Nothing is known in the published fossil record that could be ancestral to the Chiroptera (mainly because the primitive Chiroptera have not been found), and reference to the highly varied Insectivora in the "wastebasket" sense is not helpful. Known tenrecoid insectivores show no special dental similarity to the earliest known bat (personal observations, courtesy of Dr. G. L. Jepsen).

Edinger, however, did not contest the notion that in the Eutheria an exposed midbrain is probably primitive. She wrote (1964, p. 18): "As further progress in brain evolution was cerebral, neocortical advancement, subordinate role and overlap of the midbrain was a general phenomenon. It occurred in very different degrees at different times in the different branches of lower as well as higher mammals. In some of the former, an exposed

tectum may have remained in the primitive eutherian position; but in various species, during a period of 60 million years, the tectum became secondarily exposed through drives centered in, for example, its acoustic colliculi." In the above quotation, taken from the summary of the paper, Edinger clearly maintained that there was an exposed midbrain in the primitive Eutheria.

Edinger, as a result of her inquiry into the endocast of the pantothere *Amblotherium* (B.M. No. 47758), implied that there was no exposed tectum in the first Theria as in *Amblotherium* in which (p.14) "... the tectum ... was on a level below the dorsal brain surface, superposed by the cerebral hemispheres."

The main body of Edinger's paper argued for the independence of an exposed midbrain from the poorly or highly developed cerebral hemispheres. This contention, quite independent of various implications of what is and what is not primitive in the brain of various groups of mammals, is not questioned or debated here.

Edinger further asserted that the exposed midbrain of early Tertiary mammals is not a primitive holdover of the ancestral therapsid condition but is a newly emerged midbrain from an ancestral condition in the upper Jurassic and lower Cretaceous mammals, in which (p.18) "... an expanded but still palaeencephalic cerebrum overlapped a midbrain which was still of the reptilian type, as were the hindbrain and other characters in these most ancient mammals." Edinger pointed out (p. 18): "Conclusions are necessarily speculative. Of the tectum, there exist no actual documents between the corpora bigemina of early Mesozoic therapsid Reptilia and the corpora quadrigemina of Neozoic Mammalia. Its condition in the middle Mesozoic had to be concluded from the brain of three individuals."

COMPARATIVE ASPECTS OF THE MICROSYPID CRANIUM

The rather fundamental and important difference in cranial construction exists between Eocene notharctines,² adapines, and

¹ The reference to the order Chiroptera was based on a crushed endocast that lacked midbrain exposure. Other than the fact that the endocast has enlarged lobes posteriorly, which can be interpreted as enlarged acoustic colliculi, there is no additional evidence that the specimen represents a bat. Jepsen (1966, p. 1337) has recently noted that the skull on which Edinger based her conclusions is a heavy-boned cranium and not the skull of a flying mammal. Jepsen identified the specimen as a miacid carnivore.

² For illustrations of *Notharctus*, *Adapis*, and *Plesiadapis*, see Gregory (1920), Stehlin (1912-1916), and D. E. Russell (1959, 1964), respectively.

anaptomorphids (the last known from only one crushed specimen of *Tetonius homunculus* partly described by Matthew in 1915), on one hand, and *Plesiadapis* and *Microsyops*, on the other. If, for the sake of this discussion one were to refer to the greatest degree of constriction between the anterior and posterior moieties of the skull as the line of demarcation between the facial and the cerebral cranium, this fundamental difference becomes quite apparent. The cerebral part of the skull in both Paleocene *Plesiadapis* and the Eocene *Microsyops*, although very broad, is distinctly shorter than the facial part. The facial skull is clearly more dominant and larger than the cerebral cranium. The two skull parts are sharply separated by the mid-cranial constriction. On the other hand, in the Eocene *Notharctus*,¹ *Smilodectes*, *Adapis*, and *Tetonius*, the cerebral skull gains importance in three closely correlated ways. One feature is the relatively greater expansion of the cerebrum compared with the primitively smaller condition of the neopallium. Second, there is a pronounced reduction in the relative size of the facial skull which can probably be correlated with a reduced importance of the sense of smell. A reduction in olfaction consequently resulted in a reduced surface area of the ethmoidal scrolls for olfactory epithelium which in turn resulted in a shortening and narrowing of the muzzle. Third, as a result of cerebral expansion, the pronounced constriction between the facial and cerebral skulls became much less obvious.

D. E. Russell (1964) made detailed comparisons of the cranial features of *Plesiadapis* with those of *Notharctus*, *Smilodectes*, *Adapis*, and *Pronycticebus*. I add and comment on the pertinent known details of the microsyopid skull as it relates to Russell's treatment. Russell's comparative study is the most factual and exhaustive of the comparative anatomy of early Tertiary primate skulls to date. I do not attempt to compile information here given by that author, which was verified by me, or facts that have no direct

¹ For detailed information on primitive primate cranial anatomy, I have relied heavily on the monographs of Gregory (1920) and Gazin (1958) for *Notharctus* and *Smilodectes*, of Stehlin (1912-1916) for *Adapis*, and of D. E. Russell (1964) for *Plesiadapis* and *Pronycticebus*.

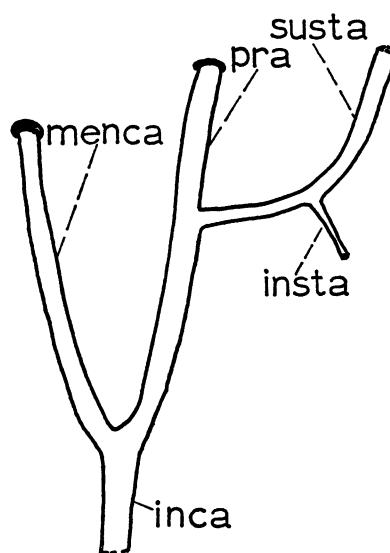


FIG. 21. Reconstructed carotid circulation in the basicranium of *Microsyops* cf. *M. latidens*.

Abbreviations: inca, internal carotid artery; insta, inferior stapedial artery; menca, medial entocarotid artery; pra, promontory artery; susta, superior branch of stapedial artery.

bearing on microsyopid anatomy. Comments are made here only on certain features of the only adequately known leptictid skull, that of the Oligocene *Leptictis*. The skull of this genus, in my opinion, is still the most primitive well known, available cranium of an insectivore, with special bearing on many primitive features of the primitive prosimian skull. The information presented here on the skull of *Leptictis* is based on one of the four excellently preserved skulls (A.M.N.H. Nos. 9316, 38915, 38916, and 38919) and confirmed on the other three specimens.

The premaxilla of *Microsyops* is enlarged, but to a much lesser degree than in *Plesiadapis*. The enormous premaxillae of the latter genus are in touch with the frontals, but in *Microsyops* there is no premaxilla-frontal juncture. The maxilla broadly separates the latter two bones.

The lacrimal foramen is outside the orbit, as in *Plesiadapis* and *Notharctus*. In *Microsyops* this foramen is rather far up in both the skull itself and on the lacrimal. Although A.M.N.H. No. 55284 is badly crushed in the critical regions of both sides, it is fairly clear that the foramen, clearly preserved on a chip of bone on the right side, was smaller

than its homologue in *Plesiadapis*. In *Plesiadapis* this foramen is not so high on the skull and appears to be more antero-ventral on the lacrimal itself than in *Microsyops*. The figures of skulls of *Adapis* given by Stehlin (1912-1916) seem to show this foramen on, or slightly inside, the anterior border of the orbit. D. E. Russell's line drawing of *Adapis* (1964, fig. 19) shows, however, the lacrimal foramen outside the orbit. In *Leptictis* this foramen is small to medium-sized, and it is barely inside the superior portion of the orbit.

In *Microsyops* the posterior entrance to the infraorbital canal from inside the orbit is apparently uniquely double, at least among early Tertiary prosimians and *Leptictis*. The anterior exit of the infraorbital canal, i.e., the infraorbital foramen on the side of the muzzle, is a single opening as in *Plesiadapis* and *Leptictis*. D. E. Russell (1964) reported that, in some species of *Adapis*, the latter foramen is double on the muzzle. This condition is also true on the only known skull of *Tetonius* (A.M.N.H. No. 4194).

As far as it can be determined from A.M.N.H. No. 55286, there is no irregularly exposed area of the ethmoid (i.e., an "os planum") inside the orbit either in *Microsyops* or in *Leptictis*, as was noted for *Adapis*, *Pronycticebus*, and *Plesiadapis* by Russell.

Apparently there was no frontal-maxillary contact inside the orbit of *Microsyops*. The anterior orbital wing of the palatine makes rather broad contact with the lacrimal as in *Leptictis* and thus broadly separates the frontal from the maxillary. Russell, on the other hand, reported long frontal-maxillary contact in *Plesiadapis*, *Adapis*, and *Pronycticebus*, accompanied by the necessary reduction of the anterior orbital wing of the palatine. For notharctines, information is lacking on this point. At first, it would appear that the latter condition may be primitive for the primate orbit. Recent lemurs and lorises (except *Perodicticus*), however, have long palatine wings in contact with the lacrimal, preventing any frontal-maxillary contact (see D. E. Russell, 1964, p. 107). *Leptictis*, recent tupaiids, microsyopids, species of lemurs, and lorises (with the above-noted exception) probably reflect the primitive condition that antedated the

frontal-maxillary contact in *Plesiadapis*, *Adapis*, and *Pronycticebus*.

As in notharctines and adapines, the posterior nares are broad and wide in *Microsyops*. In *Plesiadapis* and in *Leptictis* these openings are much smaller and narrower. Both *Plesiadapis* and *Leptictis* share the presence of a postpalatine spine that originates in the middle of the thick postpalatine torus. In *Microsyops* and in *Plesiadapis* M¹ is under the anterior pocket of the orbit but does not extend anterior to it. In *Leptictis* as Butler (1956b, p. 465) also noted, M¹ is anterior to the orbit. Although *Microsyops* has a thickened postpalatine torus, it completely lacks even traces of a postpalatine spine.

In *Plesiadapis* and *Adapis*, as well as in *Microsyops*, the posterior palatine canal (the incisura for the posterior palatine artery, not to be confused with the posterior palatine foramen, usually more anterior on the secondary palate) is represented by a groove lateral to the posteriorly running crest of the palatine. In *Leptictis* the postpalatine canal is a distinct, tear-shaped foramen in the identical position as are the grooves in *Plesiadapis*, *Adapis*, and *Microsyops*.

Although comparative aspects of auditory bulla construction in primates and pertinent groups are briefly discussed below, it may be noted here that notharctines, adapines, and microsyopids have no ossified external auditory tube. Leptictids and tupaiids also lack an auditory tube. In spite of the fact that *Plesiadapis* has a prominent ossified external auditory tube, it seems unlikely that this structure was primitive in primates.

The occipital condyles (and the foramen magnum) of both *Plesiadapis* and *Microsyops* face directly posteriorly. There is no apparent indication in these two genera of an incipient trend for the gradual shifting of the atlas under the cranium. In notharctine and adapine skulls there is a definite advance toward the characteristic grade of having the occipital condyles gradually pass under the skull, so diagnostic of modern prosimian crania.

THE EAR REGION: Although A.M.N.H. No. 55286 does not have a bulla preserved with it, it seems fairly certain, as McKenna (1966, p. 15) has noted, that a bulla was



FIG. 22. Artist's reconstruction, under the direction of the author, of the head of *Microsyops lundeliusi*. Slightly less than natural size.

present. My conclusions based on the ear region of A.M.N.H. No. 55286 are similar to those reached by McKenna, who studied the specimen before me. There is no apparent contact of the bulla with either the alisphe-noid or the basisphenoid. The tympanic process on the medial part of the ventral surface of the petrosal, however, must have had a functional role in connection with either an ossified or, less likely, cartilaginous entotympanic or ectotympanic bulla.

There is a rather fundamental unity of construction between the ear regions of *Microsyops* and those of *Leptictis*, but with notable differences in many details. It should be remembered that it is not known whether microsyopids had an entotympanic or ectotympanic bulla. After the ear region of an excellently preserved *Leptictis* skull (A.M.N.H. No. 9316) was cleaned, a wealth of detail (see pl. 43) not described or figured by Butler (1956b) was revealed. A.M.N.H. No. 55286 (*Microsyops latidens*) from the Huerfano Formation and A.M.N.H. No. 9316 (*Leptictis caniculus*) are skulls about equal in size but different in construction.

In *Leptictis* (A.M.N.H. No. 9316) the promontorium appears to adhere medially much more snugly to the basioccipital—a tenuous point of comparison because, in the only good ear region of *Microsyops*, the petrosals seem to have been shoved ventrally. The degree of this distortion cannot be determined accurately without additional uncrushed specimens. The dorsal boundaries of the tympanic chamber were considerably less concave (when viewed from a ventral aspect) in *Microsyops* than in *Leptictis*. In *Leptictis* the ventromedial part of the promontorium is flat, and the entire medial part gradually extends ventrally to become flush with the lateral wall of the basioccipital. If plates 42 and 43 are consulted it will be apparent that the promontorium of *Microsyops* is rather different from that of *Leptictis*.

In *Leptictis* there is a tiny bony extension,¹ or bridge, from the posteroventral projection of the tegmen tympani to the posterolateral

part of the promontorium between the foramina ovale and rotunda. This small bridge-like structure covers a very small part of the facial canal. There is no indication on A.M.N.H. No. 55286 that *Microsyops* had this structure.

The mastoid part of the petrosal is relatively larger and broader in *Leptictis* than in *Microsyops*. Posterolateral to the jugular foramen (posterior lacerate foramen) and medial to the petromastoid, there is a distinct, although small, paroccipital process in *Leptictis*. In *Microsyops* there appears to be no sign of this usual place of origin for the digastric muscle.

Relying exclusively on the illustrations in D. E. Russell (1964, figs. 15–18) and in Saban (1963, figs. 44–48) for the ear region of *Plesiadapis*, I made the following comparisons with that of *Microsyops*. The bony partitions of the *Plesiadapis* tympanic cavity are completely absent from *Microsyops*. The epitympanic recess appears to be relatively smaller in *Microsyops* than in *Plesiadapis*. Medial to the promontorium, between it and the basioccipital, there is a spacious cavity. Its equivalent is completely lacking in *Microsyops*. This cavity, one of the pockets of the hypotympanic sinus, seems to be present in *Adapis* (see Saban, 1963, fig. 51), and similarly *Notharctus* also has a large and distinct hypotympanic sinus medial to the promontorium. The cochlear aqueduct is not exposed posteromedially in *Microsyops*, as it is in *Plesiadapis* and *Adapis*.

The following comparisons can be made between certain aspects of the carotid circulation in *Leptictis*, *Microsyops*, and *Plesiadapis*. In both *Leptictis* and *Microsyops* a very similar pattern of grooves can be seen on the ventral surface of the promontorium (see text fig. 21). In *Leptictis* the promontory artery (providing the grooves correspond to the exact passage of the blood vessels in question) leaves the tympanic cavity and enters the braincase through a foramen at the anterior tip of the promontorium. Such does not appear to be the case in *Microsyops*. Butler (1956b, fig. 3) described and figured a foramen in *Leptictis* for the superior ramus of the stapedial artery medial to the posterior third of the epitympanic recess and anterior to the facial canal. There are indications, al-

¹ The specimen that Butler (1956b) studied was damaged and apparently had lost this little bony projection. While preparing A.M.N.H. No. 9316, I broke this small structure on the right side but managed to retain it intact on the left side (see pl. 43).

though A.M.N.H. No. 55286 is not well preserved at this point, that there was a similar foramen in *Microsyops*, although relatively more anterior than the one in *Leptictis*.

There is no evidence against the presence of a medial entocarotid in leptictids or microsypids. There is a rather spacious canal medial to the promontorium in *Microsyops*, and a somewhat smaller one in *Leptictis*. This canal probably housed both the entocarotid and the inferior petrosal sinus. McKenna (1966, fig. 3) has shown, in my opinion correctly, the medial entocarotid of *Microsyops* (= *Cynodontomys*) to be relatively larger than that of *Leptictis* (= *Ictops*). Butler (1956b, pp. 472-473) noted that the canal for the medial entocarotid of creodonts closely corresponds to the canal that carries the inferior petrosal vein in insectivores. Butler also cited Matthew's view that the medial entocarotid (= the medial branch of the carotid) was lost in the earliest Insectivora and the lateral branch disappeared in the creodonts, the latter having retained the medial entocarotid. It appears from Butler's interpretation of the carotid circulation of *Leptictis* that he accepted Matthew's dictum. Butler (p. 473) added, however: "It is not impossible that primitively an artery accompanied the inferior petrosal vein into the skull, eventually becoming the internal carotid artery of most mammals." He apparently meant this condition was primitive for the Theria. Butler did not consider that in *Leptictis* the canal medial to the petrosal may have housed the medial entocarotid.

McDowell (1958, p. 208) suggested that the insectivore-primate stock, ancestral to the "Menotyphla" and primates, had already lost the medial entocarotid. McDowell (1958, p. 178) illustrated the auditory region of *Leptictis* and labeled the canal medial to the promontorium the carotid groove.

Briefly, the following pattern of carotid circulation was probably present in primitive placentals (Van Valen, 1966), *Microsyops*, and *Leptictis*. The internal carotid artery entered the tympanic cavity and branched into two large rami, the medial entocarotid and the promontory artery. The medial entocarotid artery probably entered the circle of Willis at the level of the anteromedial limit of the promontorium. The promontory artery

ran on the surface of the promontorium for about one-third of the length of the latter, before it gave off the lateral stapedia artery. The stapedia passed through the crura of the stapes and probably a short distance following that point split into a rather small inferior stapedia artery and a larger superior branch. There is no evidence from the osteology for either a posterior ramus of the stapedia or for a Vidian artery.

Unfortunately, the carotid circulation of *Plesiadapis* is poorly known. The opinions of several competent workers differ on the interpretation of basicranial osteology that pertains to the carotid circulation. I do not find evidence in the description of D. E. Russell (1964) that contradicts or confirms the presence of a medial entocarotid in *Plesiadapis*. McKenna (1966, pp. 9-11) did not mention either the absence or presence of the medial entocarotid, but he figured the *Plesiadapis* carotid circulation as having lost this blood vessel. The apparently large sample of isolated petrosals of *Plesiadapis* (D. E. Russell, 1964, pp. 97-98) appears to add to the confusion. Saban (1963, fig. 48) figured two supposed petrosals of *Plesiadapis* which show widely differing and widely branching and anastomosing sulci supposedly for the various branches of the stapedia and the "entocarotid" of Saban. The latter appears to me to have been a trace of the promontory artery rather than of the medial entocarotid. In spite of the wide variation present in the isolated petrosals, D. E. Russell (1964) maintained that there was a large promontory and a relatively much smaller stapedia artery. These vessels were not surrounded by bony canals but apparently ran in open grooves on the surface (partially) of the promontorium.

McKenna (1966, p. 11), contrary to Butler (1956b), who maintained that the leptictid bulla was formed by the petrosal, stated that it was an entotympanic one. McKenna's (1966, p. 12) recent views on the leptictid bulla and its implications concerning the bulla of primates are worth citing here since they closely pertain to the present discussion: "... in the Cretaceous the leptictid entotympanic may have been small and associated with the petrosal alone. It may have been cartilaginous rather than ossified. Prior to ossification, fusion of the entotympanic

cartilage may have simply given way to a descending wing of the petrosal. Ontogenetic evidence from lemurs and lorises favors the second alternative, so that it appears that a basic difference in mode of bulla formation between primates on the one hand and tupaiids and lepidictids on the other dates back at least to the beginning of the Tertiary." Essentially, McKenna suggested in this statement that a petrosal bulla was an ordinal character among the primates in the earliest Tertiary. However, he (1966, pp. 10–11) also considered the possibility that the ancestors of *Plesiadapis* had no "... fusion of the entotympanic to the petrosal or there was no outgrowth of a bulla from the petrosal, depending on the mode of origin of the primate bulla in the Paleocene."

No skulls or basicrania have been reported for any of the many genera of the diversified pre-Eocene prosimian primates, with the exception of the well-known single cranium of a very old individual of *Plesiadapis* from the late Paleocene. At present 17 genera of Paleocene and Cretaceous primates, belonging to five or six families, are known. Their dentitions undoubtedly reflect a broad adaptive difference and a common ancestry from insectivore origins. The adaptive shift of the earliest primates in the Cretaceous from their ancestors did not necessarily (most probably did not) involve all the modifications that came to characterize some Paleocene and latter prosimians. *Plesiadapis* was undoubtedly ecologically and adaptively (in a broad sense) as much of a primate as any of the recent prosimian genera, although it had fissured claws and lacked the characteristic postorbital bar and the enlarged neopallium of later primates. Similarly, the first varied groups of earliest prosimians, adaptively little different from their insectivorous ancestors, probably did not have the bulla construction that came to characterize later prosimians. The descending wing of the petrosal may or may not have been rudimentary in the earliest prosimians.

In addition to McKenna's (1966, pp. 10–11) doubts that the earliest prosimians possessed a petrosal bulla, the evidence derived from the only adequate specimen of *Plesiadapis* concerning the homology of the bulla is equivocal. There are contradictions in the

interpretations of D. E. Russell (1959 and 1964) and between Russell's views and McKenna's (1966) treatment of the same specimen.

D. E. Russell (1959, p. 312) wrote: "[The bullae] *dérivent seulement de l'os petreux. Il n'y a pas d'anneau tympanique mais l'ectotympanique forme un long tube osseux qui s'allonge derrière la surface glénoïdienne jusqu'à l'extérieur du crâne. Il est recouvert partiellement par un petit processus post-glenoïdien et, à son tour, remonte sur le processus mastoïdien.*" In 1964 (pp. 93–95) Russell gave a different interpretation: "... *il semble que seuls l'ecto- et l'ento-tympanique participent à sa constitution . . . L'anneau tympanique de Plesiadapis n'est pas libre, mais complètement soudé; il entoure presque l'extrémité médiane du long conduit auditif osseux constitué par l'ectotympanique. Sa présence fonctionnelle est nettement indiquée par la crête annulaire que présente la paroi interne du mur latéral de la bulle. Le long du bord ventral de S_4 et perpendiculairement à lui, s'attachent 3 ou 4 parois servant de contreforts entre le rebord annulaire et la bulle. Il n'est pas possible de savoir si le reste de la bulle, du côté médian était formé par une ossification entotympanique indépendante.*"

Russell (1964, p. 99) further wrote: "*Les sutures unissant la bulle au mastoïde, et celui-ci au squamosal, sont complètement fusionnés. Toutefois, parmi les os avoisinant ventralement le tube auditif, on peut reconnaître le squamosal qui, sous sa forme d'apophyse post-glenoïde, surmonte ce tube, surmontant lui-même à son tour le mastoïde. Ce dernier contact peut être suivi jusqu'au trou stylo-mastoïdien, ou il disparaît. De l'autre côté du trou stylo-mastoïdien, la fente suture audessus du canal de la carotide interne correspond peut-être au point d'union de la bulle et du mastoïde, mais aucune suture ne le prouve.*"

McKenna (1966, p. 10), however, stated: "... *Plesiadapis* has an auditory bulla, in fully grown individuals apparently composed of an ossification completely continuous with the petrosal—a characteristic of all known adult primates. It is not known whether this bulla represents entotympanic-petrosal fusion; if we judge from late ontogenetic stages of lemurs . . . , it probably does not. The bulla of *Plesiadapis* is continued laterally by a long osseous meatus . . . which

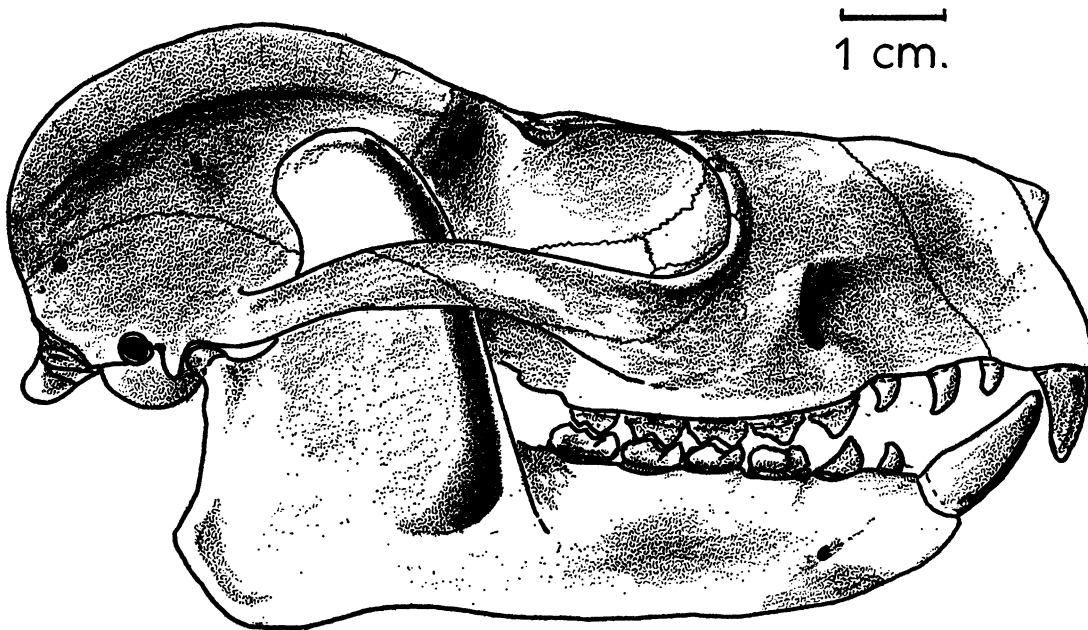


FIG. 23. Reconstruction of the skull of *Microsyops lundeliusi*.

Russell interprets as an expanded tympanic ring. The relationship of the tympanic ring to the main part of the bulla of *Plesiadapis* thus bears a certain resemblance to various non-primates and, among primates, it bears a greater resemblance to tarsioids, catarrhines, and lorisoids than to lemuroids." McKenna's (1966, fig. 3) diagrammatic illustration of the plesiadapid bulla can be taken as ambiguous. The non-ectotympanic portion, the homology of which, in my opinion, is still possibly unsolved, is illustrated as a ventral extension of the petrosal. This structure is stippled, but stippling on McKenna's figures applied both to the entotympanic and the petrosal. The eutherian entotympanic is a *de novo* cartilage bone in the known members of the infraclass and it is, as far as known from embryological evidence, independent of the petrosal.

Judged from the published evidence based on the skull of the very old individual of *Plesiadapis*, there are three possible alternate explanations for the non-ectotympanic part of the plesiadapid bulla: 1. It is composed only of the entotympanic which is fused to the petrosal as it occurs in very old individuals of tupaids (see Van Valen, 1965a, p. 144). 2. It is formed by the entotympanic and a flange of the petrosal, which fused either

early or late in ontogeny or in the adult individual. 3. The bulla medial to the ectotympanic is completely formed by the petrosal, with no trace of an entotympanic. The last explanation is the most likely.

Very little is known of the construction of the bulla among the early Tertiary erinaceoids. The earliest known erinaceoid skull with an intact ear region (S.D.S.M. No. 4048) is from the Whitneyan of South Dakota. The relatively huge bullae are formed by the petrosal, the alisphenoid, and the basisphenoid—a discovery made by M. C. McKenna (personal communication) and confirmed by subsequent observations of my own. If this bulla construction is primitive for the earliest erinaceoids recognizable from the dentition (a not very likely possibility), erinaceoids (excluding leptacids from this descriptive but in the present usage not formally taxonomic category) could be ruled out from the ancestry of primates. Any further speculation on this point, however, is useless, until erinaceoid skulls at least as old as the late Cretaceous or Paleocene are found.

A brief discussion of the homologies of dermopter and rodent bullae may be helpful here, because they may throw indirect light on the microsyopid as well as the pri-

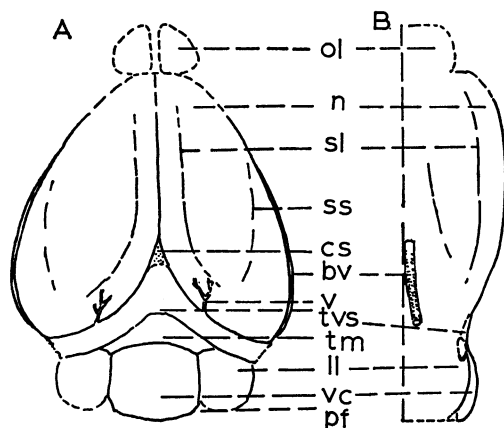


FIG. 24. Endocranial cast based on *Microsyops lundeliusi*, A.M.N.H. No. 55284, and *Microsyops annectens*, A.M.N.H. No. 12595, lateral view. A. Dorsal. B. Lateral view. Compare plate 41, figures 4, 5.

Abbreviations: bv, blood vessel; cs, confluens sinuum; ll, lateral lobe; n, neopallium; ol, olfactory lobe; pf, paramedian fissure; sl, sulcus lateralis; ss, sulcus suprasylvianus; tm, tectum mesencephali; tvs, transverse sinus; v, vein (leads into transverse sinus); vc, vermis cerebelli.

mitive primate bulla, thus adding further to the accumulating information on this aspect of the skull in the earliest prosimians.

Van der Klaauw (1931, p. 35) said of the dermopterian bulla that it was anteriorly fused with the squamosal, posteriorly with the mastoid and in older individuals with the exoccipital, and that the external auditory tube also fused with the neighboring elements. I have verified these various fusions in adults (U.S.N.M. Nos. 122766 and 239191). Van Kampen (1905, pp. 462-463), following the embryological studies of Parker (1885), showed that the dermopterian bulla was composed exclusively of the ectotympanic. Parker (1885, p. 252) had described the auditory region pertinent to this discussion in an embryo of *Galeopithecus volans*, 5.5 inches in length, as follows: "The annulus is very instructively imperfect with the next stage (fig. 4) where it already forms a vertical opening or slit with bony lips. Here (fig. 1) it lies under the tegmen tympani as a shallow saucer-like bone, projecting in front, binding its hinder and front crura inside the squamosal, and developing a rudiment from the hind crus which will become the hinder and lower part of the

vertical bony meatus." In older embryos, as Parker's detailed figures showed, the tympanic ring sends out the auditory tube, thus apparently indicating that the bulla is wholly ectotympanic, without a trace of any role played by the entotympanic.

McKenna (1961) and A. E. Wood (1962, p. 245) have suggested that rodents were derived from plesiadapids. That the actual ancestors of the first rodents were plesiadapids is not proved, and such ancestry is unlikely. Not only are the homologies of the bullae distinct, but the known paramyid rodent ear region is more primitive than the ear region of *Plesiadapis*.

A. E. Wood (1962, p. 245) discussed the condition, but not the homology, of the bulla in paramyids, the earliest and most primitive family of rodents, and noted that the bulla was not fused to the skull in the earliest forms but that it became co-ossified with the cranium in the later forms. Dawson (1961, p. 5, pl. 2) referred to the loose bulla of the middle Eocene sciuravid *Sciuravus* as a tympanic bulla, probably meaning an ectotympanic one. Van Kampen (1905, p. 553) clearly stated that, in all recent rodents (and also in lagomorphs), the ectotympanic invariably forms the bulla, and the entotympanic, which is not present, or any other element does not enter into the formation of the auditory bulla.

In conclusion, the ear region of the late Paleocene *Plesiadapis* bears a greater similarity to that of notharctines and adapines than to that of *Microsyops*. The anatomy of the ear region in *Microsyops* is the major obstacle to an unquestioned allocation of microsyopids to the Primates. The ear region of *Microsyops* may be regarded, until proved otherwise, as very primitive, and close to and easily derivable from the ear region of the presently unknown primate ancestors.

POSTCRANIAL REMAINS OF MICROSYOPIDS

It is almost certain that many specimens of postcranial remains of microsyopids are scattered in various early Tertiary collections in North American museums. The lack of association with dental remains of virtually all but one specimen of a tibia (see below) renders microsyopid postcranial osteology almost

completely unknown. Although microsyopids are among the more abundant fossils in rocks of Wasatchian and Bridgerian age, there are no other undoubted skeletal remains which, with reasonable certainty, can be accepted as having belonged to a microsyopid.

A.M.N.H. No. 17493 from the upper Huerfano Formation includes specimens of the proximal third of a right tibia, a left astragalus, and about nine badly fractured vertebrae in "museum-association" with the mandible that can be identified as *Microsyops lundeliusi*. A brief comparison with Huerfano species of similar size quickly revealed that the postcranial material represented specimens of the hyaenodontid *Sinopa*.

A.M.N.H. No. 19197 consists of an excellently preserved calcaneum from the B₂ horizon of the Grizzly Buttes locality in the Bridger Formation, catalogued with a mandible of *Microsyops elegans*. The calcaneum almost certainly belongs to a paramyid rodent, not to *Microsyops*.

U.S.N.M. No. 13440 from the lower beds of the Bridger Formation is a tibia (see pl. 47, figs. 1-5) probably correctly associated with recognizable fragments of upper teeth of *Microsyops elegans*. Approximately two-thirds of the tibia is preserved. The most striking feature of this bone is the considerable mediolateral flattening of the entire shaft. Although some of the flatness is due to crushing, most of it was natural for the specimen. On the proximal surface, the outer articular facet, the outer tuberosity, and the facet for the fibula have been sheared off. On the medial side of the proximal end, the inner articular facet and the inner tuberosity are slightly below the level of the outer tuberosity. There is only a lateral spine of the tibia on its proximal end; this structure, however, is large and bulbous. On the posterior and somewhat medial part of the proximal surface and slightly posterolateral to the outer articular surface, there is a distinct concave surface, possibly an area of attachment for the posterior crucial ligament. The anterior border of the tibia is clearly defined by the continuous crest which runs distally from a point shortly distal to the proximal end. The fracture of the lateral part of the proximal end prevents any inter-

pretation of the nature of articulation of the fibula with the tibia. The proximal half of the tibia is considerably wider than what is seen of its distal half—the usual condition of the mammalian tibia.

