BULLETIN OF THE PEABODY MUSEUM OF NATURAL HISTORY, YALE UNIVERSITY

The *Bulletin of the Peabody Museum of Natural History* was published as peer-reviewed monographs from inception in 1925 through 2004. Volumes reported on original research in the natural sciences based on the collections of the Peabody Museum of Natural History at Yale University, covering diverse topics that include evolution, phylogeny, taxonomy, systematics, biology, botany, zoology, invertebrate and vertebrate paleontology and paleoecology, paleobotany, and archaeology.

Beginning with Volume 47 (2006), the *Bulletin of the Peabody Museum of Natural History* was converted to a journal format.
Journal issues are available from BioOne Complete at https://bioone.org/.

The original monograph series incorporated the *Bulletin of the Bingham Oceanographic Collection,* which ceased independent publication with Volume 19, Article 2 (1967). The *Postilla* series, which ceased publication with Number 232 (2004), was merged into the journal. These archives are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at https://elischolar.library.yale.edu/.

This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
https://creativecommons.org/licenses/by-nc-sa/4.0/

Yale PEABODY MUSEUM OF NATURAL HISTORY

P.O. Box 208118 | New Haven CT 06520-8118 USA | peabody.yale.edu

Systematics, Functional Morphology and Macroevolution of the Extinct Mammalian Order Taeniodonta

ROBERT MILTON SCHOCH

College of Basic Studies and Department of Geology
Boston University

and

Peabody Museum of Natural History
Yale University

BULLETIN 42 • 21 JULY 1986
PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
NEW HAVEN, CONNECTICUT 06511

Bulletins published by the Peabody Museum of Natural History, Yale University, are numbered consecutively as independent monographs and appear at irregular intervals. Shorter papers are published at frequent intervals in the Peabody Museum *Postilla* series.

The *Peabody Museum Bulletin* incorporates the *Bulletin of the Bingham Oceanographic Collection,* which ceased independent publication after Vol. 19, Article 2 (1967).

Communications concerning purchase or exchange of publications should be addressed to the Publications Office, Peabody Museum of Natural History, Yale University, 170 Whitney Avenue, P.O. Box 6666, New Haven, CT 06511, U.S.A.

Printed in the United States of America
ISBN No. 0-912532-04

CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

FOREWORD

This monograph was written as a doctoral dissertation in the Department of Geology and Geophysics at Yale University during the period 1979 to 1982 while the author held a National Science Foundation Graduate Fellowship. The monograph was essentially complete by the summer of 1982 and was reviewed by the dissertation committee (Drs. John H. Ostrom and Keith S. Thomson of Yale University, Dr. J. David Archibald of San Diego State University, and Dr. Malcolm C. McKenna of the American Museum of Natural History) during the fall of 1982. On 14 December 1982 the dissertation was successfully defended at a public defense held in the Department of Geology and Geophysics at Yale. The dissertation was submitted to the Graduate School of Yale University in the spring of 1983, and the degree of Doctor of Philosophy was conferred in May 1983.

In June 1983 the monograph was submitted to the Publications Office of the Peabody Museum of Natural History, Yale University, for consideration as a volume in the series *Bulletin of the Peabody Museum of Natural History.* Besides reviews from the dissertation committee, additional reviews of the monograph were solicited from Drs. Leo J. Hickey and Bruce Tiffney, both of Yale University. In December 1983 the monograph was accepted for publication. A grant proposal was submitted to the National Science Foundation requesting publication support for the monograph, and funds were awarded in November 1984. The publication of the monograph is supported by NSF Grant BSR-8410831. However, all opinions and conclusions expressed in this monograph are solely the author's responsibility.

The monograph was complete by September 1982; only minor editorial changes have been made to it since then. One addition to the Taeniodonta has come to my attention since September 1982, and this addition came too late to be incorporated into the final monograph or dissertation. Dr. Robert E. Weems has brought to my attention that recently a single tooth referable to a taeniodont was found outside of the Rocky Mountain intermontane sedimentary basins of western North America. This specimen, a lower left third or fourth premolar, was collected by Dawn Hepler on 11 April 1981 from probable upper Paleocene strata of the Black Mingo Group approximately 0.8 km north of St. Stephen, South Carolina. The tooth is referable to *Ectoganus gliriformis lobdelli* (Simpson, 1929) Schoch, 1981, and is described in detail elsewhere.[1] Here it is important to note that this single specimen records a considerable geographic range extension for the Taeniodonta.

---

[1] Schoch, R. M. 1985. Preliminary description of a new Late Paleocene Land-mammal fauna from South Carolina, U.S.A. *Postilla* (Yale University) 196: 1–13.

ACKNOWLEDGMENTS

My dissertation committee consisted of Drs. John H. Ostrom (chairman), Keith S. Thomson, J. David Archibald and Malcolm C. McKenna. I thank them for their help and support.

I thank Drs. Malcolm C. McKenna and Richard H. Tedford (AMNH: abbreviations for institutions are given on p. 6), Drs. R. Dehm, K. Hessig and P. Wellnhofer (BAWSM), Dr. B. Engesser (BNM), Dr Mary Dawson (CM), Mr. Alden Hamblin (DNHM), Dr. William D. Turnbull and Mr. J. Clay Bruner (FMNH), Mr. Charles Schaff (MCZ), Dr. Robert M. West (MPM), Dr. Donald Baird (PU), Dr. John A. Wilson (TMM), Dr. William Clemens, Jr. (UCMP), Drs. Robert W. Wilson and Larry G. Marshall (UK), Dr. Robert Sloan (UM), Dr. Barry S. Kues (UNM), Dr. Thomas Bown (USGS), Drs. Robert J. Emry and C. Lewis Gazin and Mr. Robert Purdy (USNM), Dr. Jason A. Lillegraven (UW), and Dr. John H. Ostrom and Miss Mary Ann Turner (YPM) for permission to examine specimens in their care. I thank Drs. R. M. West and J. H. Hutchison for finding, and kindly allowing me to borrow, AMNH 107954, a partial skeleton of *Stylinodon*. I thank Dr. Robert T. Bakker for pointing out USNM 22483 to me and for helpful discussions.

I thank Dr. J. David Archibald, Dr. Leo J. Hickey, the late Mr. William Kohlberger, Dr. Spencer G. Lucas, Mr. Earl Manning, Mr. James U. McClammer, Jr., Dr. Malcolm C. McKenna, Dr. John H. Ostrom and Dr. Keith S. Thomson for many useful discussions.

I thank J. David Archibald, Debera Edwards, Adriana M. Goetz, Barbara Honey, Geraldine Kochan, Monica Lack, Patricia Lewis, Carmencita Luna, Anne P. Pettit, Robert H. Pettit, Linda Reichlin, Leslie Ruppert, C. Alicia Schoch, Marguerita C. Schoch, Milton R. Schoch and Costas Tsentas for logistic support in visiting some of the above institutions.

I thank Abbie Rabinowitz for drawing the skulls in Figures 1, 9, 10, 11, 17, 25, 28–30 and 56; Nienke Prins for drawing Figures 2–8, 12–16, 18–23, 26, 27, 31–42, 48, 55, 59, 60 and the dentitions in Figures 1, 9–11, 17, 25, 28; Jim Farelly for drawing Pl. 7, fig. 1; and Ruth Yanai for drawing Pl. 61, fig. 2. I thank Dr. David E. Schindel for the use of photographic equipment and Mrs. Miriam Schwartz for help in using the Yale Computer Center text-editing program.

I gratefully acknowledge financial support from the National Science Foundation (NSF Graduate Fellowship and Publication Grant BSR-8410831); the Peabody Museum of Natural History, Yale University; and the Yale University Graduate School. Facilities were provided by the Department of Geology and Geophysics and Peabody Museum of Natural History, Yale University, and by the College of Basic Studies and Department of Geology, College of Liberal Arts, Boston University. I thank the Geological Society of America for permission to reproduce various figures, plates and parts of text previously published in the Geological Society of American Bulletin (Schoch 1981b). I thank my wife, Cynthia Pettit Schoch, for her continuing encouragement and help in typing and proofreading of the final manuscript. My son, Nicholas Robert Schoch, helped provide the inspiration needed in editing this monograph. Finally, I thank Zelda Edelson and Millie Piekos (both of the Peabody Museum Publications Office) for their help in seeing this volume to publication.

Official Acknowledgement of NSF Support and Disclaimer

This material is based upon work supported by the National Science Foundation under Grant BSR-8410831. Any opinions, findings, conclusions or recommendations expressed in this publication are those of the author and do not necessarily reflect the views of the National Science Foundation.

YALE UNIVERSITY PEABODY MUSEUM OF NATURAL HISTORY BULLETIN NO. 42
307 PP., 60 FIGS., 65 PLS., 1986

SYSTEMATICS, FUNCTIONAL MORPHOLOGY AND MACROEVOLUTION OF THE EXTINCT MAMMALIAN ORDER TAENIODONTA

ROBERT MILTON SCHOCH

ABSTRACT

The Taeniodonta is an archaic order of extinct eutherians known from Puercan (early Paleocene) to Uintan (middle Eocene) strata of the Rocky Mountain intermontane sedimentary basins of western North America and from late Paleocene strata of South Carolina. Taxonomic revision of the order establishes that there are eight genera and twelve species of taeniodonts currently known. The eight genera of the order Taeniodonta form two monophyletic clades, here designated families: the Puercan to Torrejonian (middle Paleocene) conoryctids (*Onychodectes, Conoryctella, Conoryctes* and *Huerfanodon,* from oldest to youngest) and the Puercan to Uintan stylinodontids (*Wortmania, Psittacotherium, Ectoganus* and *Stylinodon,* oldest to youngest). All supposed taeniodonts which have been variously reported from outside of western North America are here excluded from the Taeniodonta on morphological criteria and relegated to other orders.

The sister-group of the Taeniodonta may lie among the late Cretaceous "leptictimorphs" (perhaps the "palaeoryctids" or "pantolestids"). The conoryctids and stylinodontids evolved independently of, but somewhat parallel to, each other. Major evolutionary trends which characterize the conoryctids include: increase in the crown hypsodonty of the cheek teeth; a tendency toward molarization of the posterior premolars and reduction of the anterior premolars; increase in the relative size of the canines; increase in the robustness and depth of the face and mandible; and overall increase in size. Functional morphologic studies suggest that conoryctids were medium-sized (5–15 kg) omnivores, although they perhaps became progressively more herbivorous throughout their evolution.

The stylinodontids were already well differentiated with the appearance of the most primitive known member of the family, *Wortmania* of the Puercan. With *Psittacotherium,* large size and the other essential features of the typical stylinodontid morphotype were well established. These features were progressively modified in *Ectoganus* and *Stylinodon.* Progressive stylinodontid trends include: increase in the relative size of the canines and anterior premolars; the development and elaboration of a bilophodont condition of the molar crowns; increase in crown hypsodonty of the cheek teeth; development and elaboration of root hypsodonty, culminating in all of the teeth being rootless and evergrowing; increase in depth and robustness of the skull and mandible; the development and enlargement of large, laterally compressed and recurved claws on the manus; modifications of the carpal and tarsal series toward a more serial condition; increase in the relative robustness of the limb bones; and increase in total body size. Functional morphologic studies suggest that stylinodontids were active diggers, rooters and grubbers. In terms of modern analogues, an advanced stylinodontid may be thought of as an aardvark with the head of a pig.

Although general trends can be observed in conoryctid and stylinodontid evolution, the genera of each family cannot be related in a strictly "ancestor–descendant" fashion. Indeed, the Uintan *Stylinodon,* the latest known and in many ways most derived taeniodont, may have a separate ancestry from all other known taeniodonts since the Puercan.

ABSTRAKT

Die Taeniodonta ist bekannt ausschliesslich von den niedrigen paleocaenen bis zur Mitte der eocaenen Schicht der Felsengebirgen zwischengebirgigen sedimentaeren Talbecken Nordamerikas. Die Schwestergruppe der Taeniodonta liegt vielleicht unter den Leptictimorphen. Die bekannten Taeniodont-Gattungen bilden zwei monophyletische Kladden: frue-mittlere paleocaenen Conoryctiden (*Onychodectes, Conoryctella, Conoryctes, Huerfanodon* von den aeltesten bis zum juengsten) und frueh-paleocaenen bis zu den mittleren eocaenen Stylinodontiden (*Wortmania, Psittacotherium, Ectoganus, Stylinodon* von den aeltesten bis zum juengsten).

Die kennzeichnenden Hauptentwicklungen der Conoryctiden umfassen: Die Steigerung in Krone-Hypsodontie in Wangezaehnen; die Backzahnisierung der hinteren Vorbackzaehnen; die Einrenkung der voranstehenden Vorbackzaehnen; die Steigerung in verhaeltnismaessiden Groesse der Eckzaehne; die Steigerung in Gesichtsstaerke und deren Tiefe ebenso in dem Kinnbacken; und die Steigerung der Koerpergroesse. Strukturanalytische morphologische Forschungen schlagen vor, dass die Conoryctiden mittelgrosse(5–15 kg) alles Verschliegende waren, obwohl sie vielleicht im Laufe ihrer Evolution plantfressenderer wurden.

Zunehmende Stylinodontid-Richtunen umfassen; Die Steigerung in verhaeltnismaessigen Groesse der Eckzaehnen und voranstehenden Vorbackzaehne; die Entwicklung und die Vervollkommnung eines bilophodonten Zustands der Backzaehnenkrone; die Steigerung in der Krone-Hypsodontie der Wangenzaehne; die Entwicklung und die Vervollkommnung der Wurzelhyposondontie; die Steigerung der Tiefe und der Staerke von der Hirnschale und der Kinnbacken; die Entwicklung und die Vergroesserung der grossen, seitlich gedraengten zurueckbogenen Klauen und des Manus; die Abaenderungen der Handwurzel- und Tarsalserien gegen einen periodischeren Zustand; die Steigerung der Koerpergroesse. Strukturanalytische morphologische Forschungen schlagen vor, dass die Stylinodontiden grabens-, wurzelns- und wuehlenstaetig waren. Angesichts modernen Vergleiche gaelte ein vorschrittener Stylinodontid als eine Aardvark mit dem Kopf eines Schweines.

Obwohl die allgemeine Evolution in Conorcyctiden und Stylinodontiden zu beobachten ist, darf die Gattungen jeder Familie in einer streng unmittelbaren "Vorfahren–Abkoemmling"-Verhaeltnis nicht verstanden werden. Der mittlereocänen *Stylinodon,* welcher der spaetest bekannter und vielfach vorgeschrittener Taeniodont ist, koennte eine getrennte Abstammung von der anderen bisherigen Taeniodonten seit dem fruehen Paleocaene haben.

1. INTRODUCTION, TERMINOLOGY, MEASUREMENTS

INTRODUCTION

The Taeniodonta is an order of archaic eutherian mammals known exclusively from the early Tertiary of western North America. Their remains are found in Puercan (early Paleocene) to Uintan (middle Eocene) strata, spanning about 20 million years, of the Rocky Mountain intermontane sedimentary basins. A few dubious specimens of "taeniodonts" have been reported outside of North America, but none of these have been substantiated as unequivocally referable to the Taeniodonta and most are referable to other orders (see below, Chapter 3, "Other Supposed Occurrences of Taeniodonts").

Taeniodonts ranged in size from that of a large house cat to that of a medium-sized pig or hog (up to 110 kg in body weight). The eight currently recognized genera are arranged in two families. One family, the conoryctids, can be thought of as small- to medium-sized (5–15 kg) generalized, omnivorous mammals. The other family, the stylinodontids, are the standard textbook taeniodonts (cf. Romer 1966). Stylinodontids were relatively large beasts (10–110 kg) characterized by their short, wide skulls with massive mandibles and large canines. The stylinodontid body was solid and heavy, the limbs were stout, robust and powerful and the forefeet bore large, laterally compressed and recurved claws. As is suggested below, stylinodontids may have been active diggers, rooters and grubbers, feeding on tubers and other underground food resources. In terms of modern analogues, an advanced stylinodontid may be thought of as an aardvark with the head of a pig.

A number of points make the study of the Taeniodonta especially interesting:

1) The genera of taeniodonts have been regarded as constituting two parallel orthogenetic lineages by two prominent students of the order (Wortman 1897b; Patterson 1949b). Indeed, the taeniodonts have become a textbook example of differing phyletic rates of evolution in two sister clades after the separation of one from the other by a quantum shift (Simpson 1953, p. 392; Minkoff 1983, p. 305).

2) One group of taeniodonts, the stylinodontid taeniodonts, acquired relatively large body size in the early–middle Paleocene when most mammals were still relatively small. They represent one of the first eutherian radiations to attain relatively large body size, although they were soon overtaken in the middle and late Paleocene (by pantodonts, for example).

3) Most taeniodonts are characterized by crown hypsodonty as compared to most contemporaneous mammals. Furthermore, the stylinodontid taeniodonts of the middle–late Paleocene are the first mammals known to develop fully hypsodont (both crown and root) teeth (White 1959; Webb 1977).

4) The earliest Paleocene stylinodontids also had distinctive, large, laterally compressed claws on the manus. This, along with points 2 and 3, indicates that adaptively they were doing something quite different than were contemporaneous mammals.

5) The taeniodonts are a poorly understood "orphan" group (Romer 1966, 1968) which arose during the first great radiation of early Tertiary mammals at the end of the Cretaceous and beginning of the Paleocene. They have been variously (but not convincingly) linked with edentates (Wortman 1897b), pantolestids, leptictids, palaeoryctids, didelphodonts, pantodonts, apatotheres, creodonts and carnivores (McKenna 1969, 1975; Szalay 1977). In Uintan times they appear to have gone extinct without descendants.

The last comprehensive study of the Taeniodonta was by Wortman (1897b). Matthew (1937) reviewed the Paleocene taeniodonts known to him from the San Juan Basin. Gazin (1936, 1952) has made a few contributions to the study of taeniodonts and Patterson last reviewed the order in a semipopular manner over thirty years ago (1949b). Since then, little has been added to our knowledge of taeniodonts until the recent studies initiated and carried out by the present author (e.g., Schoch 1981a, 1982a, 1983a).

It is the purpose of this study to update and expand our knowledge of this little known and poorly understood order. This is done in four main sections:

1) A systematic revision of the Taeniodonta is undertaken and the known taxa are described (dental, cranial and postcranial remains: Chapter 3).

2) The stratigraphic and geographic distribution and biostratigraphy of the taeniodonts is discussed (Chapter 4).

3) Speculations are made regarding the paleobiology of the Taeniodonta (Chapters 5 and 6).

4) Relationships and macroevolutionary trends among the taeniodonts are discussed (Chapter 7).

Thus, the first two sections form the substantive basis for the hypotheses and speculations of the second two sections. It is hoped that this study will add to our knowledge of the Taeniodonta in particular, and also to our knowledge of the early Tertiary eutherian radiation in general.

The remainder of this chapter deals with certain necessary preliminaries (i.e., dental terminology, dental measurements, anatomical terminology and osteological measurements, abbreviations used) that are vital for understanding the descriptions and discussions which comprise the bulk of this work.

DENTAL TERMINOLOGY

The enlarged, gliriform upper teeth of *Psittacotherium, Ectoganus* and *Stylinodon,* which were considered to be incisors by Cope (e.g., 1877, 1884b), were definitively demonstrated by Wortman (1897b) to be homologous to the canines of other eutherian mammals and also to the canines of the conoryctid taeniodonts and *Wortmania.* This homology is based on the relation of these teeth to the premaxilla–maxilla sutures which occur over or just anterior to these teeth. The corresponding lower teeth are thus also judged to be the lower canines. Posterior to the canines, taeniodonts primitively have four premolars and three molars that are considered homologous to the premolars and molars of the typical eutherian dentition. As demonstrated by USNM 12714, a skull of *Ectoganus,* the four more anterior cheek teeth have deciduous precursors, whereas the three posterior cheek teeth (molars) do not. The teeth anterior to the canines are considered to be generally homologous to the incisors of the typical eutherian, although the exact homology of each tooth is uncertain. Matthew (1937, p. 254) homologized the teeth of *Onychodectes,* which he believed retained three incisors above and below on each side (the primitive eutherian condition), with those of the other taeniodonts. In *Onychodectes* the most anterior upper two incisors are vestigial, the posterior upper incisor is slightly enlarged, the anterior and posterior most lower incisors are vestigial, and the middle incisor (I_2) is enlarged. Thus, Matthew (1937) believed that *Psittacotherium* had only one incisor on each side above and below and he considered these to be I^3_2. However, as discussed below under the various genera, the complete incisor formula is not conclusively known for any taeniodont except *Stylinodon* (and *Stylinodon* has only been well known since 1958 when a complete skull of *Stylinodon* was found: FMNH PM 3895) and the homologies hypothesized by Matthew (1937) are far from certain. Thus, here I arbitrarily label the most posterior incisors I^3_3 and those progressively more anterior, if present, I^2_2 and I^1_1.

Terminology for the orientations and details of crown morphology used here follow eutherian tooth nomenclature as standardized by Szalay (1969, table 1, fig. 1) and Zhou and others (1975, table 1, fig. 1). The crown details are named on the basis of their topographic relationships to one another. On the basis of what appears to be a close relationship between the taeniodonts and palaeoryctids (discussed below) and the generally stereotypic and well-documented basic underlying molar crown pattern common to all eutherians, the terminology applied to the crowns of taeniodont teeth may imply homology as well as analogy with the generalized eutherian morphotype (except where noted). The same terminology is used for the premolars as for the molars without necessarily implying homology between the crown features of the premolars and those of the molars.

DENTAL MEASUREMENTS

Lengths and widths of the crowns of the teeth of taeniodonts were taken to the nearest tenth of a millimeter using an antique vernier caliper made by P. Roch (Rolle, Switzerland). I have tested the caliper used against standards and it is both accurate and precise to better than one-twentieth of a millimeter. All lengths are strictly anteroposterior lengths taken on the tooth as it is oriented in the tooth row. On isolated teeth I oriented the tooth as it would be positioned in the tooth row, on the basis of homologous teeth in place on jaw fragments, before taking measurements. I found that this practice produced reasonably consistent results. All widths are strictly transverse (mediolateral) widths taken on the teeth as they are oriented in the tooth row and perpendicular to the lengths taken. Most taeniodont teeth are extremely worn and I found that trying to take more precise or accurate measurements is not practical, possible or necessary for the present purposes of this study (as discussed above), and recording measurements to the nearest tenth of a millimeter seems to be the upper limit of reproducibility. Statistics which have been calculated for dental measurements are described and discussed in Simpson and others (1960).

ANATOMICAL TERMINOLOGY AND OSTEOLOGICAL MEASUREMENTS

The anatomical terminology for bony elements and their orientations and features and for muscle groups is that standardly used and understood by mammalogists, following such authorities as Wake (1979), Greene (1935), Flower (1876b), Davison (1917), Mivart (1881), J. G. Savage (1957), Coues (1872), Turnbull (1970) and Wood Jones (1949). Where ambiguity may be present, it is explained in the appropriate place in the text. All measurements taken on osteological elements are self-explanatory (see tables in Appendix I) and were taken with either the same caliper used for dental measurements, a meter stick, or a steel tape. Angular measurements (in degrees) were taken with a clear plastic circular protractor.

ABBREVIATIONS USED

AC	Amherst College, Amherst, Massachusetts
AMNH	American Museum of Natural History, New York, New York
BAWSM	Bayerischen Akademie der Wissenschaften Sammlung Munchen, Munich, Federal Republic of Germany
BNM	Basel Naturhistorischen Museum, Basel, Switzerland
CM	Carnegie Museum, Pittsburgh, Pennsylvania
DNHM	Dinosaur Natural History Museum, Vernal, Utah
FMNH	Field Museum of Natural History, Chicago, Illinois
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MPM	Milwaukee Public Museum, Milwaukee, Wisconsin
PU	Princeton University, Princeton, New Jersey (The PU fossil mammal collection is now housed at the Peabody Museum of Natural History, Yale University.)
TMM	Texas Memorial Museum, Austin
UALP	University of Arizona Laboratory of Paleontology, Tucson
UCMP	University of California Museum of Paleontology, Berkeley
UK	University of Kansas, Lawrence
UM	University of Minnesota, Minneapolis
UNM	University of New Mexico, Albuquerque
USGS	U.S. Geological Survey, Paleontology and Stratigraphy Branch, Denver, Colorado
USNM	National Museum of Natural History, Washington, D.C.
UW	University of Wyoming, Laramie
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut

L	Length
W	Width
Tr	Trigonid
Td	Talonid
*	Asterisks indicate approximate measurements of damaged or worn teeth or measurements of alveoli.

All dental measurements are given in millimeters.
Tooth nomenclature follows Szalay (1969, pp. 198–203, table 1, fig. 1) and Zhou and others (1975, table 1, fig. 1).

2. PREVIOUS STUDIES

The first taeniodont to be described was *Stylinodon mirus* by Marsh in 1874, followed closely in the same year by Cope's descriptions of *Ectoganus gliriformis* and several species of "*Calamodon*" (now all considered to be synonyms of *E. gliriformis*: Cope 1874; Marsh 1874; Schoch 1981b). Cope (1874) originally considered *Ectoganus* and "*Calamodon*" to be the first North American representatives of the South American order Toxodonta. Marsh thought that *Stylinodon* resembled *Toxodon* in some respects, but stated that it "may, perhaps, have some affinities with the Edentates" (1874, p. 532).

In 1875 Marsh named the order Tillodontia (based on his genus *Tillotherium*: Marsh 1875b) and included within this order the families Tillotheriidae and Stylinodontidae. He here stated that the Tillodontia appears to have no close affinities with the Toxodonta.

In 1876 Cope named the suborder Taeniodonta (order Bunotheria) for *Ectoganus* and *Calamodon,* and considered them to be in some respects intermediate between the Edentata and Insectivora (1876a). In 1884 Cope included six suborders in his Bunotheria: Taeniodonta, Tillodonta (sic), Mesodonta, Insectivora, Creodonta and probably Prosimiae (Cope 1884c). In his classifications of 1891 and 1898 Cope included the following in the order Bunotheria: Pantotheria, Creodonta, Insectivora, Tillodonta (sic) and Taeniodonta (Gregory 1910). Cope, however, placed *Onychodectes, Conoryctes* and *Wortmania* in the Creodonta (Cope 1888d), and *Psittacotherium* in the Tillodontia (Cope 1882b). Wortman (1896b, 1897b) first recognized the Taeniodonta in its modern sense. Wortman placed the genera now recognized as taeniodonts in the suborder Ganodonta of the order Edentata and included two families in the suborder: Conoryctidae (*Onychodectes* and *Conoryctes*) and Stylinodontidae (*Hemiganus* [= *Wortmania*] *Psittacotherium, Calamodon* [= *Ectoganus*] and *Stylinodon*). Wortman viewed the conoryctids and stylinodontids as two evolving phyla forming a graded ancestor–descendant series from one genus to the next. Wortman (1896b, 1897b) viewed his "Ganodonta" as a primitive division of the Edentata (edentates which retained enamel on their teeth). He believed that the stylinodontids led to the ground sloths whereas the conoryctids led to the armadillos.

Schlosser (1911) adopted Wortman's views, but put different ranks on the suprageneric categories. Thus, Schlosser recognized the Ganodonta as a family of the Edentata and reduced Wortman's Conoryctidae and Stylinodontidae to subfamilies. However, Wortman's allying of the taeniodonts with the edentates was not universally accepted. Scott (1905) recognized the resemblances seen between the edentates and taeniodonts as due to convergence, as did Ameghino (1897, 1902, 1906a, b) and Winge (1915). Without stating where their true affinities might lie, Scott (1905) considered the taeniodonts to be a distinct order. Ameghino (1897, 1902, 1906a, b) considered the taeniodonts to be condylarths allied with the Periptychidae, whereas Winge placed them in the Insectivora as descendants of the Leptictidae (Winge 1915; Simpson 1931). Thus, Winge (1917, 1923) recognized the family Stylinodontidae (order Insectivora) composed of three tribes: Onychodectini (*Onychodectes*), Conoryctini (*Conoryctes*) and Stylinodontini (*Hemiganus* [= *Wortmania*], *Psittacotherium, Calamodon* [= *Ectoganus*] and *Stylinodon*).

Matthew (1918, 1928) also believed that many of the supposed resemblances seen between the stylinodontids and the edentates (especially ground sloths) pointed out by Wortman (1897b) were both overstated and due, at least in part, to convergence. After reexamination of the original specimens, Simpson (1931) came to the same conclusions and in general agreed with Winge (1923). In his monograph published posthumously in 1937, Matthew essentially adopted Winge's (1923) views, except that he recognized the Taeniodonta as a distinct order and proposed a new subfamily, Psittacotheriinae. Thus, Matthew (1937) recognized the family Stylinodontidae (sole family of the order Taeniodonta) composed of the Onychodectinae (*Onychodectes*), Conoryctinae (*Conoryctes*), Psittacotheriinae (*Wortmania, Psittacotherium,* and *Calamodon* [= *Ectoganus*]) and Stylinodontinae (*Stylinodon*).

Simpson (1945) adopted Matthew's (1937) classification of the Taeniodonta in its broad outlines, but reduced the number of subfamilies to two. Thus, Simpson (1945) recognized one family of the order Taeniodonta, the Stylinodontidae, composed of the subfamilies Conoryctinae (*Onychodectes, Conoryctella* [a genus described by Gazin in 1939] and *Conoryctes*) and Stylinodontinae (*Wortmania, Psittacotherium, Ectoganus* and *Stylinodon*).

Patterson (1949b), who last reviewed the order, thought the taeniodonts were "probably derived from unknown Cretaceous insectivores" (1949b, p. 243) and adopted Simpson's (1945) classification of the Taeniodonta in its entirety, adding his new genus *Lampadophorus* (= *Ectoganus*) to the Stylinodontinae in an evolutionary position intermediate between *Psittacotherium* and *Ectoganus.* Patterson (1949b) considered the conoryctines to be generally primitive relative to the stylinodontines, and thought that the successive genera of each of the subfamilies were related in ancestor–descendant relationships. Patterson (1949b) viewed *Onychodectes* as the most primitive taeniodont and as a structural ancestor for all other taeniodonts. Wortman's (1897b) and Patterson's (1949b) theories of direct ancestor–descendant relationships between the conoryctine taeniodont genera, forming one lineage, and the stylinodontine taeniodont genera forming another lineage were not completely upheld by Matthew (1937). Thus, whereas Matthew (1937, p. 277) stated that "all the evidence points to *Wortmania* as being the direct ancestor of *Psittacotherium,*" concerning *Conoryctes,* Matthew concluded (p. 254) that "it is not at all clear that it is a direct or closely approximate descendant of *Onychodectes.*"

Most recently, McKenna (1969, 1975), Lillegraven (1969) and Kielan-Jaworowska and others (1979) have suggested (on the basis of tooth morphology) that the Cretaceous palaeoryctids *Cimolestes* or *Procerberus* gave rise to the Taeniodonta. Lillegraven (1969, p. 69, fig. 40) has explicitly stated that *Procerberus formicarum,* through an intermediate (and as yet unpublished) specimen of *Procerberus* found in the early Paleocene Mantua lentil of the Polecat Bench Formation of the Bighorn Basin, Wyoming, gave rise to the Taeniodonta. On the basis of dental similarities, McKenna (1975) relegated the Taeniodonta, along with the Didelphodonta, Pantodonta and Apatotheria to his new order Cimolesta. Szalay (1977, p. 368) has countered this by uniting the "Taeniodontidae" with the Leptictidae (Leptictinae and Palaeoryctinae), Pantolestidae "and possibly the Microsyopidae" as the new order Leptictimorpha, on the basis of shared-derived characters of the astragalocalcaneal complex (see below, Chapter 7).