Although the fragment of the head of an ulna is probably correctly associated with a Bridger specimen (exact locality is not known) of *Microsyops*, A.M.N.H. No. 11441, it is neither described nor figured here. Even on the family level, this poor specimen is not adequate for meaningful comparison with other groups within its approximate size range.

TOOTH OCCLUSION

The upper molars of the early species of *Microsyops* are slightly less complicated than those of mixodectids, and the lower teeth, with the exception of the less tall metaconid than that seen in mixodectids, are essentially similarly constructed. In spite of the obvious differences of the *Gestalt* of the components of the individual teeth, which clearly reflect the differences between the two families, the wear facets, although not the shearing mode, are essentially similar in the two families.

As a point of interest it may be noted that the slightly anteroposterior shear between the poorly developed paracristid on P₄ and the homologue of the centrocrista on the small, triangular P₃, as the occlusion was in the oldest species of the known *Microsyops* lineage, did not change. As P₄ became gradually more molariform through the phylogenetic history of the genus the triangular P₃ did not change. In spite of the progressively more molarized fourth premolars, P₃ remained uninfluenced. The structure of the third premolars remained essentially the same from the late early Wasatchian *M. angustidens* to the late middle Bridgerian *M. annectens*, although only lower P₃ are known with certainty in either of the two species of *Microsyops* from the Bridger Formation.

NOTES ON MASTICATION IN MICROSYOPIDS

Remarks made on microsyopid mastication are necessarily incomplete. The evidence is spotty, and the available specimens leave a great deal to be desired. As noted above,

the microsyopid skull lacks a paroccipital process, and the digastric may therefore have originated from the area medial to the fossa on the ventral surface of the petromastoid. The glenoid fossa is not really a fossa but rather a flat articular surface that allows ample room for anterior, lateral, and medial movement of the mandibular condyle. The morphology of the glenoid fossa seems to indicate that there was much ectental motion of the mandibles.

Several lines of observation indicate that the microsyopid mandibular symphysis was mobile during chewing. No known specimens show the mandibles co-ossified at the symphysis. The wear described on the medial surface of the enlarged lower incisor clearly indicated a mobile symphysis.

There is no reliable evidence that enables the determination of the exact mode of mastication in microsyopids. Quite apart from the possible grasping function of the incisors, mastication by the molar teeth was either prolonged for a certain period of time on one side and then shifted and prolonged on the other side, or the chewing cycle consisted of one buccal excursion on one side and then one on the opposite side. The combined but probably not exactly synchronous action of the temporalis and the masseter complex resulted in the pulling back and forth of the right mandibular tooth row across the surface of the maxillary teeth. As the right mandible moved to the right side and upward, motion occurred at the mandibular symphysis. Probably both a separation of the two rami and a rotation of one incisor on the medial surface of the other occurred at that time. The fact that rotation of the incisors on their medial surfaces did occur seems to be attested by the even and continuous shiny wear facet on the medial side of the incisor of *M. lundeliusi*, A.M.N.H. No. 55285. This rotation occurred as a result of the pulling to the right and up of the right mandible (or the left one in the reversed situation), so that the medial surface of the right incisor moved slightly forward (to the right in an anterior direction) and upward in relation to the left incisor. The lower incisors, in order to be in occlusal contact with the upper ones, had to extend farther forward and more ventrally than during the occlusal contact of the molars.

There is no evidence from the wear facets of *Microsyops* that there was any purely propalinal mastication during this forward phase when the lower incisors were brought forward. It is probable that, when that occurred, the mandibular rami were slightly lowered and were brought close to the skull. Unfortunately there is not one mandible on which the angle is uncrushed or intact. There is no way to determine the relative importance of the pterygoid musculature, crucial in the execution of orthal and propalinal mandibular movements.

There is little doubt that the first three of the microsyopid upper premolars and the second and third lower ones served for anchorage of food and not for slicing or any form of chewing. The anterior upper premolars are raised distinctly above the level of the fourth premolars when the upper and lower fourth premolars and molars are in occlusal contact.

From the movable microsyopid mandibular symphysis and the supposed economy of the two alternative modes of mastication suggested above, it is most likely that these mammals chewed on one side for considerable periods of time before changing to the other. This particular mode of mastication is not unusual. Studies on the mastication of the rabbit by Ardran, Kemp, and Ride (1958) and on the kangaroo by Ride (1959) showed that these mammals chewed on one side for long periods of time. Both the rabbits and the kangaroos have a movable symphysis which I believe is probably correlated with prolonged chewing on one side at a time. Extended chewing on either side by anisognathus mammals with a solidly fused mandibular symphysis may put severe strain on the opposite dentary squamosal joint. Because of this stress, various resulting malfunctions of the condylar joint would be selected against in favor of individuals with a mobile mandibular symphysis. In addition to the general hypothesis of Scapino (1965), who rather clearly demonstrated the importance of symphyseal movement in *Canis* and showed that a loose symphysis allows contact between lower and upper molars of one side of an anisognathus skull, I believe that prolonged mastication on one side of the skull may also put a selective premium on

an unfused symphysis, provided that unusual strength at the mandibular symphysis does not have greater selective value.

I could find no living species of mammals with sufficiently similar incisors that would have allowed a reliable analogy of function with *Microsyops* except maybe for several marsupial phalangers. Although direct analogies cannot be drawn because of the lack of studies on their mastication, some comparisons with macropodids, which have morphologically somewhat similar, although functionally probably quite different, lower incisors, can yield, by contrast, valuable information.

The enlarged lower incisor of the gray kangaroo superficially resembles that of *Microsyops*. The kangaroo incisor, however, extends out horizontally from the mandible, whereas in *Microsyops* the incisor forms an angle of about 130 degrees with the horizontal ramus. In contrast to the incisor of *Microsyops*, that of kangaroos is heavily and evenly worn¹ on its superior surface. This wear on the kangaroo incisor is due to a cropping of vegetation between the lower incisors and the elongate, transversely constricted, sharp upper incisors. Ride (1959), using cinematographic and cineradiographic techniques, has convincingly demonstrated in the wallaby *Protemnodon rufogrisea* that the mandibles are loose at the mandibular symphysis during chewing and has shown the manner in which this is accomplished. In the resting position the lower incisors are pressed together and lie between the upper incisors. When the animal bites off grass cineradiographs reveal that there is wide separation of the lower incisors. Ride (p. 37) suggested: "It appears that when the animal has its mandible forward in the grasping position the incisors are invariably separated to some extent, and that the degree of separation is affected by the hardness of the food. When carrot was fed to the animal a wider separation of these incisors occurred than when leaves were taken. This observation introduces the possibility that separation is produced mechanically by the effect

of the direct pressure of the food on the incisors and not by muscular action." Ride concluded (p. 38) that incisor separation in the wallaby occurs during biting, which seems to occur when the lower and upper incisors close onto the food. His figure 1 shows that the separation of the lower incisors is symmetrical, a synchronous lateral rotation of both mandibles at the symphysis.

Although the lower incisors in *Microsyops* were posterior to and between the enlarged upper incisors when the mandibles were in a central resting position, the upper and lower incisors could be brought to apex-to-apex contact only when the lower jaw was moved forward, similar to the condition of incisor contact in most rodents. The incisors of microsyopids, however, unlike those of rodents, are not subjected to heavy wear, a fact that suggests a relatively soft fruit or herbaceous diet.

It may be appropriate to point out here that all Paleocene primate mandibles known to me that have the symphyseal region preserved indicate the presence of a loose and mobile symphysis. This is clearly the primitive condition for both eutherians and metatherians.

TRENDS IN MICROSYOPIDS

The specimens of *Microsyops* from the various Eocene localities afford a unique opportunity for studying minor evolutionary changes and their cumulative result in time. There is little doubt that most of the known species of *Microsyops* are the result of phyletic evolution from the earliest Wasatchian species recognized in North America.

The observed continuum of one sample of *Microsyops* to the next in time renders the taxonomy on the species level extremely difficult. With the exception of a few instances, which warrant special mention below, most of the taxa designated as species are really stages in the evolution of a lineage. Taxonomically, however, the time separating the various samples and the resulting size and minor morphological changes qualify as taxonomic boundaries.

As noted above, almost invariably the taxonomic criteria for the defined species of *Microsyops* are largely quantitative and involve the occurrence of minor features such

¹ Although relatively few complete lower incisors of *Microsyops* are known, some slightly worn ones are associated with heavily worn molars.

as the relative development of the talonid or the metaconid on P_4 or the mesostyle on the upper molars, the qualitative features themselves having a statistical occurrence in the larger samples examined. The results of this phyletic evolution, of course, are quite clear when we look at samples separated by relatively long periods of time, such as *M. wilsoni*

and *M. scottianus*; then the distinction becomes obvious. Were several intermediate samples not known that clearly connect the latter two species, they would be put in different genera.

Microsyops also includes species that represent a relatively distinct branching off from the previous lineage. *Microsyops lunde-*

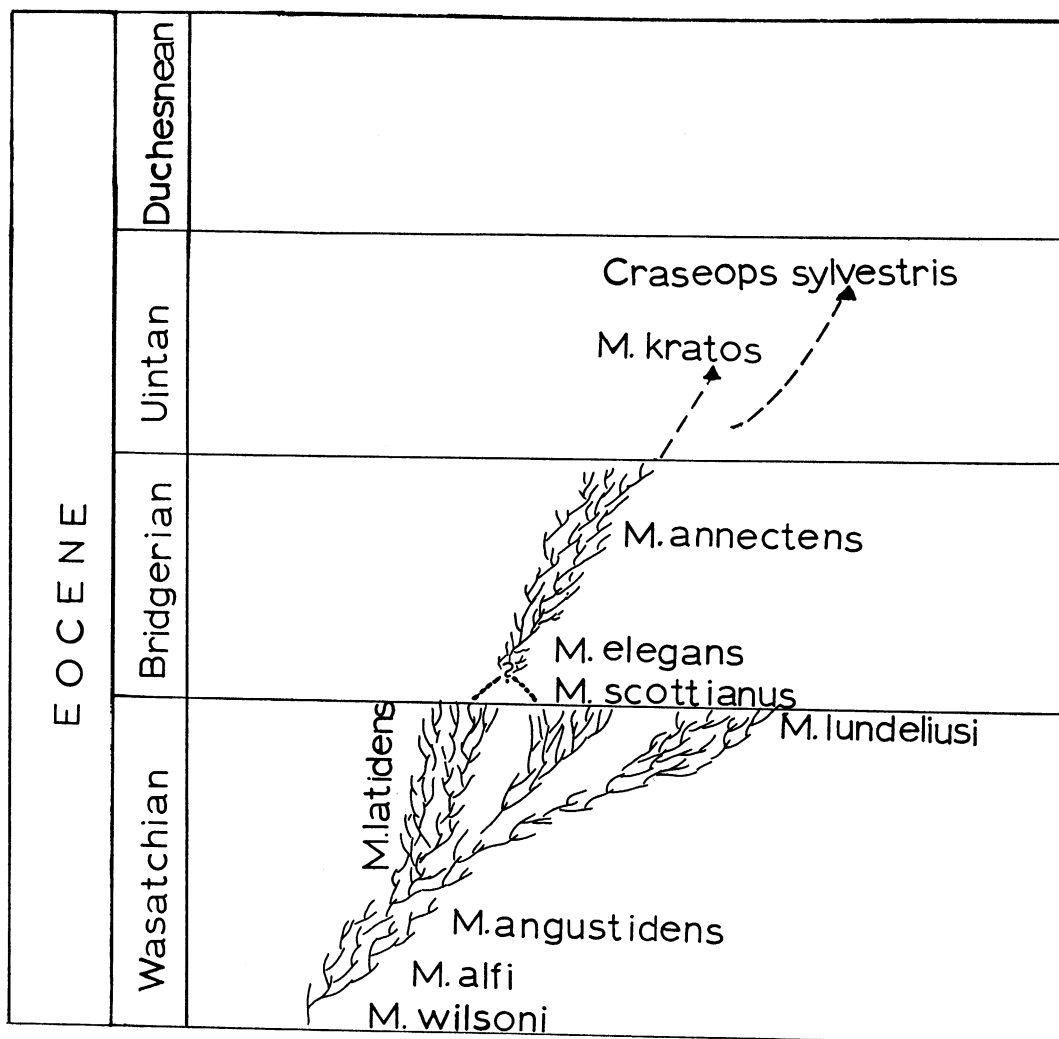


FIG. 25. An interpretation of microsyopid evolution during the North American Eocene. The "bushlike" phylogeny of the relatively better-known taxa depicts the probably undecipherable minor changes that occurred in the numerous successive populations of the Wasatchian and Bridgerian representatives. In the case of relatively very poorly known species such as the early Uintan *Microsyops kratos* and the late Uintan *Craseops sylvestris*, probable derivation is indicated by a broken line. Although the derivation of the early Bridgerian *Microsyops elegans* from *M. latidens* is likely, this is not sufficiently probable to preclude origins from *M. scottianus*. A gradual shift of the microsyopid phylogeny from left to right of the figure depicts the relative degree of size increase. The known change in morphology cannot be expressed satisfactorily by a similar graphic device.

liusi is distinct from *M. scottianus*, in addition to being larger, by having much bulkier, heavier dentition, a feature that probably points to a larger, bulkier animal. As noted elsewhere, it is likely that both the contemporaneous *M. lundeliusi* and *M. scottianus* speciated from *M. latidens*.

Instructive details can be learned about *Microsyops* in particular and tooth evolution in general if we follow the details of the evolution of the fourth premolar, the tooth that has undergone the most fundamental known change in the evolution of *Microsyops*. We can examine these changes in detail (see table 20 for a brief summary) and attempt to correlate the appearance and relative development of the various features of the lower and upper fourth premolars. Following an examination of the changes in the history of the fourth premolars, the remaining elements of the dentition are also reviewed in terms of phyletic changes.

The metacone appears as an incipient structure on P_4 of *M. alfi* and *M. angustidens*, and in the younger species of the genus it is consistently present and increases in size. The paraconule first appears in *M. latidens*; it is most strongly manifest on *M. elegans*. The metaconule also first appears in *M. latidens*, although it is much less pronounced there than the paraconule.

The paraconid of P_4 is absent from *M. wilsoni*, absent from, to weak in, *M. alfi* and *M. angustidens*, and persistently present and consistently weak in *M. latidens*, *M. scottianus*, *M. lundeliusi*, *M. elegans*, and *M. annectens*. In the only known specimen of *M. kratos* there is only a weak paracristid and no paraconid. There are no known fourth premolars in *Craseops*.

The metaconid of P_4 is completely absent from *M. wilsoni*, but it has a moderate expression in *M. alfi*. Individuals almost certainly of *M. angustidens* show a range of expression of this cusp from its complete absence to a moderate development. It remains moderate in *M. latidens* but becomes larger and subequal in both *M. scottianus* and *M. lundeliusi*. In both Bridger species the metaconid remains large, but in the Uintan *M. kratos* it is moderate. It is distinctly smaller than the protoconid (based on one specimen).

On the talonid of P_4 of *M. wilsoni* none of

the usual cusps is distinct, and the talonid (as well as the whole tooth) is designated as premolariform. In *M. alfi* the hypoconid is distinct on one specimen, and at that stage the premolar is designated as premolariform-semimolariform. The talonid of *M. angustidens* displays a condition similar to that in *M. alfi*, but, as an additional feature, the entoconid tends to be faintly manifested in the former. The term chosen to describe this condition is semimolariform. In some specimens of *M. latidens* all three of the principal cusps of the talonid are distinct, and the general condition of the tooth is designated as semimolariform-molariform. *Microsyops scottianus*, *M. lundeliusi*, *M. elegans*, and *M. annectens* have a molariform fourth premolar. *Microsyops kratos* (which may prove to be generically distinct from *Microsyops*, when the upper teeth become known) has a very poorly defined hypoconulid. The only known P_4 may represent a deciduous tooth.

The mesostyle first appears on the upper molars of *M. latidens*. It has a broad range of expression in the Lysite and La Barge samples of the species; weak to moderate forms of this structure appear in both samples. In all younger than middle Wasatchian species of the genus the mesostyle is present, although in no case is it very strong. In the Sespe *Craseops* there is an enormous development of the mesostyle, and, strongly correlated with this enlargement, the styler shelf is secondarily greatly enlarged, and the paracrista and metacrista are strikingly elongated. In retrospect, after studying *Craseops*, I believe that *M. annectens* foreshadows these features.

In *Craseops* the metaconule is virtually lost, and the paraconule crista is almost completely reduced. In general, the buccal half of the upper molar of *Craseops* has considerably broadened anteroposteriorly in comparison with that of *Microsyops*.

There seem to be no major changes in the structure of the enlarged lower incisor, but the number of specimens in which it is known is very limited. It is possible that the incisors illustrated on plate 33, figures 3, 4, are not correctly allocated to *M. alfi*, i.e., to *Microsyops*. The incisors figured (and other similar ones from Four Mile localities) resemble very closely, however, homologous teeth of later species, with one noticeable and significant

TABLE 20

OCCURRENCE OF VARIOUS FEATURES OF THE DENTITION IN *Microsyops*

(Numbers 1-8 represent a sequence in periods of time. 4 and 5 indicate that *M. latidens* persisted into the time interval in which *M. scottianus* and *M. lundeliusi* also existed. The molar mesostyle first appeared in *M. latidens* and persisted in all younger representatives of the genus.)

	Metacone	P ⁴ Paracone	Metaconule	Paraconid	P ₄ Metaconid	Talonid
1 <i>M. wilsoni</i>	Absent	Absent	Absent	Absent	Absent	Premolariform (no cusps distinct)
2 <i>M. alfi</i>	Incipient	Absent	Absent	Absent-weak	Weak-moderate	Premolariform to semimolariform (hypoconid)
3 <i>M. angustidens</i>	Present	Absent	Absent	Absent-weak	Moderate	Premolariform to semimolariform (hypoconid, occasional entoconid)
4, 5 <i>M. latidens</i>	Present	Present	Absent-weak	Weak	Moderate	Semimolariform
5 <i>M. scottianus</i>	Present	Present	Poorly known	Weak	Large	Molariform
5 <i>M. lundeliusi</i>	Present	Present	Absent-present	Weak	Large	Molariform
6 <i>M. elegans</i>	Present	Present	Present-strong	Weak	Large	Molariform
7 <i>M. annectens</i>	Present	Present	Absent-present	Weak	Large	Molariform
8 <i>M. kratos</i>	?	?	?	Absent	Moderate	Molariform

difference. The dorsal and posterior surface of the crown, which forms a shallow basin, is considerably more extensive. The crown of incisors from the Four Mile are relatively broader than incisors of undoubted microsyopids. A specimen from the upper Huerfano Formation, A.M.N.H. No. 55225, a right mandible of *M. latidens*, bears an enlarged incisor that also shows the extraordinarily broad-crowned condition seen on incisors from the Four Mile. The resemblance is striking, and it strengthens the allocation of these specimens, which are abundant in the Four Mile quarries.

If these specimens represent *Microsyops*, the following minor changes should be noted to characterize evolution in the enlarged lower incisor. The trend involved a general thickening and strengthening of the base of the incisor, a reduction in the extent of the superior crest of the tooth and, correlatively, a reduction of the broad basal part of the crown.

Even less can be said about the enlarged upper incisor because of the scarcity of specimens. This tooth is known in one specimen of *M. latidens* (pl. 36, figs. 5–8), in the type of *M. lundeliusi* (pl. 48, figs. 7, 8), and in the skull of the latter species (pl. 50, figs. 4, 5) from the upper Huerfano Formation. This incisor, although broad at the base of the crown and robustly rooted, tapers to a relatively fine point in the known specimen of *M. latidens* and in the skull of the large upper Huerfano *Microsyops*. As noted above (p. 264), the blunt and relatively low-crowned upper incisor of the type of *M. lundeliusi* (presumably correctly allocated to the type) from the Wind River Basin stands in sharp contrast to the condition seen in the upper Huerfano specimen. Accordingly doubt is expressed above (p. 267) that the large upper Huerfano sample is specifically the same as the type from the Boysen Reservoir area. Because the intraspecific variation in this tooth is not known, the problem cannot yet be solved.

The upper canine, although present, lost its importance as a canine; it is small, even slightly smaller than P^1 or P^2 . The canine, in essence, became incorporated in the anterior premolar row.

It is conceivable that the transversely con-

stricted anterior premolars evolved from the type of highly constricted narrow and long premolars seen in *Navajovius*. Because upper premolars are largely unknown among early *Microsyops*, the trends that may have occurred in these teeth cannot be described.

A general trend, established probably rather early in microsyopid evolution (probably before the beginning of the Eocene), was the establishment of the relatively greater importance of the area of incisivization than that of caninization. Specimens of *M. angustidens* already indicate the reduction of two pairs of lower incisors, the lower canine and the first lower premolar. It is fairly certain, when the lack of major change in the lower dentition as early as the early Wasatchian is considered, that the characteristic upper dentition of *Microsyops* had already evolved by that time.

One may speculate that the apparent lack of coordinated molarization of the lower and the upper fourth premolars is correlated with the asymmetrical and more drastic reduction of the lower than the upper dentition. For only two incisors lost from the upper dentition, the two incisors, the canine, and the premolar were eradicated from the lower one.

The explanation for the molarization of the microsyopid fourth premolars may be that competition with herbivores (rodents, if microsyopids were terrestrial; notharctines, if they were arboreal) of similar size placed a selective premium on a larger surface area for the whole dentition, which, in turn, was attained by the gradual molarization of the fourth premolars.

Text figure 26 shows that the plotted arithmetic mean of the length/mean posterior width of the various samples of M_2 of known microsyopids falls on a straight line. The value of b in $y = ax + b$ is zero for all practical purposes. This straight arithmetic plot strongly indicates that lineage allomorphy did not accompany size increase in the dentition; hence the data may be handled by the isometric form of the growth equation, $y = ax + b$. Owing to the inadequacy of most *Microsyops* samples, the possible allometry between the various species of the genus (species form allomorphy; see Simpson, 1953, p. 27) is not investigated here.

The evolution of *Microsyops kratos* presum-

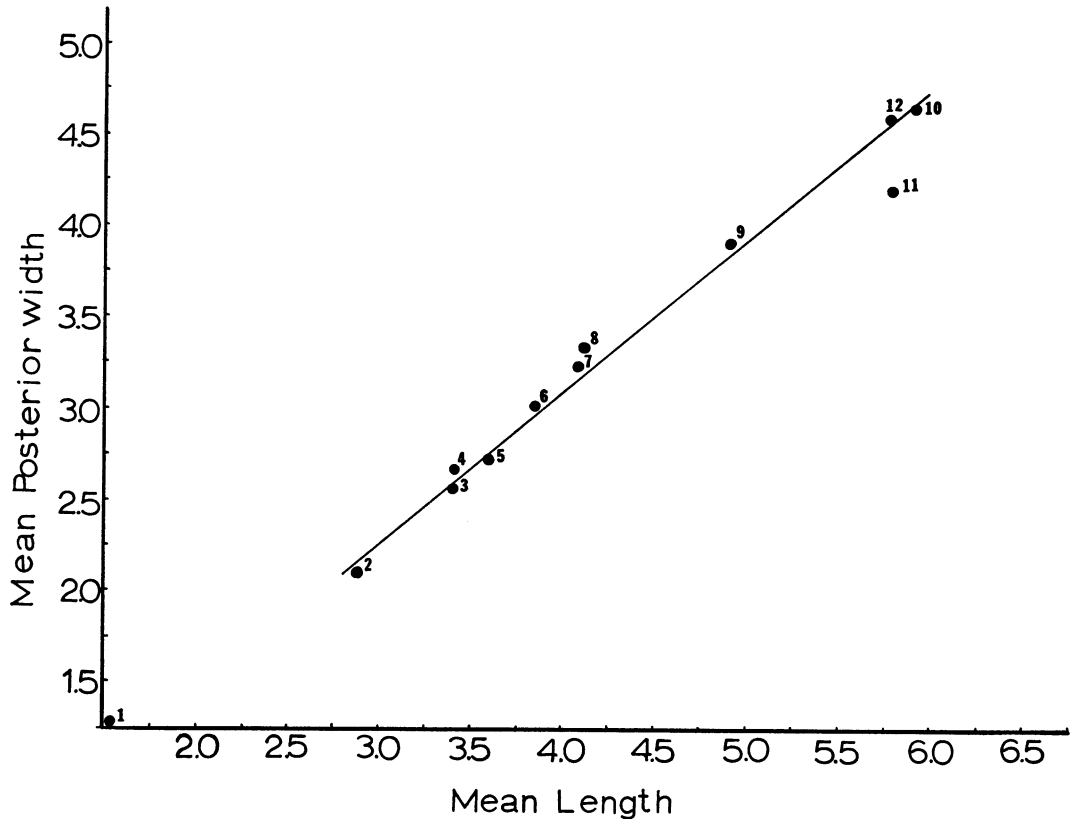


FIG. 26. The plotted arithmetic of the mean length/mean posterior width of various samples of M_2 of *Microsyops* and *Craseops* falls on a straight line. The value of b in $y=ax+b$ is approximately 0, which indicates that lineage allomorphosis did not take place with the obvious size increase. *Microsyops kratos* may be an exception, but the only known specimen of this species permits no conclusion.

Symbols: 1, *Navajovius kohlhaasae*; 2, *Microsyops wilsoni*; 3, *M. alfi*; 4, *M. angustidens*; 5, *M. latidens* from the Lysite fauna; 6, *M. latidens* from the La Barge fauna; 7, *M. elegans*; 8, *M. scottianus*; 9, *M. annectens*; 10, *M. lundeliusi*; 11, *M. kratos*; 12, *Craseops sylvestris*.

ably either from *M. elegans* or *M. annectens* may have involved changes in the length/posterior widths of the molars. Whether lineage allomorphosis took place in this particular segment of the lineage cannot be determined, because *M. kratos* is known from only one specimen and *M. annectens* also lacks an adequate sample. Number 11 on text figure 26 (representing *M. kratos*) is far off the slope of the growth line, possibly because the individual specimen plotted is well off the unknown mean value of the species.

DENTAL CONVERGENCE OF MICROSYOPIIDS AND CONTEMPORANEOUS ARTIODACTYLS

There is a remarkable degree of convergent

similarity between the upper and the lower molar structure of microsyopids and such common early artiodactyls as the Wasatchian *Diacodexis* and the Bridgerian *Homacodon* and *Sarcolemur*. The differences between these two distinct groups of Eocene mammals are listed in table 21.

The deceptive convergent feature that confused the identity of specimens from each group is the closely appressed entoconid and hypoconulid in both the microsyopids and the artiodactyls in question. The paraconid is reduced in somewhat the same way in both groups.

MICROSYOPIID AFFINITIES

The most puzzling and most important question concerning the relationships of mic-

rosyopids is: (a) is the family related to Paleocene primates such as *Plesiolestes*, *Palenochtha*, or *Purgatorius*; or (b) is it related to presently unknown but once probably existing Paleocene or Cretaceous primates distinct from paromomyids, plesiadapids, and carpolestids; or (c) did microsyopids evolve from some Cretaceous or Paleocene leptictids? Point (b) clearly cannot be discussed, as evidence is lacking. Although points (a) and (c) are not necessarily mutually exclusive, they are so treated, so as to form a working hypothesis.

The major morphological features of the leptictid and microsyopid ear region, as seen in the early Oligocene *Leptictis* (pl. 43) and in the late early Eocene *Microsyops* (pl. 42), are remarkably similar. Among the dentally rather diverse Paleocene and Eocene primates, skulls that show the ear region are known only in the late Paleocene *Plesiadapis*, the Eocene notharctines, adapines, and in the tarsiod *Tetonius*. The details of the comparisons, which are treated under the section dealing with comparative aspects of the microsyopid cranium, are not repeated here. The similarity of the ear region of *Microsyops* to that of *Leptictis* should not be overvalued, however, in deriving microsyopids from leptictids. The primitive late Cretaceous to early Paleocene leptictids and primates have not been collected, or they are unavailable, and, in particular, the homology of the microsyopid bulla is not known. The basicranium of the late Paleocene *Plesiadapis* is closer to that of *Notharctus*, *Adapis*, or *Pronycticebus* than to the more primitive ear region of *Microsyops*. It may be that the ear region of *Mic-*

rosyops represents a condition closely similar to the primitive primate ear region or is derived from it.

The dental evidence, particularly that derived from the earliest and most primitive Wasatchian sample of *Microsyops*, suggests that microsyopids are primates. The position of the recently described *Purgatorius* (Van Valen and Sloan, 1965) is briefly discussed under the section dealing with the Paromomyidae (p. 315). The genus is too early in time for meaningful comparison with even the earliest *Microsyops*. There is nothing in the known dental morphology of *Purgatorius* that would oppose the derivation of microsyopids, paromomyids, and *Purgatorius* from a common Cretaceous ancestor.

It may be significant to point out that in microsyopids, as they are known at present, premolariform P_4^1 are primitive. *Navajovius*, *Palenochtha*, *Palaechthon*, and *Paromomys* also possess premolariform fourth premolars. *Plesiolestes*, however, has a semimolariform-molariform P_4 . It must be emphasized that, in spite of the striking similarity of the primitive species of *Microsyops* to *Navajovius* and the similarity of both to primitive paromomyines, there is no evidence for a close abutment of the hypoconulid to the lingual entoconid in either paromomyids or *Navajovius*.

The enlarged premaxilla of *Microsyops* should not be taken as an indication of any relationship to plesiadapids. The enlargement of this bone is correlated with, and probably caused by, the enlargement of one or more incisors as in apatemyids, tillodonts, rodents, and tupaiids, in addition to microsyopids and plesiadapids.

TABLE 21

SYNOPTIC COMPARISON OF MICROSYOPIIDS AND SOME EOCENE ARTIODACTYLS

Microsyopids	Some Eocene Artiodactyls
P_3^3 not much elongated	P_3^3 characteristically very long anteroposteriorly
Mesostyle lacking in only primitive early Wasatchian species	Upper molars lacking a mesostyle
Paraconule and metaconule of molars smaller, less conspicuous than those of artiodactyls	Paraconule and metaconule of molars rather prominent compared with those of microsyopids
No trace of precingulid on lower teeth	Lower teeth usually having precingulid
Paraconid invariably lower than metaconid	Paraconid almost as high, or as high, as metaconid; paraconid invariably pressed very closely against metaconid

THE INSECTIVORE-PRIMATE TRANSITION

THE INSECTIVORE-PRIMATE TRANSITION and the taxonomic boundary have been referred to and in some cases briefly and vaguely discussed in the literature. In the following section I cannot hope to "solve" this interesting and important transition, because there are simply not enough facts, but I attempt to present those that are known in a framework that may generate further inquiry and elicit new information.

To discuss the insectivore-primate boundary, one is restricted mostly to known changes and inferred adaptations of dentitions and to the sparse evidence from the cranial anatomy. Many teeth, dentitions, and a few skulls of Cretaceous and early Tertiary insectivores and primates are the basis of the present evaluation. The only inferred evidence that is used relates to the dietary habits of some of the fossil forms. The inference is based largely on the vaguely consistent dietary habits of Recent primates.

It was clearly recognized by Simpson (1959c, p.268) that the most primitive known prosimians "... had acquired a rather vague but real grade distinction from the primitive insectivores." He also noted that this "... cannot be, or at least has not been, reduced to a precise diagnostic basis but it is such that most primitive primates can be readily recognized as such on a balance of their characters." Simpson (1955, pp. 436-439) himself, in discussing prosimian classification, had made penetrating comments on some aspects of this subject.

McKenna (1963b), in spite of the title of his study of Paleocene and Eocene apatemyids, did not specifically discuss the boundary. The same author in his 1966 paper on the origin of the primates, however, gave a relatively detailed examination of some characters (with emphasis on the origin of the bulla and changes in the carotid circulation) of virtually all the known groups of mammals that have immediate bearing on the insectivore-primate boundary. As all better-defined taxonomic boundaries of major categories are based on diagnosed morphological characters that reflect major morphological and adaptive differences, an attempt is made

here to delineate the earliest known primates from their taxonomically and presumably adaptively different insectivore ancestors. The very first major grade of primate evolution, which probably incorporates all known Cretaceous, Paleocene, some Eocene, and several Recent groups, is referred to as the prosimian grade,¹ briefly sketched by Simpson (1959c, p. 268).

NOTES ON SOME INSECTIVORA

It appears most probable that long, roughly transversely running paracrista and metacrista are primitive in the Metatheria and Eutheria. In the recently published lower Cretaceous therian *Pappotherium* (Slaughter, 1965) and in the Lance marsupials these features are obvious. These long and necessarily

¹ Simons (1962a, p. 24), in a generalized discussion of early Tertiary primate relationships, justified the use of the term "lemuroid" for all early prosimians as follows: "... it is surely valid to assume that the ancestral stocks of all the groups which have advanced beyond the lemur-like state (represented today by tupaiids and lemurs) went through such a level of advancement, and consequently their ancestors of the early Cenozoic can correctly be called lemuroid or lemur like." Although such a course has the merit of convenience for understanding early prosimians from the vantage point of the Recent, I cannot fully agree with Simons' descriptive characterization. With the exception of the Eocene notharctines and adapines that were truly lemur-like, the Paleocene and Eocene groups display characteristic peculiarities. The enlarged anterior teeth, the characteristic proportions of the facial and cerebral moieties of the skull, the relatively small brain, and the diagnostically modified dentitions of many groups of prosimians imply little of a lemur-like morphology. The lemuroids, which probably originated on the African continent in the pre-Eocene, are prosimians independent both phylogenetically (but from a common primate ancestry) and adaptively from the numerous families of primates of the early Tertiary. Although reference to all these families as prosimians or as primates of prosimian grade is valid, the term "lemuroid" is no substitute for the concept of a broad prosimian adaptive zone. The groups of the earliest major prosimian radiation in the Paleocene are more similar to one another than to lemuroids. The possibility that the ancestors of the anthropoid suborder may have passed through a somewhat lemur-like adaptive phase has little bearing on the diverse and abundant Paleocene groups. Even if the application of the term "lemur-like" to some "tarsioid" stock of the second major prosimian radiation in the Eocene is justifiable, it is not so to the more primitive groups in the Cretaceous, Paleocene, and Eocene.

transverse paracrista and metacrista are closely correlated with a very efficient transverse shear. Correlated with this feature of the upper molars is, of course, a rather transverse trigonid, relatively more so than the talonid, on which the paracristid and the protocristid are also wide and transverse. This sort of functional complex is undoubtedly primitive in the Eutheria also. In addition to the didelphodonts it is displayed quite clearly in certain primitive erinaceoids¹ such as *Leptacodon* and *Scenopagus*.

The upper fourth premolar of *Leptacodon*, *Scenopagus*, and *Geolabis* shows a strong centrocrista that sheared against the paracristid of the first lower molar. In the Cretaceous *Gypsonictops* the homologous upper tooth functions differently from that of the erinaceoids listed above. In addition to the lack of the posterobuccally sweeping centrocrista on P⁴, the paracrista and metacrista of *Gypsonictops* molars also differ from those of erinaceoids in their function; they more closely approximate the occlusion seen in leptictids and pantolestids. To regard *Gypsonictops* as a leptictid is much more meaningful than to regard it as an erinaceoid.

The upper molars of *Leptacodon tener*² (A.M.N.H. No. 17179) show a condition that must have been similar to the beginnings of the upper dentition of the earliest primates, or to that of the most immediate ancestors of the primates. The primate-like characters of *Leptacodon* consist of the metastyle, the strong paraconule and metaconule, the broad talonids, and the precingulid. But the tall and acute cusps and the primitive therian shear clearly distinguish *Leptacodon* from the earliest primates.

Evidence that relates to the basicranium of pre-Oligocene erinaceoids is completely lacking. M. C. McKenna (personal communication) brought to my attention the earliest known erinaceoid skull with an adequately preserved ear region (S.D.S.M. No. 4048), from the Whitneyan White River Oligocene

of South Dakota. The bulla of this specimen has components from the basisphenoid, alisphenoid, and petrosal, a condition different from the entotympanic bulla of known leptictids and tupaiids, and the presumably petrosal bulla of the known early Tertiary primate skulls.

The earliest known alleged leptictid is *Procerberus* Sloan and Van Valen (1965, pp. 6-7), placed in a monotypic subfamily. This genus, well represented from the Maestrichtian Bug Creek Anthills Quarry, is not, in my opinion, so central morphologically among the primitive groups of placentals as was stated by its authors. The weak and faintly constructed paraconule and metaconule of *Procerberus* may be not primitive but secondarily weakened. In *Gypsonictops* and undoubtedly early Tertiary leptictids³ the stylar shelf is greatly reduced, and there is no important transverse shear on the paracrista and metacrista. The latter characters are in important contrast to the primitive erinaceoid condition.

The earliest known pantolestids appear in the middle Paleocene. The pantolestine *Propaleosinopa* (including *Bessoecetor*; Van Valen, 1967) and the pentacodontine *Aphronorus*, as well as other genera, show a peculiar suite of characters that at first glance appears to have adaptive similarity to the known primitive prosimian dentition. The upper molars are not very wide transversely, and the cusps are low and tend to be, but are not completely, bulbous; there is a relatively strong hypocone. On the lower molars the trigonids are almost as low as those in most Paleocene paromomyids. The paraconids are strong, and the paracristid is angulate, as in the early prosimians. Pantolestids lack enlarged incisors and have strong canines (A.M.N.H. No. 12153). Paleocene and Eocene pantolestids, however, display a much heavier tooth wear (see, for example, specimens of *Aphronorus*, A.M.N.H. Nos. 35637, 35293, and specimens of *Pantolestes*) than is customarily found in

¹ Most of the post-Eocene erinaceoids are too advanced in many features to be considered primitive.

² The type of "*Mckennatherium libitum*" (Van Valen, 1965b), A.M.N.H. No. 35437, is a specimen of the erinaceoid *Leptacodon ladae* (Simpson, 1935) from the Torrejonian Gidley Quarry. *Leptacodon ladae* and *Leptacodon tener*, the genotype, although clearly separated by size, are congeneric.

³ For a succinct summary of the dental features of leptictids and some erinaceoids (geolabidines), see D. E. Russell (1964, pp. 44-45). The hypoconulid in some leptictids such as *Prodiacodon* transforms into several small cusps on the postcristid, a fact omitted by Russell. Whether these cusps represent the proliferation of the hypoconulid or entail new ones cannot be very important genetically.

Paleocene primates. Matthew (1909a, pp. 531–532), who noted the disposition of the *Pantolestes* teeth toward peculiar and heavy wear, remarked of the Bridger genus that this mammal may have been an aquatic form living on a mixed diet of fresh-water clams, fish, and turtles. It is most likely, then, that the superficially primate-like adaptations of pantolestids were, in effect, used for a fundamentally different mode of feeding than is postulated for the Cretaceous and Paleocene prosimians.

In addition to the primate-like families of insectivores, several genera, particularly from the European Paleocene, show primate-like adaptations in dentition. These genera, *Adunator* (leptictid), *Adapisorex* (probably leptictid-derived), and *Pagonomus* (pantolestid), were treated and illustrated by D. E. Russell (1964). The adaptations displayed by these genera are of interest because they probably reflect an independent change in the insectivorous diet in the respective families. The primate-like characters that appear to a greater or less degree in these genera are: (a) the reduced styler shelf; (b) relative to those of other genera of their respective families, the cusps are low and rather bulbous; (c) the paraconules and metaconules are strong, the trigonids are relatively low, and the upper teeth are not very wide transversely. In addition to the genera noted, the erinaceoid *Litolestes* also displays a very primate-like balance of characters.

THE APATEMYIDAE

The earliest probable apatemyid is an undescribed genus (U.K.M.N.H. No. 1410) from the Puerco of New Mexico (being studied by McKenna and others). The species represented by the specimen shows a tremendously enlarged and very procumbent anterior-most tooth and an equally procumbent but only slightly enlarged tooth behind it. The crown of the anterior incisor is broken off, but the posterolingual surface of the one following it is excavated in a fashion somewhat similar to that seen on the incisors of *Promothodectes* and *Plesiadapis*. Similarly, an undescribed Tiffanian apatemyid (P.U. No. 17465) shows probably the same two incisors enlarged in both the upper and lower dentitions. The rather strong shear against the paracrista and

metacrista of the molars of this specimen suggests independent insectivore origin for the apatemyids, as has already been stated by McKenna (1963b). As in primates, however, the anteroposteriorly oriented centrocrista can probably be correlated with the gently rounded buccal talonid wall of the occluding lower molar.

One of the most persistent differences that set apart even the earliest apatemyids from early prosimians is the peculiar, low and diminishing posterolingual part of the postcristid and the entocristid. This arrangement results in a relatively unimportant, reduced entoconid and a very indistinct talonid notch. Stated another way, the talonid is lingually wide open, a unique feature among possibly related groups. In addition to the peculiarity of the talonid, the trigonid on the first and second molars is longer and relatively wider than the talonid.

Although apatemyids are phylogenetically non-primates, they show remarkable trends that may resemble the insectivore-primate transition. From the Torrejonian *Jepsenella* through morphologically roughly intermediate forms to the Chadronian and Orellan *Sinclairiella* (for the extension of stratigraphic range of the genus, see Clemens, 1964) there is a striking reduction in the height of the trigonid and in the height of the cusps on both the upper and lower molars. From the *Jepsenella* to the *Sinclairiella* state the postvallid appears to change from a nearly vertical position to an anterolingually leaning condition.

THE TUPAIIDAE

Quite recently thorough studies have been made of the cranial morphology of *Tupaia* by Spatz (1964, 1966), and a comprehensive review of tupaiids was published by Van Valen (1965a) who has allocated the European Paleocene *Adapisoriculus* to the Tupaiidae. Van Valen also voiced the opinion that the tree shrews are not primates but an independent group of leptictid-like insectivores. McKenna (1966) has recently discussed aspects of tupaiid morphology in relation to the origin of Primates and concluded that the tupaiids are leptictid-like insectivores (*sensu lato*).

One of the greatest obstacles to a realistic evaluation of the controversial family is the

paucity of undoubted fossil tupaiids. *Adapisoriculus minimus* and *A.? germanicus* may or may not be tupaiids. I consider the Lutetian *Messelina* Tobien (1962, p.35), originally allocated to the Erinaceidae, as one of the most likely fossil tupaiid candidates. The lower teeth of *Messelina tenera* are at least as similar to tupaiid lowers as are those of *Adapisoriculus*. Also, the upper teeth of *Messelina* bear a much more striking resemblance to the unworn dentition of *Ptilocercus* (U.S.N.M. No. 311313) than do those of *Adapisoriculus* to the uppers of any of the Recent tupaiid species.

The dentition of the most primitive living tupaiid, *Ptilocercus*, does not greatly resemble that of primitive and early prosimians. The general lack of conules in tupaiids is rather striking in relation to the strong and bulbous ones of paromomyids, plesiadapids, carpoles-tids, and microsyopids. Campbell (1966) argued that the neuro-anatomy of Recent tupaiids can be correlated with their elaborate visual system, which can explain the tupaiid brain as a result of convergent evolution with that of primates. Another study on the Recent forms by Martin (1966) concluded that the unique reproductive anatomy of these mammals warranted ordinal separation of tupaiids from primates.

Recently Sorenson and Conaway (1964) published a rather thoroughly documented paper on the behavior of tree shrews in captivity. The four species studied (*Tupaia tana*, *T. longipes*, *T. gracilis*, and *T. minor*), in spite of the morphological (i.e., skeletal) similarity, showed marked behavioral differences. *Tupaia tana*, the largest species, is clearly set off from the other three by its size, by being exclusively a ground dweller (a very clumsy climber), and by being basically carnivorous. The other three species are excellent climbers and, although insects are in the diet of all, are basically frugivorous. *Tupaia tana*, on the other hand, showed a much greater preference for mice and canned horse meat than for the various fruits preferred by the other species.

It appears to me that in *T. tana* the clearly carnivorous feeding habit is a new behavioral modification which has not had its effect on the animal's morphology. The teeth of *Tupaia tana* are rather low-cusped, like those of the other tupaiids; the mandibular condyles

are high above the level of the tooth row, testifying to a herbivorous and frugivorous ancestry; and the temporal musculature is accordingly weak " . . . the mice are slowly masticated by the weak jaws" (Sorenson and Conaway, 1964, p. 83). The Sorenson and Conaway study illustrates the extremely important pre-adaptive nature of a behavioral change that may channel future morphological changes of the feeding and locomotor complexes of a species. Although tupaiids are, more likely than not, insectivores (*sensu lato*), they are capable of furnishing insights into some of the probable changes that canalized the separation of the earliest primates from their insectivore ancestry.

THE PAROMOMYIDAE

The paromomyids, with the plesiadapids, represent one of the best-known families of Paleocene primates and, in addition to *Teilhardina belgica*, are probably the most primitive of the known prosimians. A synoptic classification of the family, presented below, will aid the discussion and gives my present views of paromomyid classification based on the presumed affinity of the genera involved. My grouping is different from that of Van Valen and Sloan (1965). I agree with Van Valen and Sloan (1965) in following McKenna's (1960) reasoning and consequent rejection of Simpson's (1955) family name Phenacolemuridae.

Family Paromomyidae Simpson, 1940

Subfamily Paromomyinae Simpson, 1940

Tribe Paromomyini (Simpson, 1940), new rank

Paromomys

Phenacolemur

Palaechthonini, new tribe

Palaechthon

Palenochtha

Plesiolestes

?Family Paromomyidae

Subfamily Purgatorinae Van Valen and Sloan, 1965

Purgatorius

Purgatorius has recently been described by Van Valen and Sloan (1965). Through the courtesy of Drs. Van Valen and Sloan, all the original material and additional specimens of *Purgatorius* are illustrated here (pl. 57). It is virtually impossible to distinguish the only

Maestrichtian specimen, the type of *Purgatorius ceratops* (U.M. No. VP1547) from Harbicht Hill, from *Purgatorius unio* from the Puercan Purgatory Hill. The talonid of the Cretaceous species may be relatively narrower transversely than that of the Paleocene species, but such a difference is plainly impossible to confirm on the basis of one tooth. At present I follow Van Valen and Sloan (1965) in maintaining the two species, although the specific distinctness of *Purgatorius ceratops* from *P. unio* has yet to be proved.

Contrary to Van Valen and Sloan's (1965) allocation of *Purgatorius* to the Paromomyidae, I am reluctant to accept the latter family as a dumping ground for all early or primitive primates and question the validity of such a move. In comparison with the Palaechthonini (the more primitive tribe of the paromomyids), *Navajovius*, and the earliest *Microsyops*, the following features of *Purgatorius* appear to be distinct and presumably more primitive than those of other Paleocene and Eocene prosimians. The styler shelf is distinctly wider. The paracone and metacone are taller, less bulbous, and more acute. The paraconule and metaconule are less strong and less bulbous and consequently the cristae around these are more distinct. The trigonids are taller, and the metaconid and protoconid are slightly taller and less bulbous. The paraconid is not completely separable from the paracristid. The talonid is probably slightly narrower than the trigonid and is conspicuously narrower than the talonid in the Paromomyidae in general. The postvallid is more vertical.

Although *Purgatorius* may not be a paromomyid, the following characters of the genus (in addition to the total balance of the characters) seem to support its primate affinities. The cusps are relatively rather bulbous on both the upper and the lower molars; the metastyle is present on the metacrista; the protocone is characteristically displaced in an anterior direction, almost lingually aligned with the paracone; and M_3 is longer than M_2 . The relatively wide styler shelf of *Purgatorius* would be a uniquely primitive feature among early prosimians.

Since the hypodigm of *Purgatorius unio* consists of isolated teeth, no undoubted fourth premolars are known for the species.

If the allocations of P_4 by Van Valen and Sloan (1965) and P^4 in this paper (separated from the Purgatory Hill Quarry sample by Van Valen) are correct, then *Purgatorius* had premolariform fourth premolars. A more thorough knowledge of this important genus is needed.

All three genera referred to the Palaechthonini (*Palaechthon*, *Palenochtha*, and *Plesiolestes*) are Torrejonian in age. *Plesiolestes*, described by Jepsen (1930), is probably the most primitive undoubted paromomyid, but it is also the most poorly known.

The excellent collection of this genus at the Princeton Museum, recovered after the description of the type specimen in 1930, badly needs description, thorough illustration, and extensive comparison with *Purgatorius*, other paromomyids, *Pronothodectes*, picrodontids, *Navajovius*, and primitive *Microsyops*.

It may be noted here that *Plesiolestes* has a semimolariform-molariform lower fourth premolar; the trigonid of this tooth is not so fully developed as that of the following molar. Upper teeth of *Plesiolestes* are known but not yet described.

As stated above, the Palaechthonini give us the basis for an understanding of the dental features of Paleocene primates, closest in time to the unknown stem primates. The styler shelf has virtually disappeared from the Palaechthonini. The cusps on both upper and lower molars are low and bulbous. The paraconules and metaconules are large and bulbous, and the preparaconule and postparaconule and postmetaconule crista are indistinct in *Palaechthon* and *Palenochtha*. The hypocone and precingula and postcingula are present. A distinct metastyle is present on the metacrista. The enamel is slightly wrinkled on the teeth. The fourth premolar is variable from being premolariform to being semimolariform-molariform. P^4 has a small but distinct metacone. The hypoconulid on the lower molars is low and not very distinct. M_3 is longer than M_2 .

The Paromomyini, as understood here to include *Paromomys* and *Phenacolemur*, are more advanced in dentition than the Palaechthonini. The more advanced dentition of the Paromomyini involves a general trend to flatten and spread out the posterolingual area of the upper molars, a consequent ob-

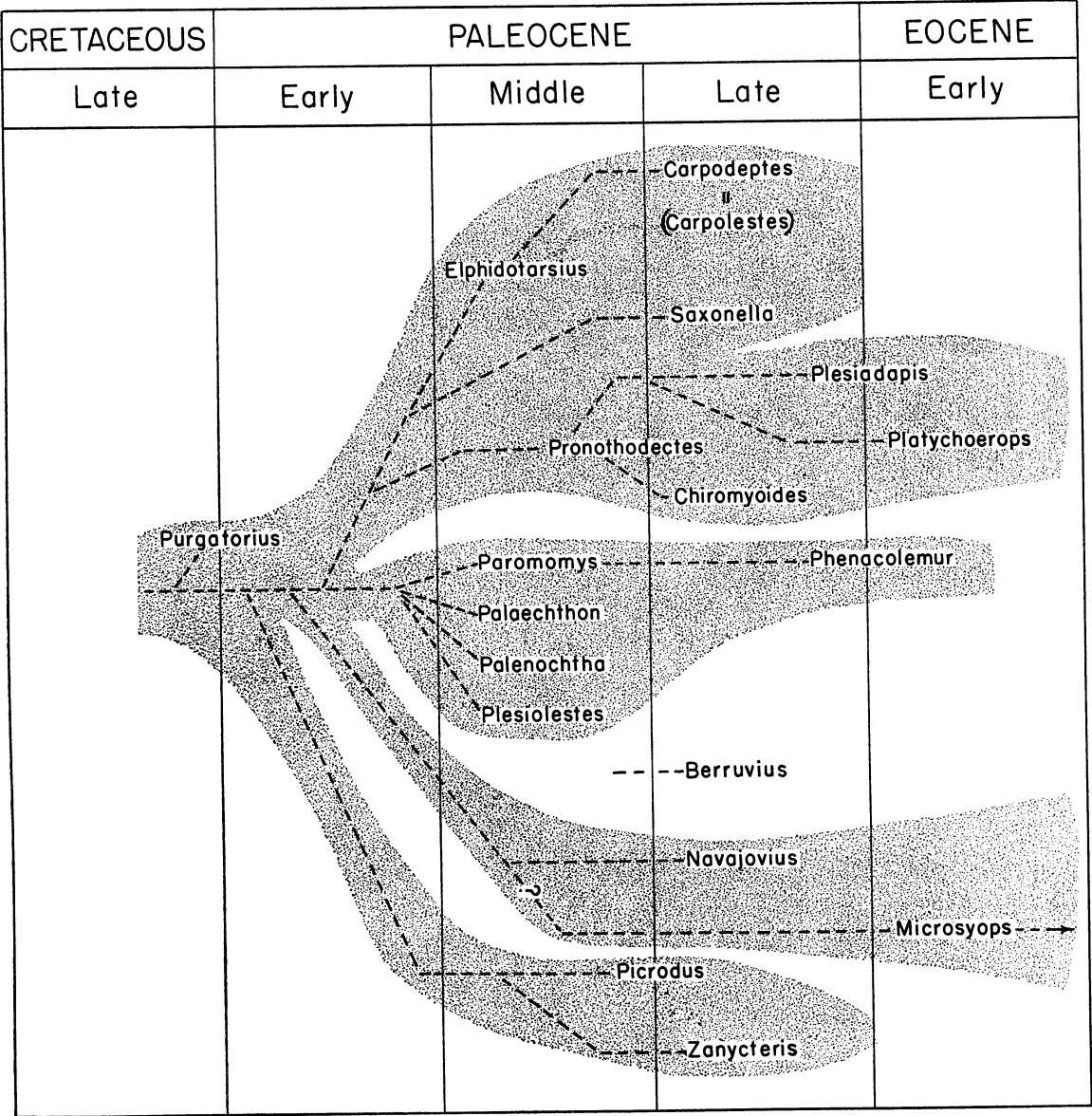


FIG. 27. Suggested interrelationship of genera of Paleocene primates. Although virtually all Eocene primates are omitted from the chart, a possible tie of *Microsyops* with paromomyid-like ancestors is suggested.

literation of the metaconule, and an extreme reduction in the number of premolars in *Phenacolemur*. Simpson's (1955) thoroughly documented study should be consulted on the latter two genera. Their further treatment is not pertinent here to an inquiry of primitive dental features of the earliest prosimians.

THE PLESIADAPIDAE AND CARPOLESTIDAE

The plesiadapids are the only Paleocene primates in which a skull is relatively well known (see D. E. Russell, 1959, 1964). The most primitive known member of the family is the Torrejonian and Tiffanian *Pronotho-*

dectes. In the Torrejonian this genus already possessed the single enlarged anterior lower tooth characteristic of the family. The molar structure of *Pronothodectes* (see excellent illustrations in Simpson, 1955) displays some very interesting general features, different from those of *Purgatorius* and known paromomyids. The protocone is relatively less displaced in an anterior direction to align lingually with the paracone than is the protocone of paromomyids and *Purgatorius*. The "non-skewed" character of the protocone also characterizes *Navajovius*, *Microsyops*, and *Saxonella*.

D. E. Russell (1964, pp. 129–130) noted the very close resemblance between the upper incisors of *Saxonella* and those of *Plesiadapis*, but dismissed it: "... *mais cette ressemblance s'étendrait probablement aux incisives supérieures des Phénacolemurides, des Omomyines ou des Anaptomorphines, si elles étaient connus.*" Considering the striking resemblance of the fourth premolar and the molars of *Saxonella* to those of *Pronothodectes*, I believe that this similarity¹ is more than convergence.

In spite of the structure of the highly specialized plagiaulacoid premolars, the carpolestines (*Elphidotarsius*, *Carpolestes*, and *Carpodectes*) have molars that indicate close origins from primates that were also ancestral to plesiadapids. Although Simpson (1937, p. 162) did not advocate very close ties between the carpolestids and plesiadapids, he wrote the following about *Elphidotarsius*: "... *M₂₋₃* are almost exactly like those of *Pronothodectes*, so much so that were this form known from those teeth alone it would have to be defined as a species of *Pronothodectes*." My studies confirm this point.

THE PICRODONTIDAE²

It was Simpson (1937) who first suggested that picrodontids might be primates. McGrew and Patterson (1962) did not, however, consider this probable. McKenna (personal communication), Van Valen (personal communication), and I (Szalay, 1968) have independently maintained that picro-

dontids are primates. The possibly paromomyid-derived picrodontids have upper molars adaptively roughly similar to those of *Phenacolemur* and strongly suggest a highly frugivorous diet. McGrew and Patterson (1962, p. 6) also supported the view that the exoedaenodont ("... the enamel at the base of the crown extends out far beyond the necks of the teeth...") teeth of picrodontids reflected a frugivorous diet.

The picrodontid dentition (no adequate skulls are known) is a very advanced and specialized one and does not show the primitive features of early primates. However, the peculiar picrodontid dentition illustrates the remarkable adaptive range that was already achieved among Paleocene prosimians.

Furthermore, it is of interest to note the avenues of extreme specialization among early prosimians. These various extreme expressions of the directions of adaptations suggest the general nature of the selection pressure that probably was responsible for the evolution of the earliest prosimians, i.e., the first major radiation of the primates. *Phenacolemur*, the carpolestids, and the picrodontids seem to demonstrate repeatedly the molding by major selection pressures of the prosimian feeding mechanism toward a frugivorous-omnivorous specialization.

ORDINAL CHARACTERS AND ANCESTRY OF EARLIEST PROSIMIANS

Any attempt to delineate the earliest prosimians from their adaptively similar and horizontally very close insectivore relatives is extremely difficult, if not impossible. The origin of most major taxa is rarely delimited from that of their adaptively similar (but in retrospect less successful) close relatives. The taxonomic difficulties in diagnosing all primates in a coherent order are virtually insurmountable at present. I have focused my attention therefore on the members of the first major prosimian radiation—species from the Cretaceous (one specimen is known), Paleocene, and the Eocene. Many of the features cited as indicative of these early prosimians necessarily apply to the adaptively similar primate-like insectivores and some of the primitive condylarths.

The presumed features that differentiated

¹ A similarity that has also been noted by L. Van Valen (personal communication).

² While the present paper was in press, my review of the Picrodontidae (Szalay, 1968) was published.

the adaptively insectivorous primate ancestors from the earliest prosimians are poorly known and restricted almost entirely to the dentition.

As the cusps are reduced in height, they become more bulbous, and correspondingly the conules also become accentuated. As a result of the reduction in cusp height the trigonid becomes relatively low. In the late Puercan and probably Maestrichtian *Purgatorius* the trigonid is, primitively, high. In the same genus there is a broader styler shelf than in any of the later primates. All known Paleocene primates, with the exception of *Purgatorius*, are characterized by the virtual absence of the styler shelf. The upper teeth of early primates are also much narrower transversely than, for example, those of leptictids. A shortening of the facial skull and a broadening of the zygomatic arches also appear to be primate features in comparison with the non-primate-like Insectivora of the Mesozoic and early Tertiary.

Of course, the independent evolution of several primate-like families of insectivores makes the taxonomic boundary difficult to delineate. If the record ever becomes well enough known to define the earliest primates from other groups on the basis of their time of appearance, then matters may become easier. Even with a better-known record, it is unlikely that horizontal classification can ever be discarded. Any attempt to impoverish an order such as the Primates from its early "side branches," to make it increasingly a vertical category, would be a distinctly non-biological taxonomic practice. In spite of the numerous remarks to the contrary in the literature (e.g., McGrew and Patterson, 1962), I prefer to allocate doubtful groups to the orders to which they are strongly suspected to belong and use those as meaningfully queried major categories rather than to overburden the already much-abused Insectivora. Thus, at present, I believe that *Purgatorius*, picrodontids, and microsypids (the latter doubtfully) are primates, whereas apatemyids and tupaiids are not. It is obvious that the freezing of taxonomic boundaries is not advocated here. On the contrary, a constantly renewed examination of taxonomic boundaries and their meaning should not stop as new discoveries come to light.

My study indicates that one of the following three groups may have been ancestral to the Primates during the latter part of the Cretaceous: (a) unknown stocks of leptictids, (b) erinaceoids, or (c) primitive condylarths.

Although the upper dentition of one of the early erinaceoids, *Leptacodon tener*, is rather primate-like, there is no conclusive evidence for erinaceoid derivation of the primates. Primates almost certainly did not originate from genera such as the Cretaceous *Procerberus*. That genus was claimed to be central, in morphology, for many orders, including the primates (Sloan and Van Valen, 1965). In my opinion, this peculiar and unusual leptictid has no bearing, or only an indirect one, on primate (and condylarth) origins. The almost complete lack of a paraconule and metaconule on the upper molars shows an adaptive trend completely opposite to the accentuated, bulbous conules of the earliest prosimians. It is conceivable, however, that other leptictids will prove to be very revealing as to primate origins.

A possible origin for primates from arctocyonids was indicated by Van Valen (1966, fig. 16). *Protungulatum*, the first Cretaceous ungulate (a probable arctocyonid; see Sloan and Van Valen, 1965), and the early prosimians share many morphological and functional similarities in dentition. The reduced styler shelf, the virtual absence of the paracrista and the metacrista, and the rather low and somewhat bulbous cusps characterize the beginning of both condylarths and primates. The repeated occurrence of fascinating cases of convergence during the early Tertiary between various groups of the two orders may rest partly on genetic ties in the Cretaceous that are closer than suspected. In spite of their similarities, however, even the earliest and most primitive known taxa can be easily recognized as either primates or condylarths on the total balance of their characters.

SELECTION AND THE INSECTIVORE-PRIMATE TRANSITION

Following the above examination, the question naturally arises: What were the selective forces operating on the ancestors of primates that resulted in the adaptations of the earliest prosimians?

The following discussion attempts to outline an explanation for the adaptive changes of early prosimians from their insectivore ancestors and also applies with equal weight to several groups of primate-like insectivores such as the apatemyids and mixodectids.

It is evident from the examination of the known early prosimian record and the primate-related insectivore record that the primates differentiated from their ancestry through a complex of characters and not by any one diagnostic modification. The earliest testimony to this change has, as yet, been derived only from the dentition. It is safe to assume, however, that the various features of the early prosimian dentition reflect a rather important shift in the nature of the whole feeding mechanism. Sporadic finds of primate skulls in the early Tertiary confirm this shift as a change from the insectivorous diet (i.e., a carnivorous diet in a special sense) of the insectivore ancestry to a herbivorous one. This change in diet, which concomitantly affected the feeding mechanism, was not an absolute one, as the insectivorous-carnivorous mode of life of many recent primates of any of the suborders testifies. Nevertheless, only an increase in the feeding on fruits, leaves, and other herbaceous matter explains the first radiation of primates.

What were the possible stages in this adaptive shift from a primarily insectivorous habitus to an essentially frugivorous-herbivorous one? We may speculate to explain the facts as follows. A large, unoccupied, or partly occupied, frugivorous-herbivorous adaptive zone must have been available. The first evolutionary changes that were necessary for exploring these opportunities were behavioral. Once a preference for, or at least sustained interest in, small fruits, berries, and leaves was established at the expense of a more insectivorous diet, selection could start operating toward a more efficient chemical and oral digestion. Alterations in the oral digestion, of course, also involved changes in the dentition itself. The usual diet of soft-bodied invertebrates captured by a strict insectivore is quickly sliced and swallowed by the animal. Attempts to grind tough-shelled seeds or fibrous fruits probably very often resulted in a breakage of the tall and acute cusps. With selection for less tall and more

bulbous cusps and increased ability for ectental mastication, grinding became radically more efficient.

It is well known that the tip of a cusp on a tooth is the result of cessation of mitotic growth of an area of the inner enamel epithelium (Butler, 1956a). The height of a cusp or cusplule is determined by the relative mitotic growth on the slopes of the cusp. This relatively higher point (the cusp), which was formed in areas where there was relatively less growth than in the surrounding areas, is the result of differential growth of the inner enamel epithelium. To phrase it somewhat differently, the relative mechanical stresses set up by the growing inner epithelium determine the relative height of cusps and cusplules on the molar pattern of both insectivores and primates, as well as in other mammals. It is easy to see, then, once the necessary behavioral changes took place in "pre-primate" insectivores, that genetic changes, to result in lower-cusped teeth, must have been relatively minor. For this assumption, one also assumes that growth rates of different portions of the inner epithelium are subject to relatively minor genetic causes.

A previously not fully exploited primary food source of fruits, leaves, and other material probably was increasingly utilized by several groups of therians¹ some time during the second half of the Cretaceous. One of these groups was undoubtedly the early prosimians. The mixodectids, the apatemyids, the ptilodontid multituberculates, the eutherian plagiomenids, and probably the Cretaceous marsupial *Glasbius* were occupants, in addition to the primates, of the frugivore-herbivore-omnivore adaptive zone for small mammals. Text figure 28 is an attempt to show the great adaptive similarity of many groups of mammals to the early prosimians and the consequent difficulty in delineating the insectivore-primate boundary.

It appears fairly reasonable to assume that the earliest primate radiation was not an isolated or unique phenomenon, but part of a major radiation of many groups of small

¹ Frugivorous multituberculates existed in great abundance before and during the Cretaceous and during the early Tertiary.