3. SYSTEMATIC REVISION AND DESCRIPTIONS

INTRODUCTION TO THE SYSTEMATIC REVISION

Practical or applied taxonomy (as opposed to theoretical systematics), by its very nature, may necessarily involve some subjective judgments on one level or another. In my systematic revision of the Taeniodonta I have recognized as species *distinct* clusters of specimens which share the same or very similar morphologies. When within such a species certain characters vary or grade from one extreme to another, and it is possible to separate out most specimens into two or more groups, I have recognized these groups as subspecies (cf. Simpson 1943, 1961). Genera are used to distinguish groups of species which are closely similar morphologically as compared to other species or, in the case of monotypic genera, for a single species which is widely different from other genera and species. The scope of morphologies that are encompassed by any one taeniodont genus is partly determined by the way the concept of the genus has been used for taeniodonts (and mammals more generally) in past studies (cf. Wortman 1897b; Matthew 1937; Patterson 1949a, b). Furthermore, I have strived for monophyletic taxa on every level. All primary taxonomic judgments are made solely on the basis of morphology; extrinsic stratigraphic and geographic data are recorded, and discussed in a separate section, but do not form the basis for taxonomic distinctions. The "species" here recognized are admittedly "morphological species"; no claim is made for their correspondence to the "biological species" of the neontological world, although I have taken criteria of extant species (such as the range and coefficients of variation of measurements seen in extant species; cf. Simpson and others 1960; Gingerich 1974; Gingerich and Schoeninger 1979; Gingerich and Winkler 1979; Yablokov 1974) into account when distinguishing and formally recognizing fossil taxa. The diagnoses of the taxa serve to distinguish (differentiate) the taxon concerned from other taxa within a higher taxon: they are not definitions of the taxa involved in any absolute sense (cf. Simpson 1945, p. 22, for a discussion of the difference between diagnosis and definition). The formal nomenclature strictly follows the rules and recommendations of the International Code of Zoological Nomenclature (Stoll and others 1964). A description and discussion section follows each genus where all known dental, cranial and postcranial remains of the genus are described and differences between the species and subspecies within any genus are pointed out, as well as major similarities and differences relative to the other genera of taeniodonts.

SYSTEMATIC PALEONTOLOGY

ORDER TAENIODONTA COPE, 1876a

Equals or includes:

Stylinodontidae Marsh, 1875b, p. 221.
Taeniodonta Cope, 1876a, p. 39.
Ectoganidae Cope, 1876a, p. 39.
Calamodontidae Cope, 1876a, p. 39.
Hemiganidae Cope, 1888d, p. 310.
Ganodonta Wortman, 1896a, p. 259.
Conoryctidae Wortman, 1896a, p. 260.
Stylinodontia Marsh, 1897, p. 137.
Conoryctinae Schlosser, 1911, p. 414.
Stylinodontinae Schlosser, 1911, p. 414.
Onychodectini Winge, 1917, p. 105.
Conoryctini Winge, 1917, p. 105.
Stylinodontini Winge, 1917, p. 106.
Onychodectinae Matthew, 1937, p. 238.
Psittacotheriinae Matthew, 1937, p. 237.
Taeniodontidae Szalay, 1977, p. 368.
Conoryctellini Schoch, 1982a, p. 470.
Wortmaniinae Schoch, 1982a, p. 470.
Psitacotheriini Schoch, 1982a, p. 470.
Ectoganini Schoch, 1983b, p. 205.

Included Genera. *Onychodectes* Cope, 1888d; *Conoryctella* Gazin, 1939; *Conoryctes* Cope, 1881a (= *Hexodon* Cope, 1884a); *Huerfanodon* Schoch and Lucas, 1981b; *Wortmania* Hay, 1899; *Psittacotherium* Cope, 1882b (= *Hemiganus* Cope, 1882e); *Ectoganus* Cope, 1874 (= *Calamodon* Cope, 1874 = *Dryptodon* Marsh, 1876b = *Conicodon* Cope, 1894 = *Lampadophorus* Patterson, 1949a); and *Stylinodon* Marsh, 1874.

Distribution. Puercan (early Paleocene) to Uintan (middle Eocene) of western North America; upper Paleocene strata of South Carolina (see Foreword).

Discussion. I recognize the Taeniodonta as a monophyletic taxon whose members share the following derived character-states: relatively narrow upper molars, with protocones, protoconules and metaconules small and placed far lingually, paracones and metacones moderate-sized, punctate and placed far labially with reduced stylar shelves; pre- and postcingula lacking on upper molars; hypocone absent or developed by a splitting off from the protocone; lower molars lack cingulids; trigonids and talonids of all molars subequal in size (length and width); trigonids bear subequal protoconids and metaconids; molars decrease in size posteriorly, hypoconulid/talonid not expanded on M_3. Taeniodonts can also be distinguished by a tendency toward hypsodont cheek teeth. In relatively primitive forms (*Onychodectes, Conoryctella, Conoryctes, Huerfanodon* and *Wortmania*) this takes the form of "tooth-base" or "crown" hypsodonty (White 1959) characterized by the labial extension of the enamel on the lower cheek teeth and the lingual extension of the enamel on the upper cheek teeth. In more advanced taeniodonts (*Psittacotherium, Ectoganus* and *Stylinodon*) this form of hypsodonty is combined with "root" hypsodonty (White 1959) in which the roots of the cheek teeth fuse and become evergrowing. Taeniodonts are also characterized by the possession of a leptictimorph astragalocalcaneal morphology (Szalay 1977).

In this section I revise only the genus- and species-level taxonomy of the Taeniodonta, diagnose the two families of taeniodonts, document the temporal and geographic distribution of the taeniodonts and describe the known remains of the Taeniodonta. The phylogeny, classification (above the genus level) and evolution of the Taeniodonta are discussed in a following section (Chapter 7). However, in this section the term "conoryctid" refers to the genera *Onychodectes, Conoryctella, Conoryctes* and *Huerfanodon* and the term "stylinodontid" refers to the genera *Wortmania, Psittacotherium, Ectoganus* and *Stylinodon.*

Conoryctidae Wortman, 1896a

Type Genus. *Conoryctes* Cope, 1881a.

Included Genera. *Onychodectes* Cope, 1888d; *Conoryctella* Gazin, 1939; *Conoryctes* Cope, 1881a; *Huerfanodon* Schoch and Lucas, 1981b.

Distribution. Puercan (early Paleocene) to Torrejonian (middle Paleocene) of western North America.

Revised Diagnosis. Taeniodonts with relatively narrow, triangular-shaped P^{3-4}; well-developed crown hypsodonty of the cheek teeth; P^4 with incipient metacone; P_4 with small talonid heel.

Onychodectes Cope, 1888d

Onychodectes Cope, 1888d, p. 317.

Type Species. *Onychodectes tisonensis* Cope, 1888d (= *Onychodectes rarus* Osborn and Earle, 1895).

Included Species. Only the type species.

Distribution. Puercan of New Mexico and Utah.

Revised Diagnosis. Small taeniodonts; teeth moderately hypsodont (relatively less hypsodont than *Conoryctella*); P^4 nonmolariform with a well-developed protocone, paracone and incipient metacone, parastyle, stylocone and metastyle; P^4 metastylocone small to moderately well developed; lower molar trigonids bear large, subequal and sharply punctate protoconids and metaconids with only slightly smaller, lingually placed paraconids; lower molar talonids bear high and punctate hypoconids, slightly smaller and punctate entoconids and smaller hypoconulids.

Onychodectes tisonensis Cope, 1888d
(Figs. 1, 2)

Onychodectes tisonensis Cope, 1888d, p. 318. (See synonymies under the subspecies.)

Type Subspecies. *Onychodectes tisonensis tisonensis* Cope, 1888d.

Included Subspecies. The type subspecies and *Onychodectes tisonensis rarus* Osborn and Earle, 1895.

Diagnosis. Same as that for the genus.

Onychodectes tisonensis tisonensis Cope, 1888d
(Table 23; Figs. 3e–g, h–l, 4c–h, 5a–i, 6c, d, g–k, 7; Pls. 1, 2, 3; Pl. 4: figs. 1–5, 9, 10; Pl. 5: figs. 1–4, 6–9, 13–15; Pl. 6: figs. 7–9; Pl. 8: figs. 3–8, 11, 12; Pl. 9: figs. 11, 12, 15–18, 21–24)

Onychodectes tisonensis Cope, 1888d, p. 318.
Onychodectes tissonensis (*lapsus calami*): Osborn and Earle, 1895, p. 40.
Onychodectes tissonensis (*lapsus calami*): Wortman, 1897b, p. 97.
S. tissonensis (*lapsus calami*): Wortman, 1897b, p. 97.
Onychodectes tisonensis: Matthew, 1937, p. 239.
Onychodectes n. sp.?: Robison and Lucas, 1980, p. 302.
Onychodectes tisonensis tisonensis: Schoch, 1981b, p. 938.

Type Specimen. AMNH 3405, right and left maxillae with P^4–M^3, left dentary with M_2 and associated right astragalus (Pl. 4: figs. 1–5; illustrated by Cope 1888d, Pl. 5, figs. 8, 9). Several different individuals of *O. t. tisonensis* have been catalogued under AMNH 3405; any of these specimens that can be demonstrated to be from the same individual as Cope's illustrated specimens may be regarded as part of the type specimen (see Cope 1888d, p. 318).

Horizon and Locality of the Type. Collected by David Baldwin in 1885 from presumably Puercan strata of the Nacimiento Formation, San Juan Basin, New Mexico.

Referred Specimens. AMNH 902a, upper molar ($M^{2(?)}$); AMNH 3405 (not the type specimen, see above), left maxilla with P^4–M^2, proximal part of right femur, proximal part of right tibia, and distal part of left tibia (Fig. 6c, d, g–k; Pl. 5: fig. 3; Pl. 8: figs. 3–8); AMNH 3407, right and left dentary fragments with left P_{1-2}, right and left P_3–M_1, right M_{2-3}, roots of left C_1, right P_{1-2}, alveoli for left M_{2-3}; AMNH 3408, left dentary fragment with $P_{2(?)}$, M_{1-3}; AMNH 3409, left dentary fragment with P_4–M_1; AMNH 3411, left maxilla with P^4–M^2 (Pl. 5: fig. 1) and right dentary fragment with P_3–M_3 (Pl. 5: figs. 14, 16, 17) and postcranial fragments; UCMP 36514, right maxilla fragment with P^4–M^3 (Pl. 4: figs. 9, 10): all from presumably Puercan strata of the Nacimiento Formation, San Juan Basin, New Mexico.

AMNH 785, skull with left P^4, M^{2-3} and right M^{2-3}, alveoli for right and left I^3, C^1, P^{1-3}, right P^4, right and left M^1, left dentary fragment with M_{2-3} and right dentary fragment with roots of P_2 and complete P_3–M_3 (Pl. 3; Pl. 6: figs. 7, 8); AMNH 786, right dentary fragment with M_{1-2}, roots of C_1, P_{2-4}, alveolus for P_1; AMNH 812, right dentary fragment with M_2, alveoli for P_4–M_1; AMNH 822a, right dentary fragment with M_2; AMNH 27678, left dentary fragment with P_4–M_2; UCMP 31293, left maxilla with P^4–M^1 and partial P^3, M^2; UCMP 31817, left dentary with P_{2-4}; UCMP 31819, right dentary with P_4–M_2 and alveolus for M_3; UCMP 68687, left P^4 and two isolated lower molars; UCMP 92156, right dentary fragment with M_{2-3} and roots of M_1; UCMP no number, left maxilla with P^3–M^2, left dentary fragment with roots of P_{3-4} and complete M_{1-3} and edentulous right dentary fragment; UK 8114, left maxilla with M^2; UK 8116, left P^4 (Pl. 5: fig. 7); UK 9417, left M_1; UK 12711, left dentary fragment with M_{1-3}; USNM 15535, right dentary fragments with P_3, M_{1-3}; USNM 15536, right maxilla with P^4–M^1 (Pl. 5: fig. 4): all from Puercan strata of the Nacimiento Formation, De-na-zin Wash, San Juan Basin, New Mexico.

AMNH 16406, left dentary fragment with P_2–M_1, alveoli for P_1, M_{2-3}; AMNH 16408, right dentary fragment with M_{1-2} and alveoli for C_1–P_4 and M_3 (Pl. 6: fig. 9); AMNH 16409, left dentary fragment with P_4–M_1, M_3; AMNH 16410, left dentary fragment with P_2–M_1, alveoli for C_1–P_1, both humeri, proximal part of the left ulna, sacrum, radius and other postcranial fragments (Figs. 3e–g, 4c–h, 5a, b; Pl. 5: fig. 13; Pl. 7: figs. 2–5; Pl. 8: figs. 11, 12; Pl. 9: figs. 21–24); USNM 15534, left dentary fragments with P_{3-4}, M_{2-3} and roots of P_{1-2} (Pl. 5: figs. 15, 18, 19): all from Puercan strata of the Nacimiento Formation, Alamo Wash, San Juan Basin, New Mexico.

AMNH 16411, isolated teeth and tooth fragments including two incisors, right P^4, right $dP^{4(?)}$, left P_3, right and left M_2, right M_3 and postcranial fragments (Pl. 5: figs. 8, 9); AMNH 16528, skull and lower jaws with right $I^{2(?)}$, left C^1–P^1, right and left P^2–M^3, roots of right and left I_2 and C_1, right and left P_1, left P_2, right and left P_3–M_3, right manus, left pes and miscellaneous vertebrae (Figs. 3h–l, 5c–i, 7; Pls. 1, 2; Pl. 7: figs. 6, 7; Pl. 9: figs. 11, 12, 15–18); AMNH 58059a, right $M_{2(?)}$: all from Puercan strata of the Nacimiento Formation, Kimbeto Wash, San Juan Basin, New Mexico.

AMNH 27608, (?)left M^2; AMNH 58172, right $M_{3(?)}$; UCMP 74792, left $M^{2(?)}$; UCMP 89695, left $M^{2(?)}$: all from Puercan strata of the Nacimiento Formation, Betonnie Tsosie Wash, San Juan Basin, New Mexico.

AMNH 36070, left M^2 (Pl. 5: fig. 6); AMNH 36071, left P^4: both from Puercan strata of the North Horn Formation, Wagonroad local fauna, Emery County, Utah.

Revised Diagnosis. Subspecies of *Onychodectes tisonensis* with relatively simpler crowned premolars and molars than in *O. t. rarus*; anterior internal accessory cusp absent on P_4; external accessory cusp between trigonid and talonid lobes of M_{1-2} absent.

Onychodectes tisonensis rarus Osborn and Earle, 1895

(Table 23; Figs. 3a–c, 4a, b, 5j, k, 6e, f; Pl. 4: figs. 6–8, 11, 12; Pl. 5: figs. 5, 10–12; Pl. 6: figs. 1–6; Pl. 8: figs. 8, 10; Pl. 9, figs. 1–8, 13, 14, 19, 20)

Onychodectes rarus Osborn and Earle, 1895, p. 42.
Onychodectes rarus: Wortman, 1897b, p. 97.
Onychodectes rarus: Matthew, 1937, p. 249.
Onychodectes tisonensis rarus: Schoch, 1981b, p. 938.

Type Specimen. AMNH 824, left dentary fragment with M_{1-2} (Pl. 4: figs. 6–8).

Horizon and Locality of the Type. Puercan strata of the Nacimiento Formation, De-na-zin Wash, San Juan Basin, New Mexico.

Referred Specimens. AMNH 3040a, (?)right maxilla with M^2 and partial roots of M^1 and M^3; AMNH 3576a, isolated right and left M_3, right dentary fragments with P_4, M_2, scapula, vertebrae and other postcranial fragments (Figs. 3a–c, 4a, b, 5j, k, 6e, f; Pl. 8: figs. 9, 10; Pl. 9: figs. 1–8, 13, 14, 19, 20): both from presumably Puercan strata of the Nacimiento Formation, San Juan Basin, New Mexico.

AMNH 27679, right maxilla with M^{1-2} and left dentary fragment with M_{1-2}; UCMP 68668, right dentary fragment with P_4; UK 9416, right M_1, left M_2 (Pl. 5: figs. 10–12) and dentary fragments; UK 13000, left dentary fragment with P_4–M_1, alveoli for P_{2-3}: all from Puercan strata of the Nacimiento Formation, De-na-zin Wash, San Juan Basin, New Mexico.

AMNH 16405, left maxilla with P^3–M^2 and roots of M^3, right dentary with canine stub, parts of P_{1-2} and complete P_4–M_3, left dentary with canine, root of P_1 and complete P_2–M_3 (Pl. 4: figs. 11, 12; Pl. 6: figs. 1–6); AMNH 16407, left dentary fragment with P_{3-4} and anterior part of M_1, roots of P_2; AMNH 23090, left maxilla with P^4–M^2: all from Puercan strata of the Nacimiento Formation, Alamo Wash, San Juan Basin, New Mexico.

Revised Diagnosis. Subspecies of *Onychodectes tisonensis* with the following characters moderately to well developed (as compared to *O. t. tisonensis*): P^4–M^3 slightly broader and with better developed ectocingula; lower premolars slightly more molariform with better developed talonids on P_{3-4} and an anterior internal accessory cusp on P_4; M_{1-2} with external accessory cusp or cusps between the trigonid and talonid lobes.

?*Onychodectes* sp.

(Figs. 3d, 6a, b; Pl. 8: figs. 1, 2; Pl. 9: figs. 9, 10)

Referred Specimen. AMNH 3404, (?)right ilium (Pl. 8: figs. 1, 2), lumbar vertebra (Pl. 9: figs. 9, 10) and other bone fragments from presumably Puercan strata of the Nacimiento Formation, San Juan Basin, New Mexico.

Discussion. This specimen was collected by David Baldwin for E. D. Cope in 1885 from the San Juan Basin, New Mexico. According to the AMNH label, it originally may have included an upper jaw fragment with molars identifiable as *Onychodectes*. However, I have not been able to locate this maxilla. While several individuals (some nontaeniodont) are catalogued under AMNH 3404, a (?)right ilium and lumbar vertebra are in the size range of *Onychodectes* and may be referable to this genus.

Description and Discussion of *Onychodectes*

I consider *Onychodectes rarus* Osborn and Earle, 1895, to be a junior subjective synonym of *Onychodectes tisonensis* Cope, 1888d, at the specific level. *Onychodectes rarus* is based on AMNH 824, the diagnostic feature being an external cusp between the trigonid and talonid lobes of M_{1-2}. AMNH 16405, a left maxilla with P^3–M^2 and both lower dentaries with incomplete C_1–M_3 (Pl. 4: figs. 11, 12; Pl. 6: figs. 1–6) referred to *Onychodectes rarus* by Matthew (1937, p. 249), bears this external accessory cusp on M_{1-2} but not on M_3, and also possesses a small anterior internal accessory cusp on P_4. P^4–M^2 of AMNH 16405 are somewhat broader and have better developed ectocingula than some specimens of *Onychodectes tisonensis* (Matthew 1937). However, these are all rather minor and variable features in *Onychodectes*; when a number of specimens are lined up side by side there is a continuous gradation from one extreme to the other. Thus, most specimens (e.g., USNM 15534, AMNH 3411, AMNH 16410; Pl. 5: figs. 13–19) lack an external cusp on the lower molars and have at most an incipient anterolingual cusp on P_4. AMNH 27679 possesses a very small, incipient external cusp on M_1; UK 9416 (Pl. 5: figs. 10–12) possesses a small external cusp on M_1; AMNH 3576a and UK 13000 both have a small external cusp on the talonid of P_4 and a small anterolingual accessory cusp on P_4; and AMNH 3576a has two small external cusps between the trigonid and talonid lobes of M_2. Other specimens which bear the characters attributed to *O. rarus* by Matthew (1937) in varying degrees of development are: AMNH 3040a, AMNH 16407, AMNH 23090, AMNH 27679 and UCMP 68668.

Likewise, the size of both the upper and lower molars of specimens of *Onychodectes* is somewhat variable (Table 23), but there are no clear gaps and the majority of coefficients of variation range from approximately five to nine. Much of this size variation may be due to the extremely worn condition of these teeth and the consequent difficulty in measuring homologous points on different specimens. Although more specimens in a better state of preservation might demonstrate that *Onychodectes* is composed of more than one species, it is most reasonable to assign all specimens to one species at the present time. The variable, but recognizable, morphological differences are here relegated to subspecific status.

The probable dental formula of *Onychodectes* is I^3_3 C^1_1 P^4_4 M^3_3 (Fig. 1), although there is the possibility that only two upper incisors were present (cf. Matthew 1937, p. 240). The incisors are of moderate size with I^3 and I_2 slightly enlarged.

The canines of *Onychodectes* are sharply pointed and of moderate size. P^1_1 are small, simple, pointed teeth and are single-rooted. P^2 is two-rooted and oval in cross-section, being compressed transversely and elongated anteroposteriorly. P^3 is triangular in cross-section and bears a large paracone labially and a moderate protocone lingually.

P^4 (Pl. 5: figs. 7, 8) is roughly triangular in cross section and labially bears a large oval paracone elongated anteroposteriorly with at most an incipient metacone on its posterior face. Labially, P^4 bears a very slight ectocingulum, a minute parastyle with a slight stylocone and a small metastyle with a small metastylocone. Lingually, P^4 bears a moderate-sized protocone flanked by pre- and postcingula. The precingulum connects the anterior base of the protocone to the parastyle and bears a small pericone. The postcingulum connects the posterior

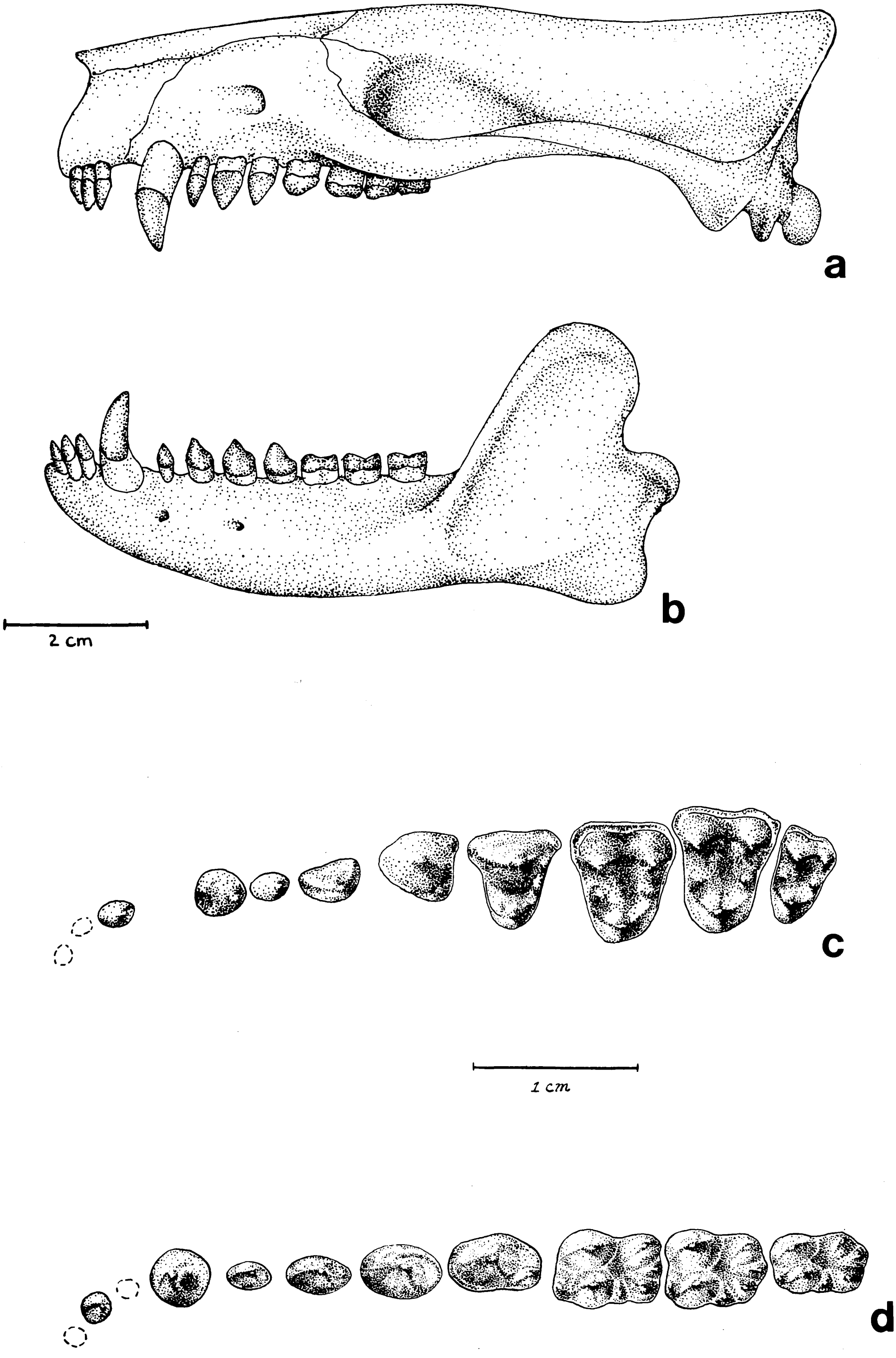


FIG. 1. Restoration of the skull, mandible and dentition of *Onychodectes tisonensis tisonensis*, based primarily on AMNH 16528 and AMNH 785. *a*) Left lateral view of skull. *b*) Left lateral view of mandible. *c*) Occlusal view of upper left dentition. *d*) Occlusal view of lower right dentition.

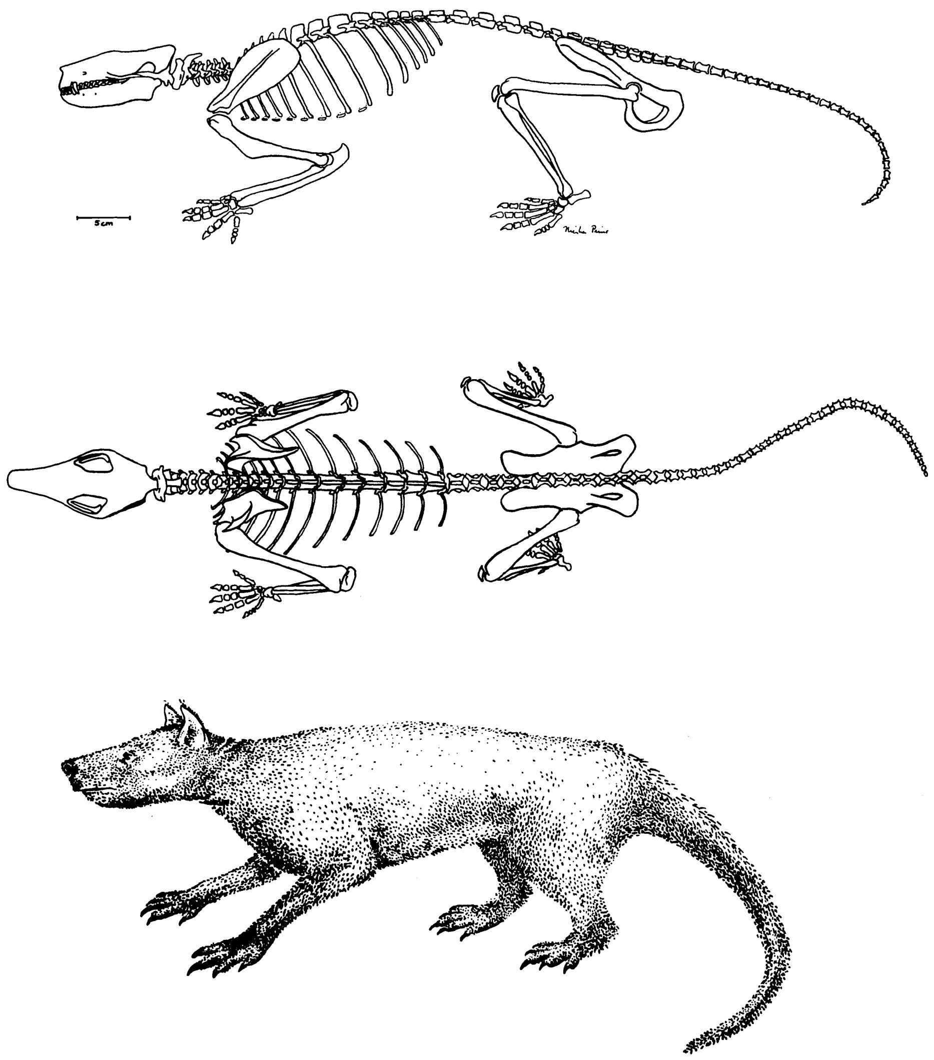


FIG. 2. Reconstructed skeleton and life restoration of *Onychodectes tisonensis* based on specimens described and illustrated in the text and plates. *Top:* left lateral view of the reconstructed skeleton. *Middle:* dorsal view of the reconstructed skeleton. *Bottom:* life restoration.

base of the protocone to the metastyle and bears a small "metaconule" flanked labially by a smaller "hypocone" (the homologies of these cusps are not certain).

M^{1-3} (Pl. 4: figs. 1, 9–12; Pl. 5: figs. 1–6) decrease in size posteriorly, but otherwise are of similar morphology. These teeth bear moderate-sized, subequal, conical, punctate, labially appressed and lingually inclined paracones and metacones. Labially, M^{1-3} bear well-defined and minutely cuspidate parastyles, ectocingula and metastyles. Their stylar shelves are at most extremely narrow. The trigon basins are shallow. On the lingual edge of the teeth M^{1-3} bear moderately small and poorly defined protocones that are slightly recurved labially. Small protoconules (paraconules) and metaconules occur relatively labially along the far anterior and posterior edges of M^{1-3}.

P_{2-4} (Pl. 2; Pl. 5: figs. 13–19) are all simple, nonmolariform, double-rooted teeth that increase in size posteriorly. Anteriorly, P_{2-4} bear large, high, anteroposteriorly elongated and laterally compressed protoconids that are sharp and slightly recurved posteriorly. Posteriorly, P_{2-4} bear small talonid heels that increase in relative size from P_2 to P_4.

M_{1-3} (Pl. 2; Pl. 5: figs. 10–19; Pl. 6) decrease in size posteriorly, but otherwise are of similar morphology. The trigonids and talonids are subequal in size, subcircular in cross-section and not particularly compressed anteroposteriorly. The trigonids bear large, subequal and sharply punctate protoconids and metaconids with only slightly smaller paraconids. The talonids bear high and punctate hypoconids, slightly smaller and punctate entoconids and smaller hypoconulids. Minute ectoconulids and mesoconids may both be variably present; one or two minute external cuspids are sometimes present on the anterior part of the talonid lobe.

All of the cheek teeth are moderately hypsodont and show the characteristic taeniodont trait of "rolling eruption" (Patterson 1949b) with enamel extending far lingually on the upper cheek teeth and far labially on the lower cheek teeth.

Associated with AMNH 16411 is a molariform tooth (Pl. 5: fig. 9) which because of its enamel color (it is slightly lighter in color than the other teeth associated with it, presumably of the same individual) and its dimensions (relatively small and transversely widened: length is 4.7 mm, width is 6.5 mm) appears to be a right dP^4 of *Onychodectes.* This tooth bears a large conical paracone, a slightly smaller metacone positioned well labially, a narrow stylar shelf, slight ectocingulum, medium-sized and broad (but broken) parastyle, small mesostyle, and a shallow ectoflexus. The trigon basin is relatively shallow and bears a poorly defined protocone lingually, an incipient paraconule, pre- and postparaconule wings, an incipient metaconule and pre- and postmetaconule wings. This tooth lacks any cingula, as do other teeth of taeniodonts. It is very hypsodont (the enamel extends far down the lingual face of the tooth), but it is very shallow labially.

Skull

Two skulls of *Onychodectes* are known: AMNH 785 and AMNH 16528 (Pls. 1, 3). Both are relatively poorly preserved and have been described in detail by Matthew (1937, p. 241–43), fig. 58; Pl. 58: fig. 4).