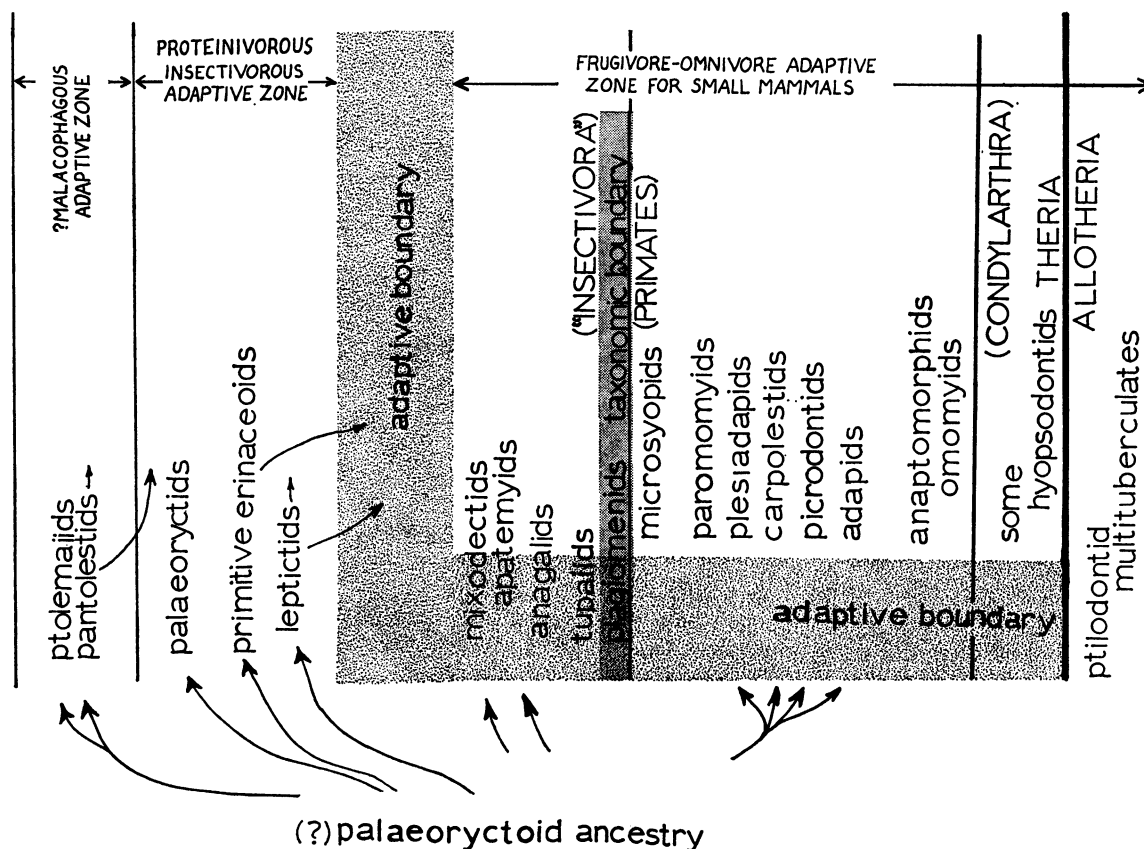


FIG. 28. Chart representing conjectural working hypothesis of inferred feeding habits of several groups of small, primitive mammals, primarily Paleocene and Eocene families. The diagram shows the close adaptive similarity of several non-primate and non-condylarth families to early primates and small condylarths, and the consequent difficulty in drawing the non-primate-primate boundary among several families with an inadequate fossil record. It is likely that taxonomic and adaptive boundaries will not coincide even when taxonomic questions have been settled by more ample evidence.

The term "proteinivorous" indicates probably a high percentage of animal protein in an animal's diet, ranging from various invertebrates to small vertebrates. "Malacophagous" and "insectivorous" diets, would designate special cases of a primarily proteinivorous food consumption. An omnivorous diet, as understood here, includes a certain percentage of animal proteins, but the bulk of the food intake is various plant proteins and other vegetable matter. A herbivorous diet (with specializations within this category, such as frugivorous) should designate a strict consumption of vegetable matter of all kinds.

The arrows showing derivation of the various placental families are not intended strictly.

(probably partially arboreal) mammals during the latter part of the Cretaceous. These assorted groups, along with the primates, further exploited a vacant adaptive zone, or one partly or less effectively occupied, all responding to roughly similar selective forces. The success of the first major prosimian radiation may very well have helped to determine the decline and eventual extinction of mixodectids and ptilodontid multituberculates and probably greatly contributed to the

decline of apatemyids and plagiomenids as well.

The origin of the primates and the primate-like groups was a response to opening opportunities in a new adaptive zone, or a considerably enlarged one, the similar selection pressures resulting in a whole series of parallel adaptations in closely related lineages and in some less closely related. Although the original response for this selection pressure manifested itself in a seemingly different

morphology of the adapted features of these groups, the differences were only expressions of their respective ancestry; the selection pressures acting on them were the same. Once an enlargement of some of the anterior teeth and a relatively well-adapted crushing, meshing dentition were attained, convergence (or parallelism) or divergence continued, depending on further evolution and the morphology of the groups involved.

Although evidence other than that derived from the dentition is limited, we may be able to correlate some of the known cranial features with the adaptive shift advocated above. There are some notable common adaptive features in the crania (see sections dealing with the cranial morphology of *Mixodectes* and that of *Microsyops*) of the late Paleocene *Plesiadapis*, the early Eocene *Microsyops*, the middle Paleocene *Mixodectes*, and the early Oligocene *Sinclairiella*. The ptilodontid multituberculate skull also bears adaptive similarity to skulls of these therians. The snout is relatively short in comparison with snouts in leptictid and erinaceoid skulls, and the zygomatic arches are laterally broad and strong, presumably for the additional bulk of a stronger masseter muscle complex.

The shortening of the snout may be correlated with the reduction or crowding of the antemolar dentition and partly with a more efficient use of the manus. The lessening importance of olfaction and the increased role of stereoscopic vision may have influenced the economy of ontogeny to reduce the extensive snout region.

A brief note is added here concerning the function of the enlarged incisors of apatemyids, mixodectids, microsyopids, most paromomyids, carpolestids, plesiadapids, and picrodontids. In conjunction, the enlarged incisors of ptilodontid multituberculates are also commented on. Buettner-Janusch and Andrew (1962), in criticizing Avis (1961) for the latter's general refusal to accept the view that recent prosimians use the tooth comb for fur scraping and combing, implied that in all

prosimians the enlarged and procumbent lower incisors evolved for the purpose of fur combing. The evidence presented by Buettner-Janusch and Andrew appears to be overwhelmingly convincing that, at least in lemurids and lorises (including *Galago*), the lower incisors and the incisiform canine have the primary function of combing and grooming the fur of the animal and its social partners. Simons (1962b) specifically endorsed the reasons for the origin of procumbent incisors only in the tupaiids, lemurids, and lorises. His view is realistic and is all that both behavioral and morphological evidence permits one to conclude. There is no evidence for postulating fur combing and grooming as a selective value of one or two pairs of enlarged procumbent incisors among the earliest prosimians and the adaptively extremely similar prosimian-like insectivores such as the apatemyids and mixodectids.

The fur comb consists of two pairs of incisors and the incisiform procumbent canine in lorises and lemurids. The individual elements of the fur comb, although procumbent, have slender, transversely constricted crowns which are not significantly enlarged. The premolars in the mandible following the canine are robust in these two families and, at least in lorises, are higher-crowned than the canine and the incisors. In some paromomyids, plesiadapids, carpolestids, picrodontids, microsyopids, mixodectids, and apatemyids the enlarged lower incisors are distinctly strongly rooted and long-crowned. The opposing upper incisors in almost all these groups, in which the upper incisors are known, are stout, firmly anchored teeth, usually equipped with pronglike cuspules. The adaptive similarity of plesiadapid, mixodectid, and ptilodontid multituberculate upper incisors is indeed very striking. Their use probably involved a great expenditure of stress resistance and anchorage in tearing and snapping off leaves, fruits, or possibly even underground vegetation and roots.

SUMMARY

CONTRARY TO THE PRACTICE of many earlier workers, the author of the present paper clearly separates the Paleocene Mixodectidae and the Eocene Microsyopidae.

The following species and genera of the insectivore mixodectids are considered valid: *Mixodectes pungens*, *Mixodectes malaris*, *Elpidophorus elegans*, *Elpidophorus minor*, *Eudaemonema cuspidata*, *Dracontolestes aphantus*, and *Remiculus deuschi*. Various Puercan fossils other than *Dracontolestes* probably have been incorrectly allocated to the family. The cranial and postcranial anatomy of mixodectids is virtually unknown.

An undoubted derivation of mixodectids from any of the known Cretaceous or Paleocene families is not possible. Mixodectids may have originated from some unknown Cretaceous palaeoryctids, erinaceoids, or near-erinaceoid group. Leptictid ancestry for the family is not likely, because even the earliest leptictids are shown to be more advanced than mixodectids in certain important features of the molar teeth. Close ties of mixodectids with *Adapisoriculus* and Recent tupaiids are not improbable.

The possibility of a close plagiomenid-mixodectid affinity is re-examined, and some new evidence is described and illustrated. There is no direct or meaningful indirect evidence to confirm a derivation of plagiomenids from the Mixodectidae. Allocation of the Mixodectoidea to the Dermoptera is considered to be unjustified. *Thylacaelurus* is not a plagiomenid. Its affinities may lie with insectivores close to the dimylid stem.

The Eocene Microsyopidae are known from the following species and genera: *Microsyops wilsoni*, new species, *M. alfi*, *M. angustidens*, *M. latidens*, *M. scottianus*, *M. lundeliusi*, *M. elegans*, *M. annectens*, *M. kratos*, and *Craseops sylvestris*. Microsyopid cranial anatomy is described in detail; the postcranial anatomy is virtually unknown. From the evidence of the dental morphology, the microsyopids may be derivable from the earliest primates. Because it is not known whether Cretaceous and early

and middle Paleocene primates had the relatively advanced basicrania of late Paleocene *Plesiadapis* and Eocene prosimians, the primitive basicranium of *Microsyops* is not necessarily decisive against the inclusion of microsyopids in the Primates. As opposed to the usual practice of overburdening the Insectivora and using it as a "wastebasket," the microsyopids are placed, although with a query, in the Primates.

The late Paleocene *Navajovius* is allocated, with a query, to the Microsyopidae. *Navajovius? mckennai*, new species, from the Wasatchian Almagre facies of the San José Formation is poorly known.

The insectivore-primate transition was probably initiated at the end of the Cretaceous or earlier by behavioral and physiological adaptations. As behavioral modifications (particularly preference for fruits, leaves, and similar foods as opposed to a predominantly insectivorous diet) affected the feeding habits and behavior, selection gradually altered the morphology and function of the feeding mechanism. The primitive therian and eutherian molar shear was gradually de-emphasized by a reduction of the long paracrista and metacrista, a straightening out of the centrocrista, and the acquisition of more bulbous and less acute cusps and conules. As prevallid-postvallum and postvallid-prevallum shear lost relative importance, the trigonid became narrower and less tall, and the talonid gained functional importance. The teeth, with other parts of the feeding mechanism, became more suitable for mastication and other aspects of oral digestion of a predominantly frugivorous-herbaceous diet.

The apatemyids and tupaiids are considered to be independently derived families from the Insectivora, not the Primates. The Paleocene picrodontids, extremely specialized frugivores derived from early primates, epitomize (with other prosimians) the nature and direction of selection pressures responsible for the origin of the Primates.

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PLATES 17-57

PLATE 17

1-4. *Mixodectes pungens*, enlarged lower incisors, A.M.N.H. No. 2557b, Nacimiento Formation, San Juan Basin, New Mexico. 1, 2. Lingual view. 3, 4. Buccal view. Half of the crown of the lateral incisor and the entire crown of the medial incisor are missing. $\times 5$.

5-10. *Mixodectes malaris*, *Deltatherium* zone, Nacimiento Formation, New Mexico. 5-8. Enlarged incisors (crowns broken) and anteriormost premolar, U.K.M.N.H. No. 13751. 5, 6. Occlusal view. 7. Buccal view. 8. Lingual view. 9, 10. P³, partially embedded in hard matrix, U.K.M.N.H. No. 9539, occlusal view. $\times 10$.

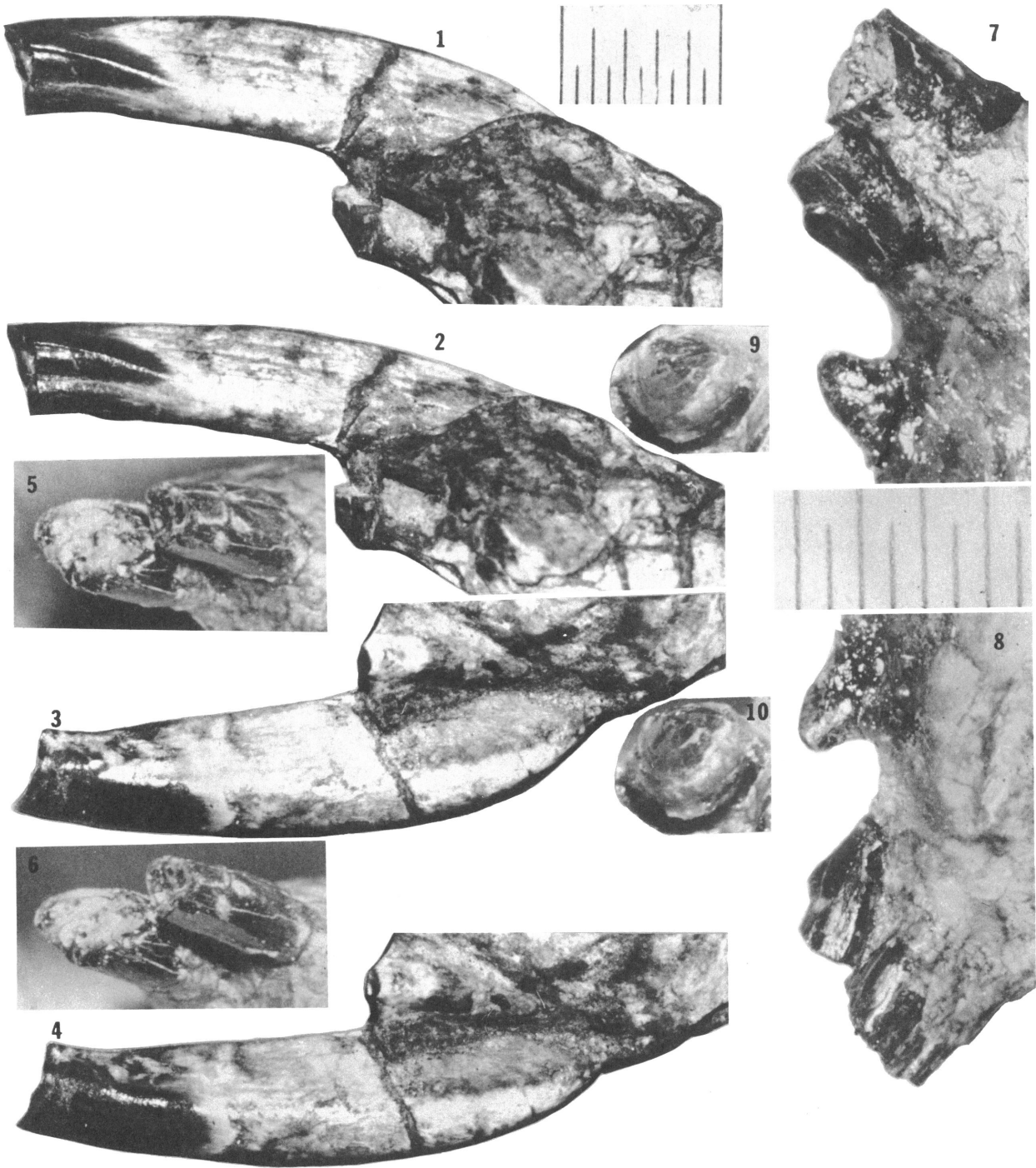


PLATE 18

Mixodectes pungens, A.M.N.H. No. 16018, Nacimiento Formation, San Juan Basin, New Mexico. 1, 2. Left and right mandibular fragments with left P_4 - M_1 and right M_{2-3} , occlusal view. $\times 5$. 3, 4. Right mandible with M_{2-3} , medial and lateral views. $\times 3$.

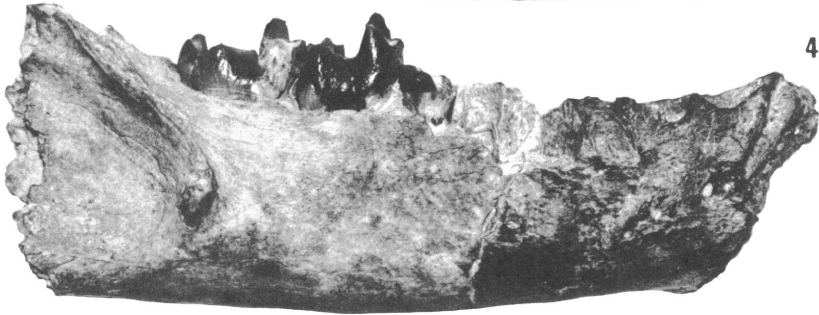
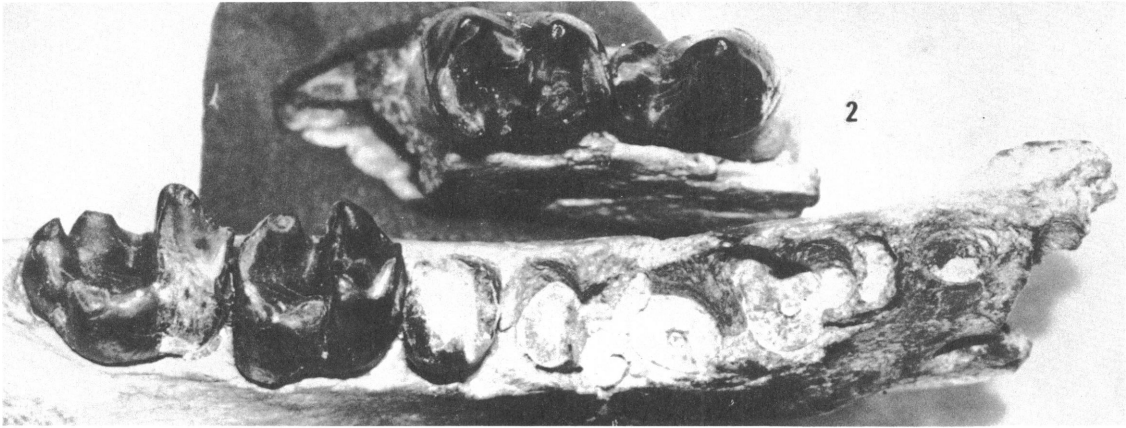
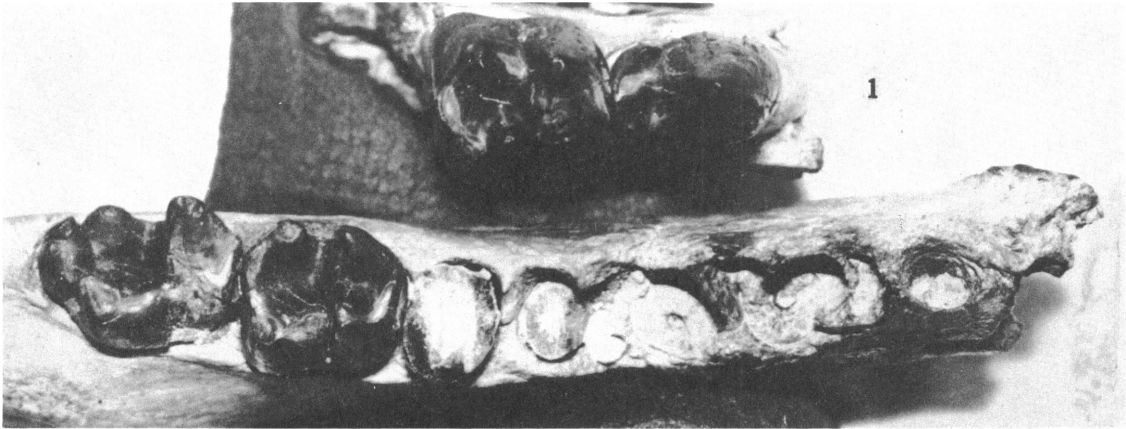


PLATE 19

Mixodectes pungens, Nacimiento Formation, New Mexico. 1, 2. Partial right mandible with P_3 - M_3 , A.M.N.H. No. 3081, lateral view. $\times 3$. 3, 4. Left M_{1-3} , A.M.N.H. No. 16021, occlusal view. $\times 5$. 5, 6. Right P^4 - M^3 , A.M.N.H. No. 16593, occlusal view. $\times 5$.

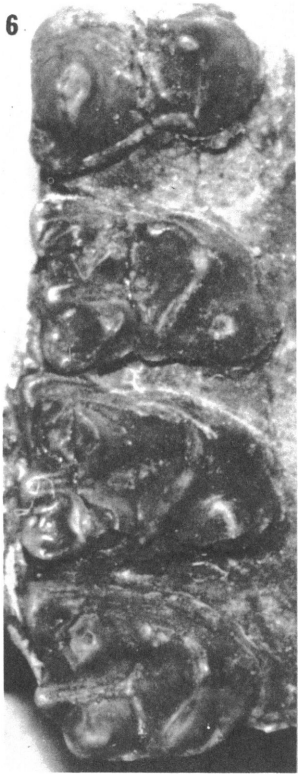
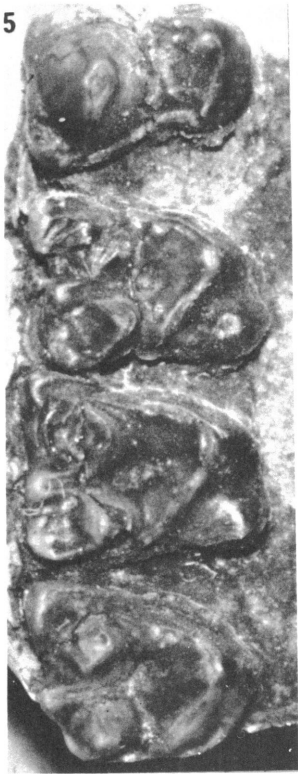
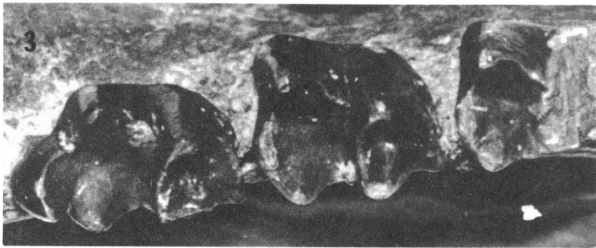


PLATE 20

Mixodectes pungens, Nacimiento Formation, New Mexico. 1-4. Right mandible fragment, U.S.N.M. No. 15396. 1. Ventral view. 2. Dorsal view. 3. Lateral view. 4. Medial view. 5. Lateral view of left mandible, A.M.N.H. No. 2557b. The enlarged medial incisor may be in an unnatural position either because of crushing or faulty repositioning and cementing during preparation. $\times 3$.

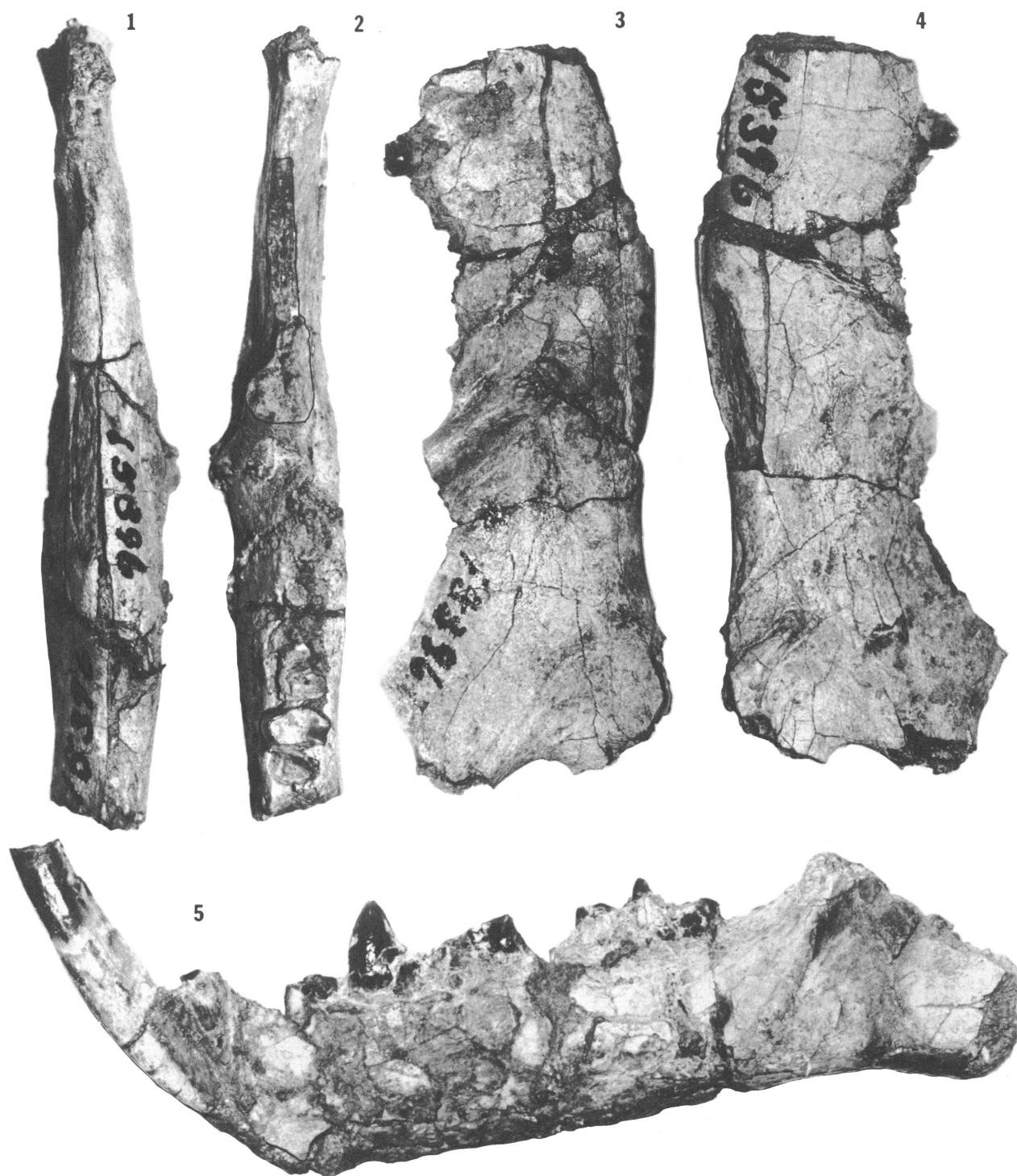


PLATE 21

1-3. *Mixodectes pungens*, Nacimiento Formation, New Mexico. 1, 2. Skull fragment, consisting of posterior portion of the facial skull and anterior segment of the cerebral skull, A.M.N.H. No. 16038. 1. Ventral view; to the left is the anterior part, and to the right, the posterior part. 2. Dorsal view; at the top is the posterior part, and the broader anterior segment of the specimen faces downward. 3. Ventral view of badly preserved partial skull, A.M.N.H. No. 16593. $\times 3$.

4, 5. *Mixodectes malaris*, occlusal view of P^3 (?), P^4 - M^3 . Portions of M^1 and M^2 are buried in the hard matrix, U.K.M.N.H. No. 13816, *Deltatherium* zone, Nacimiento Formation, New Mexico. $\times 5$.

6, 7 and 10, 11. *Mixodectes malaris*, right M^{1-3} , showing characteristic wear surfaces for the genus, A.M.N.H. No. 833, Nacimiento Formation, New Mexico. 6. Lingual view. 7. Buccal view. 10, 11. Occlusal view. $\times 5$.

8, 9. *Mixodectes malaris*, left M_{2-3} , U.K.M.N.H. No. 14022, Nacimiento Formation.

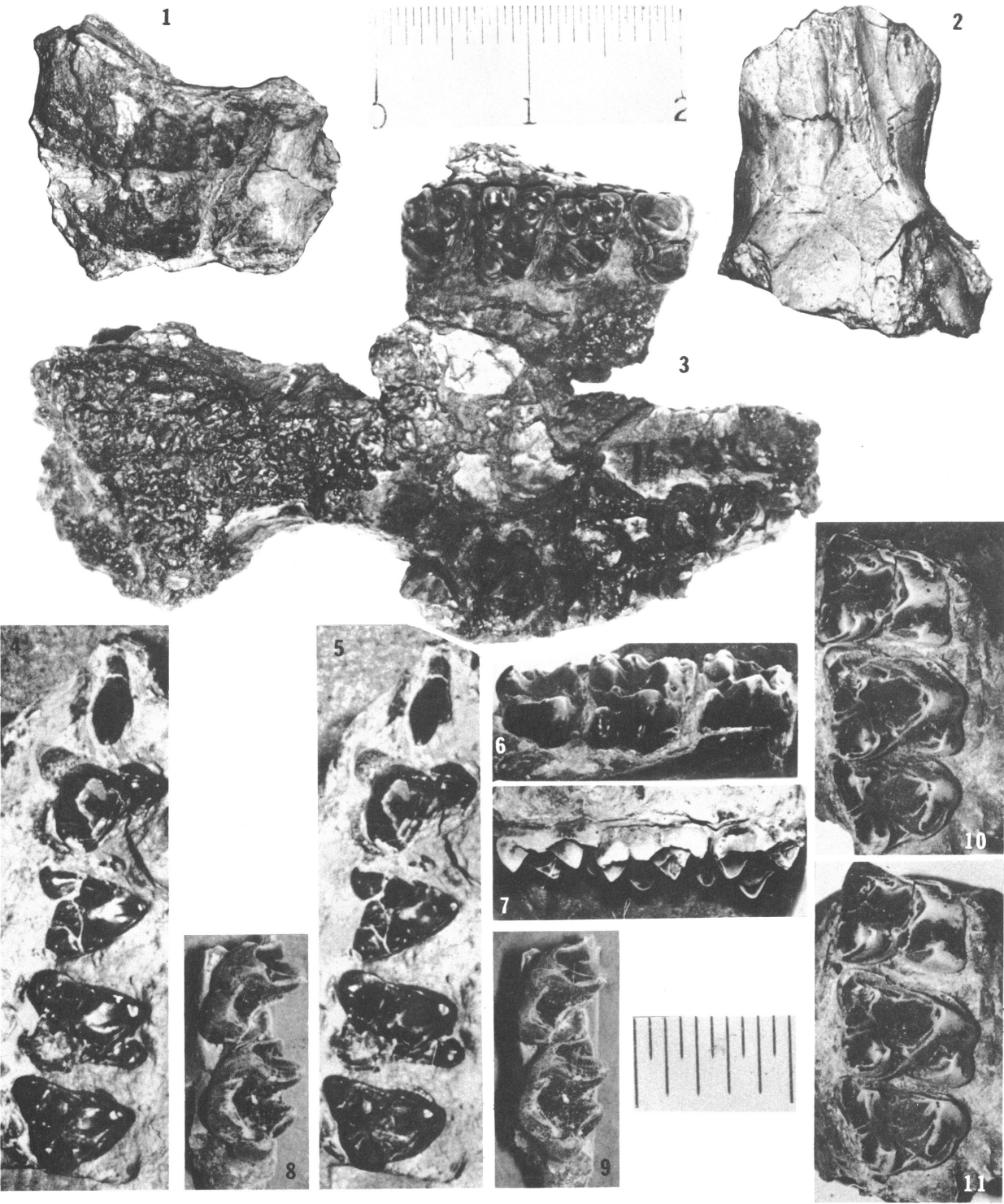


PLATE 22

1-4. *Mixodectes malaris*, *Deltatherium* zone, Nacimiento Formation, New Mexico. 1, 2. Fragmentary lower jaw showing the approximate relation of the rami, U.K.M.N.H. No. 9540. $\times 3$. 3, 4. Slightly distorted fragmentary left maxilla with roots of P^3 , lingual half of P^4 and M^{1-3} , U.K.M.N.H. No. 9542. $\times 5$.

5-8. *Mixodectes pungens*, Nacimiento Formation, New Mexico. 5, 6. Right P_4 , M_{1-3} , A.M.N.H. No. 16597. 7, 8. Right M_{1-3} , A.M.N.H. No. 16727. $\times 5.5$.

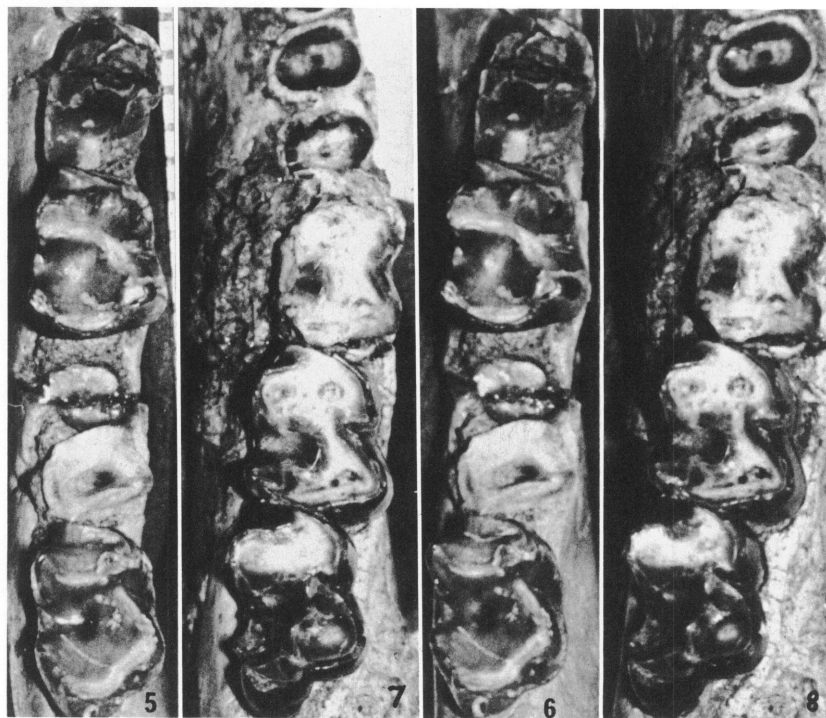
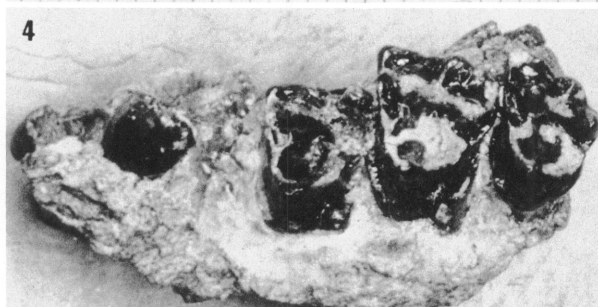
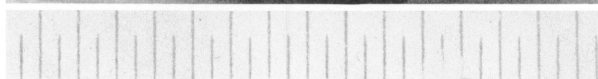
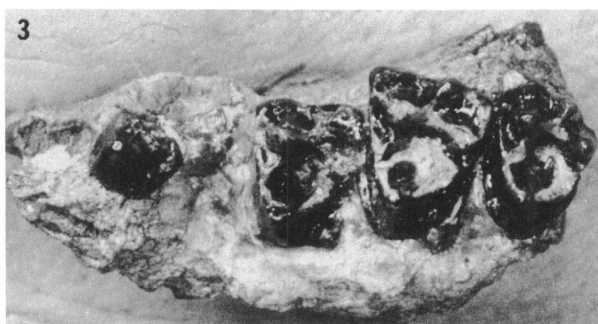


PLATE 23

1-4. *Dracontolestes aphantus*, talonid of M_2 on left of 1 and 2, U.S.N.M. No. 15719; M_{2-3} on right of 1 and 2, U.S.N.M. No. 16180, type, North Horn Formation, Emery County, Utah.