As Matthew (1937, p. 241) noted, the skull of *Onychodectes* is "strikingly insectivore-like in its proportions and in many characteristic points of construction." This further corroborates taeniodont affinities to "leptictimorphs" (sensu Szalay 1977), especially *Procerberus, Cimolestes* and allies as postulated by McKenna (1969, 1975) and Lillegraven (1969), among others, on the basis of dental characters, and by Szalay (1977) on the basis of tarsal characters (see below, Chapter 7).

The skull of *Onychodectes* is long and narrow, with a long muzzle in which the anterior teeth (incisors, canines and premolars) are well separated. The nares are terminal and the nasals are long, extending to above M^1, and expanded posteriorly. This posterior expansion is unlike that in the early Tertiary "insectivores" (Matthew 1937), but is probably a retained primitive (symplesiomorphous) character (see Novacek 1980, table 5); it is also seen in all other genera of taeniodonts. The premaxillae are relatively large and extend posteriorly between the maxillae and nasals to a point above P^1 or P^2. The infraorbital foramen is relatively large and placed above P^3. The anterior root of the zygoma joins the lateral aspect of the skull above P^4 and the zygomatic arch is relatively narrow. The anterior margins of the orbits are above M^1 and there is no postorbital process.

The posterior skull roof is also long and narrow with a low sagittal crest. Ventrally, the pterygoid flanges are thin, bladelike and not widely separated. The glenoid fossa is short and rounded and the postglenoid process is small and short. The mastoids are not enlarged; other features of the basicranium and ear region are not preserved.

The lower jaw of *Onychodectes* is relatively long and shallow with a broad and flat coronoid process that is not recurved posteriorly. The angle of the mandible is slightly expanded posteriorly. The condyle is set at, or very slightly above, the tooth row, is short anteroposteriorly, and very slightly expanded transversely. Internally, the dental foramen is prominent and set ventral and anterior to the condyle. The symphysis is weak and shallow, incompletely fused, and long anteroposteriorly. The incisors, canines and premolars are relatively well separated and do not contact interstitially.

Axial Skeleton

Vertebrae

The axial skeleton of *Onychodectes* is poorly known. As Matthew (1937) noted, there are a few isolated, incomplete and badly crushed vertebrae associated with AMNH 3404, AMNH 3405, AMNH 3576a (listed as 3476 by Matthew?), AMNH 16410 and AMNH 16528 (Fig. 3; Pl. 9); however, the identification of some of these as of *Onychodectes* is questionable (see above). Matthew (1937, p. 243) stated that "part of a cervical centrum indicates a very short neck"; however, I have not located any vertebrae that are undoubtedly cervical in the AMNH collections other than a piece included in AMNH 3576a which represents the right side of the atlas.

From the fragmentary material, the dorsal (thoracic) vertebrae appear to be considerably smaller than the lumbars (although this is based on vertebrae of different individuals). The tall spine, which is directed posteriorly, of an anterior thoracic vertebra is preserved in AMNH 3576a along with a badly crushed posterior thoracic vertebra. A fragmentary and heavily encrusted lumbar vertebra is preserved in AMNH 3404. None of these vertebrae show any remarkable features, but all follow the typical mammalian form (cf. Mivart 1881).

A number of caudals are preserved, especially in AMNH 16528. They are relatively large, especially the proximal caudals. Posteriorly, the caudals become long and slender. The neural arches are reduced and lost in the caudal vertebrae, but they retain relatively strong anterior and posterior transverse processes, a median spine and reduced anterior and posterior articular surfaces on the more proximal caudals.

Two large chevron bones are also preserved with AMNH 16528. The sides are joined in the midlines proximally and form anteroposteriorly elongated plates distally which lie on either side of, and enclose, the caudal artery.

Sacrum

Parts of the sacrum of *Onychodectes* are preserved in AMNH 3411 and AMNH 16410 (Fig. 3e, f; Pl. 8: figs. 11, 12). These are in a poor state of preservation, but appear to be composed of two expanded, heavily fused vertebrae.

Pectoral Girdle and Forelimb

Scapula

A small part of the right scapula is preserved in AMNH 3576a (Fig. 4a, b; Pl. 9: figs. 19, 20), including the coracoid process, the glenoid cavity and the base of

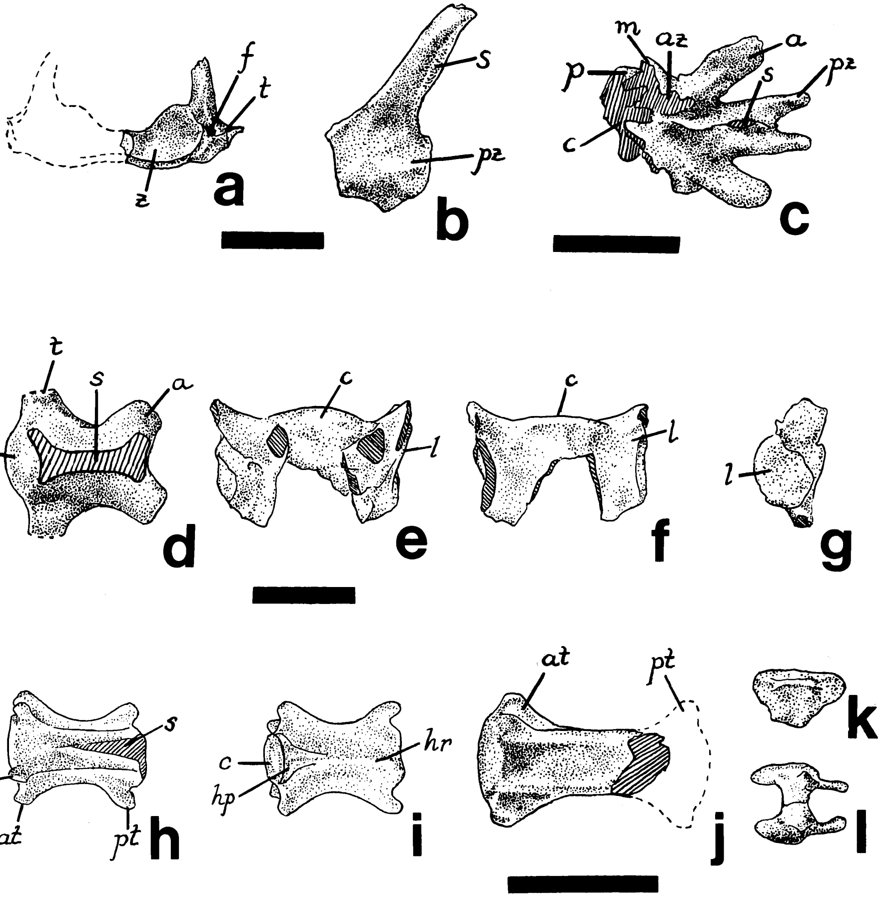


FIG. 3. Selected vertebrae and sacrum of *Onychodectes tisonensis*. *a*) Posterior view of right side of atlas, AMNH 3576a. *b*) Left lateral view of neural spine of anterior thoracic vertebra, AMNH 3576a. *c*) Dorsal view of posterior thoracic vertebra, AMNH 3576a. *d*) Dorsal view of posterior lumbar vertebra, AMNH 3404. *e*) Dorsal view of sacrum, AMNH 16410. *f*) Ventral view of sacrum, AMNH 16410. *g*) Left lateral view of sacrum, AMNH 16410. *h*) Dorsal view of anterior vertebra, AMNH 16528. *i*) Ventral view of anterior caudal vertebra, AMNH 16528. *j*) Dorsal view of posterior caudal vertebra, AMNH 16528. *k*) Left lateral view of chevron bone, AMNH 16528. *l*) Ventral view of chevron bone, AMNH 16528.

Abbreviations: a = anapophysis; at = anterior transverse process; az = anterior zygapophysis; c = centrum (vertebrae); c = anterior central articular surface (sacrum); f = foramen; hp = hypapophysial prominence; hr = hypapophysial ridge (= ventral median ridge); l = lateral mass; m = metapophysis; p = articular facet for capitulum of rib; pt = posterior transverse process; pz = posterior zygapophysis; s = neural spine; t = transverse process; z = articular surface of the atlas.

Scale below elements *a* and *b* is 1 cm long and is for elements *a, b, k, l*. Scale below element *c* is 1 cm long and is for element *c*. Scale below element *e* is 2 cm long and is for elements *d–i*. Scale below element *j* is 1 cm long and is for element *j*.

the spine. There does not appear to be anything particularly distinctive about this scapula.

Humerus

The humerus, well preserved in AMNH 16410 (Fig. 4f–h; Pl. 7: figs. 4, 5), is moderately long and slender. The head is of moderate size and the articular surface extends far distally on the posterior side (as noted by Matthew 1937, p. 244, and Wortman 1897b, p. 100). The bicipital groove is deep and both the greater and lesser tuberosities are well developed. The deltoid ridge is long, thin

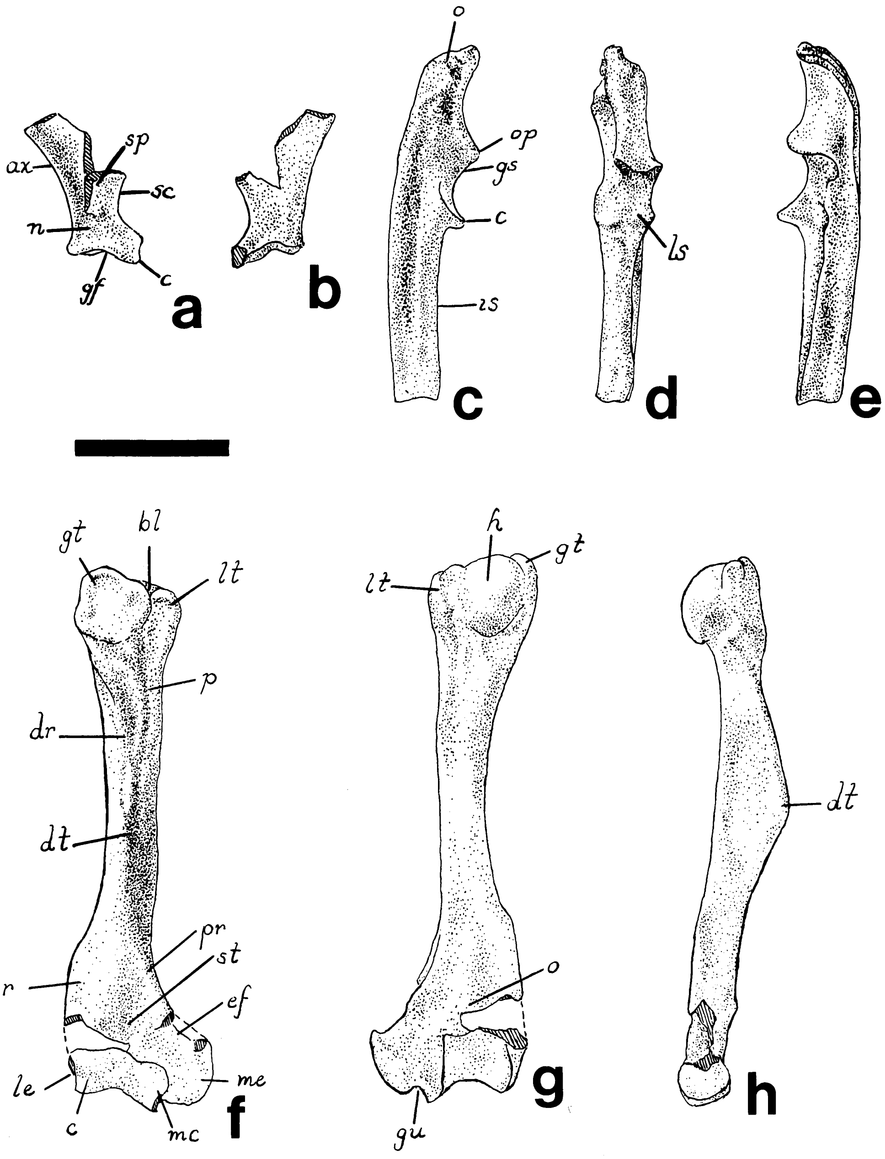


FIG. 4. Scapula, ulna and humerus of *Onychodectes tisonensis*. *a*) Lateral view of right scapula, AMNH 3576a. *b*) Medial view of right scapula, AMNH 3576a. *c*) Medial view of left ulna, AMNH 16410. *d*) Anterior view of left ulna, AMNH 16410. *e*) Lateral view of left ulna, AMNH 16410. *f*) Anterior view of right humerus, AMNH 16410. *g*) Posterior view of right humerus, AMNH 16410. *h*) Lateral view of right humerus, AMNH 16410.

Abbreviations: ax = axillary border; bl = bicipital groove; c = coracoid process (scapula); c = coronoid process (ulna); dr = deltoid ridge; dt = deltoid tuberosity; ef = entepicondylar foramen (= supracondylar foramen); gf = glenoid fossa; gs = semilunar notch (= greater sigmoid cavity); gt = greater tuberosity; gu = groove for ulnar nerve(?); h = head; le = latera epicondyle; ls = radial notch (= lesser sigmoid cavity); lt = lesser tuberosity; mc = medial condyle (= trochlea); me = medial epicondyle; n = neck; o = olecranon (ulna); o = olecranon fossa (humerus); op = olecranon process (sensu stricto); p = pectoral ridge; pr = pronator ridge; sc = scapular notch; sp = spine; sr = supinator ridge; st = supratrochlear foramen.

Scale is 3 cm long.

and prominent, extends for two-thirds the length of the humerus and projects anteriorly at about the middle of the shaft. The supinator ridge is distinct, although not especially prominent. The distal end of the humerus is relatively wide with a large internal condyle and a moderate-sized entepicondylar foramen. The olecranon fossa is moderately shallow and lacks a foramen. The capitulum and trochlea are distinct and their articular surfaces for the ulna and radius form a fairly smooth curve.

Ulna

The proximal half of a left ulna is preserved with AMNH 16410 (Fig. 4c–e; Pl. 7: figs. 2, 3); evidently this bone was complete when Matthew (1937, p. 244) described it. The olecranon is prominent and rugose with bony ridges flaring out posteriorly both medially and laterally. The semilunar notch (greater sigmoid cavity) is large and deep, and the articular surface extends far down the medial side of the shaft. The radial notch (lesser sigmoid cavity) is large, but somewhat flattened. The coronoid process is sharp and extends high above the shaft, as does the olecranon process (sensu Greene 1935, fig. 37). The shaft is somewhat flattened laterally with a moderate interosseus crest and bears a groove on the proximointernal side extending under the coronoid process as well as a deep groove in the middle of the shaft externally. Matthew (1937, p. 244) stated that the ulna "is as long as the humerus" and described the distal part of the ulna as follows: "The distal end of the shaft is somewhat narrowed, with a prominent oblique crest on its posterointernal and posterior face; this end is also slightly widened at the radial facet and is strongly oblique with a small convex knob for pisiform and cuneiform."

Radius

The heads of the right and left radii are preserved in AMNH 16410 (Fig. 5a, b; Pl. 9: figs 2–4). The head is oval-shaped (viewed proximally) and the upper part of the shaft (neck) is round in cross section and bears a moderate tuberosity. Also preserved with AMNH 16410 is the crushed distal end of the right radius; it bears no unusual or distinctive features.

Forefoot

A partial right manus of *Onychodectes tisonensis* is preserved with AMNH 16528 (Fig. 5c–i; Pl. 7: fig. 6). The carpus of *Onychodectes* consists of eight bones: proximally (listed medially to laterally) the scaphoid, lunar and cuneiform (missing in AMNH 16528), centrally the centrale and distally the trapezium (missing in AMNH 16528), trapezoid (missing in AMNH 16528), magnum and unciform. Additionally, laterally and articulating with the proximoflexor surface of the cuneiform is a large pisiform. The manus bears five metacarpals and five sets of phalanges. The first (medial) and fifth (lateral) digits are reduced in size relative to the second through fourth.

Scaphoid

Seen dorsally, the scaphoid is a thin bone elongated mediolaterally. Seen proximally, the scaphoid is subtrapezoidal in shape with two dorsopalmad convex articular surfaces, medially and laterally, separated by a shallow valley (accentuated by crushing in AMNH 16528) for articulation with the distal surface of the radius. Medially, at right angles to the proximal surface of the scaphoid, is a thin, convex articular surface elongated dorsoventrally which fits into a cor-

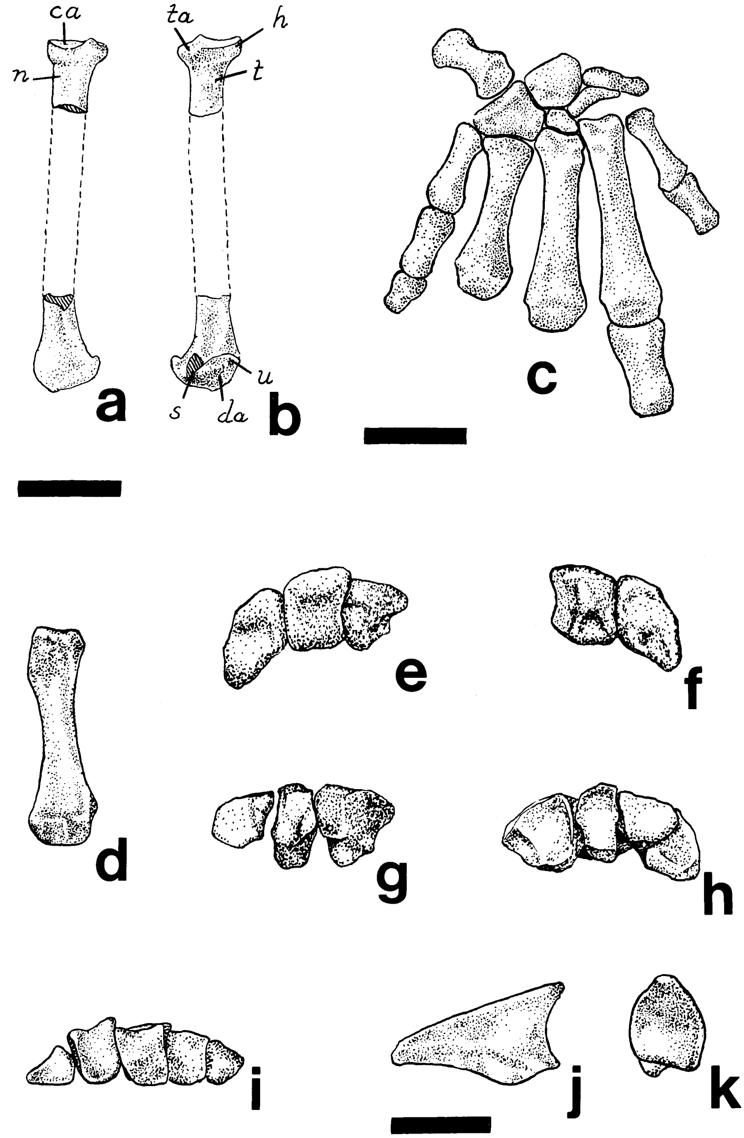


FIG. 5. Radius and manus of *Onychodectes tisonensis*. *a*) Anterior view of proximal and distal ends of right radius, AMNH 16410. *b*) Posterior view of proximal and distal ends of right radius, AMNH 16410. *c*) Anterior (dorsal) view of partial right manus, AMNH 16528. *d*) Posterior (ventral) view of right second metacarpal, AMNH 16528. *e*) Proximal view of right scaphoid, lunar and unciform, AMNH 16528. *f*) Distal view of right lunar and scaphoid, AMNH 16528. *g*) Proximal view of right centrale, magnum and unciform, AMNH 16528. *h*) Distal view of right unciform, magnum, centrale and scaphoid, AMNH 16528. *i*) Proximal view of metacarpals one through five, AMNH 16528. *j*) Lateral or medial view of ungual phalanx, AMNH 3576a. *k*) Proximal view of ungual phalanx, AMNH 3576a.

Abbreviations: ca = articular surface for capitulum of humerus; da = distal articular surface for carpals; h = head; n = neck; s = styloid process; t = tuberosity; ta = articular surface for trochlea of humerus; u = surface for ulna(?).

Scale below element *a* is 2 cm long and is for elements *a* and *b*. Scale below element *c* is 1 cm long and is for elements *c* and *d*. Scale below element *j* is .5 cm long and is for elements *e–k*.

responding, slightly concave groove on the medioproximal edge of the lunar. Distally, the scaphoid bears two slightly dorsopalmad concave surfaces, separated by a ridge which runs from the dorsal edge to the ventral edge of the scaphoid. The medial concave surface articulates with the trapezium whereas the lateral surface articulates with the centrale.

Lunar

Seen dorsally, the lunar is five sided with a long side proximally, two shorter sides medially and laterally at right angles to the proximal surface, which contact the scaphoid and cuneiform respectively, and two shorter angled surfaces distally; the medial one rests on the unciform. The surface for articulation with the radius is convex dorsoproximally, covers the proximodorsal surface of the lunar and runs far down the dorsal surface. Seen proximally, the lunar is rectangular in shape and slightly longer anteroposteriorly than transversely. Medioproximally, the lunar bears a slight groove for articulation with the scaphoid and laterally the lunar bears a slight anteroposteriorly concave surface for articulation with the cuneiform. Seen distally, the lunar comes to a sharp point dorsally where the articular surfaces for the centrale, magnum and unciform meet. Posteriorly, the lunar is only one-third as high and bears a shallow valley behind the dorsal articular surface described above. Within this valley is a deep, round pit which articulates with the proximal central protuberance of the magnum to form a "ball-in-socket" joint.

Centrale

Seen dorsally, the centrale is thin and elongated transversely; approximately a third of it lies under the lunar whereas the other two-thirds lies under the scaphoid. Seen proximally, the centrale bears a large, rather flat surface medially for articulation with the scaphoid. Laterally, the centrale bears a flat, triangular-shaped surface for articulation with the lunar. Seen distally, the centrale bears a large surface which is slightly convex dorsopalmad and also slightly concave transversely for articulation with the trapezoid. Laterally, approximately perpendicular to the surface, the centrale bears a small, flat surface which contacts with the proximomedial edge of the magnum.

Pisiform

Articulating with the proximoventral surface of the cuneiform (missing in AMNH 16528 and not known for *Onychodectes*) is the large pisiform. Anteriorly the pisiform bears a large, slightly concave (transversely) facet for articulation with the cuneiform. The pisiform is long posteriorly (ventrally) and slightly deepened dorsoventrally (proximodistally) with a slightly expanded and rugose posterior (ventral) head.

Magnum

The dorsal surface of the magnum is rather small and irregularly shaped; it fits between the unciform, lunar, centrale, trapezoid and third metacarpal. Ventrally, the magnum is expanded and much larger than the dorsal surface. Seen in proximal view, the magnum is rectangular in outline, elongated anteroposteriorly and compressed transversely. There is a prominent protuberance in the middle of the proximal face that bears a hemispherical articular surface which fits into the round pit on the distal surface of the lunar, forming the ball-in-socket joint described above. Dorsoproximally, relatively flat to slightly convex articular surfaces for the lunar and centrale form the sides leading up to this protuberance. Dorsolaterally, the magnum bears a triangular-shaped, slightly dorsopalmad convex and proximodistally concave surface for the unciform. Dorsomedially the magnum bears a similar, but smaller, articular surface for the trapezoid. Distally, the magnum is deeply concave dorsopalmad and slightly convex transversely. The entire distal surface of the magnum forms an articular surface for the proximal articular surface of the third metacarpal.

Unciform

The unciform is the largest carpal of *Onychodectes*. In dorsal view it forms a large, semitriangular wedge (thinning laterally) that contacts with the cuneiform, lunar, magnum and metacarpals three, four and five. Proximomedially, the unciform bears a dorsopalmad and transversely convex articular surface that contacts the lunar. Medially, it bears a proximodistally concave, dorsopalmad extended groove which articulates with the magnum. Dorsolaterally, the unciform bears a dorsopalmad convex, and slightly concave proximodistally, surface that articulates with the cuneiform. In distal view, the unciform forms a quadrilateral in outline and medially bears a surface, which is deeply concave dorsoventrally and slightly concave transversely, for articulation with the proximal surface of the fourth metacarpal. Laterally, the unciform bears a similar surface that is narrow transversely and articulates with the head of the fifth metacarpal.

Metacarpals

The metacarpals are five in number; metacarpals one and five are reduced relative to the other three. Metacarpal one is a small, somewhat flattened, bone. The proximal end bears an articular facet for the trapezium, which is convex both dorsoventrally and mediolaterally. As Matthew (1937, p. 245) noted, the first metacarpal has no facet for the second and "was apparently divergent, but not opposable" although "this does not of course preclude possible movement of the digit, including the trapezium, in this direction." The distal ends of all the metacarpals are expanded, relatively squared-off and strongly convex dorsally. Ventrally, in the middle of the articular surface is a small spine elongated proximodistally (as in the metatarsals, but less pronounced; see below). The distal articular surfaces of metacarpals one and five are also slightly convex mediolaterally, whereas those of two through four are only very faintly convex mediolaterally.

The second metacarpal is almost the length of the third, but less robust. The proximal end bears a mediolaterally concave and dorsoventrally convex articular surface for the trapezoid. Medially, it bears a large, flat facet for the trapezium. Laterally, there is a large, concave facet for metacarpal three, and as metacarpal two slightly overlaps three, the proximolateral border contacts the magnum.

Metacarpal three is the largest and most robust of the series. The proximal end bears a large articular facet into which the magnum fits; this is concave mediolaterally and convex dorsoventrally. Medially, there is a small, deep facet which contacts metacarpal two. Proximolaterally, there is a dorsoventrally concave facet which articulates with the unciform. Laterodistal to this facet and tucked underneath it is a concave facet for articulation where metacarpal three overlaps metacarpal four.

Metacarpal four is slightly smaller than metacarpal two. Proximally it bears a dorsoventrally convex facet for the unciform. Medially, and dorsally and ventrally, there are small convex facets for articulation with the third metacarpal. Laterally, there is a large, concave facet for articulation with the fifth metacarpal.

Metacarpal five is short and small, but wide, with a flattened shaft. Proximomedially it bears a convex articular facet for metacarpal four. Proximally it bears a convex (both dorsoventrally and mediolaterally) articular facet for the unciform. Laterally, metacarpal five also bears a large external process which is broken off in AMNH 16528.

Phalanges

A number of short, stout proximal and medial phalanges, along with several distal unguals, are preserved with AMNH 16411, AMNH 16528 and AMNH 3576a. It is not exactly determinable which of the phalanges go with which foot (fore or hind), except that the larger ones appear to belong to the pes and the smaller ones to the manus. The proximal row in each foot (especially in the pes) may have been slightly longer than the medial row.

All of the phalanges are flattened, widest proximally and narrow distally. The proximal articular facets are concave both mediolaterally and dorsoventrally; these facets are either vertical, or at an acute angle (facing dorsally), to the horizontal plane of the bone. The distal ends are not expanded, but convex dorsoventrally and either straight across mediolaterally or slightly concave. Evidently, movement was limited to extension-flexion and a moderate amount of hyperextension of the claws.

The ungual phalanges are small, sharp, unfissured claws, which are oval to subtriangular in cross-section. The unguals of the fore- and hindfeet are not distinguishable from each other.

Pelvic Girdle and Hindlimb

Ilium

A bone that may represent part of the ?right ilium of *Onychodectes* is included with AMNH 3404 (Fig. 6a, b; Pl. 8: figs. 1, 2). The ilium appears to have been moderately long and broad.

Femur

A poorly preserved proximal part of a right femur is catalogued under AMNH 3405 (Fig. 6c, d; Pl. 8: figs. 5, 6). The greater trochanter is the most prominent muscle attachment. The lesser trochanter is of moderate size and somewhat internally placed. The third trochanter is small but distinct, set high on the shaft of the femur and recurved anteriorly. The intertrochanteric fossa is broad and shallow and the shaft flattened (although this is exaggerated to an unknown degree by crushing in the specimen).

Tibia

A proximal part of a right tibia and a distal part of a left tibia are catalogued under AMNH 3405 (Fig. 6g–k; Pl. 8: figs. 3, 4, 7, 8). These fragments are poorly preserved (being partly encrusted with an ironstone concretion) and do not appear to differ from the conventional mammalian type. The fibula (not preserved) was not fused to the tibia. The distal articular surface of the tibia complements the corresponding surface of the astragalus described below.

Patella

A patella is preserved with AMNH 3576a; it is subcircular in outline and rather flat (Fig. 6e, f; Pl. 8: figs. 9, 10).

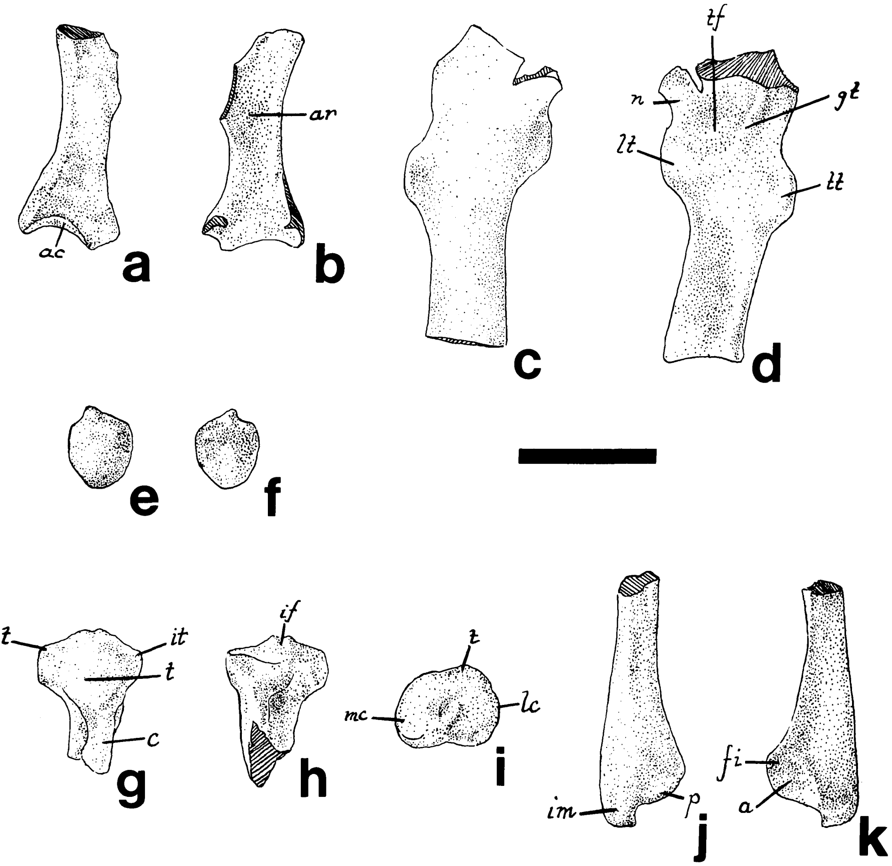


FIG. 6. Ilium, femur, patella and tibia of *Onychodectes tisonensis*. *a*) Lateral view of (?)right ilium, AMNH 3404. *b*) Medial view of (?)right ilium, AMNH 3404. *c*) Anterior view of right femur, AMNH 3405. *d*) Posterior view of right femur, AMNH 3405. *e*) Anterior view of patella, AMNH 3576a. *f*) Posterior view of patella, AMNH 3576a. *g*) Anterior view of proximal part of right tibia, AMNH 3405. *h*) Posterior view of proximal part of right tibia, AMNH 3405. *i*) Proximal view of proximal part of right tibia, AMNH 3405. *j*) Anterior view of distal part of left tibia, AMNH 3405. *k*) Posterior view of distal part of left tibia, AMNH 3405.

Abbreviations: a = surface for astragalus; ac = acetabulum; ar = auricular surface; c = crest; et = external tuberosity; fi = surface for fibula; gt = greater trochanter; if = intercondyloid fossa (= intercondyloid notch); im = internal malleolus; it = internal tuberosity; lc = lateral tuberosity; lt = lesser trochanter; mc = medial condyle; n = neck; p = descending process; t = tuberosity; tf = intertrochanteric fossa; tt = third trochanter.

Scale is 3 cm long.

Hindfoot

A partial left pes of *Onychodectes* is preserved with AMNH 16528 (Fig. 7; Pl. 7: fig. 7). The tarsus is composed of the usual seven elements: calcaneum, astragalus, navicular, cuboid (missing in AMNH 16528 but present in AMNH 3576a), ectocuneiform, mesocuneiform and entocuneiform (missing in AMNH 16528). There are five metatarsals and digits; the first and fifth are greatly reduced in size.

Astragalus

In general shape and morphology, the astragalus of *Onychodectes* is similar to that of *Procerberus* (Szalay 1977) and *Prodiacodon* (Szalay 1966). The proximal body and distal head are distinct and separated by a moderately long and relatively constricted neck. The head and neck are oriented at an angle of approximately 30 degrees medial to the long axis of the body of the astragalus. The trochlear crests are oriented at an angle of approximately 10 degrees lateral to the long axis of the body. The trochlear crests are distinct and the tibial and fibular facets are oriented vertically. The lateral and medial parts of the trochlea are asymmetrical. The lateral trochlear surface is very slightly higher than the medial trochlear surface and slightly concave dorsally. The lateral crest is longer than the medial crest and extends further anteriorly and posteriorly. The trochlear fossa is shallower than in *Prodiacodon*; the deepest point is in about the center of the body. The medial trochlear surface is slightly convex dorsally. The articular surface of the trochlea extends through an angle of about 180 degrees. A superior astragalar foramen is absent.

Ventrally, although an astragalar canal is absent, there appears to be the slightest trace of a vestigial plantar astragalar foramen (this feature is seen with reasonable certainty only in AMNH 16528 and may be an artifact of preservation or preparation or both). If this feature really does occur in *Onychodectes,* it is similar to *Prodiacodon* in this respect (Szalay 1966). The interarticular sulcus is deep. The calcaneoastragalar facet is moderately concave, long and rectangular-shaped, and more closely resembles that seen in *Procerberus* than that in *Prodiacodon.* The long axis of the calcaneoastragalar facet is oriented laterally at an angle of approximately 35 degrees from the long axis of the body. The sustentacular facet is roughly pentagonal in shape and slightly convex proximomedially–distolaterally.

The head bears the naviculocuboid-astragalar facet. This is convex distally, semicircular in shape and covers about 180 degrees. As in *Prodiacodon,* the facet is broadest laterally and tapers medially and then proximally. Matthew (1937, p. 247) states that "there is a distinct astragalo-cuboid facet"; there does appear to be a convex lateral facet on the head of the astragalus, but it is not particularly distinct.

Calcaneum

The calcaneum of *Onychodectes* is similar to that of *Procerberus* and *Prodiacodon.* The tuber calcanei is of moderate length, deep, and bears a very slightly expanded head; the medial surface is very slightly concave. The proximal end bears a distinct horizontal groove (fossa for the tendon of Achilles?). The medial and lateral processes of the tuber calcanei are not pronounced.

Dorsally, the astragalocalcaneal facet is obliquely set to the horizontal plane of the bone. It is long, relatively rectangular in shape and convex, facing distomedially. The long axis of the astragalocalcaneal facet is at an angle of about 45 degrees to the long axis of the calcaneum. Distal and medial to this facet is the moderate-sized, triangular to oval-shaped, calcaneal sustentacular facet which is slightly concave and lies approximately in the horizontal plane of the bone as a whole. These two facets are separated by a shallow depression, the interosseous fossa which held the interosseous ligament (Szalay 1966).

The peroneal tubercle is broken off in the known calcanea of AMNH 16528 and AMNH 3405 [although it may have been present on AMNH 16528 when Matthew (1937) described the foot of *Onychodectes*]. However, it was apparently prominent and expanded laterally as in *Prodiacodon.* The distal end of the calcaneum bears the large, triangular-shaped, slightly concave cuboid facet. The latter is vertical to the horizontal plane of the bone and faces distally and only very slightly medially.

Navicular

The navicular is relatively small and thin with a long, thin process which extends medially around the head of the astragalus. The proximal astragalonavicular facet is deeply concave and dish-shaped. Laterally, the navicular bears a small, rectangular facet for articulation with the cuboid. Distally, the navicular bears two distinct, flat, oval-shaped articular surfaces for the ecto- and mesocuneiform. These facets are set at an angle of about 120 degrees to one another. The facet for the entocuneiform is obliterated by poor preservation, but as Matthew (1937, p. 247) noted, it appears to be reduced.

Ectocuneiform

The ectocuneiform is relatively large and deep, thinning ventrally. Dorsally, it is rectangular in shape. Distomedially it bears a large, triangular, concave facet for articulation with the navicular. Distolaterally, it bears a thin, deep, flat surface for articulation with the cuboid. On the medial side distally it bears two suboval facets, one dorsally and the other ventrally, for articulation with the second metatarsal. Distally, the ectocuneiform bears a large, deep, concave facet for articulation with the proximal end of the third metatarsal.

Mesocuneiform

The mesocuneiform is only about half the size of the ectocuneiform. It is square in shape, seen dorsally, and deep. Proximally, it bears a flattish articular surface for the navicular. Distally it bears a slightly concave articular surface for the second metatarsal. The medial face has several small facets for articulation with the apparently reduced entocuneiform.

Cuboid

In dorsal view, the cuboid is rectangular in shape, slightly elongated proximodistally, and pinched mediolaterally in the center. Proximally, and facing very slightly laterally, is a large, slightly convex (in both directions) facet for articulation with the calcaneum. The proximomedial corner bears a small, concave facet for articulation with the astragalus, and another flat facet just distal to the last for articulation with the navicular. The cuboid fit between the navicular and calcaneum such that the navicular and calcaneum did not make contact. In the center of the medial side of the cuboid is a dorsally concave facet which extends distoventrally to become a dorsoventrally convex facet; this facet articulated with the lateral side of the ectocuneiform. Distally, the cuboid bears a large, deeply concave (dorsoventrally) facet for articulation with the fourth and fifth metatarsals. Ventrally, the cuboid bears a small, round, convex proximomedial facet and a larger, ovoid, convex distolateral facet elongated proximolaterally–mediodistally. These surfaces apparently contacted the soft parts of the ventral surface of the foot. Distal to the latter is a deep, transverse groove (for the tendon of the *peroneus longus* muscle?).

Metatarsals

Metatarsals one and five, the proximal end of three and the distal ends of two and four are preserved in AMNH 16528 (Fig. 7; Pl. 7: fig. 7). The second metatarsal is preserved in its entirety in AMNH 3576a and the fourth metatarsal is preserved in its entirety in AMNH 16410 (Fig. 7c). The metatarsals are up to twice as long as the metacarpals, but the shafts and distal ends are only slightly larger than those of the corresponding metacarpals. Metatarsals one and five are somewhat reduced, but less so than metacarpals one and five.

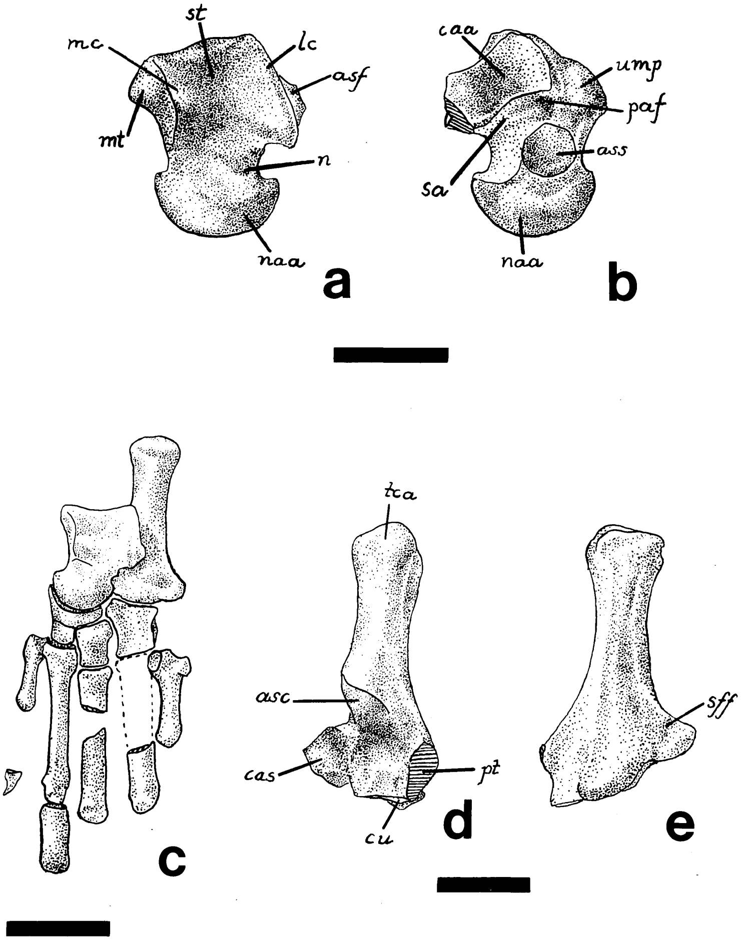


FIG. 7. Astragalus, calcaneum and pes of *Onychodectes tisonensis*. *a*) Proximal (dorsal) view of left astragalus, AMNH 16528. *b*) Distal (ventral) view of left astragalus, AMNH 16528. *c*) Anterior (dorsal) view of partial left pes, AMNH 16528 (metatarsal four is from AMNH 16410). *d*) Proximal (dorsal) view of left calcaneum, AMNH 16528. *e*) Distal (ventral) view of left calcaneum, AMNH 16528.

Abbreviations: asc = astragalocalcaneal facet; asf = astragalar fibular facet; ass = astragalar sustentacular facet; caa = calcaneoastragalar facet; cas = calcaneal sustentacular facet; cu = cuboid; lc = lateral crest of trochlea; mc = medial crest of trochlea; mt = medial tibial facet of trochlea; naa = naviculoastragalar facet; n = neck; paf = plantar astragalar foramen; pt = peroneal tubercle; sa = interarticular sulcus (sulcus astragali); sff = sustentacular groove; st = superior trochlear facet and trochlear fossa; tca = tuber of the calcaneum; ump = ventromedial process.

Scale below element *a* is 1 cm long and is for elements *a* and *b*. Scale below element *c* is 2 cm long and is for element *c*. Scale below element *d* is 1 cm long and is for elements *d* and *e*.

Metatarsal one is short, slender and deep. The proximal end bears a large, deep articular surface which is deeply concave mediolaterally and slightly convex dorsoventrally for articulation with the entocuneiform. Laterally, there is a narrow facet for articulation with the second metatarsal. The distal ends of metatarsals one through four are relatively squared-off, strongly convex dorsoventrally with the articular surfaces extending well dorsally. Ventrally, in the middle of the articular surfaces, they bear a pronounced spine elongated proximodistally. Evidently, on either side of these spines were sesamoid bones, as in the cat (Mivart 1881). The proximal articular surfaces of the proximal phalanges are either vertical or inclined at an acute angle to the horizontal plane of the bones.

To a lesser extent, the same holds true for the metacarpals and phalanges of the manus (see above). This evidence indicates that *Onychodectes* was not so fully palmigrade as *Didelphis,* for instance, but rather that it could also stand more on the distal ends of its metapodials and phalanges, as in the cat.

The second metatarsal is long and slender, although more robust than the first. The distal articular surface, which takes the mesocuneiform, is quadrate in outline and narrows ventrally. It is slightly convex dorsoventrally. Medially, there is a concave facet for articulation with the entocuneiform. Laterally, there are two rounded facets, one set dorsally and the other set ventrally, for articulation with the ectocuneiform.

Only the proximal end of the third metatarsal is known, but it appears to be of a size comparable to the second and fourth. The facet for the ectocuneiform is deep and convex both mediolaterally and dorsoventrally. Laterally, there is a deeply concave fossa and dorsal and ventral facets for articulation with the fourth metatarsal.

The fourth metatarsal is long and thin. As Matthew (1937, p. 248) noted, it "is distinctly longer than the second"; however, the bones being compared are from different individuals and so the apparent differences in length may be deceptive. The proximal end is similar to the third metatarsal. The facet for the cuboid is narrow, deep and convex dorsoventrally. Medially and dorsally, it bears a moderately large, convex facet and medially and ventrally a small, flat facet; these facets articulate with the third metatarsal. Laterally, the fourth metatarsal bears a thin, deep, concave facet for articulation with the fifth metatarsal.

The fifth metatarsal is slightly over half the length of the fourth metatarsal. The shaft is flattened and widened. Proximally there is a large, convex, dorsomedial facet for articulation with the fourth metatarsal. Lateral and proximal to this is a small, flat facet for articulation with the cuboid. Laterally on the proximal end there is a prominent, projecting hemispherical process. The distal end is set obliquely to the shaft of the bone (facing slightly laterally), is only slightly expanded, convex dorsoventrally and moderately convex mediolaterally. As in metatarsals one through four, it also bears a ventral spine elongated proximodistally.

Phalanges

As described above, except for possible differences in size, the phalanges of the front and hindfeet are not distinguishable from one another.

Conoryctella Gazin, 1939

Conoryctella Gazin, 1939, p. 276.
Conoryctes: Taylor, 1981, p. 250.

Type Species. *Conoryctella dragonensis* Gazin, 1939.

Included Species. The type species and *Conoryctella pattersoni* Schoch and Lucas, 1981c.

Distribution. Torrejonian (including the "Dragonian") of New Mexico and Utah.

Revised Diagnosis. Small taeniodonts, larger than *Onychodectes* but smaller than *Conoryctes*; teeth more hypsodont than *Onychodectes* but less hypsodont than *Conoryctes*; P^4 nonmolariform with well-developed protocone and paracone, but only an incipient metacone; stylocone and parastyle absent on P^4 or only slightly developed (in contrast to *Onychodectes* and *Conoryctes* in which they usually are moderately well developed); symphysis of lower jaw unfused; lower canines relatively large, heavily invested with enamel, triangular in cross section, transversely compressed and tending toward the rootless condition seen in advanced taeniodonts; P_4 submolariform with a single protoconid anteriorly and a moderately developed talonid posteriorly; lower molar paraconids relatively large.

Conoryctella dragonensis Gazin, 1939
(Table 24; Pl. 10: figs. 5, 6)

Conoryctella dragonensis Gazin, 1939, p. 276.
Conoryctella dragonensis: Gazin, 1941, p. 15 (in part).
Conoryctella dragonensis: Schoch and Lucas, 1981c, p. 2.

Type and Only Known Specimen. USNM 15704, left maxilla with damaged P^4–M^2 and part of P^3 alveolus (Pl. 10: figs. 5, 6).

Horizon and Locality of the Type. Dragon local fauna, Torrejonian strata of the upper part of the North Horn Formation, NW ¼, Sec. 8, T.19 S., R.6 E., Emery County, Utah.

Revised Diagnosis. Largest known species of *Conoryctella*; differs from *C. pattersoni* in the following features: P^4 with slightly better developed metacone and incipient stylocone; M^{1-2} relatively wide with reduced stylar shelves, slight ectoflexi and small mesostyles.

Conoryctella pattersoni Schoch and Lucas, 1981c
(Table 24; Fig 8; Pl. 10: figs. 1–4, 7–9)

Conoryctella dragonensis: Gazin, 1939, p. 15 (in part).
conoryctine, n. gen. and sp.: R. W. Wilson, 1956, p. 82.
n. gen. et sp.: Russell, 1967, p. 68.
Conoryctella: Schoch and Lucas, 1981a, p. 225.
n. gen. and n. sp.: L. H. Taylor, 1981, p. 259.
n. gen. et sp.: Tsentas, 1981, p. 272.
Conoryctes comma: L. H. Taylor, 1981, p. 250.
Conoryctella pattersoni Schoch and Lucas, 1981c, p. 5.

Type Specimen. UNM B-1258, palate with right and left P^4–M^3 and roots of right and left P^{2-3}, right dentary with C_1, P_3–M_3 and roots of I_{1-3}, incomplete right and left ulnae (Pl. 10: figs. 1–4, 7–9).

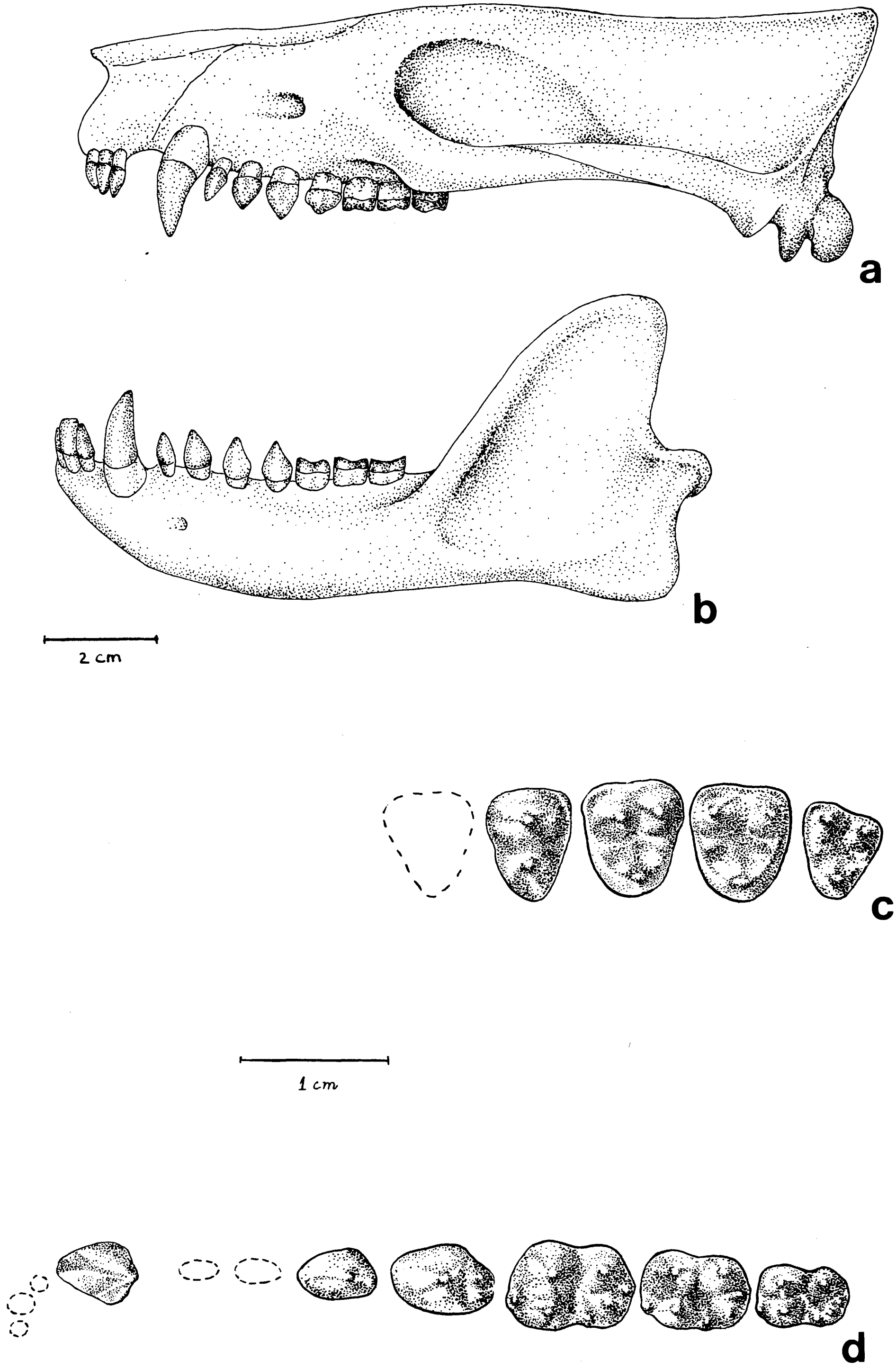


FIG. 8. Partial skull, mandible and dentition of *Conoryctella pattersoni,* UNM B-1258. *a*) Left lateral view of skull. *b*) Left lateral view of mandible. *c*) Occlusal view of known upper dentition (left P^4–M^3 and alveolus for P^3). *d*) Occlusal view of right lower dentition.

Horizon and Locality of the Type. Torrejonian strata of the Nacimiento Formation, UNM locality B-1096, Kutz Canyon, San Juan Basin, New Mexico.

Referred Specimens. USNM 15722, right dentary fragment with M_1 and base and roots of P_4; USNM 16173, fragmentary and isolated M_1 and M_2; USNM 18538, right dentary fragment with M_3: all from Torrejonian strata of the upper part of the North Horn Formation, Dragon local fauna, N.W. ¼, Sec. 8, T. 19 S., R. 6 E., Emery County, Utah.

UK 7807, right dentary fragment with M_2 and roots of M_3; UK 7888, right dentary fragment with M_2 and partial alveolus of M_1; UK 9562, left maxilla with partial M^1, complete M^2 and partial M^3 and right dentary fragment with complete M_1 and roots of C_1 and P_{1-4}; UALP 11661, left M^1: all from Torrejonian strata of the Nacimiento Formation, Kutz Canyon, San Juan Basin, New Mexico.

Diagnosis. Smallest species of *Conoryctella*; differs from *C. dragonensis* in the following features: P^4 lacks a parastyle, stylocone and metacone; P^4 postprotocrista only slightly developed; upper molars relatively narrow.

?*Conoryctella* cf. *C. dragonensis*

?*Conoryctella* cf. *C. dragonensis*: Schoch and Lucas, 1981c, p. 12.

Referred Specimen. AMNH 3412, a poorly preserved left maxilla with P^4–M^3 largely encrusted with ironstone concretion and a left upper canine: from Paleocene strata of uncertain age, Nacimiento Formation, San Juan Basin, New Mexico.

Discussion. This specimen may represent *Conoryctella,* but the teeth are so heavily encrusted with an impregnable ironstone concretion that their morphology is largely obscured and definitive taxonomic assignment thus is rendered difficult. It is described and illustrated in Schoch and Lucas (1981c, p. 12, fig. 7).

Description and Discussion of *Conoryctella*

Schoch and Lucas (1981c) have recently revised the genus *Conoryctella,* thoroughly describing and illustrating the known dentition of each species; the reader is referred to that paper.

Other than teeth, maxilla and dentary fragments, *Conoryctella* is known only from a fairly complete right dentary and the proximal ends of both ulnae preserved in UNM B-1258 (Pl. 10: fig. 9).

The mandible is similar to that of *Onychodectes,* but is slightly shorter (in relative length) and deeper. It bears a large, unfused symphysis which extends to under P_3. The ascending ramus originates posterior to M_3.

The ulna of *Conoryctella* is similar to that of *Onychodectes,* but slightly longer. The shafts of both are deep dorsoventrally and compressed transversely; however, the medial and lateral grooves are not so well developed in the ulna of *Conoryctella.* The olecranon of the ulna of *Conoryctella* is robust and heavily rugose and larger (both relatively and absolutely) than the olecranon of *Onychodectes.* The radial notch of *Conoryctella* is relatively flat and slightly larger than that in *Onychodectes*; otherwise, the ulnae of these two genera are virtually identical. The distal end of the ulna of *Conoryctella* is unknown.

Conoryctes Cope, 1881a

Conoryctes Cope, 1881a, p. 829.
Hexodon Cope, 1884a, p. 794.
non *Hexodon* Olivier, 1789, p. 1.

Type Species. *Conoryctes comma* Cope, 1881a (= *Hexodon molestus* Cope, 1884a.)

Included Species. Only the type species.

Distribution. Torrejonian of New Mexico.

Revised Diagnosis. Medium-sized taeniodonts, about the size of *Huerfanodon*; teeth relatively hypsodont (crown hypsodonty); canines lack internal grooves; P^3 nonmolariform, bears a simple large paracone and a minute to small metacone and lingual cingulum; P^4 molariform with a large protocone, smaller paracone, still smaller metacone and small parastyle, stylocone, metastyle and metastylocone; mesostyle absent on P^4; M^{1-3} bear large protocones and smaller, conical, labially placed paracones and metacones; M^{1-3} mesostyles vary from absent to moderately well developed; P_4 submolariform, trigonid bears a single large protoconid and simple talonid; lower molars with small paraconids.

Conoryctes comma Cope, 1881a
(Table 25; Fig. 9; Pls. 11, 14; Pl. 15: figs. 14–17; Pl. 16: figs. 1, 6)

Conoryctes comma Cope, 1881a, p. 829.
Conoryctes comma: Cope, 1881b, p. 486.
Hexodon molestus Cope, 1884a, p. 794.
Conoryctes comma: Cope, 1884c, p. 198.
Conoryctes comma (= *Hexodon molestus*): Cope, 1888d, p. 317.
Conoryctes comma: Wortman, 1897b, p. 101.
Conoryctes comma: Matthew, 1937, p. 250.
Conoryctes comma: R. W. Wilson, 1956, p. 82.
non Conoryctes comma: Van Valen, 1978, p. 58.
non Conoryctes comma: L. H. Taylor, 1981, p. 250.

Type Specimen. AMNH 3395, left dentary fragment with P_4–M_2, alveolus for P_2, roots of P_3 and M_3, isolated lower right canine (Pl. 15: figs. 14–17; Pl. 16: fig. 6).

Horizon and Locality of the Type. Collected by David Baldwin for E. D. Cope from presumably Torrejonian strata of the Nacimiento Formation, San Juan Basin, New Mexico.

Referred Specimens. AMNH 3396, palate with left C^1, right P^3, right and left P^4–M^3, mandible with left C_1, P_4–M_3, right C_1, P_3, M_2 and M_3, roots of left I_{1-3}, P_3 and right I_2, P_{1-2}, right proximal three-quarters of the humerus, and right distal end of the radius (type specimen of *Hexodon molestus*; Pl. 14: figs. 1–6, 8, 10); AMNH 3397, left dentary fragment with P_4–M_3; AMNH 3398, partial skull and mandible with four miscellaneous incisors, left C^1, right P^3–M^3, fragmentary right P_1, left P_4, M_{2-3}: all collected by David Baldwin from presumably Torrejonian strata of the Nacimiento Formation, San Juan Basin, New Mexico.

AMNH 16029, right dentary fragment with M_{1-2} (Pl. 14: fig. 9); UNM B-890, palate with right P^3–M^2 and left M^{1-2}, alvoeli for right M^3 and left P^{3-4}, M^3, loose incisor, left P_3, right P_4 and fragments of cranium (Pl. 16: fig. 1); USNM 22484, skull and jaws with right and left P^{3-4}, M^3 and left M^2, right C_1, P_2, P_4–M_2 (Pl. 11); USNM 22483, partial left manus (Pl. 14: fig. 7) cata-

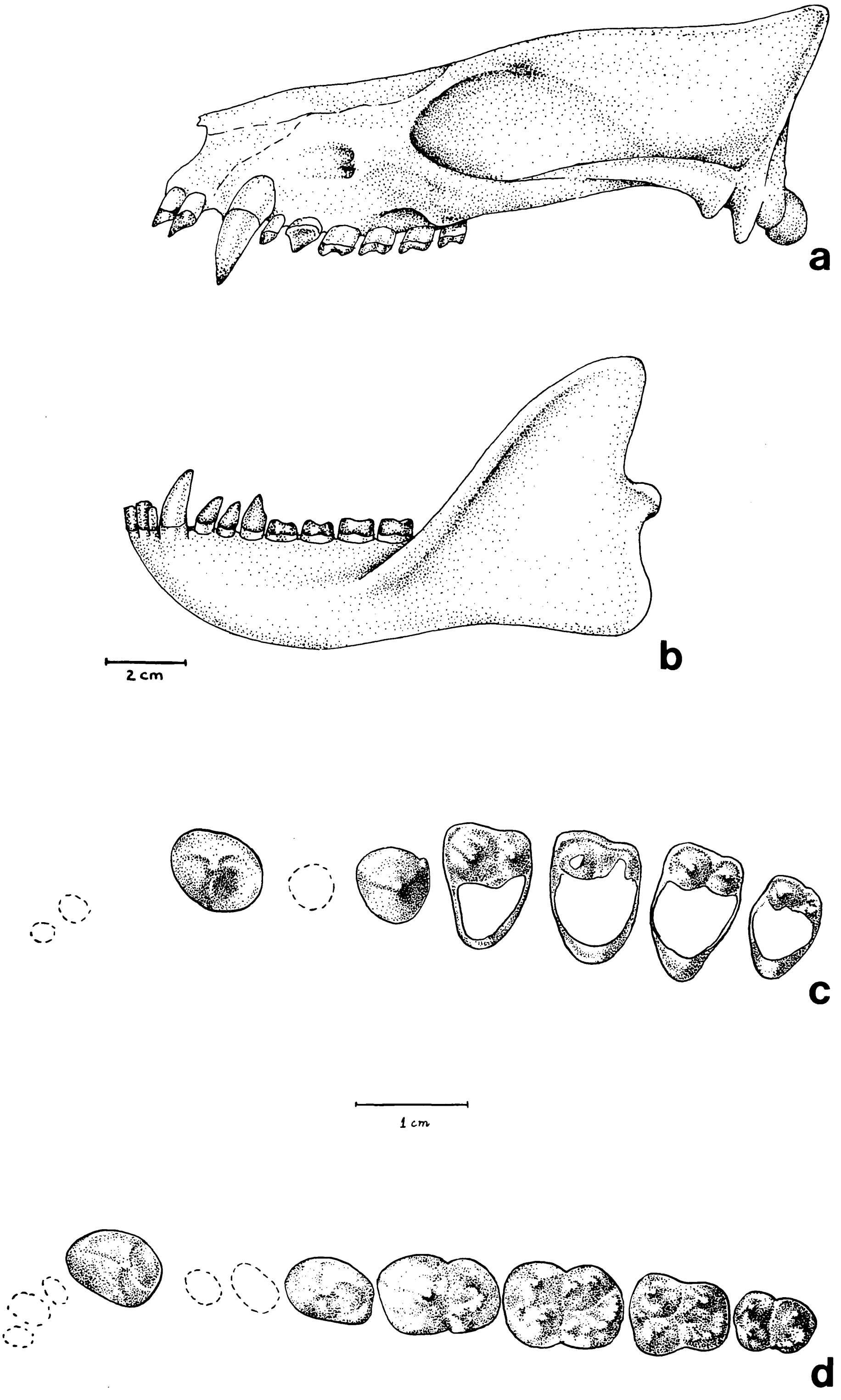


FIG. 9. Restoration of the skull, mandible and dentition of *Conoryctes comma*. Skull based primarily on USNM 22484 and AMNH 15939 (undetermined conoryctid skull). Dentition based primarily on AMNH 3395, AMNH 3396 and UNM B-890. *a*) Left lateral view of skull. *b*) Left lateral view of mandible. *c*) Occlusal view of upper left dentition. *d*) Occlusal view of lower right dentition.

logued with a skull of *Triisodon quivirensis* may actually belong to the same individual as the skull of USNM 22484 (see discussion below): all from Torrejonian strata of the Nacimiento Formation, Torreon Wash, San Juan Basin, New Mexico.

UK 8033, left dentary fragment with P_3–M_1: from UK New Mexico locality 15, Torrejonian strata of the Nacimiento Formation, SW ¼, Sec. 20, T. 22 N., R. 6 W., Sandoval County, San Juan Basin, New Mexico.

Diagnosis. Same as that for the genus.