5-9. *Remiculus deutschii*, Lemoine Quarry, France. 5, 6. From left to right: left M^1 , with no catalogue number, M.N.H.N. Nos. CR1196 (left M^1), CR312 (left M^2), and CR286 (right M^2), occlusal views. 7, 8. From top to bottom, M.N.H.N. Nos. CR928 (left lower molar), CR4415 (right P_4), and CR4417 (right lower molar), occlusal views. 9. From left to right, M.N.H.N. Nos. CR4415 (right P_4) and CR4417 (right lower molar), lingual view.

10, 11. "Mixodectid ? b" reported by Gazin (1941), right maxilla fragment with badly worn molar, U.S.N.M. No. 16200, Wagonroad local fauna, North Horn Formation, Emery County, Utah.

All $\times 5$.

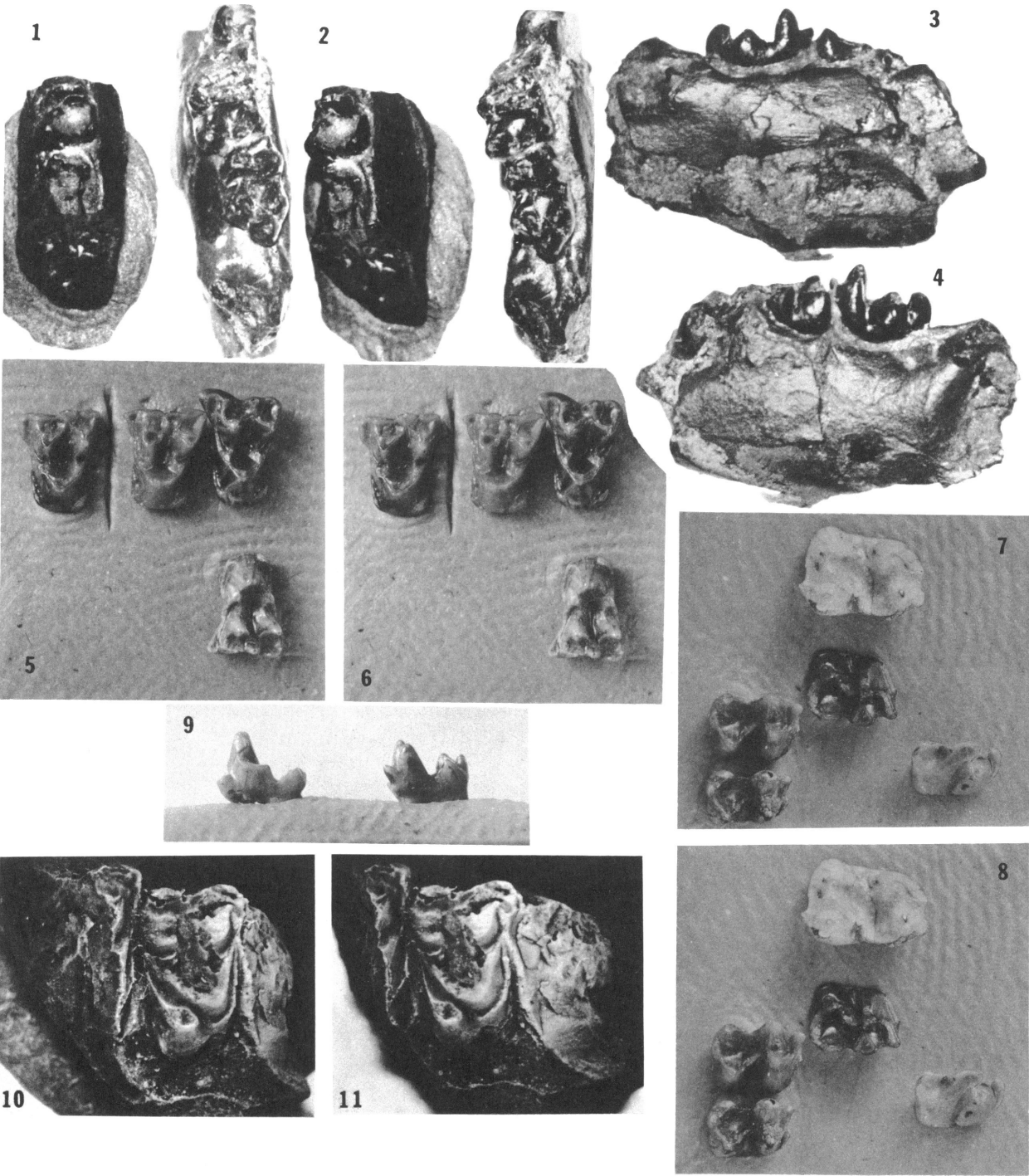


PLATE 24

1, 2. *Elpidophorus elegans*, almost complete right mandible with P_2-M_3 , A.M.N.H. No. 33856, Scarritt Quarry, Fort Union Formation, Crazy Mountain Field, Montana. 1. Medial view. 2. Lateral view. $\times 3$.

3-6. *Elpidophorus minor*, left mandible fragment with P_3-M_2 , P.U.M. No. 14201, Silberling Quarry, Fort Union Formation, Crazy Mountain Field, Montana. 3. Medial view. 4. Lateral view. 5, 6. Occlusal view. $\times 5$.

7-10. "Mixodectid a" reported by Gazin (1941), left lower molar, U.S.N.M. No. 16220, North Horn Formation, Emery County, Utah. 7. Lingual view. 8. Buccal view. 9, 10. Occlusal view. $\times 5$.

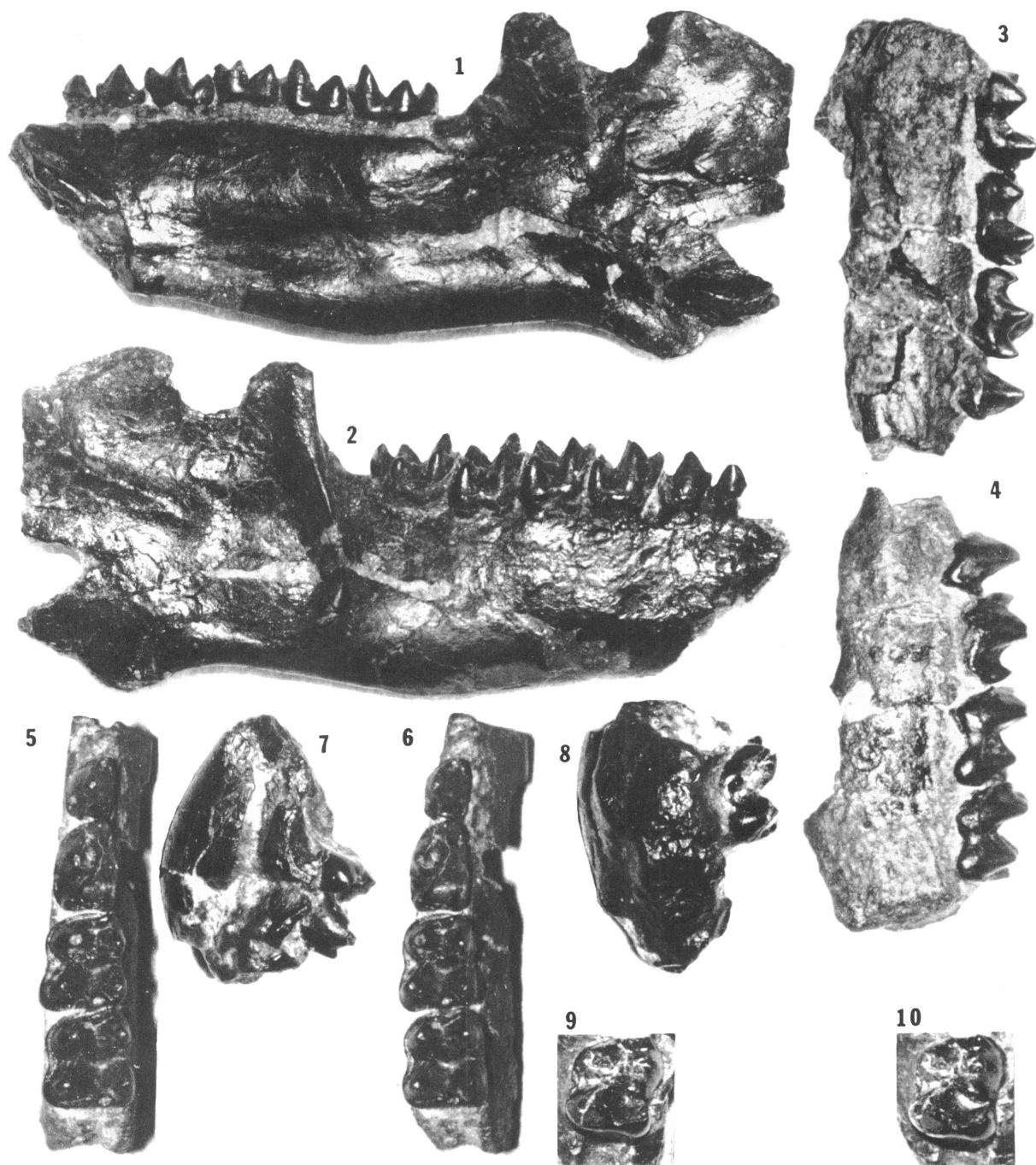


PLATE 25

Eudaemonema cuspidata, Fort Union Formation, Crazy Mountain Field, Montana.
1-4. Right horizontal ramus with canine and P_2 - M_3 , type, U.S.N.M. No. 9314. 1. Lateral view. $\times 4.8$. 2. Medial view. $\times 4.8$. 3, 4. Occlusal view. $\times 5$. 5, 6. Left M^1 and M^2 , A.M.N.H. No. 35817, occlusal view. $\times 5$. 7. Left mandible fragment, U.S.N.M. No. 9317, to show alveoli of the enlarged incisors, anterolateral view. $\times 5$. 8, 9. Right M^{1-3} , A.M.N.H. No. 35830, occlusal view. $\times 5$.

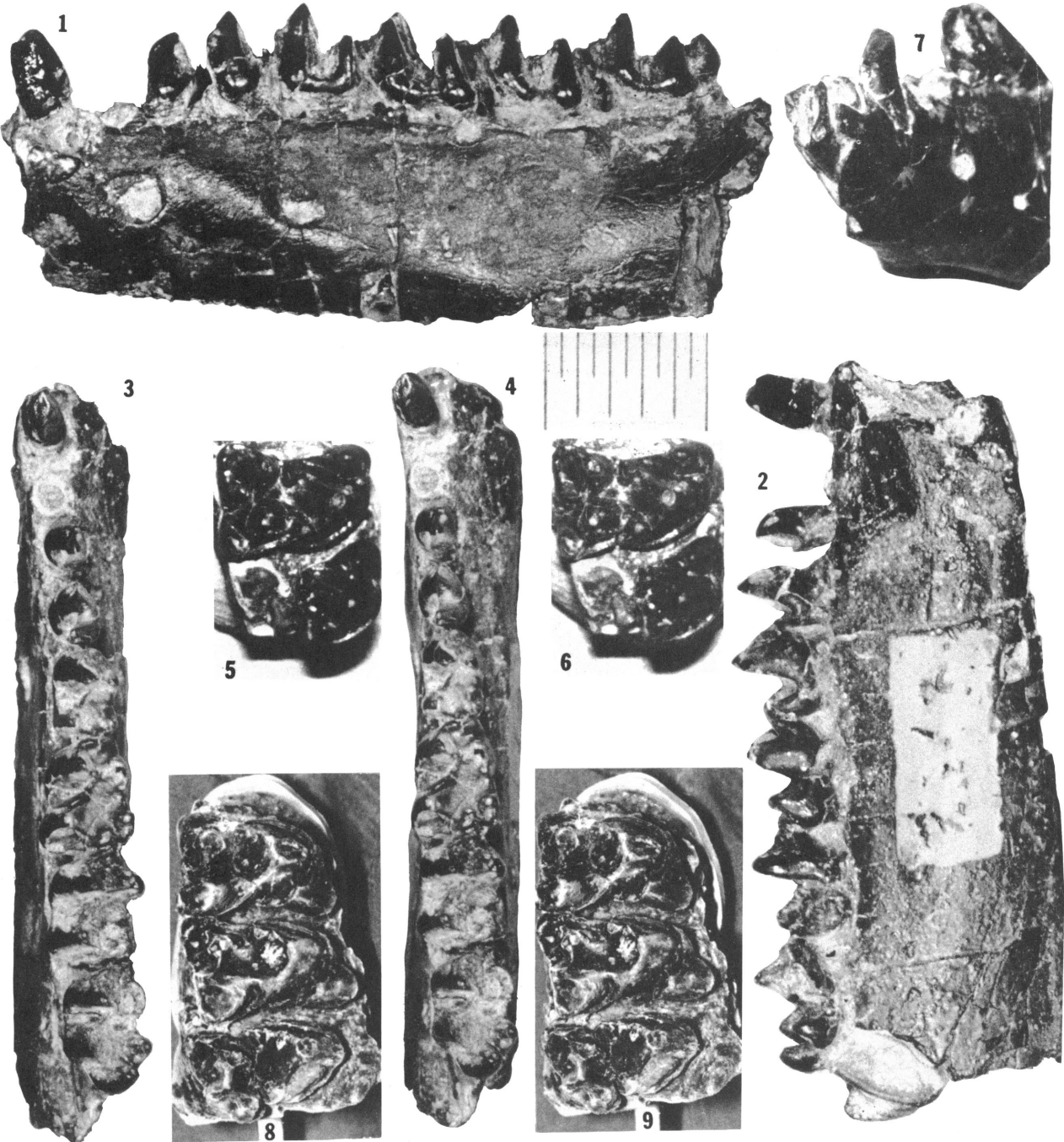


PLATE 26

1-2. *Eudaemonema cuspidata*, left P^3-M^2 , A.M.N.H. No. 35834, from Gidley Quarry, occlusal view. $\times 5$.

3-10. *Elpidophorus elegans*, Scarritt Quarry of Crazy Mountain Field, Montana. 3-6. Right upper incisor, A.M.N.H. No. 33857. 3, 4. Lingual view. 5, 6. Buccal view. $\times 5$. 7, 8. Right P_2-M_3 , A.M.N.H. No. 33856, occlusal view. $\times 5$. 9, 10. Right M^{1-2} , A.M.N.H. No. 33862, occlusal view. $\times 5$.

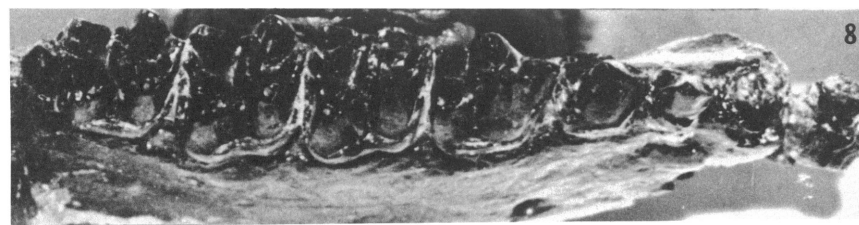
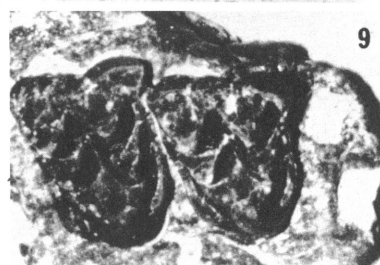
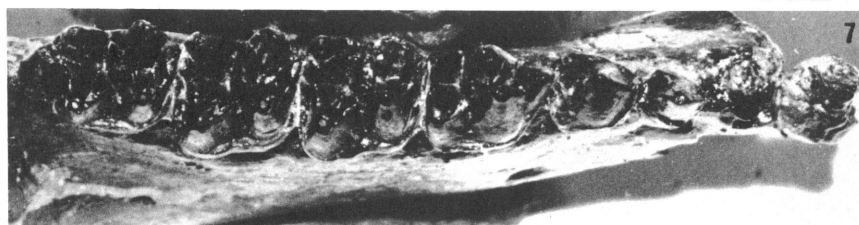
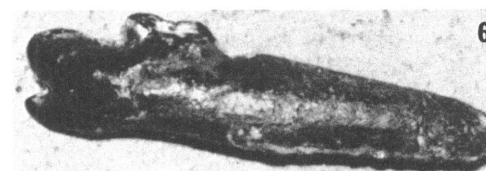
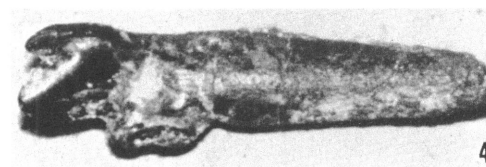
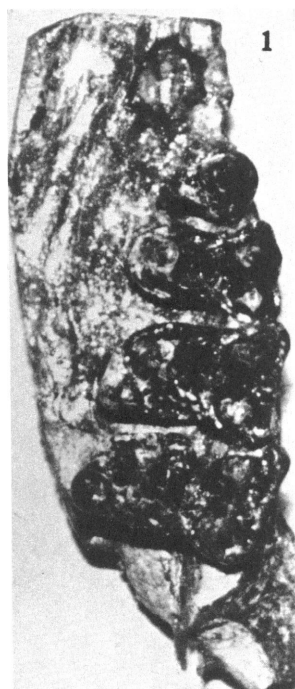


PLATE 27

1-8. *Elpidophorus elegans*, Scarritt Quarry. 1-3. Left P³-M³, P.U. No. 17639. 1, 2. Occlusal view. 3. Buccal view. ×5. 4-6. Left P²-P⁴, and part of left maxilla, P.U. No. 17637. 4, 5. Occlusal view. ×5. 6. Buccal view. ×3. 7, 8. Left premaxilla and maxilla with alveoli of I^{2(?)}, I^{3(?)}, C, P¹, P², and P³, and the following teeth: P⁴-M³, A.M.N.H. No. 35963. ×3.

9, 10. ?*Mixodectes pungens*, occlusal view of left upper molar, A.M.N.H. No. 4078, Nacimiento Formation, New Mexico. ×5.

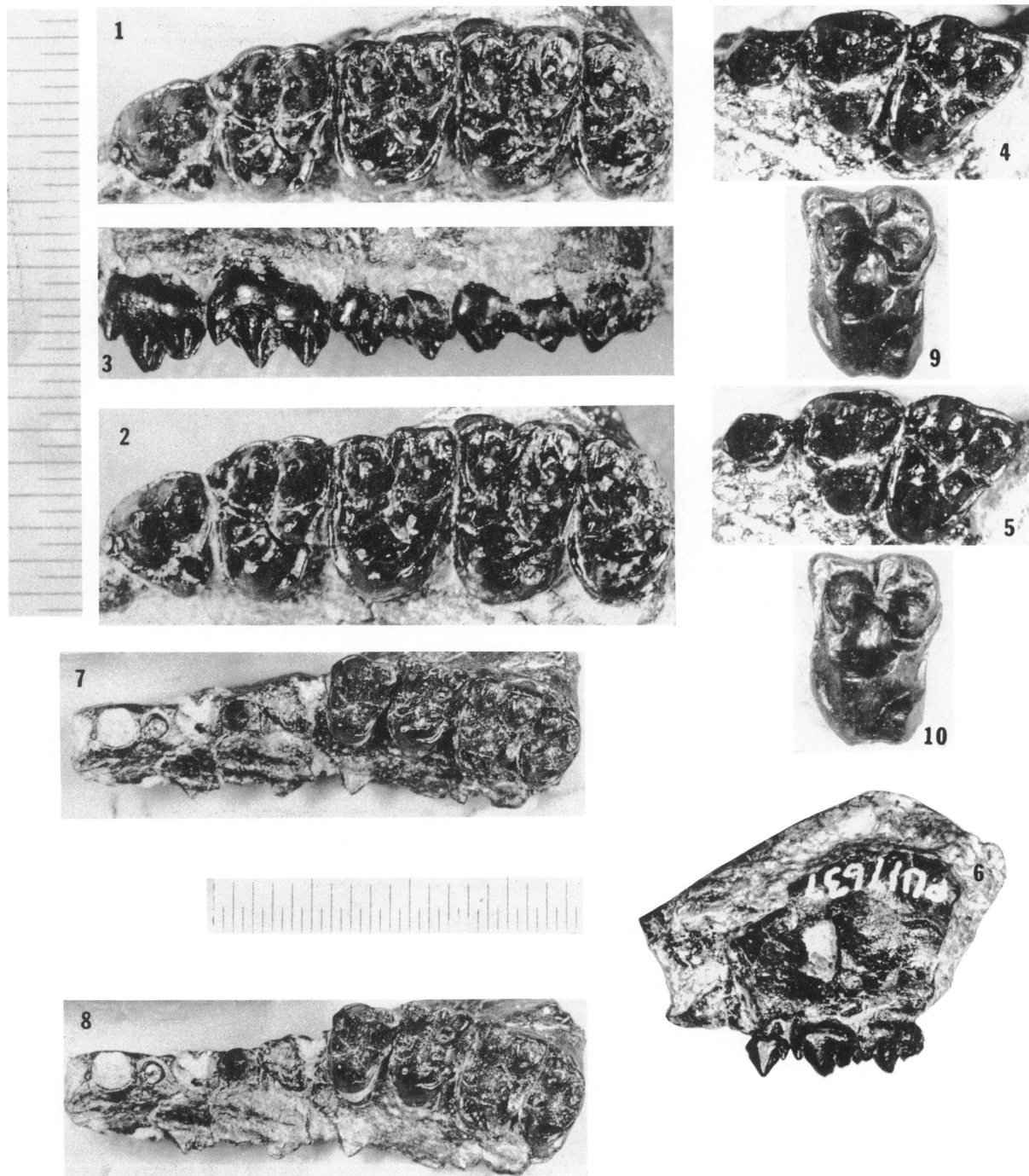


PLATE 28

1, 2. *Planetetherium mirabile*, medial view of the left mandible, primarily to show the angle of the lower jaw, A.M.N.H. No. 22206, Fort Union Formation, Bear Creek, Montana. $\times 4$.

3-5. *Plagiomene alticuspis*, crushed palate with almost complete dentition, A.M.N.H. No. 15208, from Gray Bull beds, Big Horn Basin, Wyoming. 3. Ventral view. $\times 2$. 4, 5. Right C (or an incisor) to M³, occlusal view. $\times 5$.

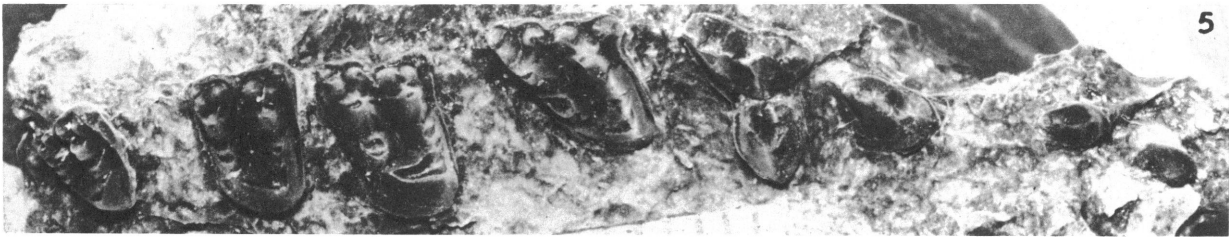
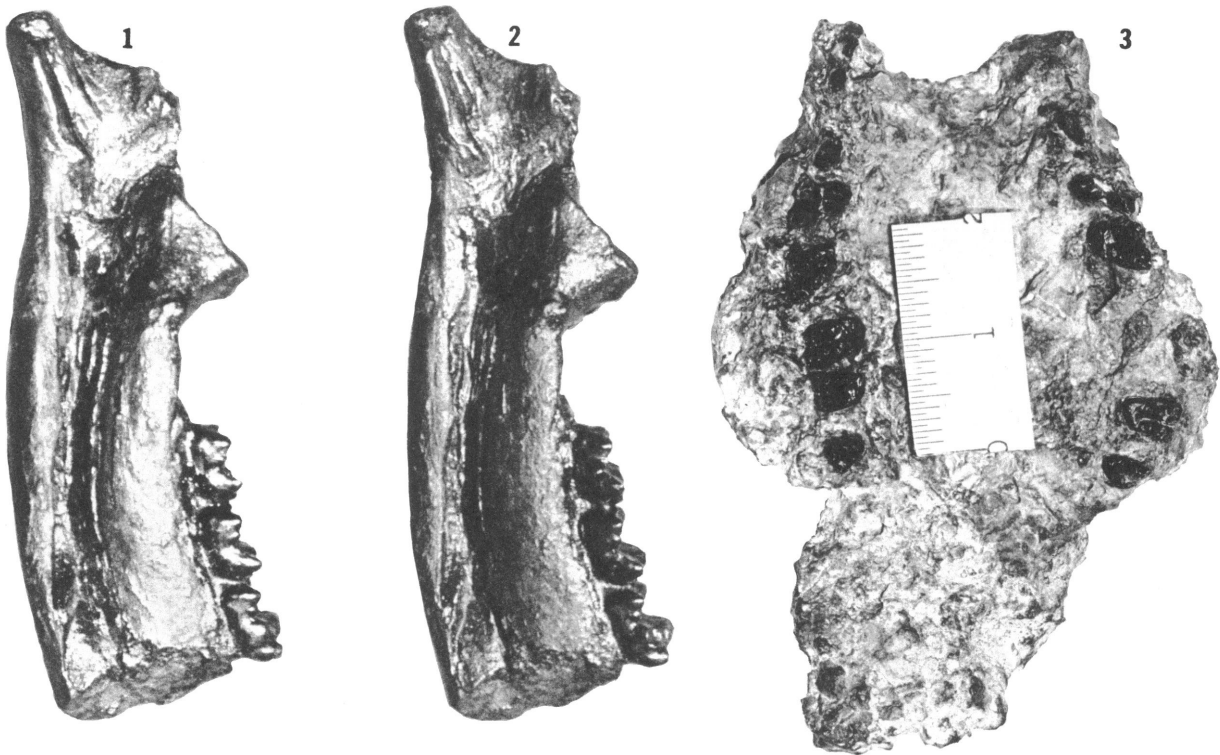


PLATE 29

1-6. *Planetetherium mirabile*, Bear Creek, Fort Union Formation, Montana. 1, 2. Left P_4-M_2 and P_4-M_3 , A.M.N.H. No. 22161 (on right of both figures) and A.M.N.H. No. 22206 (on left of both figures), occlusal view. 3-6. Left and right M^{1-2} , A.M.N.H. No. 22229, occlusal view. $\times 5$.

7-12. *Plagiomene alticuspis*, Gray Bull beds, Big Horn Basin, Wyoming. 7, 8. Left M_{1-2} , part of type, A.M.N.H. No. 15084. 9-12. Right P_4-M_2 , A.M.N.H. No. 15085. $\times 4$.

13-15. *Planetetherium mirabile*, right P^3-M^1 , C.M. No. 11671, Bear Creek, Fort Union Formation, Montana. $\times 5$.

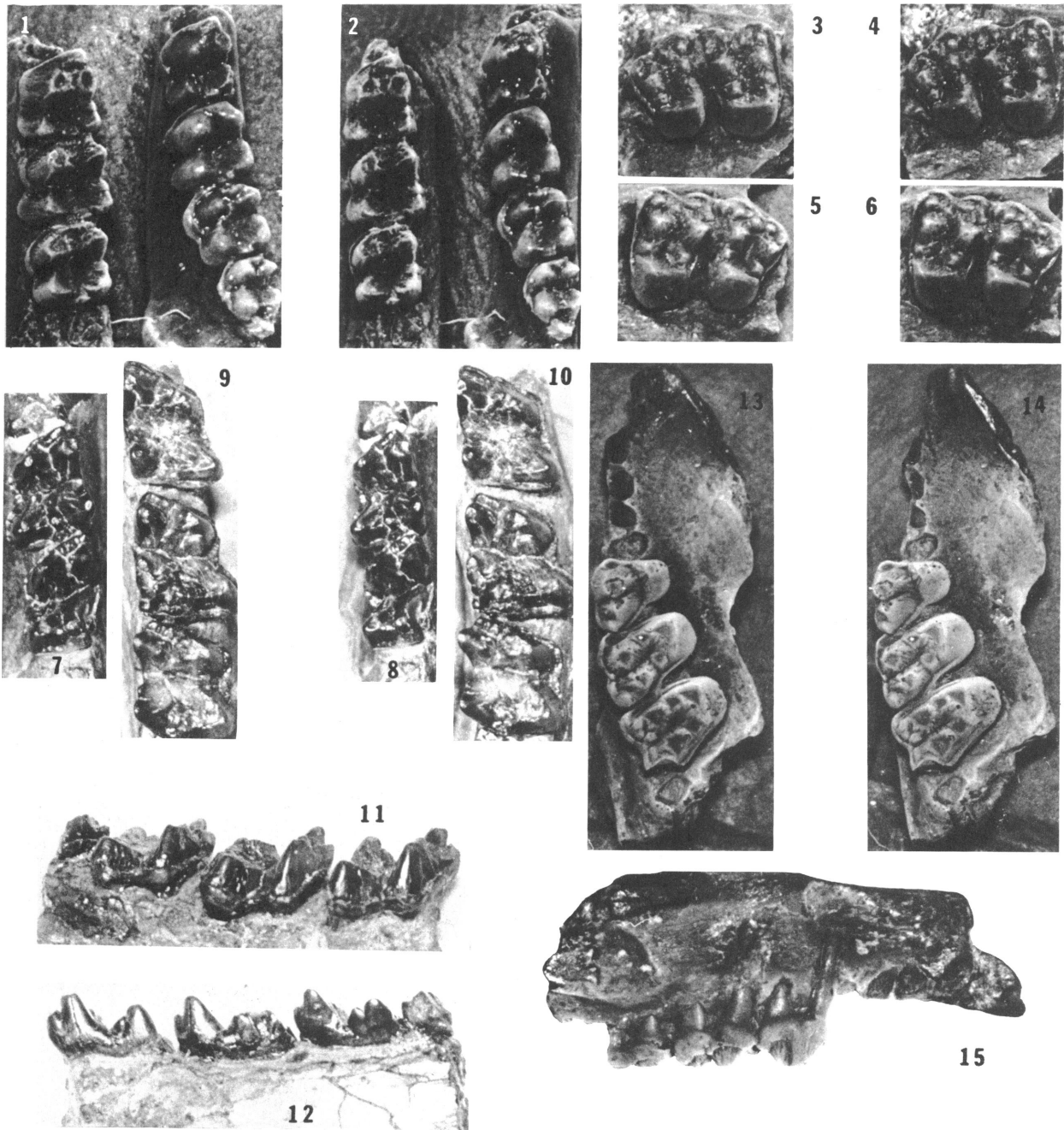


PLATE 30

1-7. *Microsyops wilsoni*, new species, composite of upper and lower dentitions (fourth premolars and molars), A.M.N.H. No. 80965, East Alheit Quarry, Wasatch Formation, Colorado. 1, 2, 4, and 5. Occlusal views. 3. Buccal view. 7. Lingual view. $\times 5$.

8, 9. *Navajovius kohlhaasae*, type, A.M.N.H. No. 17390, Tiffany beds, Mason Pocket, Colorado. 8. Posterior half of right mandible with M_{2-3} , lingual view. 9. Horizontal ramus of left mandible with incisor, P_2 , P_4-M_3 , lateral view. $\times 7$.

10, 11. *Navajovius? mckennai*, new species, left P^3-M^1 , type, A.M.N.H. No. 48612, San José Formation, Almagre facies, San Juan Basin, New Mexico. 10, 11. Occlusal view. 12. Buccal view. $\times 10$.

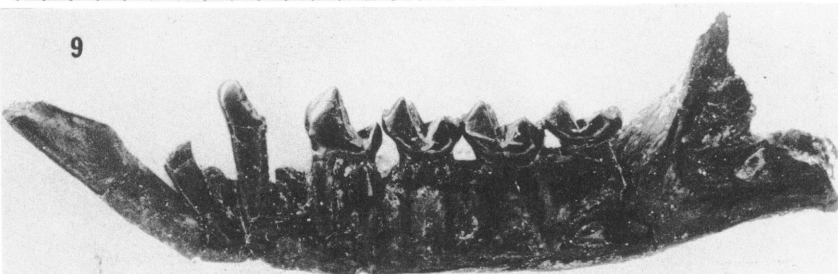
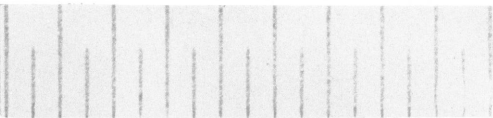
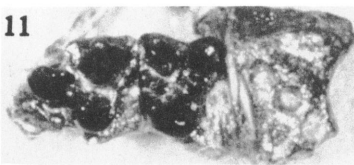
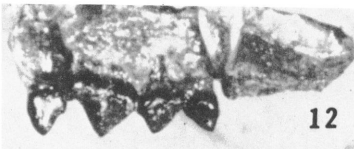
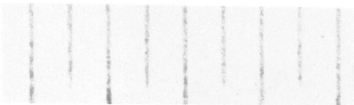
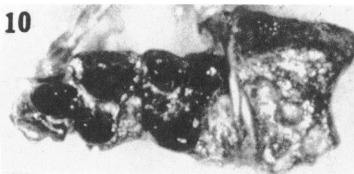
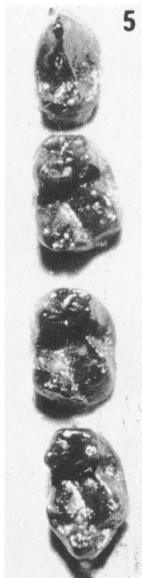
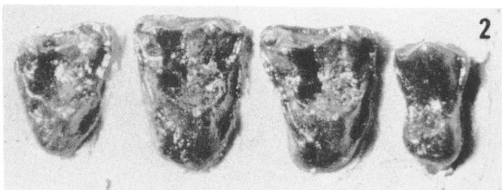
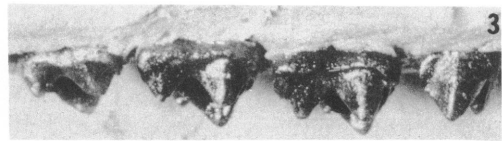
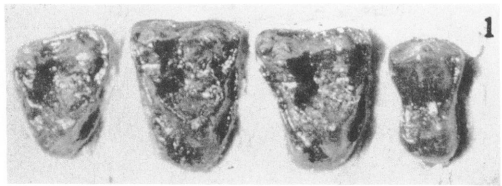


PLATE 31

1-6. *Navajovius kohlhaasae*, Tiffany beds, Mason Pocket, Colorado, A.M.N.H. No. 17399. 1-3. Upper dentition; see text for suggested homologies. 1, 2, $\times 7$; 3, $\times 12.5$. 4-6. Occlusal views of partial left lower dentition (P_2 is present only on 6; the teeth posterior to the enlarged incisor and anterior to P_4 are missing from 4 and 5), type, A.M.N.H. No. 17390. 4, 5, $\times 7$; 6, $\times 9.85$.

7-10. *Ptilocercus lowii*, right upper and lower dentition, U.S.N.M. No. 311313. Recent, from the Cameron highlands of Malaya, occlusal views. $\times 5.1$.

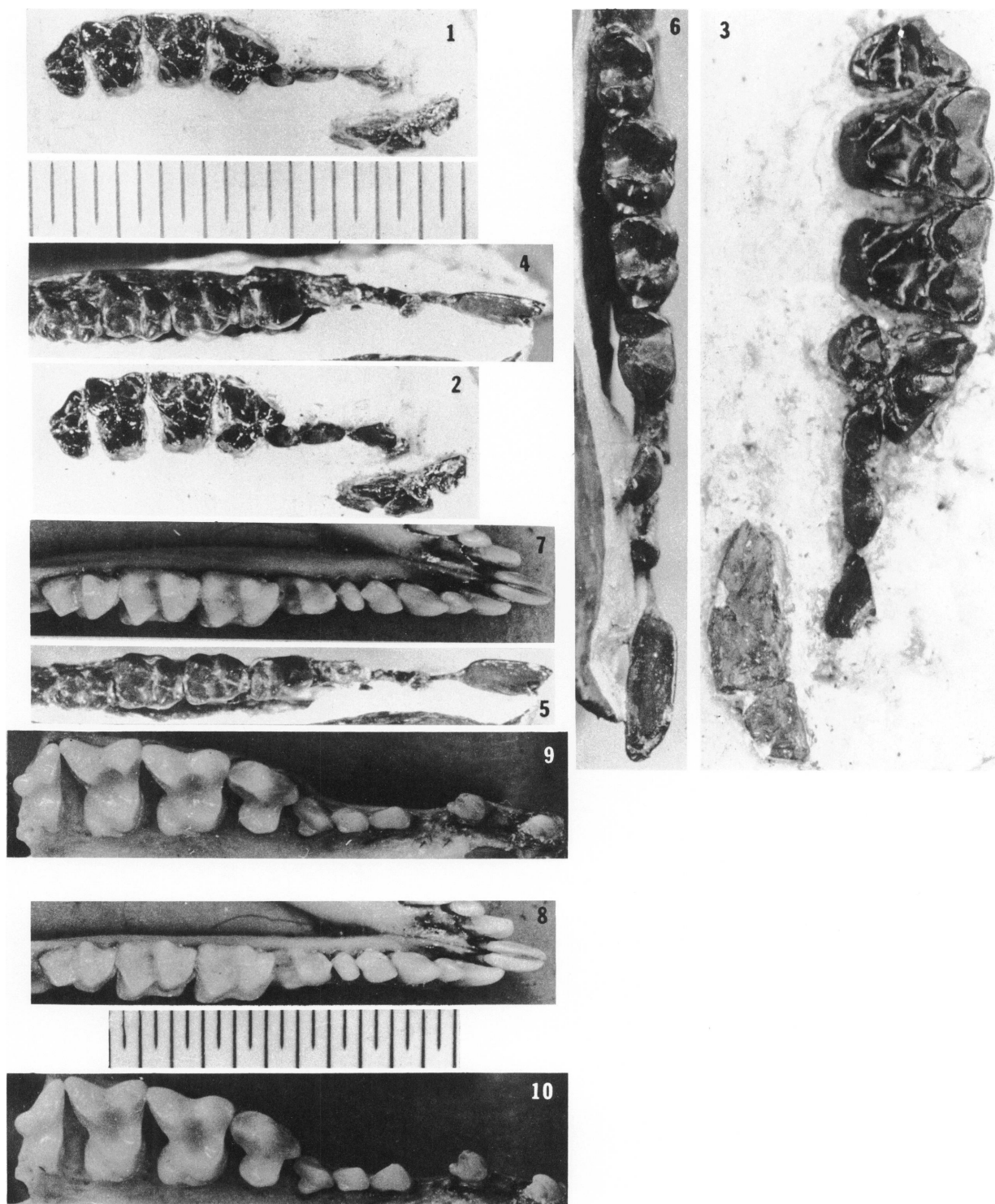


PLATE 32

1-6. *Microsyops wilsoni*, new species, Gray Bull beds of the Willwood Formation, Big Horn Basin, Wyoming. 1, 2 and on left of 5, 6. Type, partial left mandible with P₄-M₂, U.K.M.N.H. No. 8520. 3, 4 and on right of 5, 6. Right mandible fragment with P₄-M₁, U.K.M.N.H. No. 8600.

7, 8. ?*Microsyops wilsoni*, new species, right and left ?dP⁴'s, A.M.N.H. Nos. 80953 and 80954, East Alheit Quarry, Wasatch Formation, Colorado.

All ×5.

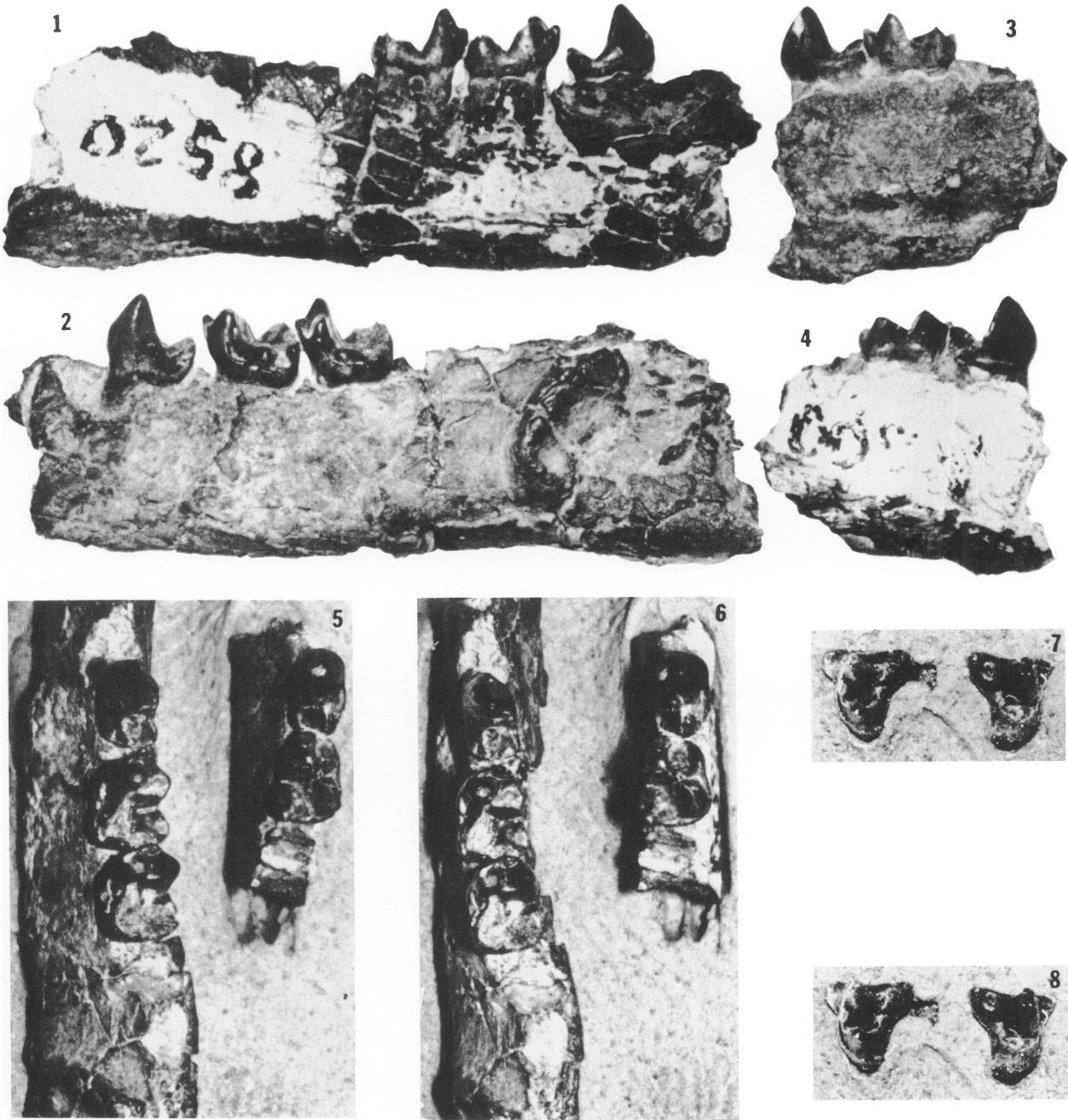


PLATE 33

1, 2. *Microsyops alfi*, left P₄-M₁, right P₄-M₁, and right M₂₋₃ (from left to right on both figures), U.C.M.P. Nos. 44062, 44063 (from Despair Quarry), and 44776E (from Timberlake Quarry), from the Four Mile Fauna, Wasatch Formation, Colorado. ×5.

3, 4. ?*Microsyops alfi*, enlarged lower incisors from the Four Mile Sand Quarry. ×5.

5-8. *Microsyops alfi*, composite of upper and lower dentitions from Despair, Sand, and Timberlake quarries of the Four Mile Fauna. ×5.

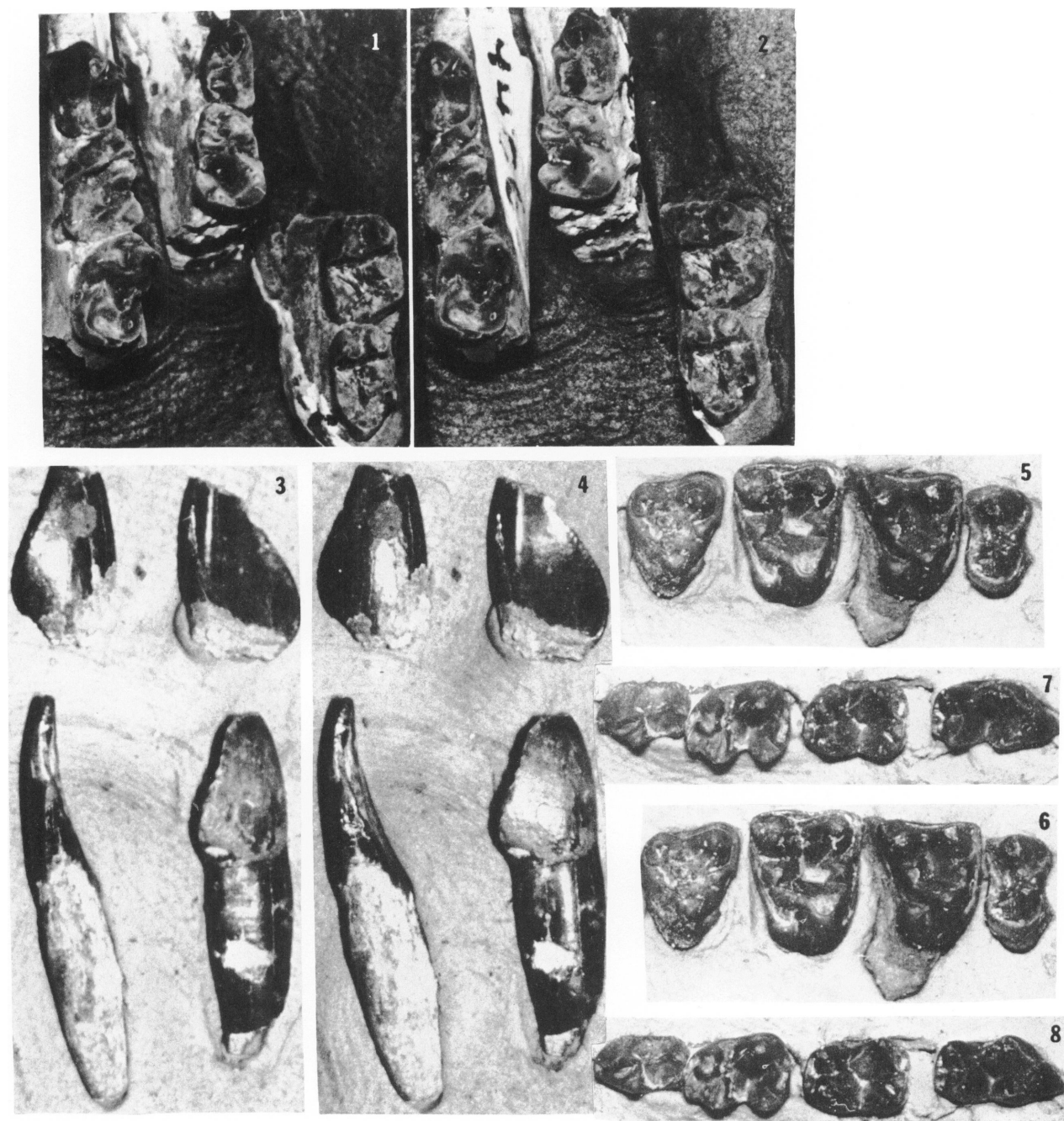


PLATE 34

1-9. *Microsyops latidens*, left P³-M³, A.M.N.H. No. 15629, from Lysite equivalent beds, "Buffalo Basin" within the Big Horn Basin, Wyoming. 1, 2. Occlusal view. 3. Buccal view. 4-6. Right P⁴-M³, U.S.N.M. No. 12138, from the Knight Member of Wasatch Formation, Sublette County, Wyoming. 4, 5. Occlusal view. 6. Lingual view. 7-9. Right P²-M², U.S.N.M. No. 12140, from the Knight Member of Wasatch Formation, Wyoming. 7, 8. Occlusal view. 9. Lingual view.

10, 11. *Microsyops scottianus*, right mandible fragment with broken incisor and P₄-M₂, A.M.N.H. No. 17473, from Lost Cabin beds, Wind River Basin, Wyoming, occlusal view. All ×5.

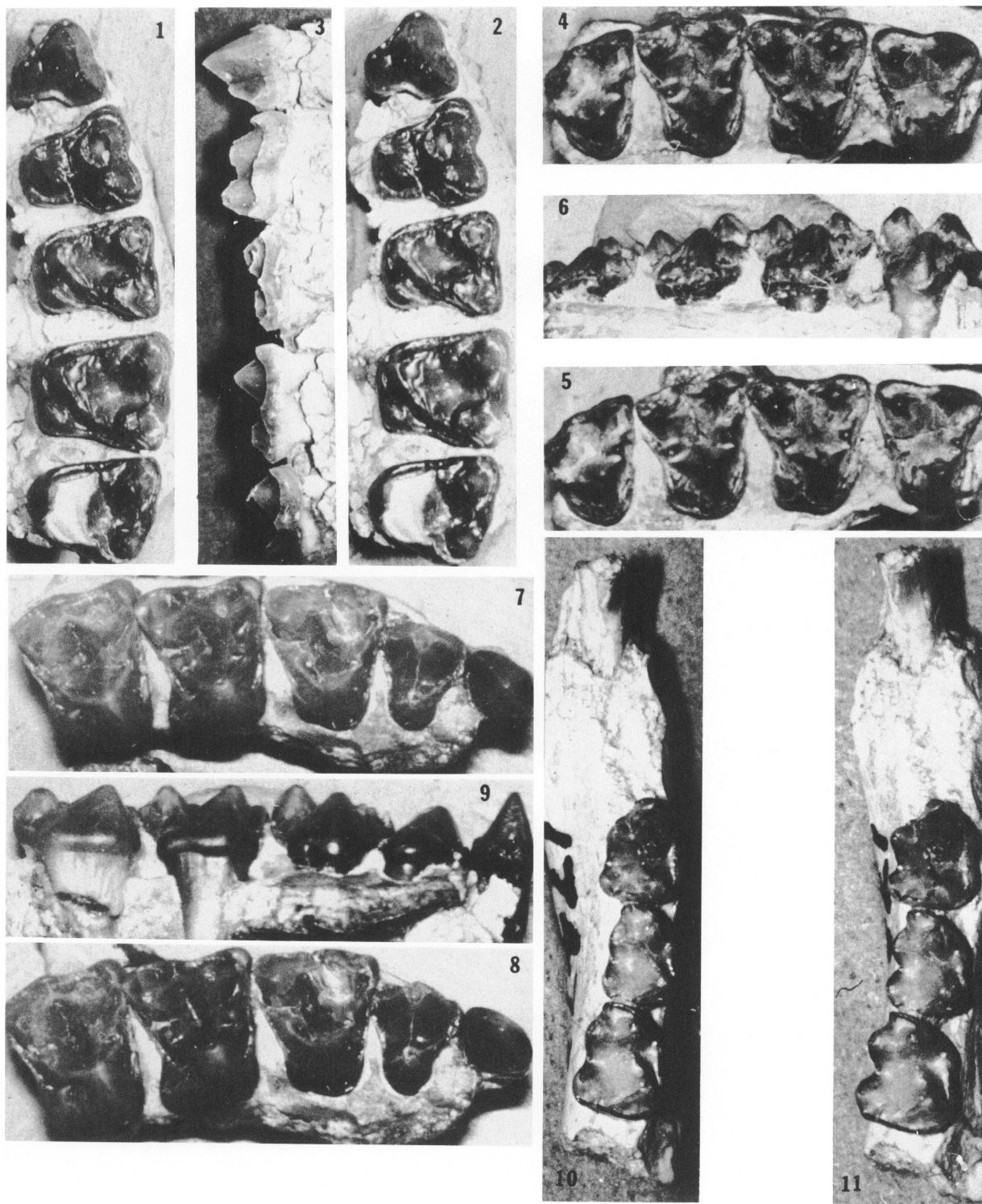


PLATE 35

- 1, 2. *Microsyops latidens*, right P_3-M_2 , Y.P.M. No. 18702, from Lysite beds of the "Buffalo Basin" within the Big Horn Basin, Wyoming, occlusal view. $\times 4.8$.
- 3, 4. *Microsyops angustidens*, left P^4-M^1 , A.M.N.H. No. 16875, from upper Gray Bull beds, Big Horn Basin, Wyoming, occlusal view. $\times 5$.
- 5, 6. *Microsyops angustidens*, type, A.M.N.H. No. 15073, left P_3-M_3 , and A.M.N.H. No. 16836, left P_4-M_2 , both from Gray Bull beds, Big Horn Basin, Wyoming. $\times 5$.
- 7, 8. *Microsyops latidens*, left P_4-M_3 , A.M.N.H. No. 12753, from Lysite beds, Wind River Basin, Wyoming, occlusal view. $\times 5$.

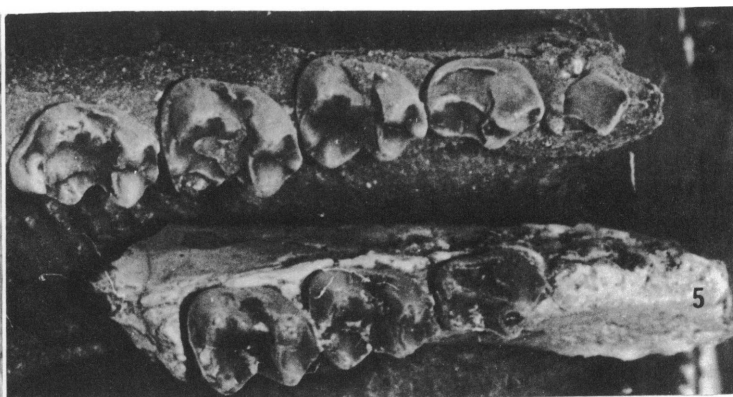


PLATE 36

Microsyops latidens. 1. Right mandible with partially broken but complete dentition, A.M.N.H. No. 14695, from Lysite beds, Wind River Basin, Wyoming, lateral view. $\times 5$. 2. Right M_{1-2} , A.M.N.H. No. 8238, from Lysite beds, Wind River Basin, Wyoming, lingual view. $\times 5$. 3, 4. P_4 - M_2 in two mandible fragments, U.S.N.M. No. 22110 (left) and U.S.N.M. No. 22114 (right), from the New Fork Member, Wasatch Formation, La Barge local fauna, Wyoming, occlusal view. $\times 5$. 5-8. Upper right incisor, U.S.N.M. No. 19319, from the New Fork Member, Wasatch Formation, Wyoming, lingual, buccal, medial, and lateral views. $\times 5$. 9, 10. Left I, P_3 - M_1 , U.S.N.M. No. 22441, Knight Member, Wasatch Formation, Wyoming, occlusal view. $\times 5$. 11, 12. Right P^4 - M^1 , U.S.N.M. No. 22107, from the New Fork Member, Wasatch Formation, Wyoming, occlusal view. $\times 5$.

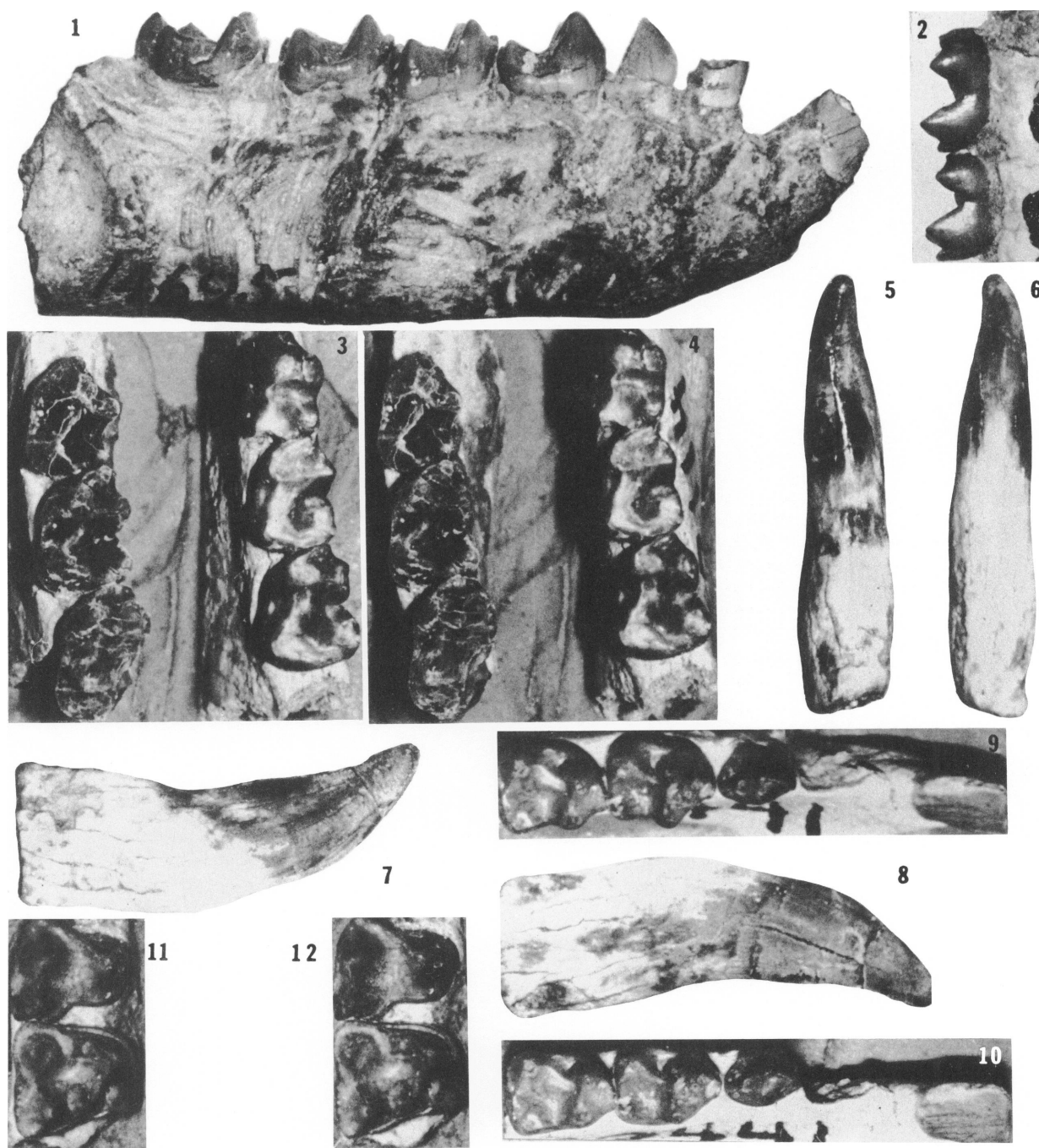


PLATE 37

1, 2. *Microsyops* cf. *M. latidens*, left and right mandible fragments with right incisor and left and right P₄-M₃, A.M.N.H. No. 55225, from the upper Huerfano Formation, A.M.N.H. locality II, Colorado, occlusal view.

3-7. *Microsyops latidens*, New Fork Member, Wasatch Formation, Wyoming. 3, 4. Left P₄-M₁, U.S.N.M. No. 19322, occlusal view. 5-7. Right P⁴-M³, U.S.N.M. No. 22107. 5. Buccal view. 6, 7. Occlusal view.

All ×5.

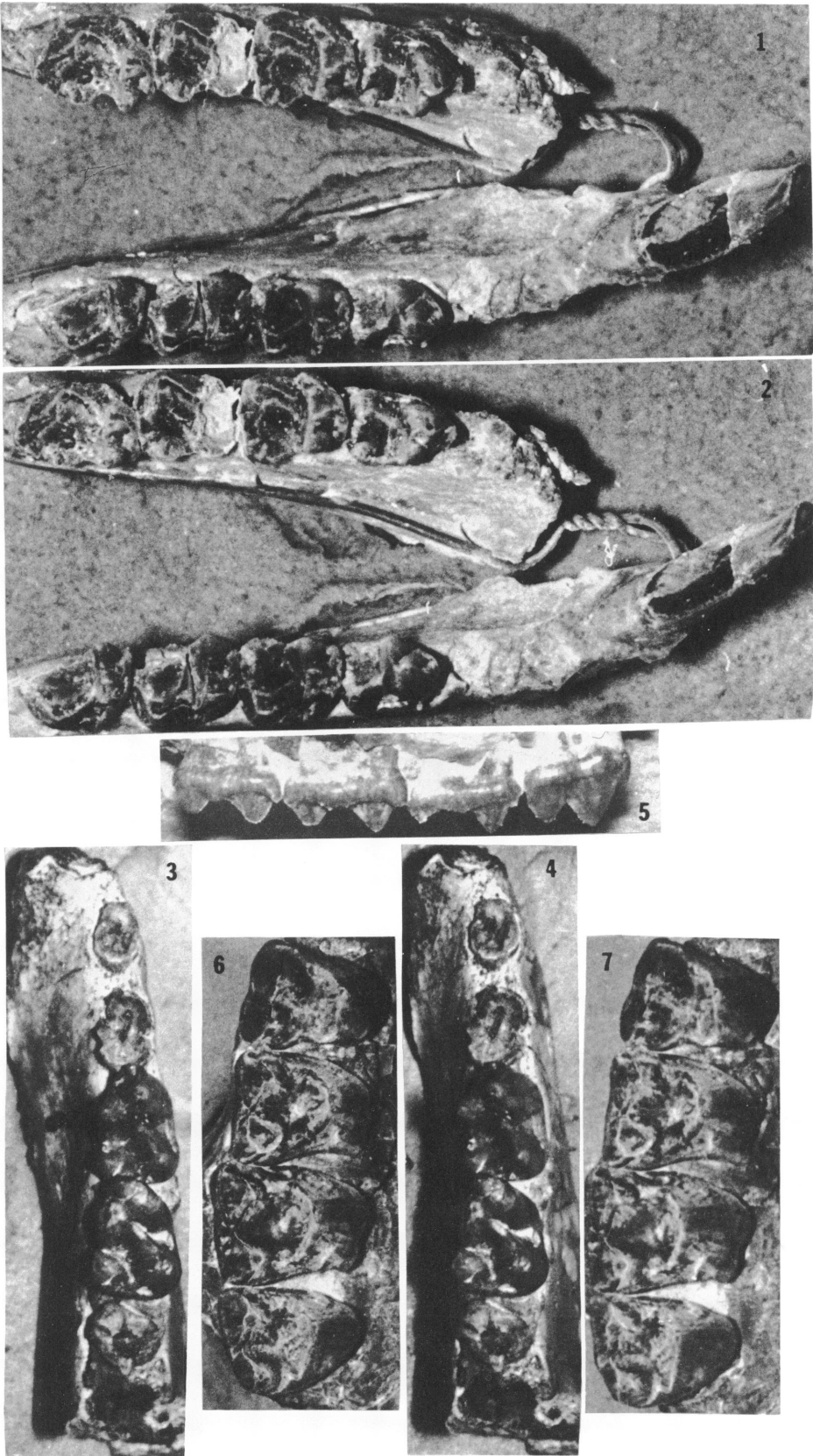


PLATE 38

Microsyops scottianus. 1-6. A.M.N.H. No. 14969, from Lost Cabin beds, Wind River Basin, Wyoming. 1, 2. P₄-M₃ in left mandible fragment (the alveoli of P₃, if the tooth ever erupted in this specimen, were filled with bone before death), occlusal view. 3, 4. Right P₃-M₂ (note presence of P₃ on right side), occlusal view. 5, 6. Right lower incisor (tip broken off) and P₂, lingual view. 7, 8. Right P₄-M₂, U.S.N.M. No. 22120, from New Fork Member, Wasatch Formation, Sublette County, Wyoming, occlusal view.

All $\times 5$.

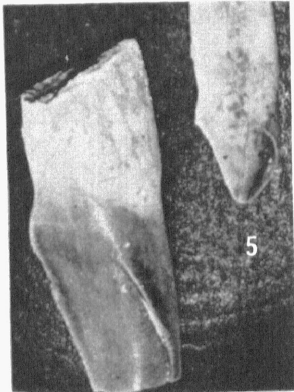
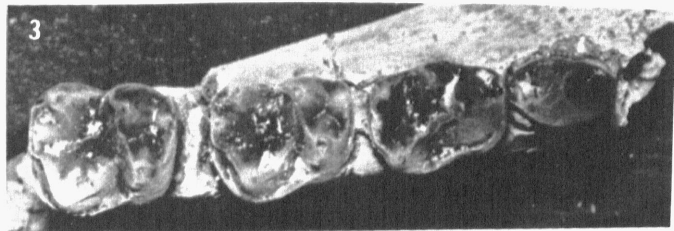


PLATE 39

- 1-4. *Microsyops scottianus*, right P_4-M_1 , A.M.N.H. No. 14703, from Lost Cabin beds, Wind River Basin, Wyoming. 1, 2. Occlusal view. 3. Lingual view. 4. Buccal view. $\times 5$.
- 5, 6. *Microsyops angustidens*, right P_4-M_3 (left) and right P_4-M_2 (right), A.M.N.H. Nos. 15690 and 15080, from upper Gray Bull beds, Big Horn Basin, Wyoming, occlusal view. $\times 5$.
- 7, 8. *Microsyops elegans*, left P_4-M_2 , type, Y.P.M. No. 11794, from lower Bridger beds, Bridger Basin, Wyoming, occlusal view. $\times 5$.
- 9, 10. *Microsyops annectens*, left M^{2-3} , U.S.N.M. No. 17817, from Bridger D beds, Bridger Basin, Wyoming, occlusal view. $\times 5$.