Description and Discussion of *Conoryctes*

Conoryctes (Fig. 9) is a monotypic genus and has been thoroughly described and revised by Cope (1888d, p. 316–17), Wortman (1897b, p. 101–02) and Matthew (1937, p. 249–54). Cope (1884a) originally proposed a separate taxon, "*Hexodon molestus,*" for AMNH 3396 (Pl. 14: figs. 1–6, 8, 10), claiming that it differed from *Conoryctes comma* (Pl. 15: figs. 14–17; Pl. 16: fig. 6) by having four lower premolars instead of three. However, in his revision of *Conoryctes,* Cope (1888d) correctly pointed out that P_1 is extremely small and single-rooted. According to Cope, the absence of P_1 in AMNH 3395, the type specimen of *C. comma,* is a preservational artifact. Otherwise, *C. comma* and *H. molestus* are indistinguishable and therefore he synonymized the two (Cope 1888d, p. 317). Van Valen (1978) has recently assigned AMNH 3224 (Pl. 15: figs. 10, 11; Pl. 16: fig. 8), the type specimen of *Triisodon heilprinianus,* to *Conoryctes comma*; however, AMNH 3224 bears a large paraconid diagnostic of *Huerfanodon* and is tentatively assignable to that genus, although indeterminate at the species level (Schoch and Lucas 1981b; also see *Huerfanodon* below).

The dental formula of *Conoryctes comma* probably is $I^2_{2\text{ or }3}$, C^1_1, P^3_4, M^3_3 (cf. Matthew 1937, p. 251). I^{1-2} are slightly enlarged and the I_2 is enlarged relative to the I_1. The canines are relatively large, projecting and deeply rooted. Apparently P^1 is absent. P^2 is small, possibly single-rooted and unicuspid.

P^3 (Pl. 16: fig. 1) is three-rooted and triangular to subcircular in cross section. It bears a large paracone and a minute to small metacone and lingual cingulum.

P^4 (Pl. 16: fig. 1) is molariform and bears a large protocone lingually and a smaller, conical paracone and metacone, both placed far labially. P^4 also bears a small parastyle, stylocone, metastyle and metastylocone. It lacks a mesostyle or ectocingulum.

M^{1-3} (Pl. 14: fig. 10; Pl. 16: fig. 1) decrease in size posteriorly, but otherwise are of similar morphology. M^{1-3} bear large protocones lingually and smaller, conical, labially placed paracones and metacones. The stylar shelves of M^{1-3} are extremely narrow and the ectoflexi are weakly developed or absent. Labially, M^{1-3} bear minutely cuspidate ectocingula; mesostyles either are absent (UNM B-890) or moderately well developed (AMNH 3396).

P_{1-2} are extremely reduced, single-rooted, and unicuspid. They are subcircular in cross section. P_3 (Pl. 14: figs. 2, 8; Pl. 16: fig. 6) is single-rooted, oriented slightly obliquely in the jaw and anteriorly bears a large, anteroposteriorly elongated and laterally compressed protoconid. A small, posterointernal talonid heel may be variably developed on P_3.

The P_4 of *Conoryctes* (Pl. 16: fig. 6) is submolariform and bears a large, simple protoconid anteriorly. The talonid is comma-shaped in cross section (hence the name *Conoryctes comma* Cope, 1881a) and bears a large hypoconid and smaller hypoconulid and entoconid.

M_{1-3} of *Conoryctes* (Pl. 14: fig. 9; Pl. 16; fig. 6) decrease in size posteriorly, but otherwise are of similar morphology. The trigonids are slightly compressed anteroposteriorly and bear large, conical protoconids and metaconids. Extremely small paraconids and paracristids are present. The talonids are subcircular in cross-section and bear moderate-sized hypoconids, smaller ectoconids and hypoconulids, and still smaller mesoconids, entoconulids and metastylids. Two smaller cusps are present on the postcristids on either side of the hypoconulids.

The cheek teeth of *Conoryctes* are hypsodont (crown hypsodonty) and show the taeniodont pattern of "rolling eruption" (Patterson 1949b) in its extreme form.

The Skulls of *Conoryctes* and *Huerfanodon*

The skulls of *Conoryctes* and *Huerfanodon* (Figs. 9, 10; Pls. 11, 12, 13; Pl. 15: figs. 1–3) are nearly identical, so far as is known, and of similar size (Table 10). Furthermore, one of the best-known skulls of a large Torrejonian conoryctid is AMNH 15939 (Pls. 12, 13), which is generically indeterminate. Therefore, the skulls of these forms will be described together. The following description is based primarily on USNM 22484, USNM 15412, AMNH 15939, AMNH 3398 and MCZ 20181.

The skulls of these forms are similar to that of *Onychodectes,* but slightly longer, wider and deeper with a shorter face and cranium, and are overall more robust. The premaxillae are short and stout, extending as a wedge between the maxillae and nasals to a point above P^1, and bear the enlarged incisors. The nares are terminal. The nasals are relatively long and narrow for a taeniodont and extend back to a point above M^{2-3} in AMNH 15939 (they are shown placed too far anteriorly in fig. 61 of Matthew 1937), whereas in USNM 15412 they only extend back to above M^{1-2}. Postorbital processes are absent, but the postorbital ridges are weakly to moderately developed and connect at the midline of the skull. They extend posteriorly to form the moderately well-developed sagittal crest. The postorbital ridges connect approximately above M^3 in USNM 22484 and AMNH 3398 whereas in USNM 15412, AMNH 15939 and MCZ 20181 they join distinctly posterior to M^3. Matthew (referring to AMNH 3398 and AMNH 15939; 1937, p. 252) states that "the lachrymals extend back to a point where they [the postorbital processes] should come, thus excluding the frontals from the orbital rim." Since the time that Matthew described AMNH 3398 and AMNH 15939, the bones of these skulls have been embedded in plaster and I cannot distinguish the lacrimals.

The maxillae are short and stout; there is a distinct doubled infraorbital foramen above P^{3-4}. The anterior border of the orbits is above M^1 and the stout anterior root of the zygomatic connects above M^{1-2}. The frontals are relatively short. Anteriorly, they suture with the nasals and maxillae in the area above M^{1-3}; posteriorly they suture with the parietals in the area of the postorbital constriction. The parietals are relatively long and narrow and meet in the midline of the skull to form the moderately well-developed sagittal crest. Posteriorly, the parietals expand transversely to form the high and well-developed occipital crest. The zygomatic arches are broad and relatively robust as compared to *Onychodectes;* their posterior connection with the squamosal is relatively strong.

Ventrally, the pterygoid flanges of MCZ 20181 are long, thin and bladelike and not widely separated, although this may be partly due to crushing of the specimen. The posterior margin of the palate of MCZ 20181 extends back to M^3. The glenoid fossae are relatively shallow, flat, transversely widened and posteriorly bounded by small postglenoid processes. The mastoid processes and occipital condyles are relatively large and transverse. Seen in posterior view, the occiput is high and broad, but not as triangular-shaped as the occiput of stylinodontids.

Mandible

The mandible of these forms is extremely similar to that of *Onychodectes* except that it is shorter, deeper and more robust with a heavier symphysis that extends under P_3. The moderately high coronoid process arises from a point lateral to the posterior part of M_3 and its anterior border is angled posteriorly. The angle of the mandible extends very slightly posteriorly, but is thick transversely and heavily rugose on its internal face; this provided the area of insertion for a strong, tendinous internal pterygoid muscle. The condyles are set slightly above the occlusal surface of the tooth row and are relatively wide transversely but narrow anteroposteriorly and moderately convex.

The Postcrania of *Conoryctes*

Preserved with AMNH 3396 are the proximal three-quarters of a right humerus and the distal end of a right radius (Pl. 14: figs. 3–6).

The humerus is nearly identical in size and morphology to that of *Onychodectes* (AMNH 16410), except that in *Conoryctes* the deltoid ridge is flattened and slightly broadened in the middle of the shaft rather than coming to a high anterior point as in *Onychodectes.*

The distal end of the radius of *Conoryctes* appears to be slightly larger and more robust than the comparable part for *Onychodectes* preserved in AMNH 16410; however, AMNH 16410 is somewhat crushed and distorted. Distally, the radius of *Conoryctes* is expanded and relatively robust (in this respect resembling YPM 39805, a radius of *Ectoganus,* Pl. 46: figs. 3, 4). The styloid process is moderately well developed and positioned relatively anteriorly. The distal facet for the carpals is large, roughly square in cross section, and slightly concave in both directions.

Cope (1884c, pl. 23e, fig. 5) illustrated the proximal end of a radius associated with the type specimen of "*Hexodon molestus.*" I have not been able to locate this piece, but it does not appear to differ in size or morphology from that of *Onychodectes.* Miscellaneous fragments of long bone are also associated with AMNH 3396. These appear to include part of the shaft of an ulna and a tibia; they do not appear to differ from those of *Onychodectes.*

As discovered by R. T. Bakker (Johns Hopkins University, personal communication, 1980), a partial left manus catalogued under USNM 23483 may be referable to *Conoryctes* (see above). This manus is extremely similar to that of *Onychodectes* (AMNH 16528, described above) except that it is approximately one and a half times the size of AMNH 16528 in most of its linear dimensions (Pl. 14: fig. 7; Table 16). As in *Onychodectes,* in *Conoryctes* the first and fifth digits are reduced relative to the second, third and fourth digits.

Matthew (1937, p. 254) stated "it would appear that *Conoryctes* had a skeleton no larger than that of *Onychodectes* and quite similar in proportions of the limb bones, although the skull is nearly twice as large, and more specialized in various particulars." However, my measurements of the skulls of *Onychodectes* and *Conoryctes* (Table 10) indicate that the skull of *Conoryctes* was only slightly larger than that of *Onychodectes.* The limb bone fragments associated with AMNH 3396 do appear to be in roughly the same size range as those of *Onychodectes,* or only slightly larger and more robust, but the partial manus of USNM 23483 is about one and a half times the size (in linear dimensions) of that of *Onycho-*

dectes (Table 16). I would judge that *Conoryctes,* and probably *Huerfanodon* also, had a relatively larger head than *Onychodectes,* and also a larger body.

Species Which Have Been Previously Referred to *Conoryctes*

Cope (1882f) named *Conoryctes crassicuspis* on the basis of AMNH 3178, a left dentary fragment with M_3 and the talonid of M_2 (illustrated in Cope 1884c, pl. 23e, fig. 6, and referred to as "*C. crassideus*" and "*C. crassidens*" by error). This species has been referred to the arctocyonid genus *Triisodon* (Matthew 1937, p. 80) and most recently to the arctocyonid genus *Goniacodon* (Van Valen 1978, p. 58).

Cope (1882f) named *Periptychus ditrigonus* on the basis of AMNH 3798, a right dentary fragment with M_2, and subsequently referred it to *Conoryctes* (Cope 1883b; 1884c, pl. 29d, caption to figs. 2–6). This species is now referred to the periptychid genus *Ectoconus* (Matthew 1937, p. 128).

Huerfanodon Schoch and Lucas, 1981b
(Fig. 10)

Huerfanodon Schoch and Lucas, 1981b, p. 683.

Type Species. *Huerfanodon torrejonius* Schoch and Lucas, 1981b.

Included Species. The type species, *Huerfanodon polecatensis* Schoch and Lucas, 1981b, and "*Triisodon heilprinianus*" Cope, 1882c, *nomen dubium.*

Distribution. Torrejonian of New Mexico and Wyoming.

Diagnosis. Medium-sized taeniodonts, approximately the size of *Conoryctes*: P^3 submolariform with a large paracone and small but distinct metacone, protocone and hypocone; M^{1-2} with well-developed and protruding mesostyles connected to the metacones by slightly cuspidate premetacristae, distinct and cuspidate parastyles, ectocingula and metastyles, and broad trigon basins with shallow valleys and cupsidate lingual margins bearing moderate-sized "protocones," "paraconules" and "metaconules"; lower canine with internal groove; lower molars with prominent paraconids and paracristids.

Huerfanodon torrejonius Schoch and Lucas, 1981b
(Table 26; Pl. 15: figs. 1–9; Pl. 16: figs. 2, 3, 5, 7)

Huerfanodon torrejonius Schoch and Lucas, 1981b, p. 684.

Type Specimen. USNM 15412, a partial skull with right P^3, right M^{1-3}, left M^{1-2}, associated fragments of the central upper incisors, partial root of right P^2, alveoli for right P^4 and left P^{2-4} plus associated right dentary fragments bearing C_1, P_4, M_1, M_3 and alveolus for P_3 (Pl. 15: figs. 1–9; Pl. 16: figs. 2, 5).

Horizon and Locality of the Type. Torrejonian strata of the Nacimiento Formation, Kimbeto Wash, San Juan Basin, New Mexico.

Referred Specimen. MCZ 20181, a crushed skull with unworn left M^{1-2} and alveoli for left C^1, P^{1-4}, M^3 and right C^1 plus an associated right dentary fragment with alveolus for P_4, roots of M_{1-2} and complete M_3 (Pl. 16: figs. 3, 7): from Torrejonian strata of the Nacimiento Formation, 2.5 km northwest of Nageezi, San Juan Basin, New Mexico.

Diagnosis. Species of *Huerfanodon* with a submolariform P_4: the trigonid bears a large protoconid with a slightly developed cingulid on its anterolingual aspect

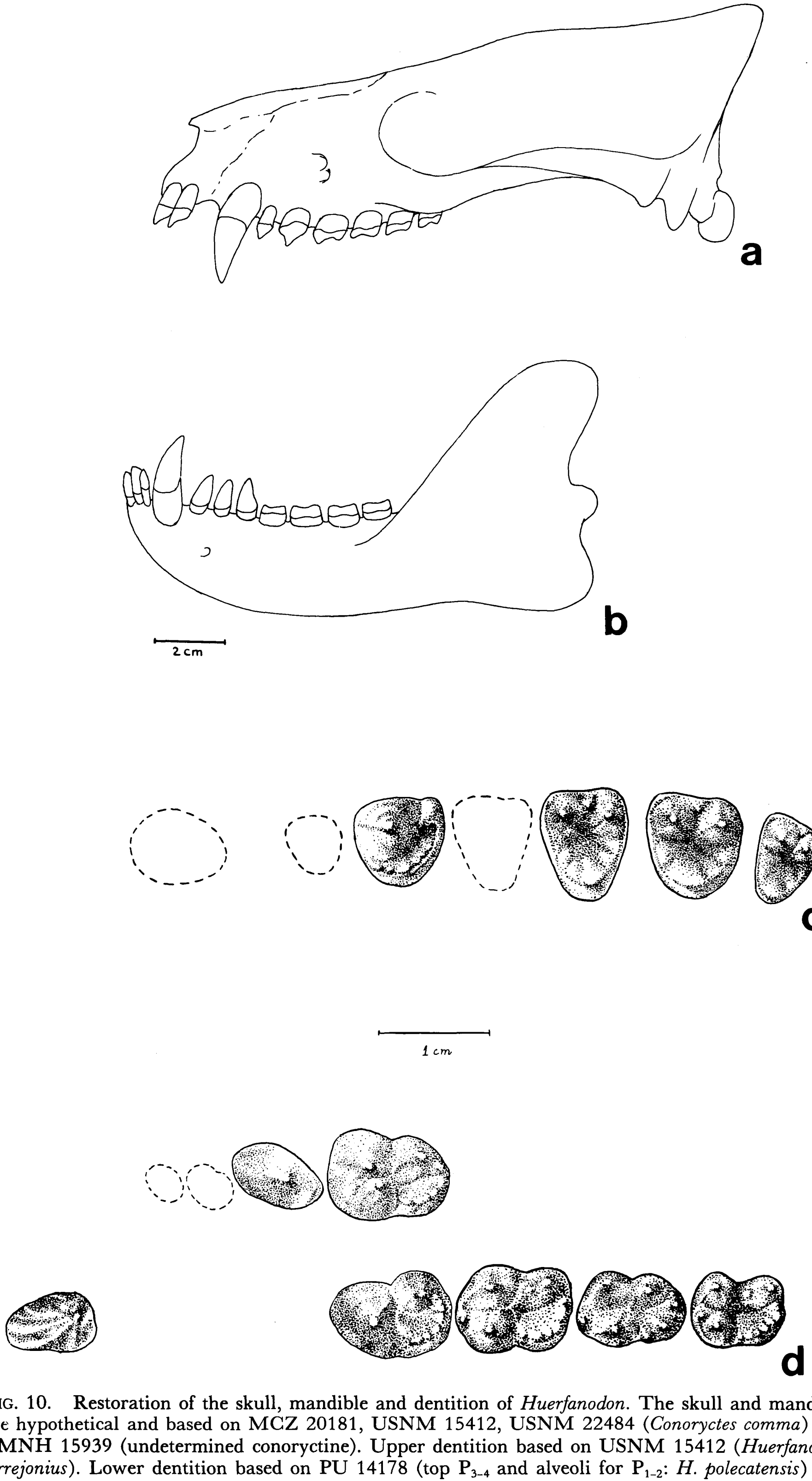


FIG. 10. Restoration of the skull, mandible and dentition of *Huerfanodon*. The skull and mandible are hypothetical and based on MCZ 20181, USNM 15412, USNM 22484 (*Conoryctes comma*) and AMNH 15939 (undetermined conoryctine). Upper dentition based on USNM 15412 (*Huerfanodon torrejonius*). Lower dentition based on PU 14178 (top P_{3-4} and alveoli for P_{1-2}: *H. polecatensis*) and USNM 15412 and AMNH 3224 (?*H.* "*heilprinianus*"). *a*) Left lateral view of skull. *b*) Left lateral view of mandible. *c*) Occlusal view of upper left dentition. *d*) Occlusal view of lower right dentition.

but lacks the large and distinct metaconid seen in *H. polecatensis;* slightly smaller dentally than *H. polecatensis.*

Huerfanodon polecatensis Schoch and Lucas, 1981b
(Table 26: Pl. 15: figs. 12, 13; Pl. 16: fig. 4)

Huerfanodon polecatensis Schoch and Lucas, 1981b, p. 688.

Type and Only Known Specimen. PU 14718, right dentary fragment with P_3–M_2, root of P_2, alveoli for C_1, P_1 and M_3 (Pl. 15: figs. 12, 13; Pl. 16: fig. 4).

Horizon and Locality of the Type. Torrejonian strata of the Polecat Bench Formation, Rock Bench Quarry, Sec. 36, T. 57 N., R. 99 W., Bighorn Basin, Wyoming.

Diagnosis. Species of *Huerfanodon* with a molariform P_4, bearing a large and distinct metaconid which approaches the protoconid in size; slightly larger dentally than *H. torrejonius.*

?*Huerfanodon "heilprinianus"* (Cope, 1882c)
(Table 26; Pl. 15: figs. 10, 11; Pl. 16: fig. 8)

Triisodon heilprinianus Cope, 1882c, p. 193.
Eoconodon heilprinianus: Matthew and Granger, 1921, p. 6 (in part).
Conoryctes comma: Van Valen, 1978, p. 58 (in part).
?*Huerfanodon "heilprinianus"*: Schoch and Lucas, 1981b, p. 690.

Type Specimen. AMNH 3224, left dentary fragment with M_2 (Pl. 15: figs. 10, 11; Pl. 16: fig. 8).

Horizon and Locality of the Type. Paleocene strata of uncertain age, Nacimiento Formation, San Juan Basin, New Mexico.

Discussion. The M_2 of AMNH 3224 bears a large paraconid as in *Huerfanodon.* However, without the P_4 it is not possible to assign it to a species and I here consider ?*Huerfanodon "heilprinianus"* a *nomen dubium* (see Schoch and Lucas 1981b, for a full discussion of this specimen).

cf. *Huerfanodon* sp.

Conoryctes comma: Simpson, 1937, p. 169.

Referred Specimen. USNM 9678, left P^3: from Torrejonian strata of the Lebo Formation ("Fort Union"), Silberling Quarry, Crazy Mountain Field, Sweetgrass County, Montana.

Discussion. This specimen, a left P^3, is in the size range of *Huerfanodon* and bears a small, but distinct, metacone and protocone; thus, it may pertain to *Huerfanodon,* but without more material it is impossible to make a definite assignment.

Description and Discussion of *Huerfanodon*

Huerfanodon has been thoroughly described and discussed in Schoch and Lucas (1981b) and the reader is referred to that paper.

Conoryctid Genus Indeterminate A

Referred Specimen. AMNH 832, right dentary fragment with roots of C_1, $P_{2(?)}$, complete $P_{3(?)}$, three upper molar fragments, right P_3 of a second individual (?) and other tooth fragments: from Torrejonian strata of the Nacimiento Formation, Escavada Wash, San Juan Basin, New Mexico.

Discussion. The above specimen documents the presence of a conoryctid in the size range of *Conoryctes* and *Huerfanodon* in Escavada Wash, but is generically indeterminate due to the incompleteness of the material.

Conoryctid Genus Indeterminate B

Conoryctes comma: Simpson, 1937, p. 169.

Referred Specimens. USNM 9597, left upper molar: from Torrejonian strata of the Lebo Formation ("Fort Union"), Gidley Quarry, Crazy Mountain Field, Sweetgrass County, Montana.

USNM 9816, two upper molars: from Torrejonian(?) strata of the Lebo Formation, Simpson's Locality 6, Crazy Mountain Field, Sweetgrass County, Montana.

USNM 9826, cheek tooth fragments: from late Torrejonian(?) strata of the Melville Formation ("Fort Union"), Simpson's Locality 28, Crazy Mountain Field, Sweetgrass County, Montana.

Discussion. The above specimens document the presence of a conoryctid in the size range of *Conoryctes* and *Huerfanodon* at these localities, but are generically indeterminate due to the incompleteness of the material.

Conoryctid Genus Indeterminate C

(Pls. 12, 13)

Conoryctes comma: Matthew, 1937, p. 250 (in part).

Referred Specimen. AMNH 15939, skull and mandible with roots or alveoli for right and left I^{2-3}, C^1 and complete P^3–M^3 (the left P^{3-4} and right P^4 have come out of the skull), alveoli for right and left I_{2-3}, C_1, M_3 and left P_{1-2}, complete left P_3, right and left P_4–M_2 (Pls. 12, 13): from Torrejonian strata of the Nacimiento Formation, Torrejon Wash, San Juan Basin, New Mexico.

Discussion. This specimen was described and figured by Matthew (1937, p. 252–54, fig. 61) as *Conoryctes comma.* However, the teeth of AMNH 15939 are extremely worn such that, whereas it represents a large conoryctid in the size range of *Conoryctes* and *Huerfanodon,* it is generically indeterminate. The left P_3 of AMNH 15939 is the only tooth in this specimen which preserves any details of the crown morphology. It is obliquely set in the jaw and anteriorly bears a large protoconid as in *Conoryctes* and *Huerfanodon.* Posteriorly there is a well-developed second conid in the position where a posterior heel is often variably developed in *Conoryctes.* In the type specimen of *Huerfanodon polecatensis* there is also a slight posterior heel in this position (Pl. 16: fig. 4). However, this conid is better developed in AMNH 15939 than in any other conoryctid specimen known to me.

Stylinodontidae Marsh, 1875b

Type Genus. *Stylinodon* Marsh, 1874.

Included Genera. *Wortmania* Hay, 1899; *Psittacotherium* Cope, 1882b; *Ectoganus* Cope, 1874; *Stylinodon* Marsh, 1874.

Distribution. Puercan (early Paleocene) to Uintan (middle Eocene) of western North America; upper Paleocene strata of South Carolina (see Foreword).

Revised Diagnosis. Taeniodonts with lower premolars set obliquely to transversely in the mandible; canines very large; skull and mandible very short and deep; large, laterally compressed and recurved claws on the manus; large and robust limb bones.

Wortmania Hay, 1899

Hemiganus: Wortman, 1897b, p. 67.
Wortmania Hay, 1899, p. 593.

Type Species. *Hemiganus otariidens* Cope, 1885a.

Included Species. Only the type species.

Distribution. Puercan of New Mexico.

Revised Diagnosis. Medium-sized taeniodonts (smaller than *Psittacotherium* but larger than *Conoryctes*) with relatively low-crowned teeth; all teeth relatively shallow-rooted; upper and lower canines enlarged and oval in cross-section; skull and mandible robust; lower premolars bear a single anteroexternal conid and a well-developed posterointernal cingulid ("talonid"); lower molars with both trigonids and talonids compressed anteroposteriorly and expanded transversely, with wear forming two blunt, transverse lophs; trigonids wider than talonids.

Wortmania otariidens (Cope, 1885a)
(Table 27; Figs. 11–16; Pls. 17–20)

Hemiganus otariidens Cope, 1885a, p. 432.
Hemiganus otariidens: Cope, 1888d, p. 311.
Hemiganus otariidens: Wortman, 1897b, p. 67.
Wortmania otariidens: Matthew, 1937, p. 271.
non *Wortmania otariidens*: Rigby and Lucas, 1977, p. 56 (based on a very worn maxilla fragment of *Entoconus ditrigonus,* S. Lucas, personal communication, 1981)

Type Specimen. AMNH 3394, partial skull with damaged and fragmentary right C^1, $P^{3-4(?)}$ and left $I^{3(?)}$, C^1, P^2–$M^{1(?)}$; lower mandible with right and left I_3, C_1, P_{3-4}, right P_{1-2}, M_2, left M_1, roots of right M_1 and alveoli for left M_2 and right M_3; associated left half of atlas, central and right part of axis, three cervical vertebrae, (?)right second metacarpal, ungual phalanx of manus, (?)left lunar, left tibia, proximal half of left femur, proximal half of left ulna, part of the right ulna (including the semilunar notch) and left radius (Pl. 17: figs. 1–3; Pl. 18: figs. 1–3; Pl. 19: figs. 2–5; Pl. 20).

Horizon and Locality of the Type. Collected by David Baldwin in 1885 from presumably Puercan strata of the Nacimiento Formation, San Juan Basin, New Mexico.

Referred Specimens. AMNH 755, left C_1 and bone fragments (Pl. 18: fig. 5); UCMP 36528, left dentary with complete P_{1-2}, roots of I_1, C_1,l P_{3-4}: both from presumably Puercan strata of the Nacimiento Formation, San Juan Basin, New Mexico.

UCMP 89280, isolated and well-worn P_2 or P_3; USNM 17655, left $P^{3(?)}$ (Pl. 17: fig. 5): both from Puercan strata of the Nacimiento Formation, Betonnie Tsosie Wash, San Juan Basin, New Mexico.

UK 12998, five (?)lower premolars (right and left $P_{1-2(?)}$ and undetermined fragment) and a right M_2; USNM 17654, right $P^{4(?)}$ (Pl. 17: fig. 6): both from Puercan strata of the Nacimiento Formation, Kimbeto Wash, San Juan Basin, New Mexico.

USNM 15428, right dentary with C_1 (Pl. 18: fig. 4; Pl. 19: fig. 1); USNM 15429, left P^4–$M^{1(?)}$ (Pl. 17: fig. 7): both from Puercan strata of the Nacimiento Formation, De-na-zin Wash, San Juan Basin, New Mexico.

AMNH 16342, left dentary fragment with P_{1-2}, roots of C_1, P_{3-4} and an associated maxilla fragment with M^2 and alveoli for M^1 and M^3 (Pl. 17: fig. 4; Pl. 18: fig. 6): from Puercan strata of the Nacimiento Formation, Alamo Wash, San Juan Basin, New Mexico.

Diagnosis. Same as that for the genus.

Description and Discussion of *Wortmania*

Wortmania is an extremely rare monotypic genus last reviewed by Matthew (1937, p. 270–77).

The teeth of *Wortmania* are very poorly known (Fig. 11). The teeth of the palate of the type specimen (Pl. 17: figs. 1–3) are heavily worn and poorly preserved. The skull has been plastered together since Matthew (1937) wrote on *Wortmania,* and the left upper cheek teeth are only set in plaster and might not be in their original positions. At the posterior part of the left maxilla, behind the tooth here interpreted as $M^{1(?)}$, is a tooth set in the plaster which is so incomplete that it cannot be determined if it belongs to *Wortmania.* Likewise, the two halves of the lower mandible (Pl. 18: figs. 1–3) have been plastered together, and the incisors, canines and two anterior right premolars are only set in plaster.

The upper incisors apparently are roughly circular in cross section and moderately large. The lower incisors are smaller than the uppers and elongated anteroposteriorly. The upper and lower canines are large and stout (Pl. 18: fig. 5).

The poorly preserved P^{1-2} are apparently short anteroposteriorly and relatively wide transversely (labiolingually). They bear large and high anteroexternal cusps; otherwise they are not distinctive.

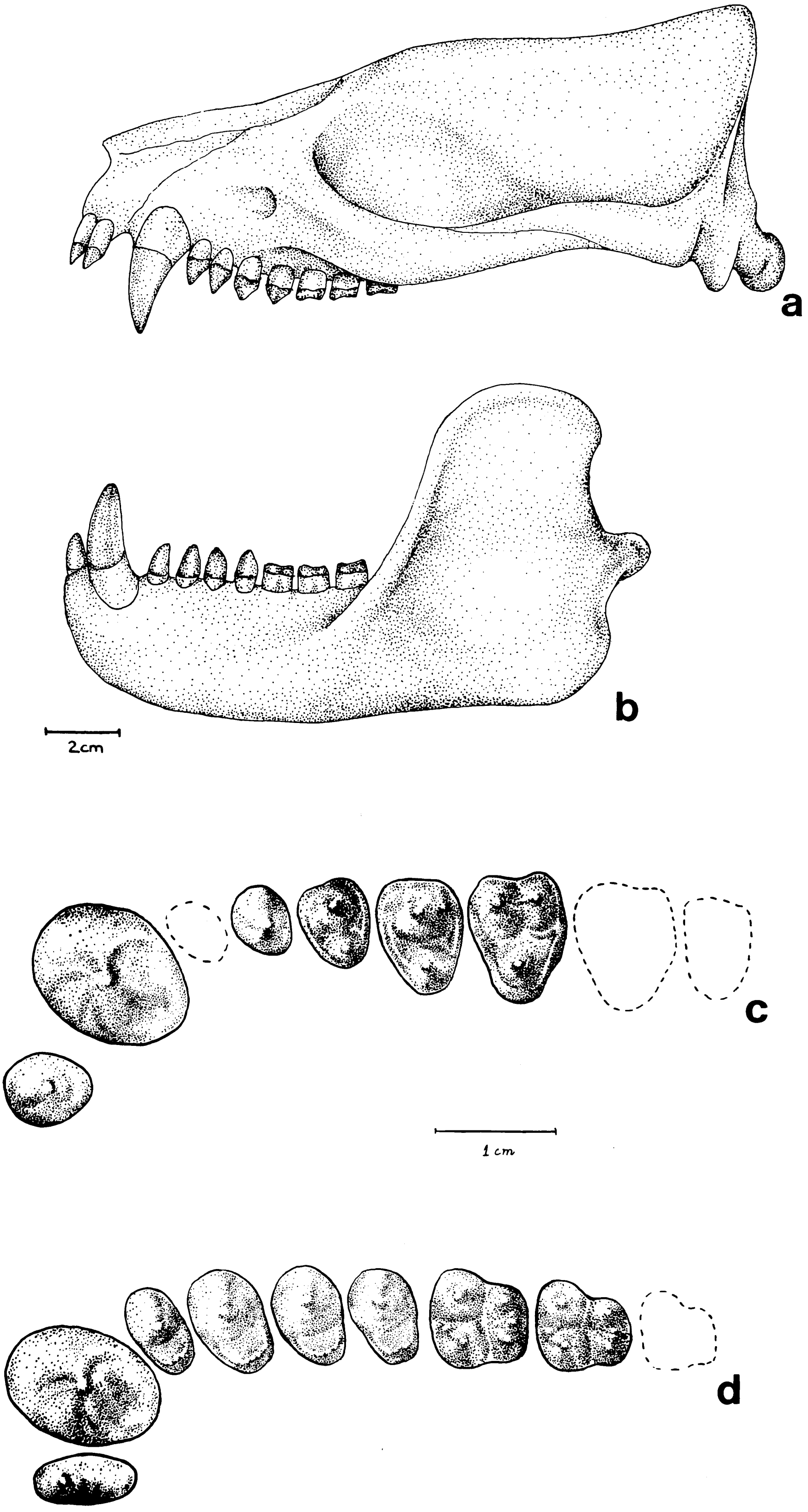
P^{3-4} (Pl. 17: figs. 5–7) bear large, centrally placed paracones labially and smaller protocones lingually, slight ectocingula, parastyles, metastyles, and para- and metacristae.