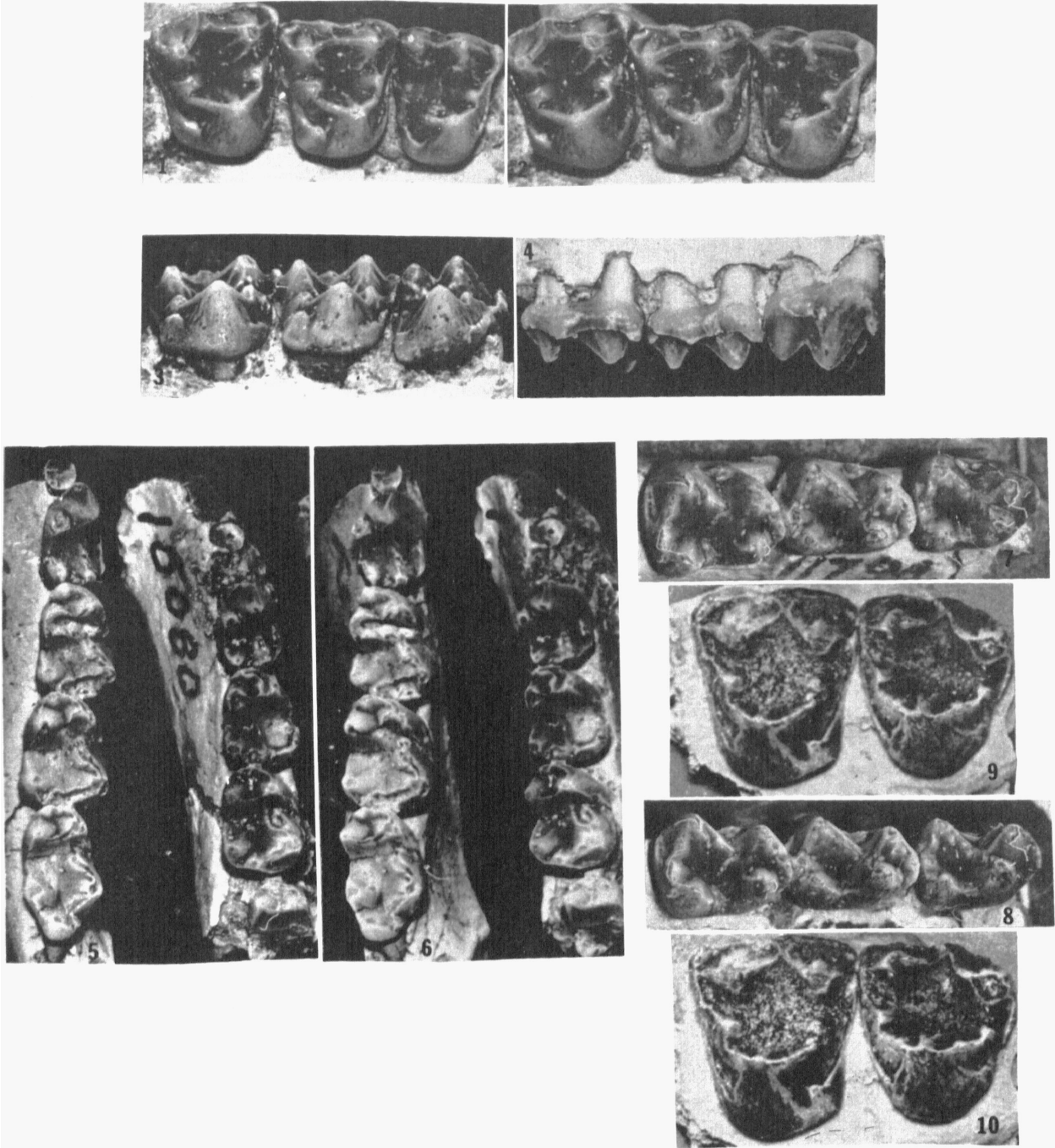


PLATE 40

1, 2. *Microsyops* cf. *M. latidens*, fragmentary right mandible with incisor and P₄-M₃, A.M.N.H. No. 55225, from the upper Huerfano Formation, A.M.N.H. locality II, Colorado, medial and lateral views.

3-5. *Microsyops latidens*, right P₄-M₃, U.S.N.M. No. 22107, from the New Fork Member of the Wasatch Formation, Wyoming. 3, 4. Occlusal view. 5. Lingual view.

6, 7. *Microsyops* cf. *M. latidens*, left P₄-M₃, A.M.N.H. No. 17482, from the upper Huerfano Formation, Colorado, occlusal view.

All $\times 5$.

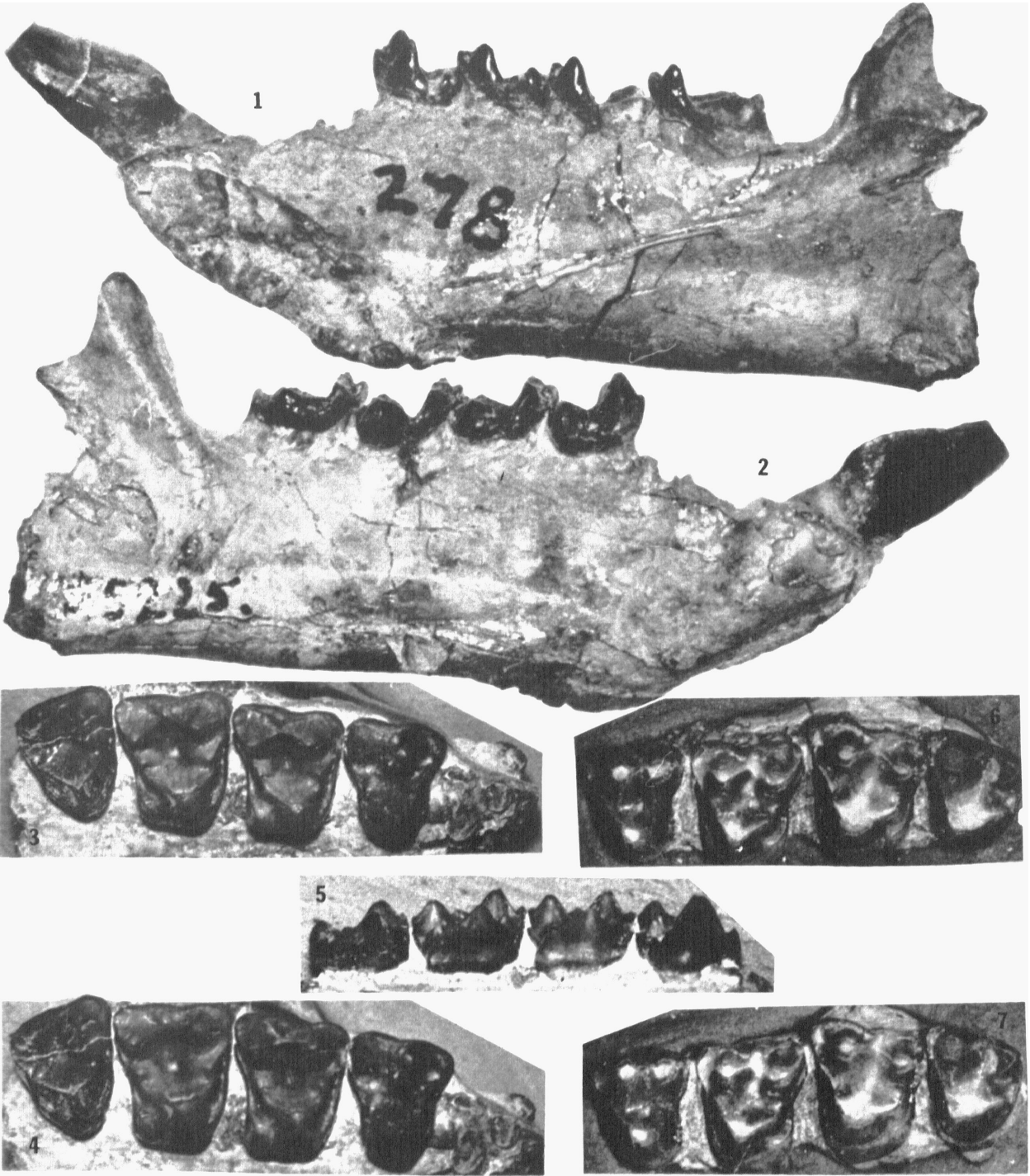


PLATE 41

1-3. *Microsyops* cf. *M. latidens*, crushed skull of young adult, A.M.N.H. No. 55286, from the upper Huerfano Formation, A.M.N.H. locality II, Colorado. 1, 2. Dorsal view. 3. Posterior view. $\times 2$.

4, 5. *Microsyops lundeliusi*, latex endocranial cast of somewhat crushed skull (see pl. 52), A.M.N.H. No. 55284, from the upper Huerfano Formation, A.M.N.H. locality II, Colorado, dorsal view. $\times 1.5$.

6-17. *Microsyops* sp., isolated upper and lower teeth catalogued under Y.P.M. Nos. 19892 and 19893, Y.P.M. locality III of Carter Mountain, Big Horn Basin, Wyoming. $\times 5$.

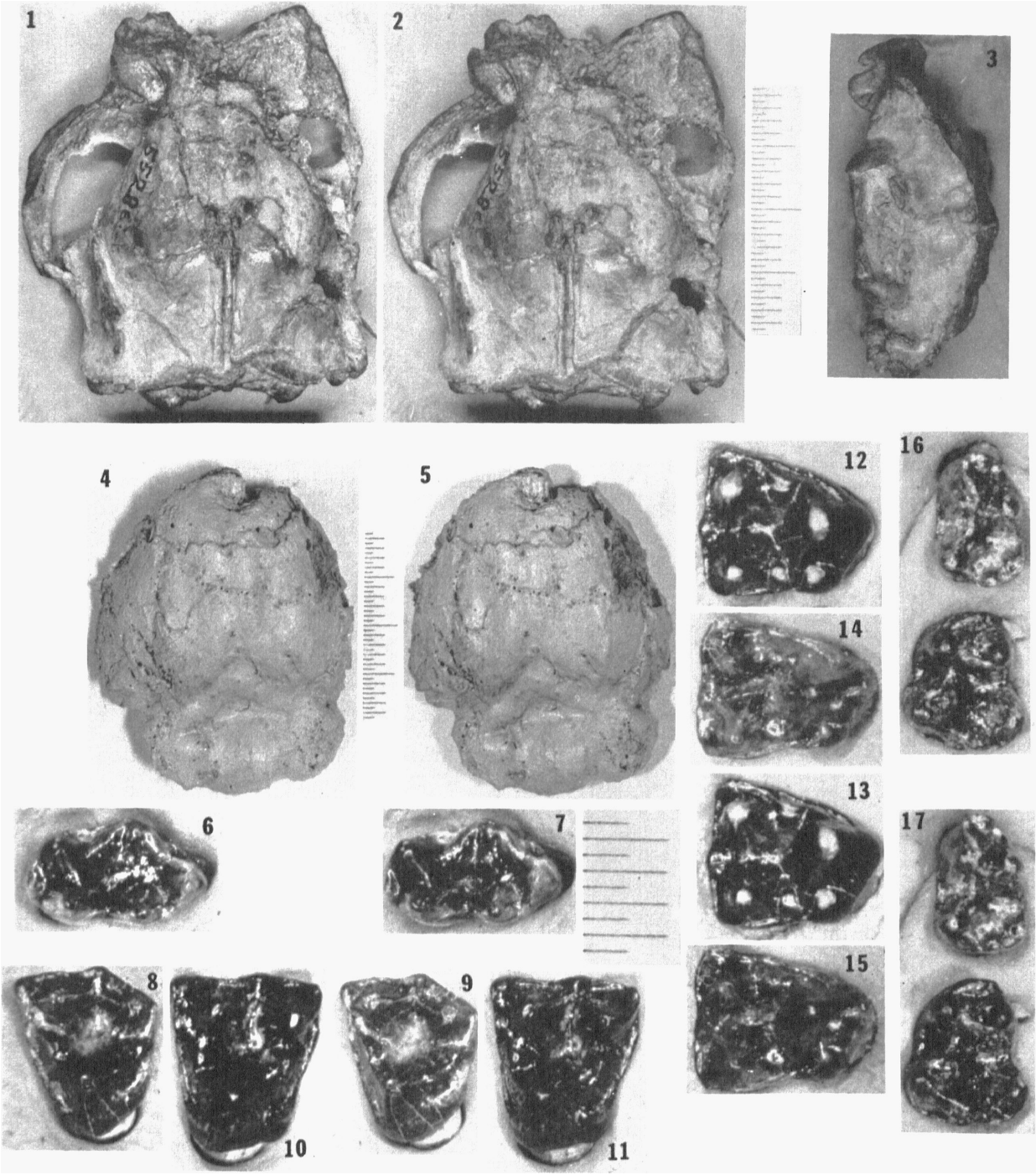


PLATE 42

Microsypops cf. *M. laudens*, A.M.N.H. No. 55286, from the upper Huerfano Formation, A.M.N.H. locality II, Colorado. 1, 2, 4, 5, and 6, 7. Skull of young adult and left and right ear regions, respectively, ventral views. 3. Lateral view of skull.
1-3, $\times 2$; 4-7, $\times 5.4$.

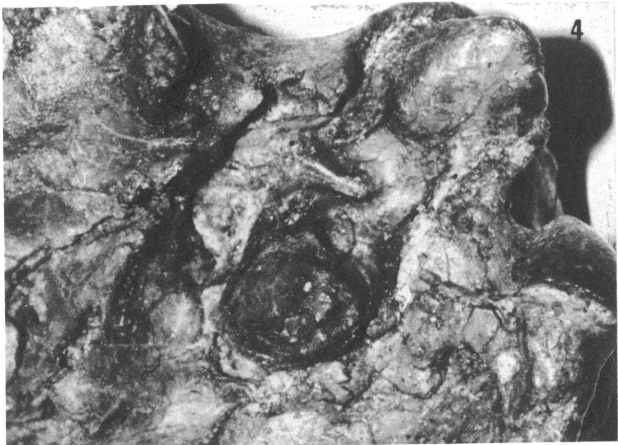
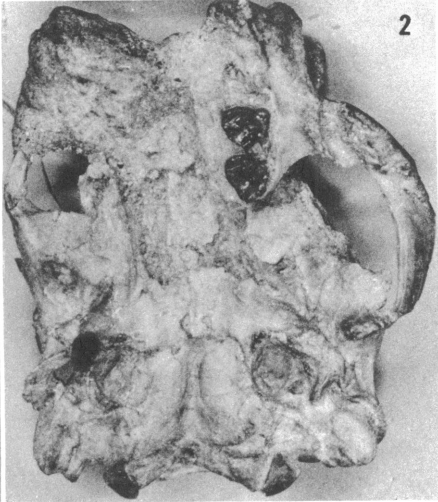
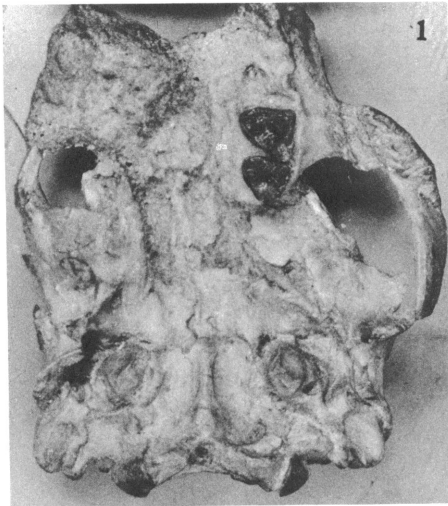


PLATE 43

Leptictis sp., A.M.N.H. No. 9316, from Oligocene beds of South Dakota, ventral view of left and right ear regions of excellently preserved skull. A bony strut bridging the facial canal lateral to the fenestra rotundum is preserved on the left ear region (1 and 2), but it is broken off on the right side. $\times 5.4$.

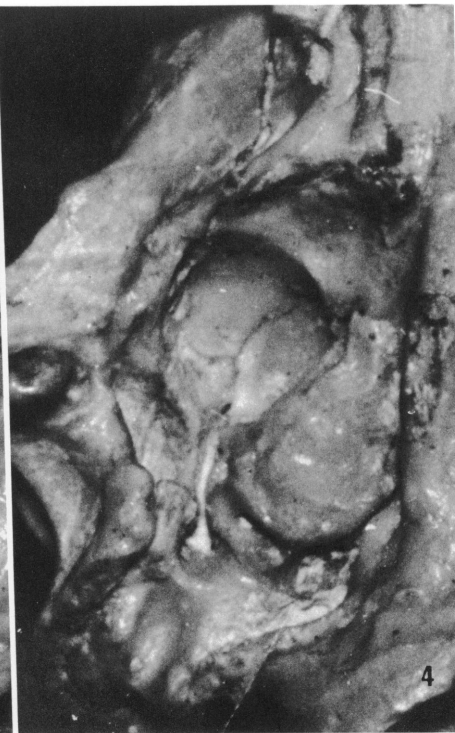


PLATE 44

Microsypops scottianus. 1-4. Left P^4-M^3 and right P^1-P^4 , U.S.N.M. No. 22117, New Fork Member, Wasatch Formation, Sublette County, Wyoming. $\times 5$. 5, 6. Left P_3-M_2 and right P_4-M_2 , U.S.N.M. Nos. 22118 (left) and 22119 (right), from the New Fork Member. $\times 5$. 7. Fragmentary left mandible, A.M.N.H. No. 14685, Lost Cabin beds, Wind River Basin, Wyoming, medial view. $\times 3$.

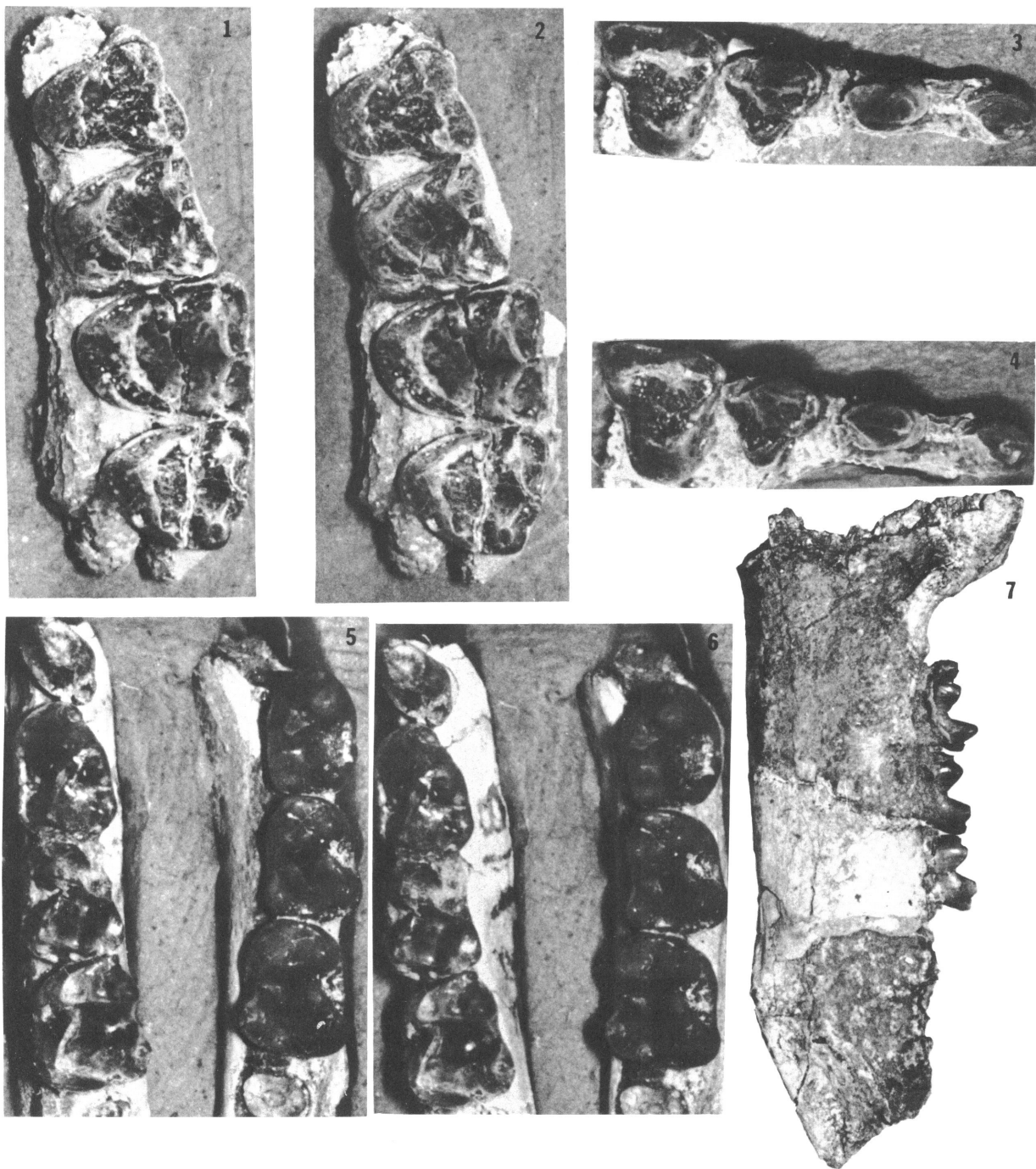


PLATE 45

1, 2. *Microsyops elegans*, type of "*Mesacodon speciosus*," fragment of right mandible with broken incisor and P_3 - M_2 , Y.P.M. No. 11790, lower Bridger beds at Grizzly Buttes, Bridger Basin, Wyoming. $\times 4.8$.

3, 4. *Microsyops lundeliusi*, left M_1 - M_3 , A.M.N.H. No. 55174, upper Huerfano Formation, A.M.N.H. locality II, Colorado, occlusal view. $\times 5.2$.

5, 6. *Microsyops* cf. *M. scottianus*, right P_3 - M_2 (left; A.M.N.H. No. 17470), and right P_4 - M_3 (right; A.M.N.H. No. 17019), Huerfano Formation, Colorado, collected in 1916, occlusal views. $\times 5$.

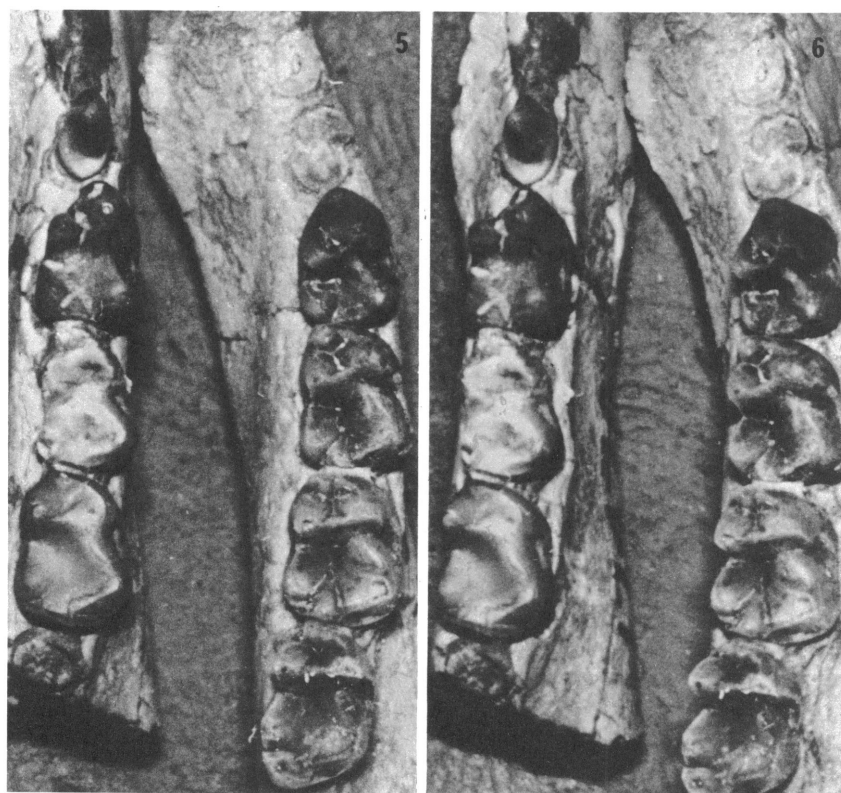
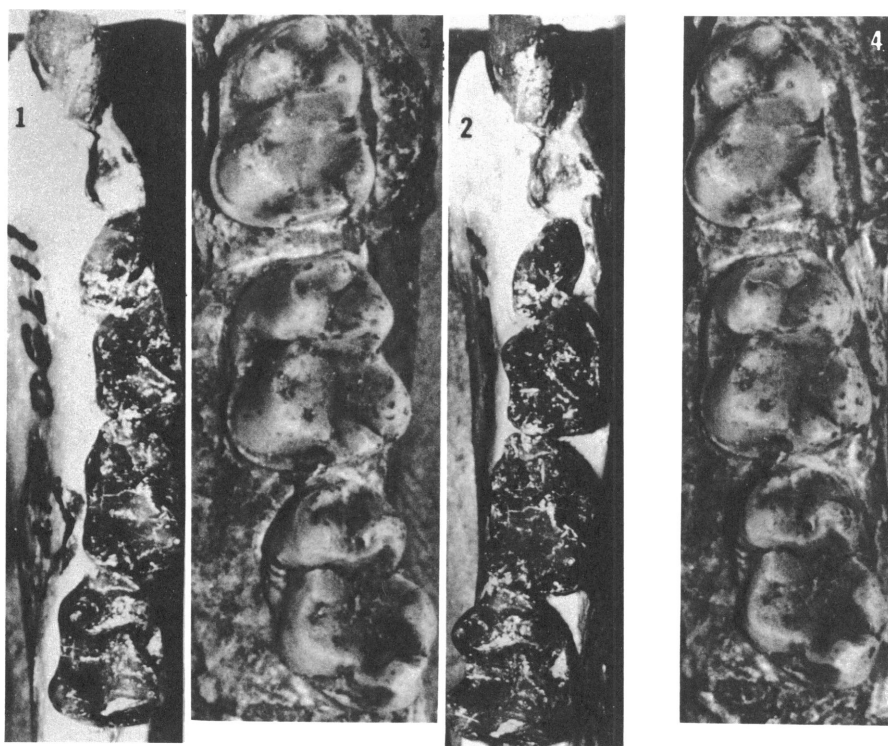


PLATE 46

Microsyops elegans, lower Bridger beds, Bridger Basin, Wyoming. 1, 2. Left P^{1-2} , lingual half of P^4 , and M^{2-3} , A.M.N.H. No. 13041, occlusal view. 3, 4. Left M^{1-3} , A.M.N.H. No. 11431, occlusal view. 5-8. Y.P.M. No. 14569. 5, 6. Right P_4-M_2 , occlusal view. 7, 8. Left M_{2-3} , occlusal view.
All $\times 5$.

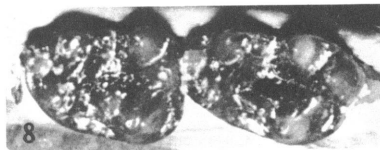
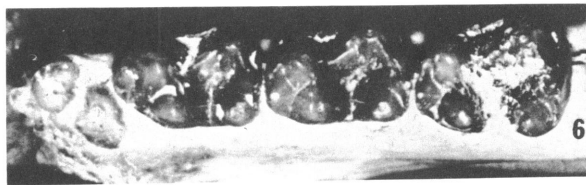
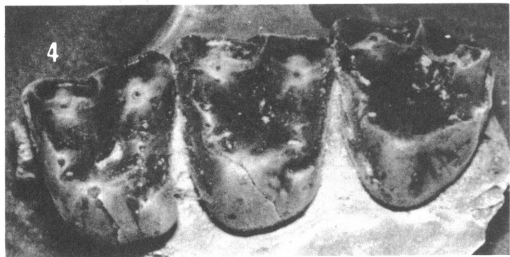
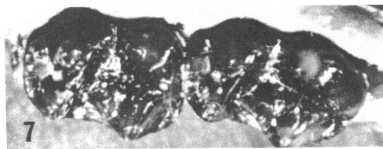
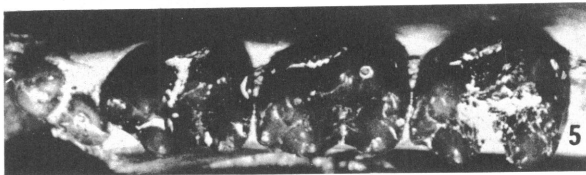
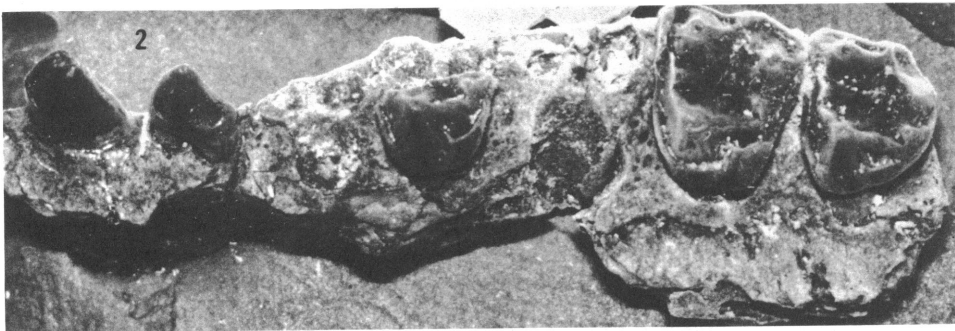
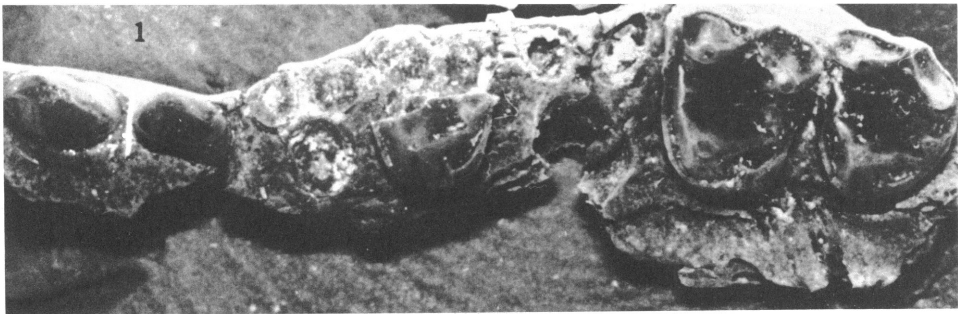


PLATE 47

Microsyops elegans, Bridger B beds, Wyoming. 1-5. Right tibia, with distal end broken off, U.S.N.M. No. 13440, anterior, posterior, medial, lateral, and proximal views. 6, 7. Partial left mandible with P₄-M₃, U.S.N.M. No. 17813, medial and lateral views.
All $\times 3$.



PLATE 48

Microsyops lundeliusi, type, U.S.N.M. No. 18371, Lost Cabin beds, Wind River Basin, Wyoming. 1, 2, 5, and 6. Fragmentary right mandible with talonid of M₁, M₂, and talonid of M₃. 1, 2. Lateral and medial views. 5, 6. Occlusal views. 3, 4, 7, and 8. Fragment of posterior part of right mandible with condyle and enlarged right upper incisor. 3, 4. Medial and lateral views. 7, 8. Buccal and lingual views.

All ×3.

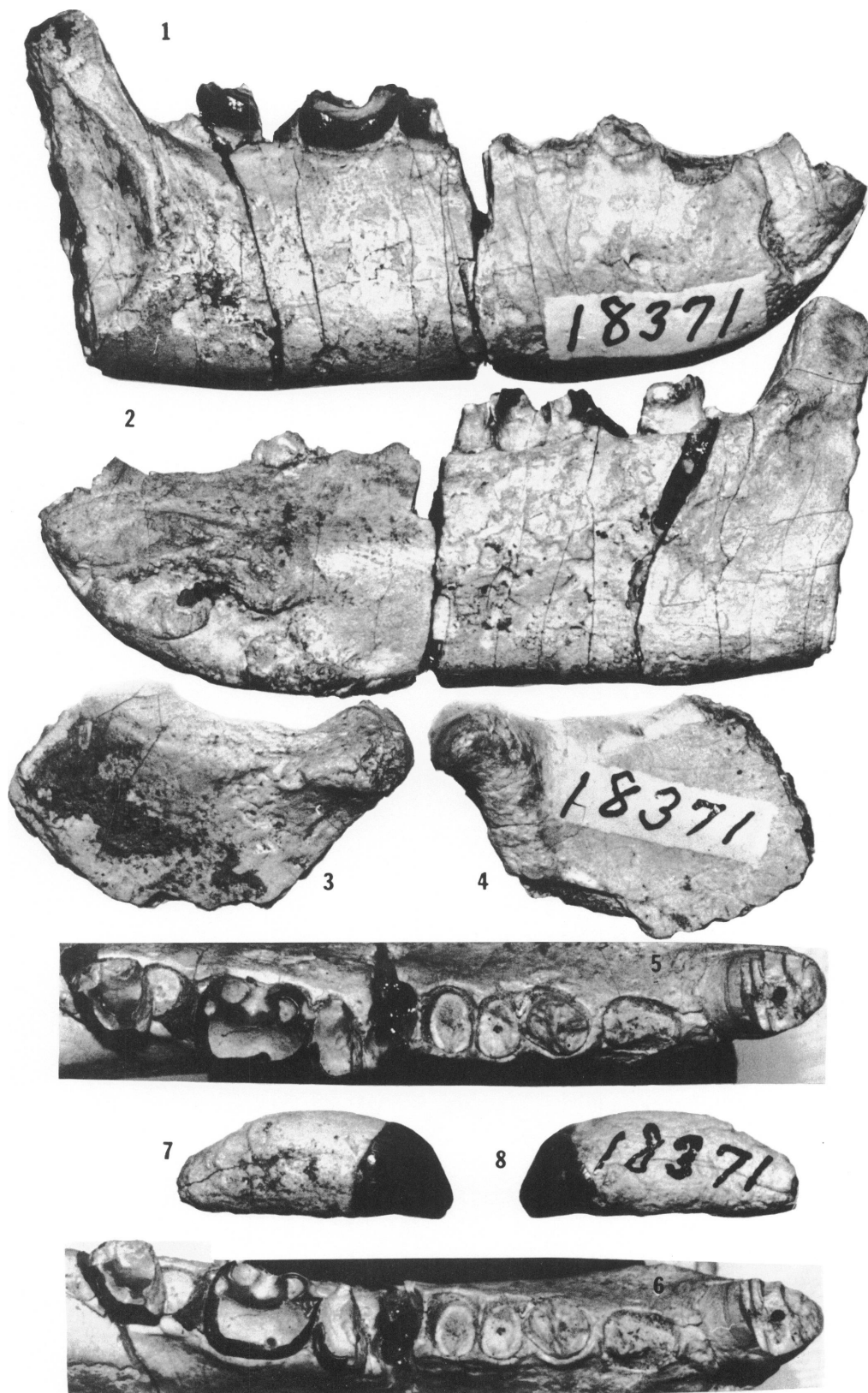


PLATE 49

Microsyops lundeliusi. 1, 2. Left P³-M³, A.M.N.H. No. 55214, Huerfano Formation, A.M.N.H. locality I, Colorado, occlusal view. 3-5. Right M¹⁻², A.M.N.H. No. 55213, upper Huerfano Formation, A.M.N.H. locality II. 3. Buccal view. 4, 5. Occlusal view. 9, 10. Left P⁴-M¹, U.C.M. No. 20807, upper Huerfano Formation, A.M.N.H. locality II, occlusal view.