M^{1-2} of *Wortmania* (Pl. 17: figs. 4, 7) bear moderate-sized protocones, large paracones displaced far labially, and slightly smaller metacones partially fused with the paracones (USNM 15429). M^{1-2} also bear slight parastyles, ectocingula, and metastyles, and may possibly bear small "protoconules" and "metaconules" (although wear on the teeth obscures these features and homologies are uncertain).

P_{1-4} (Pl. 18: figs. 3, 6) are transversely oriented in the dentary with large and high anteroexternal conids ("protoconids") and posterointernal cingulids (or "talonids"). P_{1-4} are slightly clawlike and lingually recurved.

M_{1-3} (Pl. 18: fig. 3) bear moderate-sized protoconids and metaconids and smaller paraconids. All details of the talonids on AMNH 3394 and UK 12998 have been removed by wear. Both the trigonids and talonids are slightly compressed anteroposteriorly and expanded transversely to form two blunt lophs. The trigonids are wider than the talonids.

The degree of crown hypsodonty of *Wortmania* is less than that of the smaller genus *Onychodectes.* The cheek teeth of *Wortmania* show a small degree of lingual expansion of the enamel on the upper cheek teeth and labial expansion of the enamel on the lower cheek teeth. The teeth of *Wortmania* appear to have been shallowly to moderately rooted. The roots of the type specimen (AMNH 3394) cannot be seen, but the referred (?)lower premolars of UK 12998 each bear one stout root. The molar of UK 12998 bears two roots, one underlying the trigonid and the other underlying the talonid. The upper molars of USNM 15429, USNM 17654 and USNM 17655 are all three-rooted, having two medium-sized roots labially and one large root underlying the protocone lingually.


a
b
2cm
c
1 cm
d

Matthew (1937) considered the dental formula of *Wortmania* probably to be I^1_1, C^1_1, P^3_4, M^3_3, whereas Patterson (1949b) considered it to be I^1_1, C^1_1, P^4_4, M^3_3. *Wortmania* can only be stated with certainty to have had at least one incisor above and below. Wortman (1897b) believed that *Wortmania* had two pairs of upper incisors, which does not seem unreasonable. There are also one canine above and below, at least three upper premolars, four lower premolars, an undetermined number of upper molars, and three lower molars.

Skull

The skull of *Wortmania* bears a short and deep face anteriorly and a long, relatively narrow cranium posteriorly. In general features, it is quite similar to that of *Psittacotherium.* The nasals are broad and extend far back posteriorly to above the middle of the orbits. They keep their full width for almost their entire length posteriorly. The premaxillae are relatively large and extend posteriorly as a wedge between the maxillae and nasals to a point above the posterior face of the canine and P^1. The maxillae are thick and massive. The anterior border of the orbit is above M^1, whereas the infraorbital foramen appears to be placed above P^{3-4} (many details are obscured or not preserved in the only known skull of *Wortmania,* AMNH 3394, Fig. 11a; Pl. 17: figs. 1–3). The anterior root of the zygomatic arch is thick and massive and connects to the maxilla above P^4–M^1.

Matthew (1937, p. 276) stated that "the frontals are very short, the parietals extending forward medially almost to the junction of the postorbital crests; the parietals are nearly flat, sloping out at an angle of about 45 degrees from the sagittal crest; their posterior portion is concave, sweeping up towards the occipital crest, which appears to have been wide and prominent." However, in AMNH 3394 neither the postorbital crests nor the parietal–frontal sutures are clearly discernible. What may be the frontal–parietal crest is barely visible on the left side of the skull. This begins dorsally at about the midlength of what is preserved of the skull, running ventrally and very slightly posteriorly. The flatness of the parietals and the angle which they form to one another, as noted by Matthew (1937), may be due in part to lateral crushing of the specimen. The posterodorsal edge of the sagittal crest and the extreme posterior part (occiput) of the skull are missing in AMNH 3394; however, it appears to have had moderately high and prominent sagittal and occipital crests. The occiput may have approached the triangular shape seen in *Ectoganus* and *Stylinodon,* and also probably present in *Psittacotherium.* Ventrally, only fragments of the maxilla containing the canines and cheek teeth, and perhaps part of the palate, are preserved.

Mandible

The lower jaw is known principally from AMNH 3394, AMNH 16342, UCMP 36528 and USNM 15428 (Fig. 11b; Pl. 18; Pl. 19: fig. 1). The mandible foreshadows that of *Psittacotherium* and the later stylinodontids. The mandible is short and massive, particularly deep anteriorly with a massive symphysis which extends to a point under P_{2-3}. As seen in AMNH 16342, the symphysis was unfused, at least in younger individuals. The symphysis consists of two large ovoid regions of rugose articular surfaces, one placed more dorsally and anteriorly

---

←

FIG. 11. Restoration of the skull, mandible and dentition of *Wortmania otariidens,* based primarily on AMNH 3394, AMNH 16342, USNM 15429, USNM 17654, and USNM 17655. *a*) Left lateral view of skull. *b*) Left lateral view of mandible. *c*) Occlusal view of upper left dentition. *d*) Occlusal view of lower right dentition.

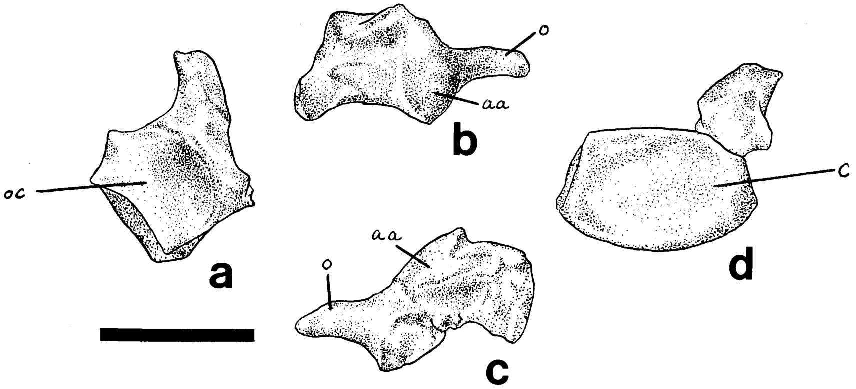


FIG. 12. Cervical vertebrae of *Wortmania otariidens,* AMNH 3394. *a*) Anterior view of partial atlas. *b*) Right lateral view of axis. *c*) Dorsal view of axis. *d*) Anterior or posterior view of cervical vertebra.
Abbreviations: aa = anterior articular surface; c = centrum; o = odontoid process; oc = articular surface for occipital condyles.
Scale is 2 cm long.

and the other ventral to the first and extending further posteriorly. Between these is what may have been a rudimentary pit for the genioglossus muscle of the tongue. This pit is well developed in *Psittacotherium* and later stylinodontids. Posteriorly, the mandible shallows slightly, and is most shallow under M_2.

The coronoid process is high and wide, squared-off and not recurved. Anteriorly, it arises from a point external to the middle of M_3. The angle is of moderate size and flat (not inflected). The condyle is moderately transverse and set at, or just slightly above, the tooth row. The reconstruction by Matthew (1937, p. 275, fig. 68) set the condyle too high above the tooth row. The mandible preserved in AMNH 3394 is slightly distorted because the left side has been broken and repaired, setting the condyle too high. Its true position is better seen in USNM 15428 (Pl. 18: fig. 4; Pl. 19: fig. 1).

Cervical Vertebrae

The left half of the atlas of *Wortmania* is preserved in AMNH 3394 (Fig. 12b; Pl. 20: figs. 13, 14). Although poorly preserved, it is similar to the atlas of *Stylinodon* and to what is known of the atlas of *Onychodectes.* The transverse process is relatively small. The odontoid process and right cranial half of the axis of *Wortmania* is preserved (Fig. 12b, c; Pl. 20: figs. 9, 10). It exhibits no particularly remarkable features. Centra of three of the posterior cervical vertebrae of *Wortmania* are also known (Fig. 12d; Pl. 20; figs. 7, 8, 11, 12, 15, 16). As in all taeniodonts for which the neck is known, these are short (anteroposteriorly) and broader transversely than they are high dorsoventrally, indicating a short, stout, powerful neck. The presumed seventh cervical vertebra is relatively longer (anteroposteriorly), more massive and not so wide transversely. The neural canal of the neck was relatively large and, in all of the cervical vertebrae known, the floor of the neural canal is pierced by two foramina, one on each side. As Cope (1888d, p. 313) noted, "The longitudinal axis of the cervical centra is oblique to the horizontal, showing that the head was elevated above the body." The anterior and posterior faces of the centra are rather flat or slightly concave.

Ulna

The ulna of *Wortmania* (Fig. 13a, b; Pl. 20: figs. 1–4) is quite similar to that of *Onychodectes,* although much larger, stouter, more robust and with a broader (transversely) and more shallow semilunar notch; in these features it approaches

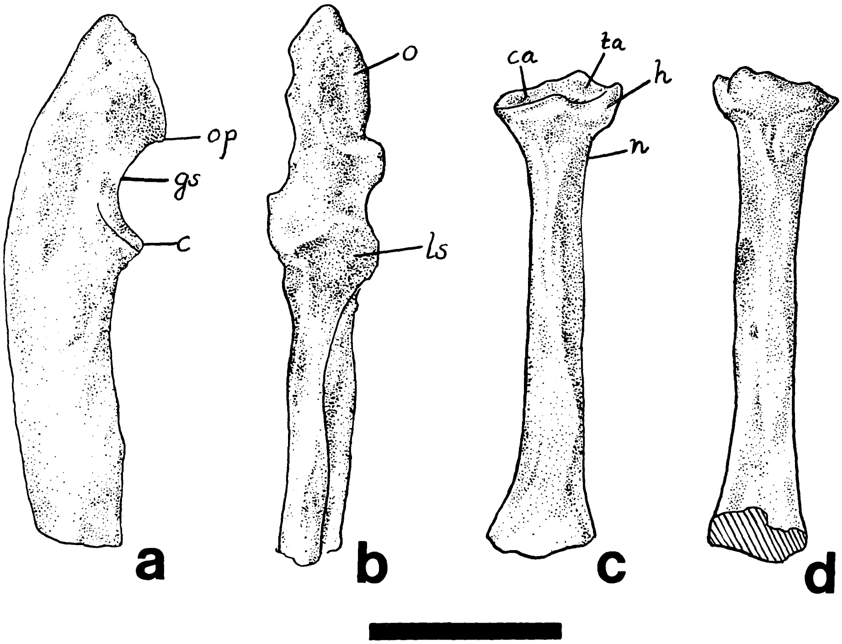


FIG. 13. The ulna and radius of *Wortmania otariidens,* AMNH 3394. *a*) Medial view of left ulna. *b*) Anterior view of left ulna. *c*) Anterior view of left radius. *d*) Posterior view of left radius.

Abbreviations: c = coronoid process; ca = articular surface for capitulum of humerus; gs = semilunar notch (= greater sigmoid cavity); h = head; ls = radial notch (= lesser sigmoid cavity); n = neck; o = olecranon; op = olecranon process; ta = articular surface for trochlea of humerus.

Scale is 4 cm long.

the condition seen in more derived stylinodontids (for example, *Stylinodon*). The olecranon, although incomplete, is large, prominent, heavily rugose, and bears medial and lateral bony ridges as in *Onychodectes*; however, these are not so well-developed in *Wortmania.* The semilunar notch is large and broad. The olecranon process (sensu Greene 1935) and coronoid process are both relatively prominent; the olecranon process is slightly higher than the coronoid process. The radial notch is large, shallowly concave transversely and set more laterally than in *Ectoganus* and *Stylinodon,* but not so far lateral as in *Onychodectes.* As in *Onychodectes,* the shaft is deep anteroposteriorly and flattened transversely with a moderate interosseous crest. It bears a shallow groove on the proximointernal side extending under the coronoid process and a deeper groove in the middle of the shaft externally. The distal end of the ulna is unknown.

Radius

The radius of *Wortmania* (Fig. 13c, d; Pl. 20: figs. 5, 6) is similar to that of *Ectoganus,* although much smaller and less robust. Posteriorly (ventrally) the head bears a large articular facet for the radial notch of the ulna. Placed well posteriorly (ventrally) is a distinct and moderately well-developed tubercle (unlike *Ectoganus* and *Stylinodon,* which lack it). The articular surface for the capitulum of the humerus is deeply concave in both directions. Distally, the shaft of the radius is slightly expanded posteriorly. The extreme distal end of the radius is not preserved.

Manus

Only three bones of the manus of *Wortmania* are preserved (Fig. 14; Pl. 20: figs. 17–22): the ?left lunar, a ?right ?second metacarpal and an ungual phalanx.

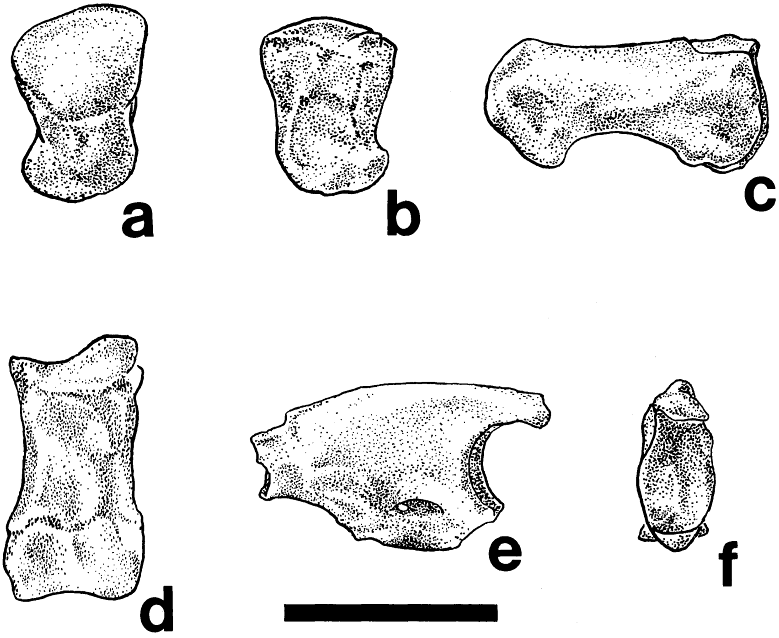


FIG. 14. Elements of the manus of *Wortmania otariidens,* AMNH 3394. *a*) Proximal view of left lunar. *b*) Distal view of left lunar. *c*) Lateral or medial view of (?)second metacarpal. *d*) Ventral view of (?)second metacarpal. *e*) Lateral or medial view of ungual phalanx. *f*) Proximal view of ungual phalanx.
Scale is 2 cm long.

The lunar was originally referred to by Cope (1888d) as "a metacarpal of the pollex" whereas the metacarpal was considered by Cope (1888d) to be a metatarsal. These misidentifications were subsequently corrected by Wortman (1897b).

The lunar is similar to that of both *Onychodectes* and *Psittacotherium.* Seen dorsally, it presents a relatively small and transversely elongated face. The proximal surface for articulation with the radius is relatively large and smoothly convex in both directions. Laterally, the lunar bears a dorsoventrally elongated and concave facet which apparently articulated with the cuneiform proximolaterally and the unciform distally. Medially and mediodistally there is a dorsoventrally convex and proximodistally concave facet which apparently articulated with the centrale which was positioned under the lunar medially. The scaphoid may have rested on the centrale in part, with the lateral edge of the scaphoid articulating with the medioproximal edge of the lunar. Seen distally, the lunar is rectangular in outline and elongated dorsoventrally. Dorsally, there is a flat, square facet which articulated with the dorsodistal half of the magnum. Ventral to this is a deep, low-set (seen distally) depression in which the raised proximal central protuberance of the magnum fits forming a "ball-in-socket" joint as described for *Onychodectes.*

The metacarpal of *Wortmania* is short, stout and deep; overall, the impression is that it is intermediate between *Onychodectes* and *Psittacotherium.* The proximal end of the metacarpal is not expanded. The far proximal surface for the trapezoid is rather saddle-shaped. It is very slightly convex dorsoventrally and deeply concave transversely with prominent medial and lateral ridges. Medially, it bears a dorsoventrally concave facet for articulation with the first metacarpal and laterally there is a similar facet for the third metacarpal. Distally, the metacarpal is

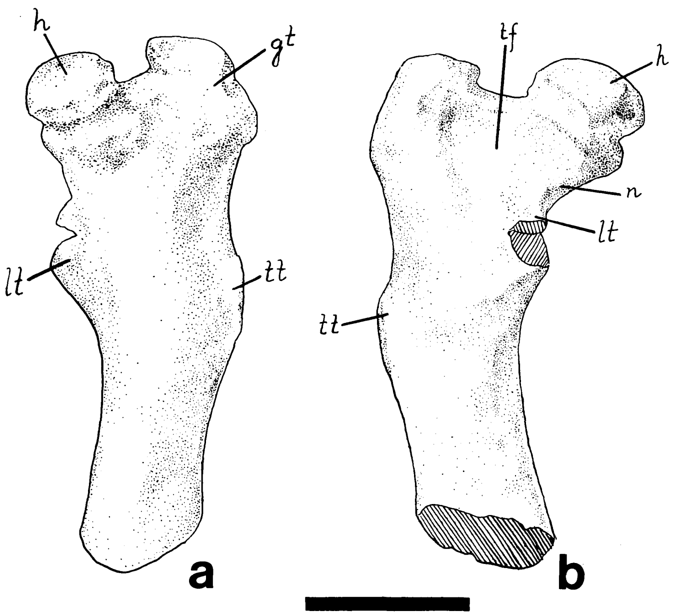


FIG. 15. The femur of *Wortmania otariidens,* AMNH 3394. *a*) Anterior view of left femur. *b*) Posterior view of left femur.

Abbreviations: gt = greater trochanter; h = head; lt = lesser trochanter; n = neck; tf = intertrochanteric fossa (= digital fossa); tt = third trochanter.

Scale is 4 cm long.

not expanded, but the distal end is squared-off. The articular surface is slightly concave transversely and deeply convex dorsoventrally. The articular surface extends slightly further proximally on the dorsolateral side. Ventrally, it bears a small median keel.

The single known ungual phalanx of the manus (probably a second, third or fourth) is nearly identical to those of later stylinodontids, except that it is proportionally smaller. It is large, high, laterally compressed and recurved with a narrow, transversely convex posterior border and a prominent ventral protuberance proximally (tuberosity for the flexor tendon) which is pierced by a transverse foramen. The proximal articular surface is deeply concave dorsoventrally and dorsally extends far proximally (as the superior process). It bears a low median keel. The ventral surface of the ungual distal to the ventral tuberosity is flat.

Femur

The proximal half of the left femur is preserved in AMNH 3394 (Fig. 15; Pl. 19: figs. 2, 3). The head is of moderate size, spherical and set on a short, stout neck. The pit for the ligamentum teres is deep and circular, but its orientation is uncertain as the epiphysis was not united to the head originally (Cope 1888d) and has since only been glued to the rest of the femur. The greater trochanter is large and prominent, extending about as high as the head proximally. Posteriorly, the lesser trochanter is also distinct, relatively large and set high on the shaft. The digital fossa is relatively large and deep; however, the greater and lesser trochanters are not connected by a distinct intertrochanteric ridge posteriorly. The third trochanter is moderately well developed, set just below the level of the lesser trochanter, and slightly recurved anteriorly. The anterior face of the shaft is smoothly convex, whereas the posterior face of the shaft is relatively flattened.

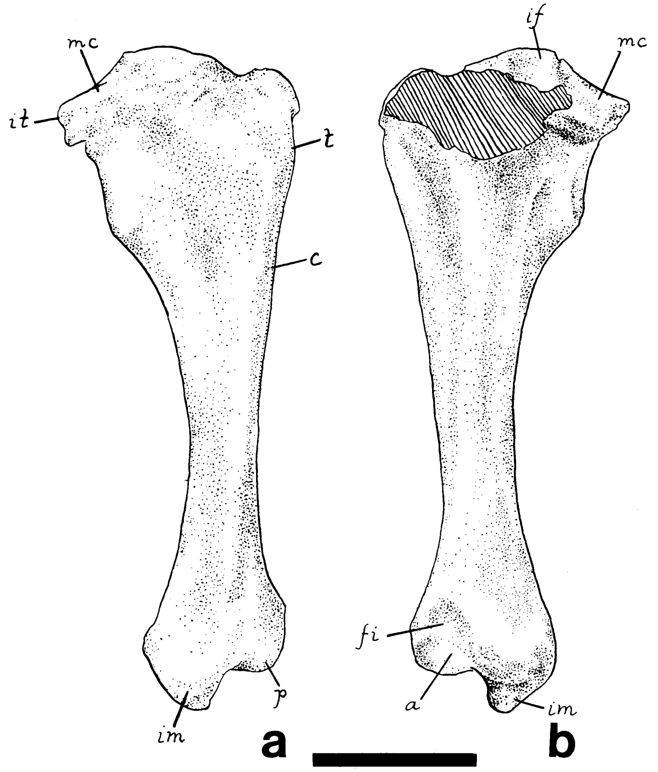


FIG. 16. The tibia of *Wortmania otariidens,* AMNH 3394. *a*) Anteromedial view of left tibia. *b*) Posterolateral view of left tibia.

Abbreviations: a = surface for astragalus; c = crest; fi = surface for fibula; if = intercondyloid fossa (= intercondylar notch); im = internal malleolus; it = internal tuberosity; mc = medial condyle; p = descending process; t = tuberosity.

Scale is 4 cm long.

Tibia

The proximal part of the left tibia of AMNH 3394 has been crushed laterally, but the main features are clear (Fig. 16; Pl. 19: figs. 4, 5). Overall, the tibia is relatively short and stout with enlarged proximal and distal ends. The proximal end preserves the large, flat internal condyle and prominent internal tuberosity. The anterior tuberosity and cnemial crest are moderately well developed. Distally, the tibia bears a large internal malleolus and externally a large concave facet for the distal end of the fibula which was not fused to the tibia; this is the same condition seen in all taeniodonts for which the tibia or fibula is known. The articular surface for the astragalus faces almost straight down and is moderately concave anteroposteriorly. Medially, it is slightly concave transversely, whereas toward the lateral edge it is slightly convex and then slightly concave again. Overall, it is similar to the tibia of *Psittacotherium,* but smaller and less robust.

Stylinodontid Genus Indeterminate
(Pl. 27: figs. 1, 2)

Undetermined Stylinodontine Genus: Robison and Lucas, 1980, p. 302.

Referred Specimen. AMNH no number, cheek tooth (Pl. 27: figs. 1, 2): from Puercan strata of the North Horn Formation, Wagonroad local fauna, Emery County, Utah.

Discussion. Although most of the crown is missing, the fused roots and labial and lingual extensions of the remaining enamel indicate that this tooth belongs to an advanced taeniodont in the size range of *Wortmania* or *Psittacotherium*.

Psittacotherium Cope, 1882b

Psittacotherium Cope, 1882b, p. 156.
Hemiganus Cope, 1882e, p. 831.

Type Species. *Psittacotherium multifragum* Cope, 1882b (= *Psittacotherium aspasiae* Cope, 1882c = *Hemiganus vultuosus* Cope, 1882e = *Psittacotherium megalodus* Cope, 1887b).

Included Species. Only the type species.

Distribution. Torrejonian of Wyoming and New Mexico; Torrejonian-Tiffanian of Montana and Texas.

Revised Diagnosis. Medium-sized taeniodonts with greatly enlarged, rooted, subgliriform canines with enamel limited to the anterior face of the tooth and with both crown and root greatly elongated; upper canine with external groove; I^3 enlarged, deeply rooted and caniniform; lower incisors of moderate size and rooted; cheek teeth moderately hypsodont with relatively shallow roots (as compared to *Ectoganus*); posterior cheek teeth double-rooted or single-rooted with traces of the fused roots; upper premolars suboval in cross-section and transversely elongated bearing a large protocone and paracone connected by low to incipient transverse anterior and posterior crests; upper molars tritubercular, suboval in cross-section and transversely elongated bearing small paracones and metacones placed far labially and anteriorly, and large protocones lingually; minutely cuspidate postmetaconule wings well developed (especially on M^{2-3}) and extending posterolabially to a point posterior and just lingual of the metacone; P_1 reduced and single-rooted; P_2 single-rooted and placed transversely in the lower jaw, bearing a large external (labial) conid and a smaller internal conid; P_4 submolariform with a transversely widened trigonid and small, lingually placed talonid; M_{1-3} decrease in size posteriorly; M_{1-3} moderately bilophodont with broader trigonids than talonids, talonids placed lingually.

Psittacotherium multifragum Cope, 1882b
(Table 28; Figs. 17–23; Pls. 21–26; Pl. 27: figs. 4–14; Pls. 28–31)

Psittacotherium multifragum Cope, 1882b, p. 156.
Psittacotherium multifragum: Cope, 1882c, p. 191.
Psittacotherium aspasiae Cope, 1882c, p. 192.
Hemiganus vultuosus Cope, 1882e, p. 831.
Psittacotherium multifragum: Cope, 1884c, p. 196.
Psittacotherium aspasiae: Cope, 1884c, p. 196.
Hemiganus vultuosus: Cope, 1884c, Pl. 32c: figs. 7–12.
Psittacotherium megalodus Cope, 1887b, p. 469.
Psittacotherium multifragum: Wortman, 1897b, p. 71.
Calamodon?: Douglass, 1908, p. 22.
Psittacotherium multifragum: Matthew, 1937, p. 255.
Psittacotherium aspasiae: Matthew, 1937, p. 269.
Psittacotherium multifragum: Simpson, 1937, p. 169.
Psittacotherium multifragum: R. W. Wilson, 1956, p. 169.
Psittacotherium multifragum?: Simpson, 1959, p. 6.
Psittacotherium cf. *P. multifragum*: J. A. Wilson, 1967, p. 159, 161.
Psittacotherium Cope, 1822 (*lapsus calami*) or *Lampadophorus* Patterson, 1949: Schiebout, 1974, p. 19.
Psittacotherium multifragum: Rigby, 1980, p. 98.
Psittacotherium multifragum: Schoch, 1981a, p. 180.

Type Specimen. AMNH 3413, mandible with left I_3, C_1, right P_2, M_1, M_2, roots of right I_3, C_1 and alveoli for left M_{2-3} and right P_1, M_3 (Pl. 21: figs. 1–4).

Horizon and Locality of the Type. From presumably Torrejonian strata of the Nacimiento Formation, near Huerfano Peak, San Juan Basin, New Mexico.

Referred Specimens. AMNH 754, partial skull and mandible with right and left I^3–C^1, fragmentary right P^1–M^1 and partial right I_3, left P_1, right and left P_4 (Pl. 24); AMNH 757, (?)lower right canine; AMNH 3416, left dentary fragment with partially erupted M_3, alveoli for M_{1-2} and crushed M_2 cemented to the outside of the jaw (type of *P. aspasiae*; Pl. 21: figs. 9, 10); AMNH 3418, right dentary with C_1 root and alveoli for P_1–M_2 and isolated right P_2 (type of *P. megalodus*; Pl. 21: figs. 5–8); AMNH 3390, left C_1, right I_3, right C^1 and upper cheek tooth (type of *Hemiganus vultuosus*; Pl. 21: figs. 11–18); AMNH 3391, right $P_{4(?)}$, left $P^{4(?)}$, undetermined cheek tooth ($P^{2(?)}$), canine tip and vertebra (Pl. 29: figs. 3, 4); AMNH 3393, broken upper cheek tooth and right C_1; AMNH 3414, left premaxilla and maxilla with I^3, C^1; AMNH 3417, left dentary fragment with alveoli for M_{1-3}; AMNH 3419, right dentary with broken C_1 and crushed molar; AMNH 88383, mandible with right and left C_1, left P_4, M_3, roots of left M_1, alveoli for right and left I_3, P_{1-3}, right P_4–M_3, partial left premaxilla and maxilla with roots of I^3–C^1, tooth, cranial and vertebral fragments (Pl. 26: figs. 3, 4; Pl. 29: figs. 5–8): all from presumably Torrejonian strata of the Nacimiento Formation, San Juan Basin, New Mexico.

UK 7749, upper cheek tooth fragments; UK 9564, canine, vertebra and hindlimb fragments; UK 9565, canine fragment; UK 9566, lower incisor; UK 9567, canine fragment; UNM NP-220, dentary fragments with right and left M_1, right M_2: all from Torrejonian strata of the Nacimiento Formation, Kutz Canyon, San Juan Basin, New Mexico.

AMNH 15938, (?)right upper incisor tip, right $P^{2(?)}$, right and left $P^{4(?)}$, left M^{1-2}, right M^3, right and left P_4, left distal tibia (Pl. 30: figs. 8, 9); AMNH 16661, upper left C^1, right and left P^2, $P^{4(?)}$, undetermined upper cheek tooth fragment, left C_1, right P_4, right and left M_1, right M_3 (Pl. 22: figs. 24–31); UNM B-850, right P^1 or P^2; USNM 15413, right and left dentary fragments with unerupted right and left M_3, deciduous C_1, deciduous $P_{1-2(?)}$ (Pl. 27: figs. 4–14): all from Torrejonian strata of the Nacimiento Formation, Torrejon Wash, San Juan Basin, New Mexico.

UK 8035, right side of skull with P^3, M^3, roots of P^2, P^4, alveoli for I^3, C^1, M^{1-2}, mandible with alveoli for right and left C_1–M_3, tooth and bone fragments (Pl. 25; Pl. 26: figs. 1, 2): from Torrejonian strata of the Nacimiento Formation, UK New Mexico Locality 15, SW ¼, Sec. 20, T. 22 N., R. 6 W., Sandoval County, San Juan Basin, New Mexico.

AMNH 3392, lower canine: from Torrejonian strata of the Nacimiento Formation, Gallegos Canyon, San Juan Basin, New Mexico.

AMNH 16560, left ulna and radius, left femur, left proximal fibula(?) and partial pes (Pl. 30: figs. 2–7; Pl. 31, figs. 3–5); AMNH 16660, mandible with right C_1, alveoli for left C_1, right and left P_1–M_3; AMNH 16662, left maxilla with C^1 and P^3 roots, alveoli for I^3, P^{1-2}, P^4, right dentary fragment with alveoli for M_{2-3}; UK 8006, edentulous mandibular symphysis with alveoli for right and left C_1–P_4; USNM 15410, left dentary with C_1 (Pl. 23: figs. 5, 6); USNM 15411, palate and partial skull with right and left C^1, right P^1, right and left P^{2-3}, left P^4, right and left M^1, left M^2, and right M^3 (Pl. 23: figs. 1–4; Pl. 31: figs. 1, 2; USNM 15410 and USNM 15411 may represent a single individual as both were collected at the same time and place and bear the same original field number):

all from Torrejonian strata of the Nacimiento Formation, Kimbeto Wash, San Juan Basin, New Mexico.

AMNH 756, dentary, canine and other tooth fragments, including a right $P_{4(?)}$ (Pl. 22: figs. 22, 23); AMNH 2453, mandible, upper and lower cheek teeth and fragments including left I^3, left P^2–M^1, M^3, right P_2, left P_4, right M_1, right ulna, radius and manus (Pl. 22: figs. 1–14; Pl. 30, fig. 1); AMNH 16731, left I^3, right P^2, left P^4, left M^3, right $M_{1(?)}$ (Pl. 22: figs. 15–21): all from Torrejonian strata of the Nacimiento Formation, Escavada Wash, San Juan Basin, New Mexico.

AMNH 36000, skull in concretion with roots of right and left C^1, right I^3, mandibular symphysis with roots of right and left C_1, alveoli for left P_{1-3}, canine and bone fragments: from Torrejonian strata of the Nacimiento Formation, Simpson's Locality 226, "northwest to westnorthwest of southeastern tip of Cuba Mesa on fourth main spur projecting southward from the mesa, mainly or wholly in sect. 3, T. 20 N., R. 2 W." (Simpson 1959, p. 5), San Juan Basin, New Mexico.

USNM 6162, canine and cheek tooth fragments including a right lower canine and left P_4: from Torrejonian strata of the Lebo Formation ("Fort Union") "from the level of and near Silberling Quarry" (Simpson 1937, p. 169), Sweetgrass County, Montana.

AMNH 100563, left P^4: from Torrejonian strata of the Fort Union Formation, Swain Quarry, Carbon County, Wyoming.

CM 1674, right $P^{4(?)}$: from Tiffanian strata of the Melville Formation ("Fort Union"), Douglass Quarry, NE of Melville, Sweetgrass County, Montana.

TMM 40147-3, fragment of incisor, fragment of canine, right $P^{3(?)}$; TMM 40147-7, edentulous right mandible fragment; TMM 40148-2, left $M^{1(?)}$; TMM 40535-86, incisor fragment; TMM 40536-119, left $P^{2(?)}$; TMM 40537-26, left $M^{1(?)}$; TMM 40537-33, left $M^{1(?)}$; TMM 40537-61, right $M^{1(?)}$; TMM 40537-91, right dentary fragment; TMM 40537-140, skull fragments in concretion and part of right upper canine; TMM 40537-68, claw; TMM 41366-1, maxillary fragments with roots of premolars and molars; TMM 41366-73, upper incisor roots in jaw fragment; TMM 41364-1, parts of clavicle, left femur, right humerus, right and left tibiae, right astragalus and other bone fragments (apparently of the same individual as TMM 41364-2, below; Pl. 28; Pl. 29: figs. 1, 2); TMM 41364-2, skull fragments with both canines and one incisor, sockets for six left cheek teeth and associated bone fragments: all from late Torrejonian(?) and Tiffanian strata of the Black Peaks Formation, Big Bend National Park, Brewster County, Texas.

Diagnosis. Same as that for the genus.

Description and Discussion of *Psittacotherium*

Schoch (1981a) pointed out that known dental remains of *Psittacotherium* are highly variable in size (Table 28). This variability may be due to several factors:

1. More than one species of *Psittacotherium* may be present, and the measurements of two or more species may grade into each other. Detailed crown and cusp morphology that might distinguish several species of *Psittacotherium* of similar size is obscured by the worn condition of most dental remains of *Psittacotherium*.
2. Many specimens of *Psittacotherium* consist of isolated teeth, and their exact positions in the tooth row are uncertain. Thus, several teeth might be presumed homologous when they are not.

3. Because many teeth of *Psittacotherium* are extremely worn or fragmentary, many measurements are little more than estimates. Measurements taken on different teeth are not necessarily taken between homologous points.

4. The hypsodont teeth of *Psittacotherium* (and taeniodonts in general) may change in size with eruption throughout the life of an individual (i.e., rolling eruption; cf. Patterson 1949b).

Due to the virtual absence of complete, or even partial, unworn teeth still in place in jaws, there is no way to judge how stereotyped or variable the various teeth in the tooth row of *Psittacotherium* are. In view of these factors, and the fact that there are no clear gaps in size between the measurements of teeth (Table 28), even though the coefficients of variation are somewhat high for a single species (Simpson and others 1960), it appears most reasonable at present to assign all specimens of *Psittacotherium* to one species (Schoch 1981a).

The dental formula of *Psittacotherium* probably is I^{1}_{1}, C^{1}_{1}, P^{4}_{4}, M^{3}_{3} (Fig. 17; contra Wortman 1897b; Matthew 1937). The number of upper incisors is uncertain. AMNH 88383 includes a complete left premaxilla which bears the root of only one enlarged upper incisor, here designated I^3. UK 8035 includes a complete right maxilla (Pl. 25) whose roots and alveoli show that *Psittacotherium* had an enlarged and rooted upper canine, four shallowly rooted upper premolars and three upper molars. The mandibles of AMNH 754, AMNH 2453, AMNH 88383 and UK 8035 (Pls. 24, 26) demonstrate that *Psittacotherium* had one set of moderately enlarged lower incisors, here arbitrarily designated I_3 (Matthew 1937 considered it to be I_2, homologous to the enlarged lower second incisor of *Conoryctes*); an enlarged and rooted lower canine; four lower premolars and three lower molars.

The upper incisors (e.g., AMNH 16731, an upper incisor of *Psittacotherium*; Pl. 22: fig. 15) are enlarged and subgliriform, forming miniature counterparts of the enlarged canines. The lower incisors (e.g., AMNH 3413; Pl. 21: figs. 1, 2) are much smaller. At eruption the crown of I_3 was completely covered with enamel. Enamel is limited to the anterior face of the incisors after wear and, as in the canines, the anterior part apparently formed a cutting/shearing implement whereas the posterior, enamel-free surfaces of the incisors and canines were used for crushing. The root of the upper incisor is grooved medially and laterally.

The upper and lower canines of *Psittacotherium* are enlarged and subgliriform. Both the crown and the root are greatly elongated. Enamel is limited to the anterior parts of the canines and is striated parallel to the length of the tooth before wear. With wear and eruption the occlusal surfaces of the canines change in size and shape such that in an old individual like AMNH 754 (Pl. 24) the upper canines consist only of large dentine stubs elongated anteroposteriorly with a small amount of anterior enamel remaining. The upper canines bear a lateral groove in the enamel of the anteroexternal surface.

The upper cheek teeth of *Psittacotherium* are fairly well known from USNM 15411 (Pl. 23; Pl. 31: figs. 1, 2), supplemented primarily by AMNH 2453, AMNH 15938 and AMNH 16731 (Pl. 22). The largest upper cheek tooth probably was P^4 or M^1. All of the upper cheek teeth are hypsodont and have the typical taeniodont pattern of greatly extended lingual enamel. The teeth are transversely widened and slightly spaced, so that they do not contact interdentally.

P^1 (considered P^3 by Matthew 1937, p. 259) is a single-rooted, small bicuspid tooth set obliquely in the jaw posterior to the outer angle of the canine. It bears a large paracone, with an incipient metacone, and a smaller protocone. The enamel is greatly extended both labially and lingually on P^1, but limited to the top of the crown anteriorly and posteriorly. Thus, with wear P^1 forms a dentine peg with thin strips of labial and lingual enamel.

P^2 is similar to P^1, but slightly larger (Table 28). Unlike P^1, the enamel of P^2 extends farther lingually than labially. P^2 bears a large, labial paracone and a smaller lingual protocone. A small posterior crest connects the protocone to the paracone.

P^3 and P^4 are of similar size and morphology. Both bear large paracones labially and variably sized, although at most small, metacones. In P^2–P^4 the lingual protocones are connected to the paracones/metacones by minutely cuspidate anterior and posterior transverse crests. Both P^3 and P^4 bear two small, fused roots labially and a larger lingual root which curves labially. Near the tooth crown all three roots are fused.

M^1 bears a small conical paracone. A metacone at the labial edge of the tooth is closely appressed to the paracone. M^1 lacks a stylar shelf or ectocingulum and there is a small, minutely cuspidate parastyle. M^1 bears a minutely cuspidate postmetaconule wing which extends posterolabially to a point posterior and just lingual to the metacone.

M^2 is similar to M^1, but the metacone is smaller and less distinct than on M^1 and there is only an incipient parastyle. The postmetaconule wing is well developed.

AMNH 15938 and AMNH 16731 include two M^3s illustrated by Matthew (1937, p. 260–61, figs. 64, 65; also cf. Pl. 22: fig. 21) that are single-rooted due to fusion of the original roots. M^3 is ovoid in cross section, with the long axis directed labiolingually. It bears a large and isolated labial paracone connected to the large and anterolingually placed protocone. The protocone is connected to the paracone by cuspidate pre- and postprotocristae. Posterolabial of the protocone on the postprotocristae is a minute hypocone.

The lower cheek teeth of *Psittacotherium* are less well known than the uppers (Pl. 22). P_{1-4} are single-rooted whereas M_{1-3} are double-rooted, although their roots are fused. P_4 is the largest tooth. M_{1-3} are hypsodont, with enamel extending farther labially than lingually.

The P_1 of AMNH 754 (Pl. 24: figs. 4, 5) is relatively small and poorly preserved. It is obliquely oriented in the jaw and may have been bicuspid like P_2. The small and shallow P_1 alveoli of AMNH 754, AMNH 88383 and UK 8035 indicate that *Psittacotherium* may have nearly lost P_1.

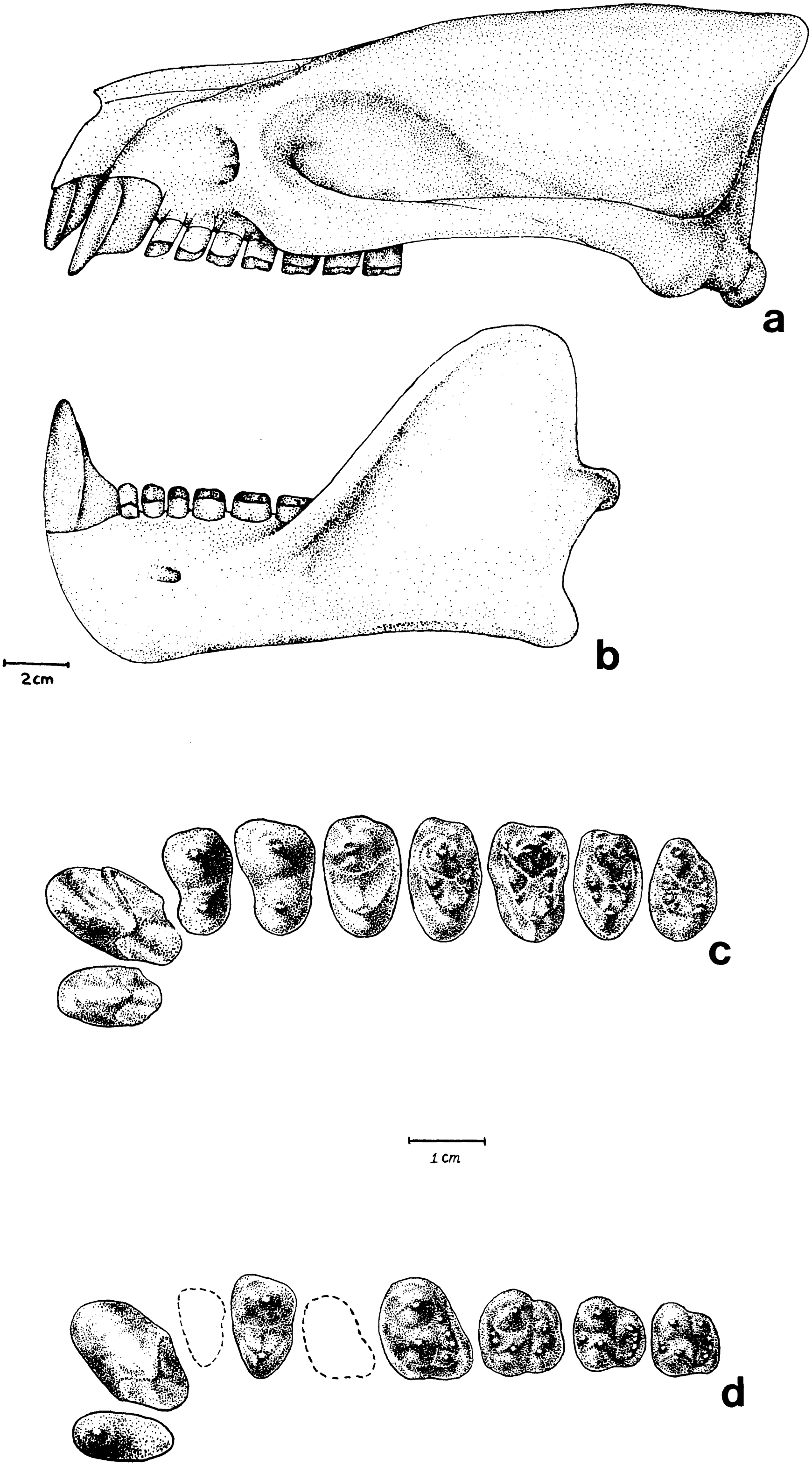
The P_2 of the type specimen of *P. multifragum,* AMNH 3413, is unworn. It is transversely oriented, simple and bicuspid, bearing a large, labial paracone and a smaller internal protocone.

The P_3 of *Psittacotherium* is not definitely known. However, squared alveoli preserved in the lower jaws of AMNH 754 and AMNH 3418 indicate that, like P_4, P_3 may have been submolariform.

AMNH 159328 and AMNH 16661 (Pl. 22: fig. 28) include moderately worn P_4s. P_4 is a submolariform and transversely bilophodont tooth. The anteroposteriorly compressed trigonid bears a large metaconid and protoconid, forming a transverse crest. A small paraconid is slightly labial of the center of the tooth. P_4

⟶

FIG. 17. Restoration of the skull, mandible and dentition of *Psittacotherium multifragum.* Skull and mandible based primarily on AMNH 754, AMNH 88383 and UK 8035. Dentition is based primarily on AMNH 3413, AMNH 2453, AMNH 16661, TMM 40148-2, TMM 40537-26, TMM 40537-33, TMM 40537-61 and USNM 15411. *a*) Left lateral view of skull. *b*) Left lateral view of mandible. *c*) Occlusal view of upper left dentition. *d*) Occlusal view of lower right dentition.


a
b
2cm
c
1 cm
d

also has a small, posterolingual, anteroposteriorly compressed talonid, which bears a large entoconid connected to the protoconid by a prominent postcristid.

The lower molars of *Psittacotherium* are unworn in AMNH 3413, AMNH 3416, AMNH 16661 (Pls. 21, 22), UNM NP-2220 and USNM 15413 (Pl. 27: figs. 11–14). M_{1-3} are essentially identical but decrease in size posteriorly. M_{1-3} are shallow-rooted, transversely bilophodont teeth with anteroposteriorly compressed trigonids and talonids. The talonids of M_{1-3} are narrower than the trigonids and placed relatively lingually. The trigonids bear subequal, conical metaconids and protoconids, variably connected by minutely cuspidate protocristids. There are minute paraconids and minutely cuspidate paracristids anterolingual to the metaconids. The talonids bear small, relatively high hypoconids and lower, cuspidate postcristids and entocristids.

Associated with USNM 15413, right and left dentary fragments with unerupted M_3s, are what appear to be the dC_1 and dP_{1-2} of *Psittacotherium multifragum* (Pl. 27: figs. 4–10). When compared to the C_1, dC_1 is sharply pointed and relatively compressed laterally with a thin, posterior enamel-free part. DP_{1-2} are extremely similar to P_2 (Pl. 21: figs. 7, 8) in being simple, bicuspid teeth with tall and thin labial cusps that are slightly inclined lingually and lingual cusps that are approximately half the height of the labial cusps and are slightly inclined labially.

Skull

The skull of *Psittacotherium* shows all of the derived stylinodontid characteristics (at least in an incipient form: Fig. 17; Pls. 23–25). Overall, it is heavily built with a short, deep face, moderately long cranium, and a high and wide occiput. The nasals are long and wide, extending far past the orbits, about two-thirds the length of the skull. Posteriorly, they broaden at a point approximately above the middle of the orbits, and then form a sharp wedge between the frontals. The frontals are laterally expanded anteriorly and suture with the maxillae just behind the anterior border of the orbits. Anteriorly, the premaxilla are large and well developed; posteriorly, they extend as a narrow wedge between the maxillae and nasals to a point above P^3. The maxillae are large and massive. The anterior border of the orbit lies above a point between P^{3-4}. There are two (AMNH 754) or three (UK 8035) infraorbital foramina placed in front of the orbit above P^3. The anterior root of the zygomatic arch is thick and massive. The lacrimal is not clearly distinct in any specimen of *Psittacotherium,* but probably was small as suggested by Matthew (1937); there is a small lacrimal foramen on the internal anterior border of the orbit of UK 8035. Posteriorly, little is known of the skull and cranium of *Psittacotherium.* It does appear to have had a moderately high sagittal crest. Based on UK 8035, *Psittacotherium* also appears to have had large mastoid processes and a high, wide, triangular-shaped occiput.

Mandible

The mandible of *Psittacotherium* is roughly intermediate between that of *Wortmania* and that of *Ectoganus* (Fig. 17; Pls. 23, 24, 26). The mandible is deep anteriorly with a massive, heavily fused symphysis which extends posteriorly to a point under P_{3-4}. The mandible shallows posteriorly and is shallowest under M_{2-3}. Anteriorly and internally there is a moderately large pit for the genioglossus muscle. Externally, there is a moderate-sized mental foramen positioned under P_3. The ascending ramus arises from a point external to M_2; the coronoid process is high and more triangular-shaped than in *Wortmania,* but not recurved. The angle is of moderate size. The condyles are transverse and set slightly above the tooth row.

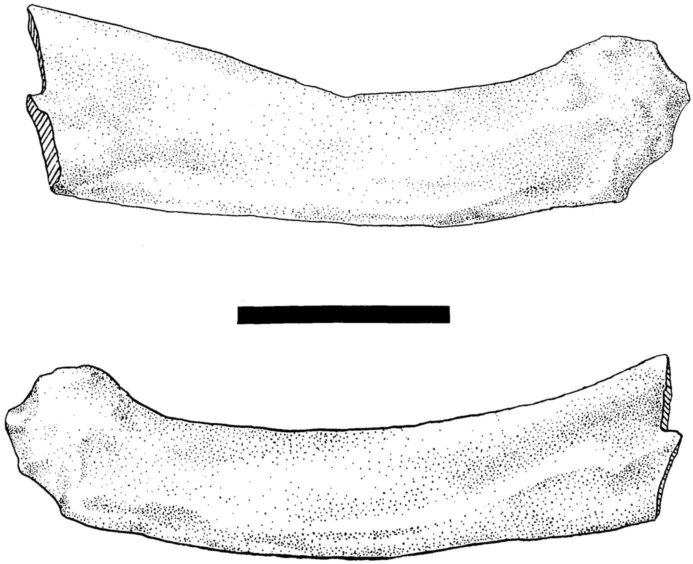


FIG. 18. Two views of the probable clavicle of *Psittacotherium multifragum*, TMM 41364-1. Scale is 4 cm long.

Pectoral Girdle and Forelimb

Clavicle

What appears to be a partial clavicle of *Psittacotherium* is preserved in TMM 41364-1 (Fig. 18; Pl. 28: figs. 7, 8). It is a large, robust, flattened and slightly recurved bone.

Humerus

Matthew (1937, p. 262) reported that the proximal and distal ends of the humerus of *Psittacotherium* were preserved with AMNH 3962. I have not been able to locate this specimen. However, the distal end of a right humerus of *Psittacotherium* is known from TMM 41364-1 (Pl. 28: figs. 5, 6). The humeral fragments that Matthew (1937, p. 262) studied were very similar in morphology to the humerus of TMM 41364-1, which is in turn extremely similar to that of *Ectoganus* (Fig. 27).

The humerus of *Psittacotherium* is short, stout and massive. Matthew (1937, p. 262) described the proximal end as follows: "The head of the humerus faces more proximal than in *Onychodectes,* much as in *Pantolambda,* but the internal tuberosity is much larger and more prominent than in the latter, as large as the external although lower set. From the front of the external tuberosity a heavy crest runs down the anterior face of the bone, towards what was presumably a high deltoid crest, as in primitive placentals generally, but the shaft of the bone is not known."

The distal end of the humerus is expanded transversely. Medially it bears a large, circular entepicondylar foramen enclosed by a strong, massive internal condyloid (pronator) ridge. The medial epicondyle is well developed, forming a prominent internal tuberosity. Laterally, the supinator ridge is well developed and recurved anteriorly. The lateral epicondyle is prominent, but not so large as the medial epicondyle. The medial trochlear crest is poorly developed and only extends as far distally as the capitulum. Mediolaterally, the trochlea is smoothly concave and the capitulum is smoothly convex. Posteriorly, the olecranon fossa is short proximodistally, but deep anteroposteriorly.

Ulna

AMNH 2453, a right ulna, radius and partial manus of *Psittacotherium multifragum* (Fig. 19; Pl. 30: figs. 1–3) has been described in detail by Wortman (1897b, p. 76–82) and Matthew (1937, p. 262–66). The following descriptions are also based primarily on AMNH 2453.

The ulna is short, deep anteroposteriorly and flattened transversely. In the middle of the shaft along its length there is a slight ridge internally, running distally from the base of the coronoid process. The posterior edge of the ulna is slightly thickened transversely. Distally, the ulna tapers only minimally and the posterior edge of the ulna has a very slight curvature. The olecranon of *Psittacotherium* is moderately large and slightly inflected medially. The semilunar notch is moderately deep and broad mediolaterally. The radial notch is relatively shallow and positioned well dorsad (anteriorly) rather than more laterally. Distally, the ulna bears a moderately large styloid process. On the styloid process there is a fairly flat facet which faces anterodistally for articulation with the cuneiform. The facet for articulation with the pisiform is not preserved in AMNH 2453.

Radius

The radius of *Psittacotherium* (Pl. 30: figs. 4, 5) is moderately short and robust and very similar in morphology to that of *Ectoganus* (described below). Seen proximally, the head is oval-shaped with the long axis directed mediolaterally. The articular surface for the humerus is smoothly and moderately concave dorsoventrally. The posterior (ventral) facet for articulation with the radial notch of the ulna is slightly convex transversely. In anterior view the head appears to be moderately expanded transversely. The tuberosity of the radius is only moderately developed. Proximally, the shaft of the radius is circular in cross section. Distally, the shaft thickens and is subquadrate in cross section. The distal end is expanded, both dorsoventrally and proximodistally, and bears a large, shallowly concave, undivided facet for articulation with the lunar and scaphoid. The anteromedially positioned styloid process is broad and blunt. The posterior surface of the shaft of the radius bears a low, rugose and proximodistally elongated ridge. The anterodistal half of the shaft of the radius is also moderately rugose.

Manus

Elements of both the right and left manus of *Psittacotherium* are preserved with AMNH 2453. The right manus (Fig. 19; Pl. 30: fig. 1) is more complete than the left. Since Wortman's (1897b) and Matthew's (1937) descriptions of the manus were written, the elements of the right manus have been glued together and solidly imbedded in plaster, the missing elements reconstructed in plastic, and the whole manus painted over. Thus, many of the articular surfaces and other features of the elements of the manus are obscured. Furthermore, I have not been able to locate all of the elements and fragments (e.g., the right centrale) described by Matthew (1937). Therefore, here I simply list and briefly discuss the elements of the manus. Wortman (1897b) and Matthew (1937, p. 263–65) have thoroughly illustrated and described the manus of *Psittacotherium multifragum*.

The carpus of *Psittacotherium* consists of eight bones: proximally the scaphoid (not preserved), the lunar and cuneiform; centrally the centrale; and distally the trapezium (not certainly identified, see Matthew's [1937] description), trapezoid (identified from fragments by Matthew [1937], see below), magnum and unciform. A pisiform was probably also present, although not preserved in any known

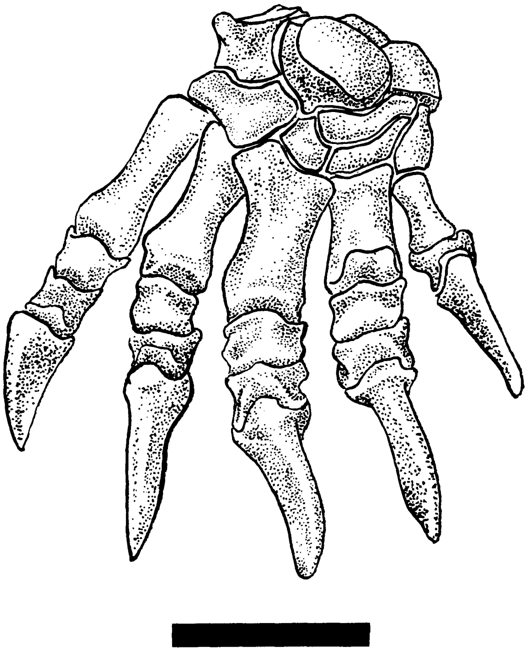


FIG. 19. The reconstructed manus of *Psittacotherium multifragum,* based primarily on AMNH 2453. Scale is 4 cm long.

specimen of *Psittacotherium.* There were almost surely five metacarpals, although only metacarpals two through four and the distal end of five are known. Miscellaneous phalanges of *Psittacotherium* are known. *Psittacotherium* probably had a single proximal phalanx and an ungual phalanx on the first digit and a full set of proximal, medial and ungual phalanges on digits two through five.

Overall, the mutual relationships of the elements of the manus of *Psittacotherium* are very similar to those of the elements of the manus of *Onychodectes.* However, the manus of *Psittacotherium* is relatively shorter and heavier than that of *Onychodectes.* This is especially seen in the second through fourth digits. In *Psittacotherium* the proximal portions of the digits are shorter and stouter than in *Onychodectes,* with greatly enlarged, laterally compressed and recurved unguals distally. What little is known of the manus of *Wortmania* is smaller, but otherwise nearly identical to that of *Psittacotherium.*

Pelvic Girdle and Hindlimb

Pelvis and Vertebrae

Wortman (1897b, p. 82–87, figs. 15–20) described and illustrated a pelvis and fourteen vertebrae (two posterior dorsal, three lumbar, and nine caudal vertebrae, AMNH 2455) from the Torrejonian of the San Juan Basin, New Mexico, which he attributed to *Psittacotherium.* Matthew (1937, p. 266) doubted that this specimen belonged to *Psittacotherium* and suggested that it might be referable to *Pantolambda cavirictus*; however, he evidently still used it in his restoration of *Psittacotherium* (Matthew 1937, pl. 64). Simons (1960, p. 19–20, pl. 16B) photographically illustrated and discussed this pelvis, comparing it to pelves of Paleocene pantodonts discovered since Matthew's work. Simons (1960) tentatively referred it to *Pantolambda cavirictus,* an assignment with which I agree.

With the elimination of AMNH 2455 from consideration, the pelvis of *Psit-*

tacotherium is unknown and only a few isolated vertebrae that may be referable to *Psittacotherium* are known.

Preserved with AMNH 3391 is a partial, crushed vertebra which has had most of the processes broken off and which is heavily encrusted by an impregnable concretion (Pl. 29: figs. 3, 4). This vertebra is relatively small (preserved height = 35 mm) with a transversely elongated centrum and a large neural spine (the latter broken off). It appears to be an anterior thoracic vertebra, but identification is not certain.

Preserved with AMNH 88383 are two ?lumbar vertebrae of *Psittacotherium* (Pl. 29: figs. 5–8). These are in relatively poor condition, but the major features are detectable. The centra are circular in cross section and relatively long anteroposteriorly. The anterior surface of each centrum is distinctly convex in both directions and tightly interlocked with the concave posterior surface of the centrum before it. The transverse processes are strong and set high dorsally. The neural spines are also well developed and angled anteriorly. What remains of the metapophyses, anapophyses and zygapophyses indicates they were large, massive, and probably tightly interlocking.

Femur

Fragmentary left femora of *Psittacotherium* are preserved in AMNH 16560 and TMM 41364-1 (Fig. 20; Pl. 29: figs. 1, 2; Pl. 31: figs. 4, 5). The femur of *Psittacotherium* is short and wide, with a flattened shaft. The head is spherical and set on a wide neck. The pit for the ligamentum teres is shallow and set low and slightly medially on the head. The greater trochanter is stout, prominent, slightly smaller than the head, and not quite so high. The digital fossa is broad and shallow. The lesser trochanter is small, relatively low-set and medially placed. The third trochanter is vestigial and set high on the lateral aspect of the shaft. The distal end of the femur is expanded transversely. The condyles are well developed and their convex articular surfaces form an arc through 180 degrees or more. The medial (internal) condyle is larger and set lower than the lateral (external) condyle. The articular surface for the patella is smoothly concave transversely, wide and extends far proximally. The intercondyloid fossa is narrow and deep. Both the internal and external tuberosities are prominent. Below the external tuberosity is a large depression elongated anteroposteriorly and slightly distoproximally; this may be the depression for the gastrocnemius muscle.

Tibia

Parts of the tibia of *Psittacotherium* are preserved in AMNH 15938 and TMM 41364-1 (Fig. 21; Pl. 28: figs. 1–4). The tibia is short and massive. Although no complete tibia is known, it appears that it was about four-fifths the length of the femur. Matthew (1937, p. 267) noted that the tibia of AMNH 15938 is "much flattened obliquely toward the proximal end," but comparison with TMM 41364-1 indicates that this is primarily an artifact of crushing of AMNH 15938.

The proximal end of the tibia is of the usual configuration, with a large medial condylar facet and a smaller lateral condylar facet. The intercondyloid fossa is relatively shallow. The tuberosity and cnemial crest are both weak.

Distally, the internal malleolus, although broken in all known specimens, was evidently well developed. The lateral descending process is poorly developed (as in *Onychodectes*). The lateral surface for the fibula is large and convex anteroposteriorly. The astragalar trochlea is strongly concave anteroposteriorly and faces distally, rather than slightly obliquely. There is only a slight anteroposterior keel in the middle of the surface which fits the corresponding fossa of the trochlear

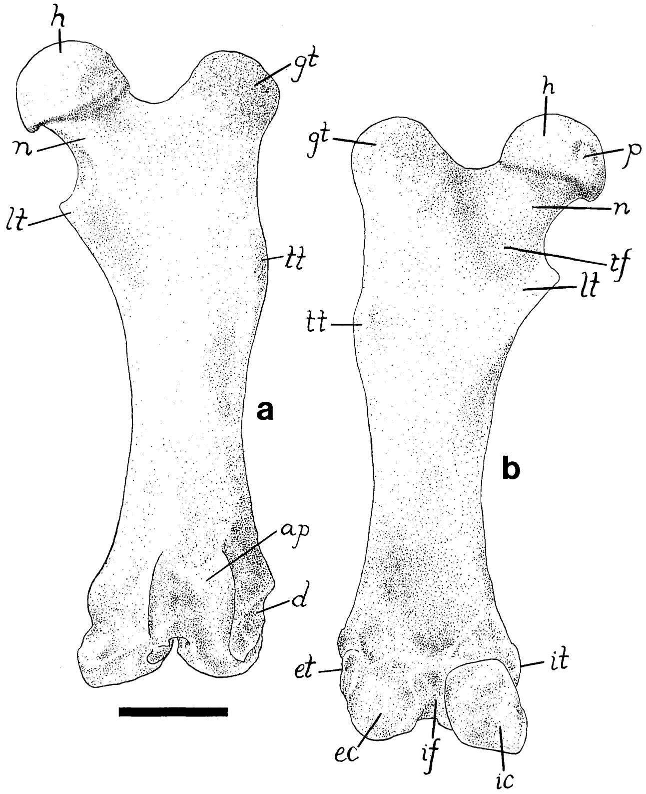


FIG. 20. A left femur of *Psittacotherium multifragum,* TMM 41364-1. *a*) Anterior view. *b*) Posterior view.

Abbreviations: ap = surface for patella; d = depression on external tuberosity; ec = external condyle; et = external tuberosity; gt = greater trochanter; h = head; ic = internal condyle; if = intercondyloid fossa; it = internal tuberosity; lt = lesser tuberosity; n = neck; p = pit for ligamentum teres; tf = intertrochanteric fossa; tt = third trochanter.