All ×5.

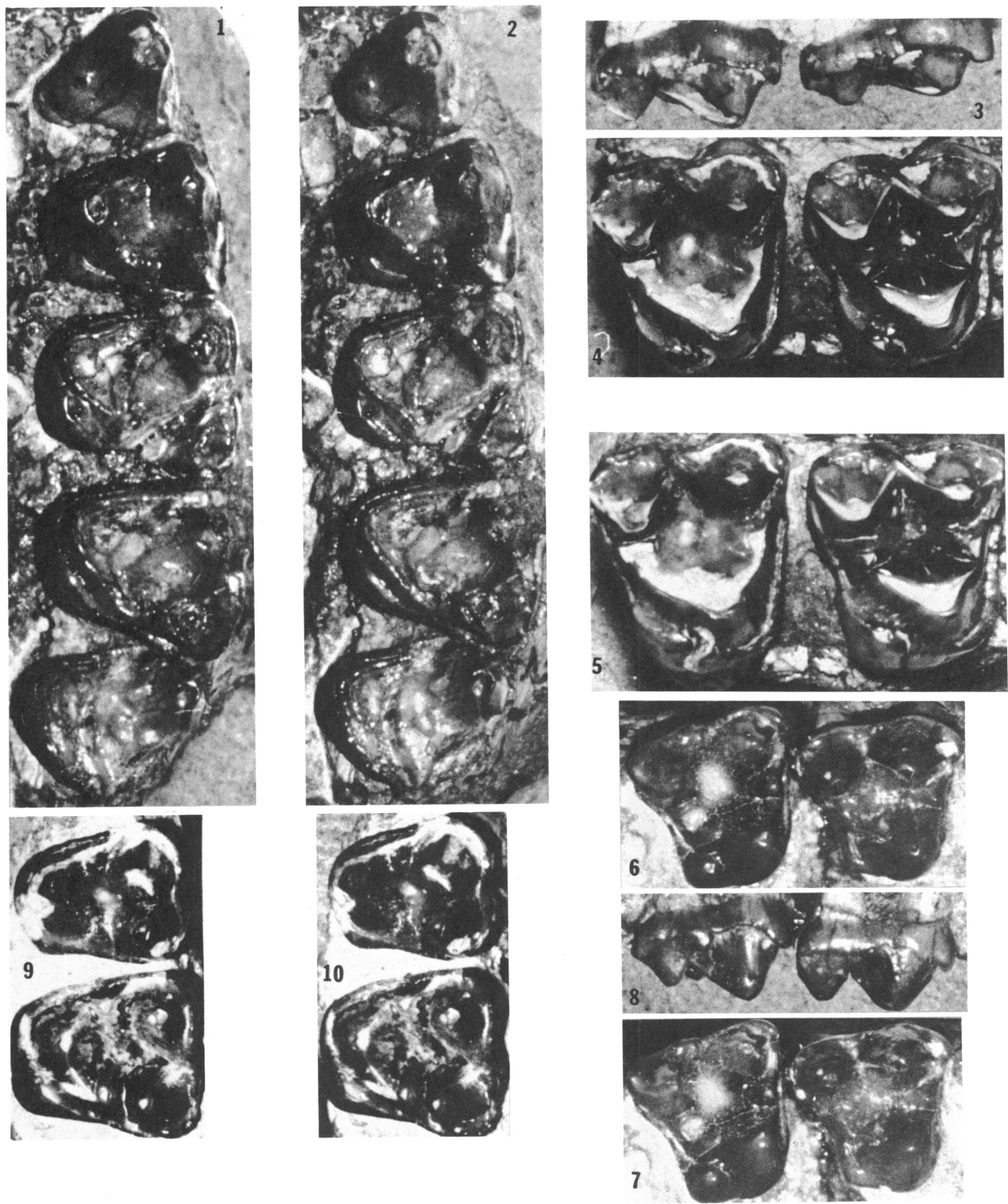


PLATE 50

Microsyops lundehiusi, upper Huerfano Formation, A.M.N.H. locality II, Colorado.
1. Almost complete left mandible, with P_2 and the angle of the mandible missing, A.M.N.H. No. 55285, lateral view. $\times 3$. 2, 3. Left P^{2-3} , U.C.M. No. 20806, occlusal view. $\times 5$. 4, 5. Right upper dentition of crushed skull, A.M.N.H. No. 55284 (see pl. 52), occlusal view; the crowns of the canine and P^2 are missing. $\times 2.75$.

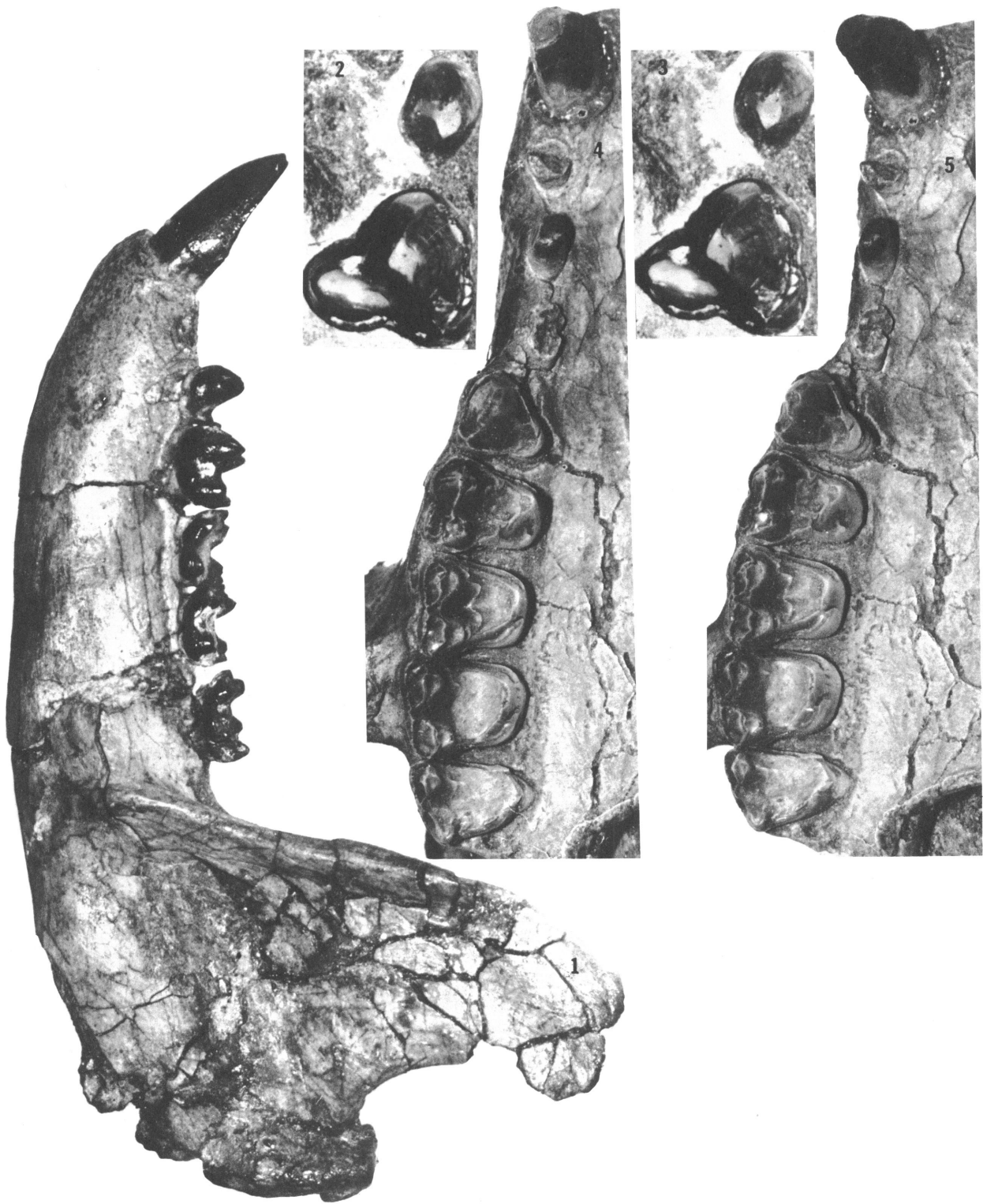


PLATE 51

Microsyops lundeliusi, upper Huerfano Formation, A.M.N.H. locality II, Colorado.
1-4. DP³⁻⁴ and unerupted M¹ (or possibly dP²⁻³ and unerupted dP⁴), A.M.N.H. No. 55208.
1, 2. Occlusal view. 3. Lingual view. 4. Buccal view. $\times 5$. 5. Almost complete left mandible
(see pl. 50, fig. 1), A.M.N.H. No. 55285, medial view. $\times 3$.

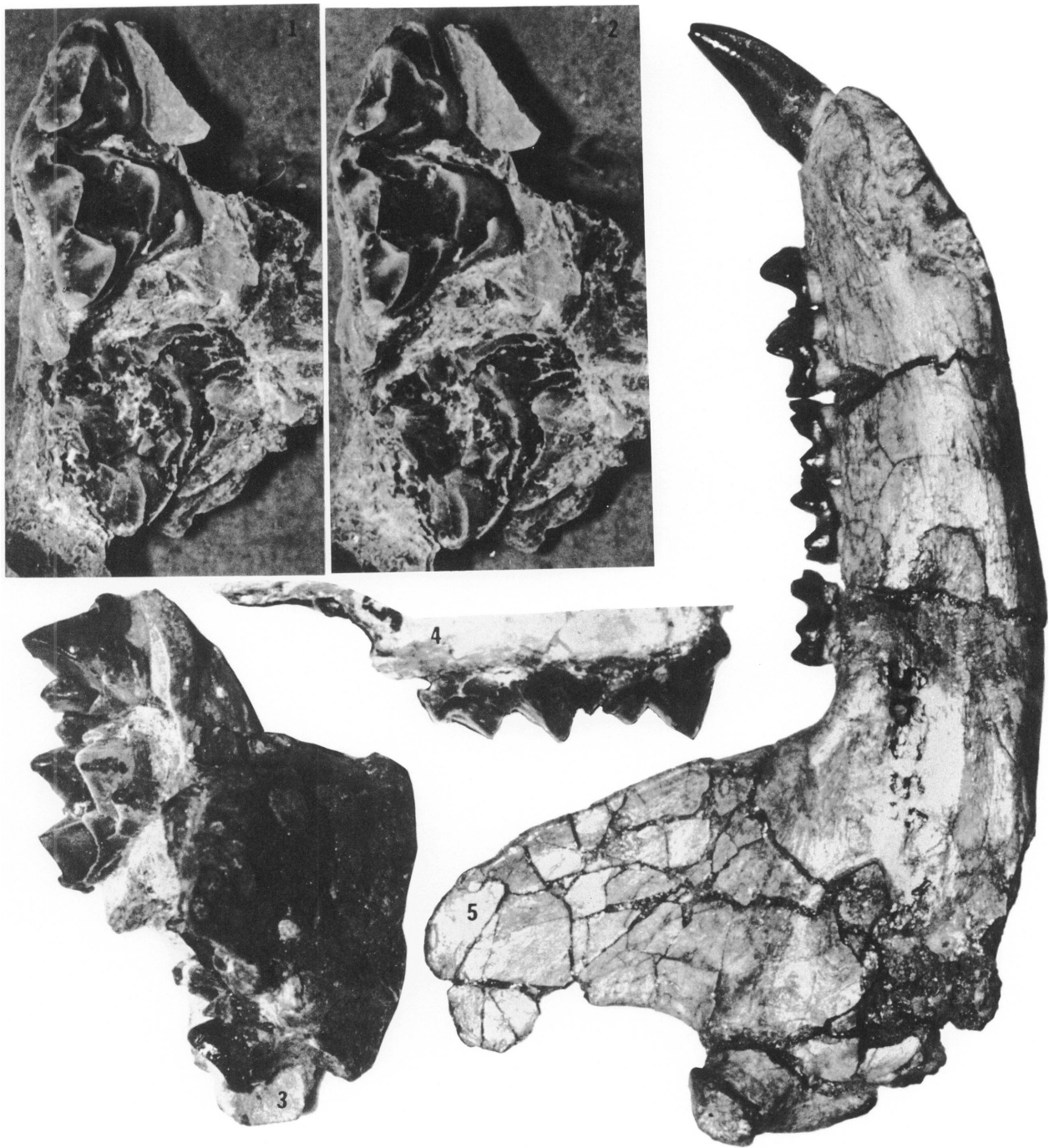
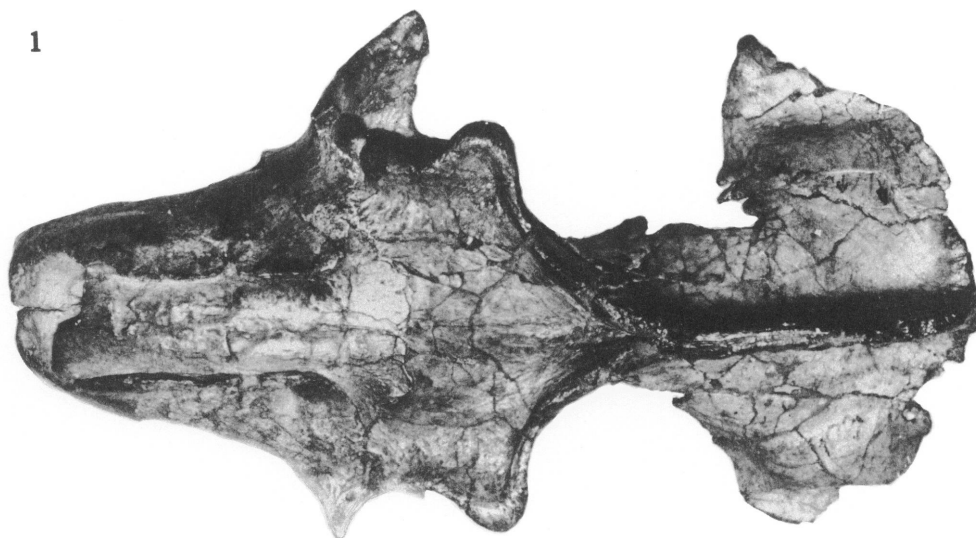


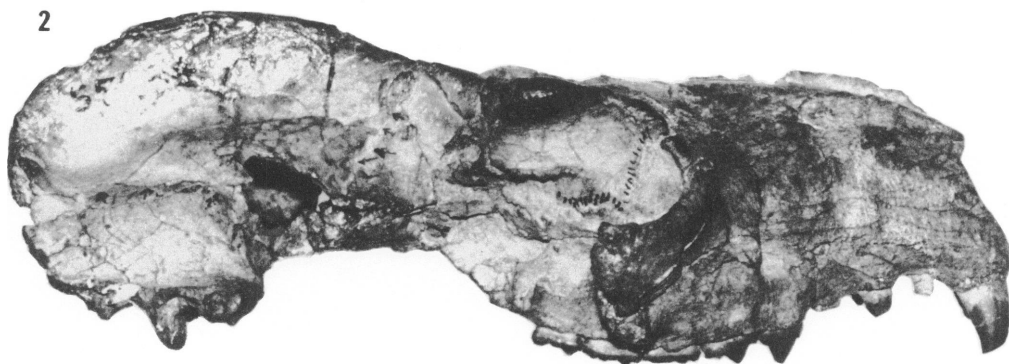
PLATE 52

Microsyops lundeliusi, incomplete, crushed skull, A.M.N.H. No. 55284, upper Huerfano Formation, Colorado. 1. Dorsal view. 2. Lateral view. 3. Ventral view. $\times 1.3$.

1



2



3

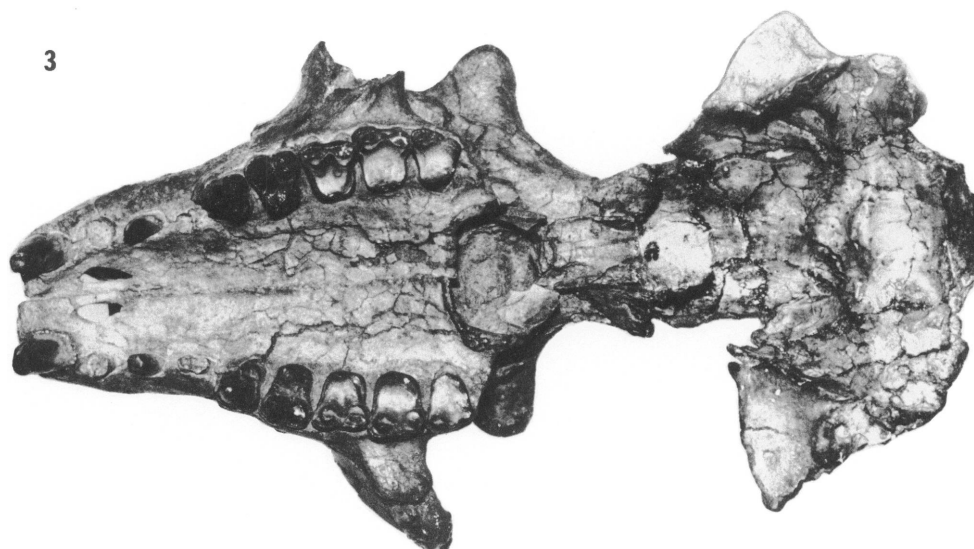


PLATE 53

Microsyops annectens. 1, 2. Left M_3 , type, Y.P.M. No. 11791, from upper Bridger beds, Henry's Fork, Bridger Basin, Wyoming, occlusal view. $\times 5.2$. 3-6. Type of "*Microsyops schlosseri*," Y.P.M. No. 13242, from upper Bridger beds, Henry's Fork, Wyoming. 3, 4. Left M_{2-3} , occlusal view. $\times 5$. 5, 6. Badly worn and shattered left M^{2-3} , occlusal view. $\times 5$. 7, 8. Right M^{1-3} , Y.P.M. No. 13258, from upper Bridger beds, Wyoming, occlusal view. $\times 5$.

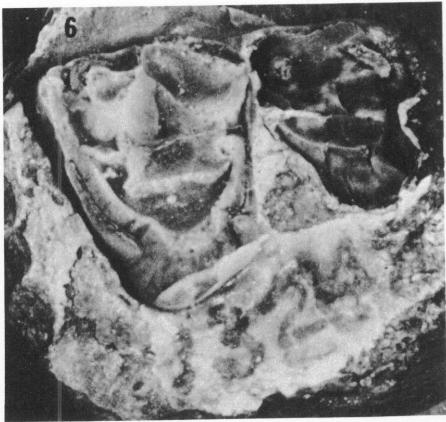
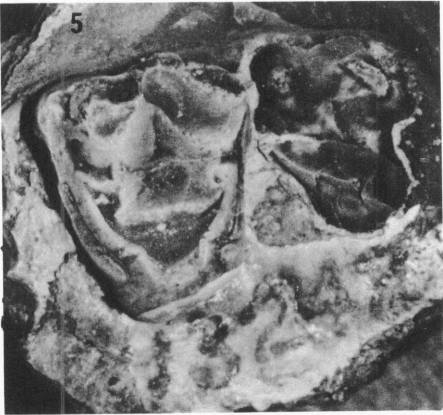
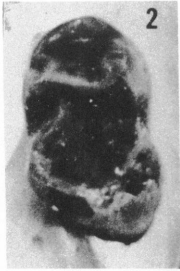
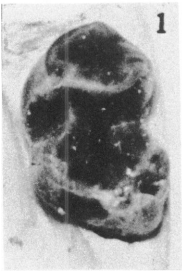


PLATE 54

Microsyops annectens. 1-4. A.M.N.H. No. 12050, Bridger D beds, Henry's Fork, Bridger Basin, Wyoming. 1, 2. Left P^4-M^3 , occlusal view. 3, 4. M_{2-3} , occlusal view. 5, 6. Left mandible fragment with broken incisor and P_4-M_2 , A.M.N.H. No. 12595, from upper Bridger beds, Henry's Fork, Bridger Basin, Wyoming, occlusal view. 7. Left M^{1-2} , Y.P.M. No. 13243, upper Bridger beds, Bridger Basin, Wyoming, occlusal view.

All $\times 5$.

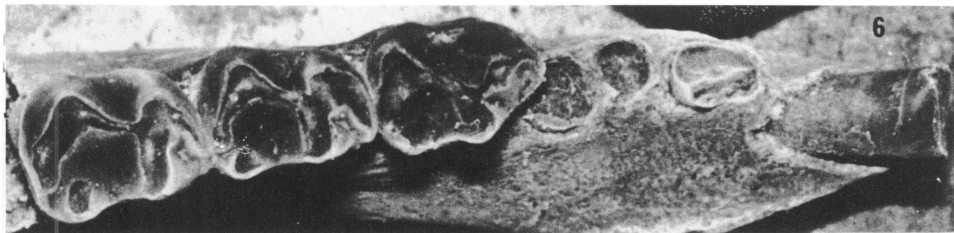
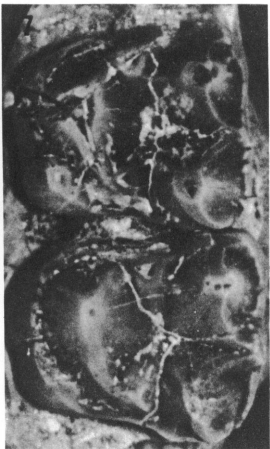
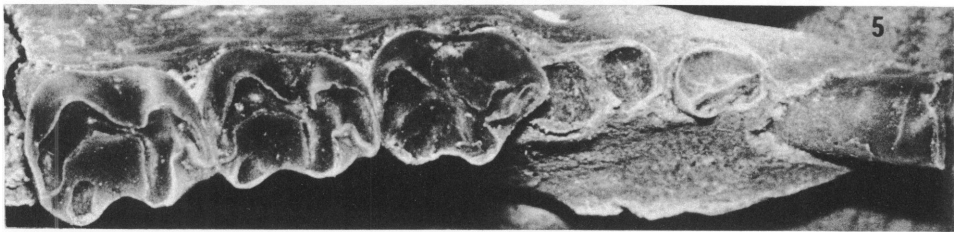
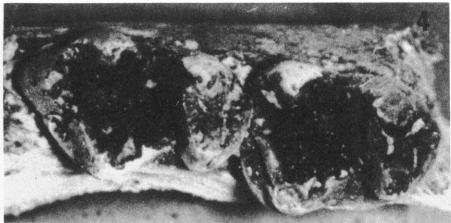
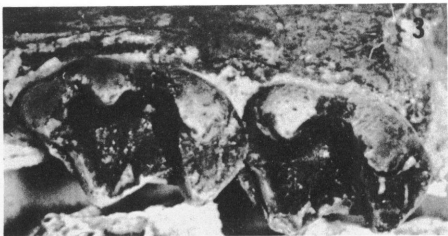
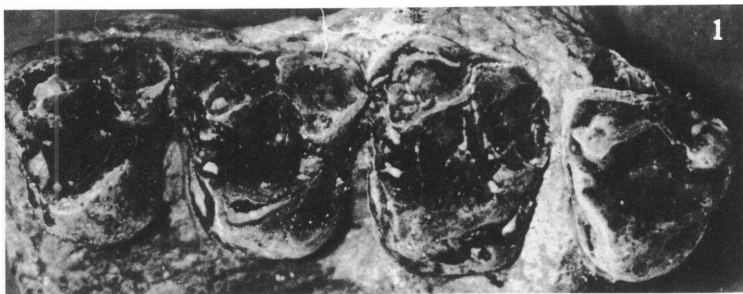


PLATE 55

Microsyops kratos, left mandible fragment with dP₃, P₄-M₃, L.A.C.M. No. CIT2032, from the Poway Formation, California. 1. Lateral view. ×3. 2. Medial view. ×3. 3, 4. Occlusal view. ×5.

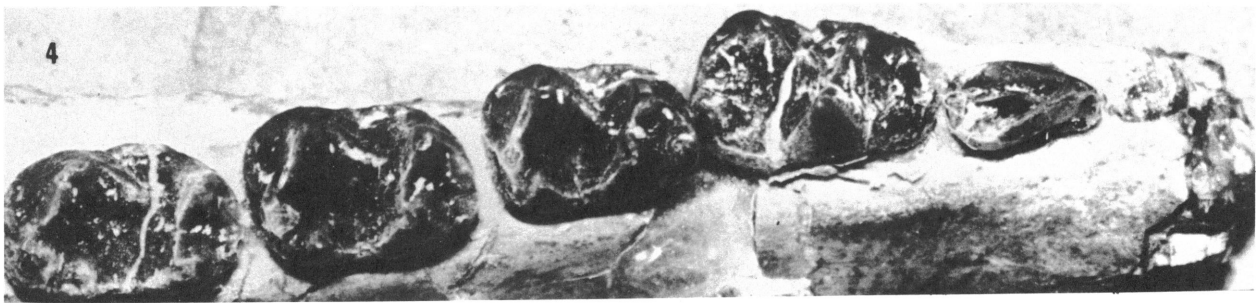
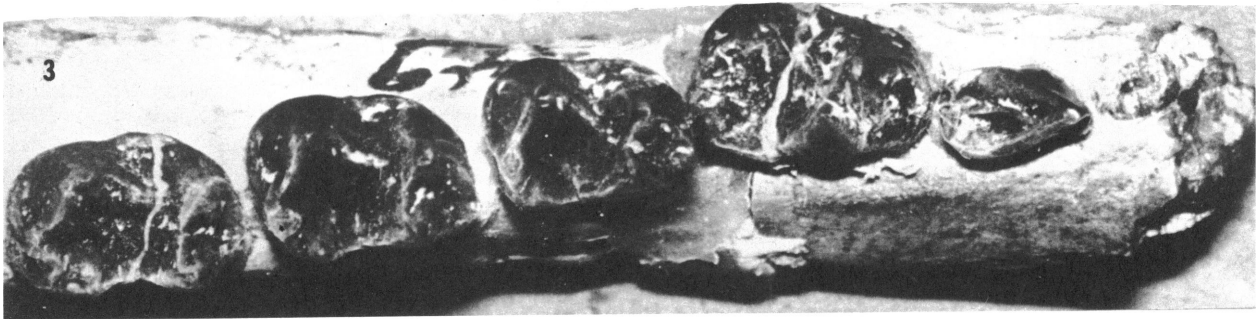


PLATE 56

Craseops sylvestris, Tapo Ranch Fauna, Sespe Formation, California. 1-5. Composite M^{1-3} , L.A.C.M. No. CIT1580, type. 1, 2. Occlusal view. 3, 4. Buccal view. 5. Lingual view. 6-9. Right M_{2-3} , L.A.C.M. No. CIT1399. 6. Buccal view. 7. Lingual view. 8, 9. Occlusal view.

All $\times 5$.

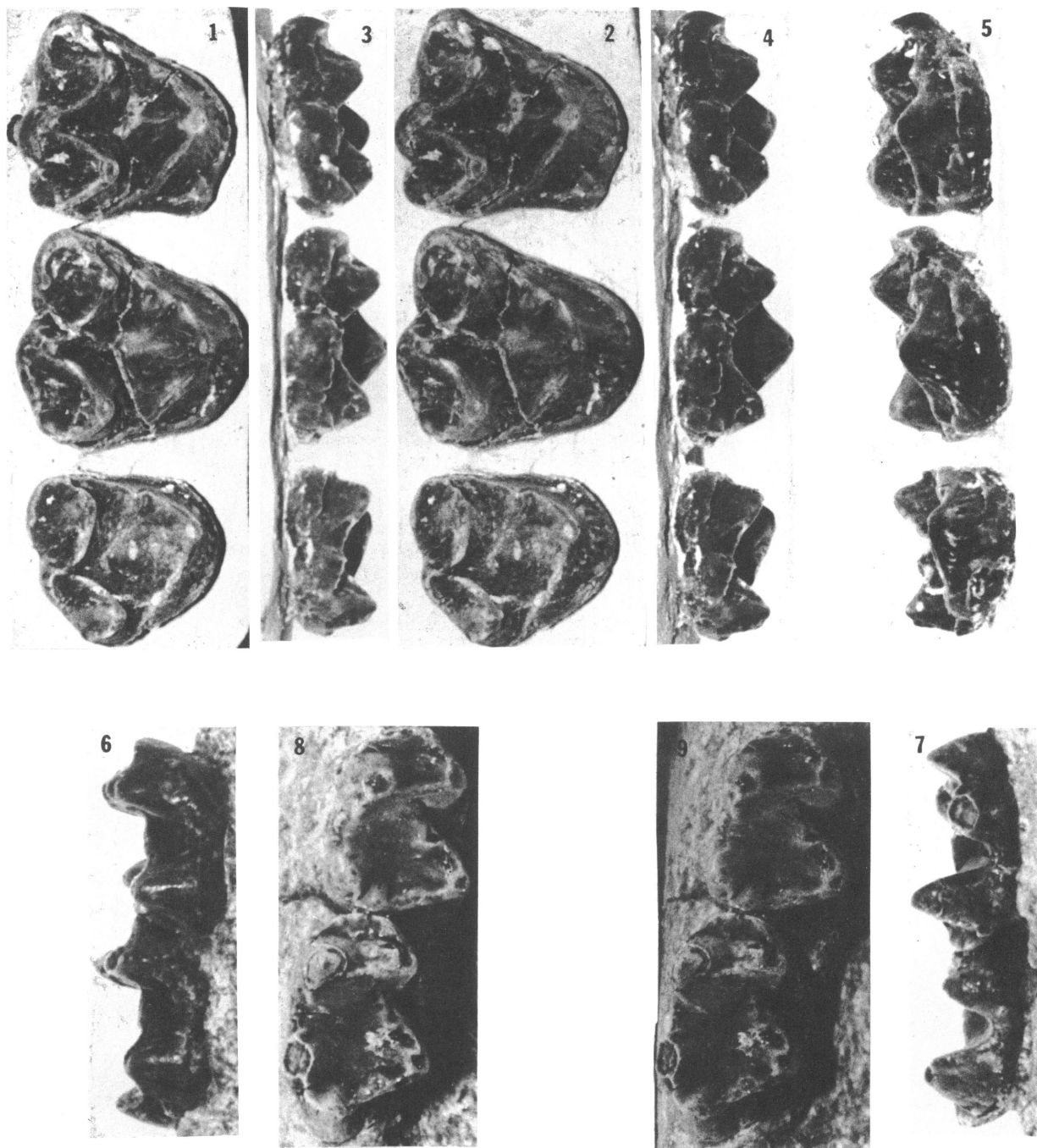


PLATE 57

1-12. *Purgatorius unio*, Purgatory Hill locality, Tullock Formation, McCone County, Montana. 1-4. Right upper molar (above), type, U.M. No. VP1597, and right upper molar (below), U.M. No. VP1652. 1, 2. Occlusal view. 3. Lingual view. 4. Buccal view. $\times 8.75$. 5-8. Right lower molar (left on 5-7, right on 8), U.M. No. VP1504, and left M_3 (right on 5-7, left on 8), U.M. No. VP1506, occlusal, lingual, and buccal view. $\times 8.75$. 9-12. From left to right, uncatalogued teeth of the University of Minnesota collection: left P^4 (?*Purgatorius*), right upper molars and right M_3 . 9, 10. Occlusal view. 11. Lingual view. 12. Buccal view. $\times 8.75$.

13-16. *Purgatorius ceratops* (?= *Purgatorius unio*), right lower molar, type, U.M. No. VP1547, from Harbicht Hill locality, Hell Creek Formation, McCone County, Montana. 13, 14. Occlusal view. 15. Buccal view. 16. Lingual view. $\times 8.75$.