Scale is 4 cm long.

surface of the astragalus. The facet of the internal malleolus is at right angles to the astragalar trochlea.

Fibula

What may be the proximal half of the left fibula is preserved in AMNH 16560 (Pl. 30: figs. 6, 7). The head and shaft are expanded anteroposteriorly and compressed transversely. The lateral side of the fibula is concave anteroposteriorly.

Pes

A partial left pes of *Psittacotherium* is preserved in AMNH 16560 (Figs. 22, 23; Pl. 31: fig. 3); this includes the navicular, all three cuneiforms, metatarsals one and two and the phalanges of two digits (reconstructed by Matthew 1937, p. 268, fig. 67, and also here, as digits two and three). With TMM 41364-1 are preserved a partial astragalus (Fig. 23c, d; Pl. 28: figs. 9, 10) and calcaneum (Fig. 23e, f) of *Psittacotherium.*

Astragalus

The proximal body of a right astragalus referable to *Psittacotherium* is preserved in TMM 41364-1. Its configuration is similar to that of the astragalus of *Ony-*

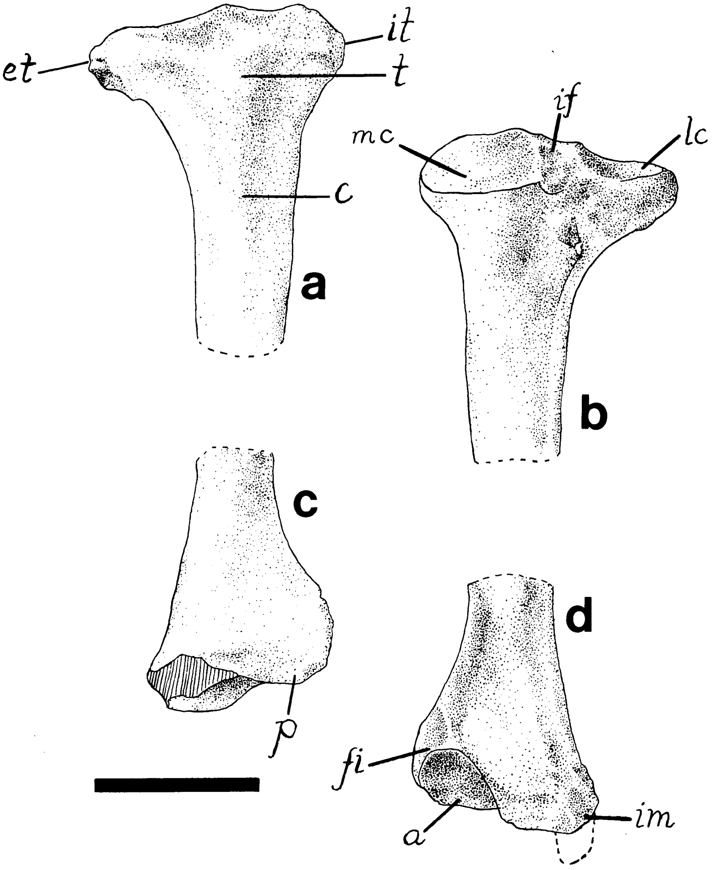


FIG. 21. The tibia of *Psittacotherium multifragum,* TMM 41364-1. *a*) Anterior view of proximal part of right tibia. *b*) Posterior view of proximal part of right tibia. *c*) Anterior view of distal part of left tibia. *d*) Posterior view of distal part of left tibia.

Abbreviations: a = surface for astragalus; c = crest; et = external tuberosity; fi = surface for fibula; if = intercondyloid fossa (= intercondylar notch); it = internal tuberosity; im = internal malleolus; lc = lateral condyle; mc = medial condyle; p = descending process; t = tuberosity.

Scale is 4 cm long.

chodectes, although somewhat compressed proximodistally and expanded transversely. The trochlear crests are not so sharp as in *Onychodectes* and are of subequal height, but the lateral trochlear crest is longer than the medial and extends further anteriorly and posteriorly. The trochlea is slightly concave transversely, but less so than that of *Onychodectes.* The tibial facet is oriented vertically whereas the fibular facet is inclined slightly laterally.

Ventrally, the calcaneoastragalar facet is large, long, oval to rectangular-shaped, concave, and closely resembles that of *Onychodectes.* The calcaneoastragalar facet is oriented laterally at an angle of approximately 40 degrees from the long axis of the body of the astragalus. The interarticular sulcus is narrow and deep. A distinct astragalar foramen does not seem to be present, although several pits are present within the interarticular sulcus. The ventroproximomedial corner of the astragalus bears a large process which extends proximally, medially and ventrally relative to the rest of the astragalus. A homologous process is seen in the astragalus of *Onychodectes,* although it is not nearly so well developed. Just distal and slightly lateral to this surface is a proximodistally concave surface. This may be a concave sustentacular facet that is appressed far proximally (as in *Stylinodon*;

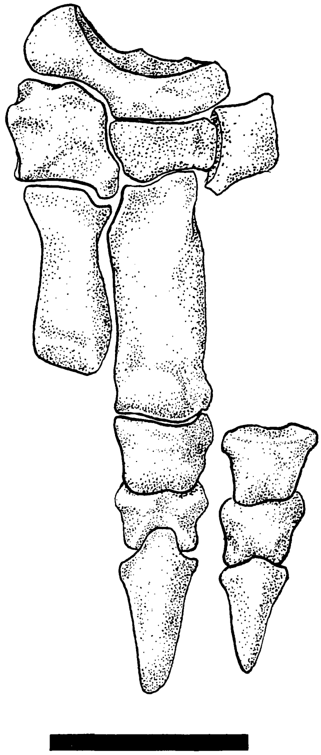


FIG. 22. Anterior (dorsal) view of the partial left pes of *Psittacotherium multifragum,* AMNH 16560. Scale is 4 cm long.

however, the sustentacular facet is convex in *Onychodectes*). Or, less likely, it may represent the intervening surface just proximal of the sustentacular facet, which is not preserved. The rest of the neck and distal head of the astragalus is also not preserved in TMM 41364-1.

Calcaneum

The proximal part of a ?left calcaneum (the tuber calcanei; Fig. 23e, f) that may be referable to *Psittacotherium* is preserved in TMM 41364-1. It is moderately long and rugose; the head is slightly expanded and inflected medially. Ventrally, it is narrower mediolaterally than it is dorsally.

Navicular

The navicular is relatively short mediolaterally and apparently made little contact with the cuboid. Proximally, the astragalonavicular facet is elongated transversely and is deeply concave both dorsoventrally and mediolaterally. The navicular tuberosity is pronounced and wrapped far around the medial side of the astragalus. Ventrally, there is also a prominent tuberosity. Distally, the navicular bears three flat facets for the three cuneiforms, arranged in a semicircle along the dorsal edge.

Entocuneiform

If properly identified, the entocuneiform is the largest bone of the cuneiform series. Seen in dorsal view, it is relatively narrow transversely, but is extremely deep. The sloping dorsomedial surface bears a wide, shallow, transverse groove which deepens ventrad. Laterally and proximally there is a proximodistally con-

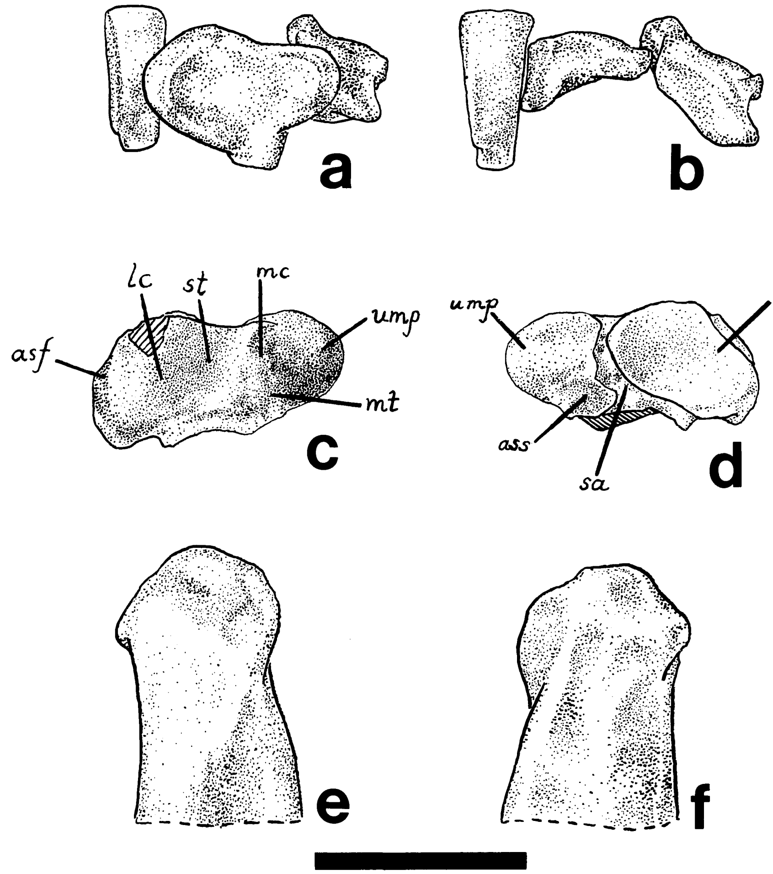


FIG. 23. Elements of the pes of *Psittacotherium multifragum*. *a*) Proximal view of ectocuneiform, navicular and entocuneiform, AMNH 16560. *b*) Proximal view of ectocuneiform, mesocuneiform and entocuneiform, AMNH 16560. *c*) Proximal (dorsal) view of partial right astragalus, TMM 41364-1. *d*) Distal (ventral) view of right astragalus, TMM 41364-1. *e*) Proximal (dorsal) view of (?)left tuber calcanei, TMM 41364-1. *f*) Distal (ventral) view of (?)left tuber calcanei, TMM 41364-1.

Abbreviations: asf = astragalar fibular facet; ass = astragalar sustentacular facet; caa = calcaneoastragalar facet; lc = lateral crest of trochlea; mc = medial crest of trochlea; mt = medial tibial facet of trochlea; sa = interarticular sulcus (= sulcus astragali); st = superior trochlear facet and trochlear fossa; ump = ventromedial process.

Scale is 4 cm long.

cave facet for articulation with the medial face of the mesocuneiform. Laterally and distally the entocuneiform bears a small, convex facet for articulation with the proximomedial corner of the second metatarsal. Proximally, it bears a deep, dorsoventrally concave facet for articulation with the navicular. Distally, it bears a narrow, deep, dorsoventrally concave, and slightly convex mediolaterally, facet for metacarpal one.

Mesocuneiform

The mesocuneiform is a relatively small bone, short proximodistally and slightly widened transversely. It is shallow, but is about twice as deep on the lateral side as on the medial side and thus comes to a point ventromediodistally. The proximal face is one large facet, slightly concave in both directions, for articulation with the navicular. The distal face forms a large facet for articulation with the second metatarsal. This face is in general shallowly concave in both directions, but medial to the midline on the dorsal border is a slightly convex protuberance that fits into a corresponding groove on the second metatarsal. The medial face of the mesocuneiform is shallow, slightly concave dorsoventrally and articulates with the lateral side of the entocuneiform. The lateral face is deep, slightly convex proximodistally and articulates with the medial face of the ectocuneiform.

Ectocuneiform

In dorsal view, the ectocuneiform is rectangular in outline (with the long axis oriented proximodistally) and expanded distomedially. It is deep ventrally. The medial face bears a proximodistally concave facet proximally for articulation with the mesocuneiform. Distally, the ectocuneiform overlaps the mesocuneiform and the mediolateral edge bears a slightly convex (in both directions), deep facet which contacts the lateral side of metatarsal two. Proximally, it bears a large facet which is dorsoventrally convex and transversely concave for articulation with the navicular. Distally, it bears a large, dorsoventrally deeply concave facet for articulation with metatarsal three. Laterally, there is a flat facet which articulates with the cuboid.

Metatarsal One

The first metatarsal is relatively reduced in length and flattened with both ends slightly expanded. The proximal end bears a slightly convex (in both directions) facet for articulation with the entocuneiform. Laterally there is a small, convex facet for articulation with the second metatarsal. The distal end bears a strong, dorsoventrally convex surface which is obliquely set such that it faces slightly medially. There may have been a medial spine or keel, as in *Onychodectes* and the second metatarsal of *Psittacotherium,* but it is not preserved in the specimen at hand.

Metatarsal Two

The second metatarsal is relatively large and robust. Proximally it is deepened dorsoventrally but compressed mediolaterally. The proximal end bears a large mediolaterally concave facet with a dorsal groove (see above) which articulates with the distal face of the mesocuneiform. Medially there are concave facets for articulation with the entocuneiform and first metatarsal. Laterally, there are facets for articulation with the ectocuneiform and third metatarsal. The distal end of the second metatarsal is expanded, squared-off and obliquely set, facing somewhat medially. It is strongly convex dorsoventrally and slightly concave mediolaterally on the medial side. Ventrally, it bears a small medial spine or keel elongated proximodistally.

Phalanges

The first and second phalanges are short, stout, flattened, and wider proximally than distally. The proximal articular surfaces are slightly concave dorsoventrally and lie at an acute angle to the horizontal plane of the bone such that they face slightly dorsad. In their centers they bear a slight median keel. The distal surfaces are strongly convex dorsoventrally and slightly concave transversely. The distal articular surface extends far ventrally on the proximal phalanges and far dorsally on the medial phalanges.

The ungual phalanges are large and moderately curved, but not high and transversely compressed as in the unguals of the manus. Transversely their dorsal surfaces are smoothly convex along their entire length. Their ventral surfaces are flat medially and distally, but proximally bear well-developed ventral processes or pads. The proximal articular surface is deeply concave dorsoventrally with a slight median ridge. The dorsal edge of the ungual extends further proximally than the ventral edge.

?*Psittacotherium* sp. or ?*Wortmania* sp.
(Pl. 27: fig. 3)

Stylinodont, near *Psittacotherium*: Gazin, 1941, p. 17.

Referred Specimen. USNM 16204, right I_3 (Pl. 27: fig. 3): from early Torrejonian strata of the North Horn Formation, Dragon local fauna, NW ¼, Sec. 8, T. 19 S., R. 6 E., Emery County, Utah.

Discussion. USNM 16204, a right I_3, is morphologically identical to the lower incisors of both AMNH 3413 (the type specimen of *Psittacotherium multifragum*) and AMNH 3394 (the type specimen of *Wortmania otariidens*). However, it is intermediate in size between these two, and therefore I am reluctant to definitely assign it to either taxon.

Ectoganus Cope, 1874

Ectoganus Cope, 1874, p. 592.
Calamodon Cope, 1874, p. 593.
Dryptodon Marsh, 1876b, p. 401.
Conicodon Cope, 1894, p. 594.
non *Calamodon* Amaral, 1935, p. 203.
Lampadophorus Patterson, 1949a, p. 41.

Type Species. *Ectoganus gliriformis* Cope, 1874 (= *Calamodon simplex* Cope, 1874 = *Calamodon arcamaenus* Cope, 1874 = *Calamodon novomehicanus* Cope, 1874 = *Dryptodon crassus* Marsh, 1876b = ?*Psittacotherium lobdelli* Simpson, 1929b = *Lampadophorus expectatus* Patterson, 1949a).

Included Species. The type species and *Ectoganus copei* Schoch, 1981b.

Distribution. Tiffanian–Wasatchian of Colorado, Clarkforkian of Montana, Clarkforkian–Wasatchian of Wyoming and Wasatchian of New Mexico; upper Paleocene strata of South Carolina (see Foreword).

Revised Diagnosis. Medium to large-sized taeniodonts; canines enlarged, rootless and compressed posteriorly with enamel limited to the anterolabial aspect; cheek teeth moderately to extremely hypsodont; M^{1-3} transversely bilophodont; P_{3-4} submolariform to molariform with talonids lingually placed and narrower than the trigonids; M_{1-3} transversely bilophodont with subequal trigonids and talonids.

Ectoganus gliriformis Cope, 1874

Ectoganus gliriformis Cope, 1874, p. 592.
(See synonymies under the subspecies.)

Type Subspecies. *Ectoganus gliriformis gliriformis* Cope, 1874.

Included Subspecies. The type subspecies and *Ectoganus gliriformis lobdelli* (Simpson, 1929b).

Revised Diagnosis. Largest species of *Ectoganus* (Table 29).

Ectoganus gliriformis gliriformis Cope, 1874

(Tables 29, 31, 32; Figs. 25c, d, 26; Pl. 32: figs. 2–10, 12–33; Pl. 35: figs. 20–22; Pl. 36; Pl. 37: figs. 1–8, 15–21; Pl. 38: figs. 5–22; Pl. 41: figs. 1–12; Pl. 42; Pl. 46: figs. 1–4)

Ectoganus gliriformis Cope, 1874, p. 592.
Calamodon simplex Cope, 1874, p. 593.
Calamodon arcamaenus Cope, 1874, p. 593.
Calamodon novomehicanus Cope, 1874, p. 594.
Dryptodon crassus Marsh, 1876b, p. 403.
Ectoganus novomehicanus: Cope, 1877, p. 159.
Ectoganus gliriformis: Cope, 1877, p. 160.
Calamodon arcamaenus: Cope, 1877, p. 163.
Calamodon simplex: Cope, 1877, p. 166.
Calamodon simplex: Cope, 1884c, p. 189.
Calamodon simplex: Wortman, 1897b, p. 88.
Calamodon arcamnaeus (lapsus calami): Wortman, 1897b, p. 89.
Ectoganus gliriformis: Gazin, 1936, p. 610 (in part).
Ectoganus cf. *simplex*: Guthrie, 1967, p. 23.
Ectoganus simplex: Schankler, 1980, p. 104.
Ectoganus gliriformis gliriformis: Schoch, 1981b, p. 938.

Type Specimen. USNM 1137, right and left I^3 and C^1 fragments, (?)right dP^{3-4}, upper (?)deciduous incisor fragment, right P_2, left dP_4, partial lower molar trigonid, partial lower molar talonid, fragmentary upper molar and associated bone and tooth fragments (Pl. 32: figs. 5–10, 16–21).

Horizon and Locality of the Type. Collected by E. D. Cope in 1874 from Wasatchian strata of the San Jose Formation, probably in Almagre Arroyo, San Juan Basin, New Mexico.

Referred Specimens. USNM 1001, left P_2, molariform cheek tooth, fragments of scapula, right humerus, ulna, magnum, ungual phalanx and other bone fragments; USNM 1012, left P^4 and canine fragments (type of *Calamodon simplex*; Pl. 32: figs. 3, 13, 22, 23); USNM: 1017, right M_2, canine and dentary fragments (type of *Calamodon arcamaenus*; Pl. 32: figs. 2, 12); USNM 1102, right P^2 (type of *Calamodon novomehicanus*; Pl. 32: figs. 4, 14, 15): all from Wasatchian strata of the San Jose Formation, probably in Almagre Arroyo, San Juan Basin, New Mexico.

YPM 11100, mandible with fragmentary right and left C_1, right P_3–M_3, root of left I_3, alveoli for right and left P_{1-2} (type of *Dryptodon crassus*; Pl. 42: figs. 3–5); YPM 11101, symphysis with right and left C_1: both from Wasatchian strata of the San Jose Formation, Almagre Arroyo (Gallinas Creek), San Juan Basin, New Mexico.

AMNH 16244, (?)incisor fragment, right and left P^{3-4}, left M^1, right P_3 (Pl. 37: figs. 1–8); AMNH 16245, left dentary fragment with crushed C_1 and P_2, complete P_3, two crushed upper molars (Pl. 36: fig. 13); AMNH 48001, left P_3, right and left P_4, left M_3 (Pl. 37: figs. 15–18): all from Wasatchian strata of the San Jose Formation, Almagre Arroyo, San Juan Basin, New Mexico.

YPM 39805, left radius (Pl. 46: figs. 3, 4): from Wasatchian strata of the San Jose Formation, San Juan Basin, New Mexico.

UNM B-970, left $P^{1(?)}$, right $P^{3(?)}$, right $M^{2(?)}$, left $P^{4(?)}$, right M_1 (Pl. 38: figs. 5–10, 14–20); UNM B-971, right $M^{1(?)}$ (Pl. 38: figs. 11–13); UNM B-973, canine fragments, partial ulna, scapula and bone fragments (UNM B-970/971/973 were all collected together and pertain to a single individual): all from Wasatchian strata of the San Jose Formation, Gobernador area, San Juan Basin, New Mexico.

AMNH 86859, upper $M^{3(?)}$, right P_4, left M_1 and canine and bone fragments (Pl. 35: figs. 20–22): from Clarkforkian strata (middle Clarkforkian?) of the "lower variegated beds" (see McKenna 1980a, p. 330), Togwotee Pass area, Purdy Basin, northwestern Wyoming. The identification of this specimen as *E. g. gliriformis* is only tentative; if it does indeed represent this taxon, it is an unusually early (stratigraphically low) occurrence. All other *E. g. gliriformis* is Wasatchian in age. Some workers might argue that, on the basis of its extremely early occurrence, AMNH 86859 should be referred to *E. g. lobdelli*. However, as stated previously, I have strived to base all of my primary taxonomic judgments solely on the morphology of the specimens involved, independent of extrinsic stratigraphic and geographic data. Fragmentary taeniodont remains, such as AMNH 86859, can be extremely difficult to identify at the species-group level. Yet, what remains of AMNH 86859 appears, to me, to most closely resemble other specimens here assigned to *E. g. gliriformis* (based primarily on the advanced degree of crown hypsodonty observed in AMNH 86859) and thus I have tentatively referred it to this taxon. I freely admit that I may be mistaken in this identification.

AMNH 4286, mandible with right and left I_3, right C_1, right and left P_1, left P_{2-3}, right and left P_4–M_3 (Pl. 42: figs. 1, 2); AMNH 4287, left P_2, right P_4, right and left M_1 (Pl. 37: figs. 19–21); AMNH 16671, right upper (?)deciduous incisor, right and left I^3–M^2, right dP^{3-4}, right M^3 and bone fragments (Pl. 36: figs. 1–12, 14–17): all from Wasatchian strata of the Willwood Formation, Bighorn Basin, Wyoming.

PU 13173, (?)right P^{3-4} and left P_4 (Pl. 41: figs. 1–12); USNM no number, canine and molariform tooth fragments, partial left maxilla, partial left femur and other bone fragments (Pl. 46: figs. 1, 2): both from early Wasatchian strata of the Willwood Formation, S. Elk Creek, Bighorn Basin, Wyoming.

CM 11497, left I^3, right C^1, (?)right P^{2-4}: from Wasatchian strata of the Willwood Formation, 4.8 km SW of the mouth of Elk Creek, Bighorn Basin, Wyoming.

UM VP6000, left dentary with C_1–P_2, M_1, M_3 and roots of right and left I_3, left P_{3-4}, M_2: from Wasatchian strata of the Willwood Formation, approximately halfway between Worland and Meeteese (Fifteen Mile Creek drainage, Cottonwood Creek), Bighorn Basin, Wyoming.

AC 2879, right dentary fragment with I_3, C_1, P_{1-2}, and M_3: from Wasatchian strata (Lysite) of the Wind River Formation, Wind River Basin, Wyoming.

Revised Diagnosis. Large *Ectoganus* with all teeth extremely hypsodont; incisors and P^{1-2}_{1-2} approach the totally rootless condition of the canine.

Ectoganus gliriformis lobdelli (Simpson, 1929b)

(Tables 29, 32; Pl. 32: figs. 1, 11, 34, 35; Pl. 33; Pl. 35: figs. 1–18; Pls. 39, 40)

Psittacotherium sp. indet.: Simpson, 1929a, p. 121.
?*Psittacotherium lobdelli* Simpson, 1929b, p. 11.
?*Psittacotherium* sp.: Patterson, 1936, p. 397.
Lampadophorus expectatus Patterson, 1949a, p. 42.
Lampadophorus lobdelli: Patterson, 1949a, p. 42.
cf. *Lampadophorus* sp.: Rose, 1981, p. 87.
Ectoganus gliriformis lobdelli: Schoch, 1981b, p. 938.
Ectoganus gliriformis lobdelli: Schoch, 1985, p. 3.

Type Specimen. AMNH 22234, right M^3 (Pl. 32: figs. 1, 11).

Horizon and Locality of the Type. Clarkforkian strata of the Fort Union Formation, Eagle Coal Mine, Bear Creek, Montana.

Referred Specimens. AMNH 22235, left I^3 (Pl. 32: fig. 35); CM 11560, right C_1 (Pl. 32: fig. 34): both from Clarkforkian strata of the Fort Union Formation, Eagle Coal Mine, Bear Creek, Montana.

PU 18345, right P^3 and right M^3 crown: from a carbonaceous clay above Coal #3, Clarkforkian strata of the Fort Union Formation, Foster Mine, Bear Creek, Montana.

FMNH P 26083, skull with right and left C^1, P^{3-4}, left M^3, alveoli for right and left P^{1-2}, M^{1-2}, right and left distal humeri, (?)left scapula, right and left ulnae, right and left femora, right and left tibiae, forefoot unguals and other bone fragments (type of *Lampadophorus expectatus*; Pls. 33, 34; Pl. 35: figs. 1, 2); FMNH P 14906, right $P_{3-4(?)}$ (Pl. 35: figs. 13–16); FMNH P 14954, fragmentary lower molar (Pl. 35: figs. 11, 12); FMNH P 15575, left P^4 (Pl. 35: figs. 3, 4); FMNH P 15008, fragmentary lower molar; FMNH P 15569, right P^3 (Pl. 35: figs. 5, 6); FMNH P 26106, right $M_{1(?)}$ (listed by Patterson 1949a, as P 26093; Pl. 35: figs. 17, 18) and lower (?)left canine; FMNH 26090, left humerus (Pl. 38: figs. 21, 22); FMNH P 26101, lower molar talonid (Pl. 35: figs. 7, 8); FMNH PM 241, left I_3 (Pl. 35: figs. 9, 10) (the above FMNH specimens compose the original hypodigm of *Lampadophorus expectatus*): all from late Tiffanian–Clarkforkian(?) strata of the Wasatch ("DeBeque") Formation, Plateau Valley local fauna, Mesa County, Colorado.

PU 18954, right M_1 and two rooted incisors (deciduous?); PU 18982, right $P^{3(?)}$, right and left P_4: both from Clarkforkian strata of the Polecat Bench Formation, west side of Polecat Bench, NW ¼, Sec. 21, T. 57 N., R. 100 W., Bighorn Basin, Wyoming.

PU 18994, right $P_{2(?)}$, right $P^{4(?)}$, right P_4, right and left M_1 and miscellaneous bone fragments (Pl. 39: figs. 16–24): from Clarkforkian strata of the Polecat Bench Formation, west side of Sand Coulee, SE ¼, Sec. 14, T. 57 N., R. 100 W., Bighorn Basin, Wyoming.

PU 20864, left $M^{2(?)}$, right and left $M^{3(?)}$, left $P_{2(?)}$, left P_4–M_2, right and left M_3 and miscellaneous tooth and bone fragments (Pl. 39: figs. 1–15): from Clarkforkian strata of the Polecat Bench Formation, SE ¼, NE ¼, Sec. 17, T. 54 N., R. 96 W., Bighorn Basin, Wyoming.

PU 21499, partial left $P_{2(?)}$, right and left P_4, right M_1, left M_3, left $P^{2(?)}$, right and left P^{3-4}, right M^1, incisor, canine tips, bone and tooth fragments (Pl. 40): from Clarkforkian strata of the Polecat Bench Formation, NW ¼, Sec. 27, T. 57 N., R. 100 W., Bighorn Basin, Wyoming.

A specimen of *Ectoganus gliriformis lobdelli* has recently been identified from upper Paleocene strata of the Black Mingo Group, approximately 0.8 km north of St. Stephen, South Carolina (see Foreword).

Revised Diagnosis. Large *Ectoganus* with P^2_2 only slightly more hypsodont than in *Psittacotherium*; posterior cheek teeth (P^3_3–M^3_3) moderately hypsodont with relatively low, rounded, bulbous crowns and relatively shallow, compressed roots.

Ectoganus copei Schoch, 1981b

Ectoganus copei Schoch 1981b, p. 938.
(See synonymies under the Subspecies.)

Type Subspecies. *Ectoganus copei copei* Schoch, 1981b.

Included Subspecies. The type subspecies and *Ectoganus copei bighornensis* Schoch, 1981b.

Diagnosis. Smallest species of *Ectoganus* (Table 30).

Ectoganus copei copei Schoch, 1981b

(Tables 30–32; Figs. 25a, b; Pl. 38: figs. 1–4; Pls. 43, 44; Pl. 45: figs. 1–4; Pl. 46: figs. 5–9)

Ectoganus gliriformis: Gazin, 1936, p. 597 (in part).
Ectoganus copei copei Schoch, 1981b, p. 938.
Ectoganus copei: Schoch, 1983a, p. 180.

Type Specimen. USNM 12714, skull and mandible with right and left I^3–M^1 (P^4s unerupted), left M^2, right and left dP^4, alveoli for right M^2 and left M^3, roots of right and left C_1, right and left P_2, left P_4 (unerupted), left dP_4, right and left M_1, left M_2, right and left M_3, roots of right P_4, alveoli for right M_{1-2} (Pls. 43, 44; Pl. 45: figs. 1–4).

Horizon and Locality of the Type. Wasatchian strata of the Willwood Formation, 13 km NW of Worland, Bighorn Basin, Wyoming.

Referred Specimens. AMNH 15633 (more than one individual), two right P_2s, right and left P_3, left $M^{2(?)}$ and other tooth fragments (Pl. 37: figs. 9–14): from

Wasatchian strata of the Willwood Formation, Fifteen Mile Creek, Bighorn Basin, Wyoming.

PU 14689, right and left dentary fragments with partial right and left C_1, right P_{1-2}: from Wasatchian strata of the Willwood Formation in the area of Sections 16, 17, 20 and 21, T. 47 N., R. 93 W., 11.3 km NW of Worland, Bighorn Basin, Wyoming.

USGS 3838, left maxilla and partial right premaxilla with roots of right and left I^3, left C^1–M^1 and partial crown of P^3, left dentary fragment with roots of C_1–P_2 and partial P_3 crown and fragments of the skeleton (Pl. 46: figs. 5–9): from Wasatchian strata in the SW ¼, SW ¼, Sec. 35, T. 48 N., R. 94 W. and in the NE ¼, NE ¼, NW ¼, Sec. 2, T. 47 N., R. 94 W., Washakie County, Bighorn Basin, Wyoming.

YPM 18618, right $P^{3(?)}$ and other tooth fragments (Pl. 38: figs. 1–4): from Wasatchian strata of the Willwood Formation, SW ¼, Sec. 25, T. 49 N., R. 97 W., Bighorn Basin, Wyoming.

Diagnosis. Small *Ectoganus* with all teeth extremely hypsodont; incisors and P^{1-2}_{1-2} approach the totally rootless condition of the canines; cusps on upper premolars larger and better developed than in *E. c. bighornensis.*

Ectoganus copei bighornensis Schoch, 1981b

(Tables 30, 32; Pl. 35: fig. 19; Pl. 45: figs. 5–19)

Ectoganus copei bighornensis Schoch, 1981b, p. 940.

Type Specimen. PU 14678, right and left P^3, right M^{1-2}, left M^3, right M_1 and canine fragments (Pl. 45: figs. 5–19).

Horizon and Locality of the Type. Early Wasatchian strata of the lower Willwood Formation, southern tip of Polecat Bench, T. 55 N., R. 100 W., Bighorn Basin, Wyoming.

Referred Specimens. PU 18052, right P^3, left M^1, left M_2, partial left M_1 and enamel fragments: from Wasatchian strata of the lower Willwood Formation, southern tip of Polecat Bench, Sec. 10, T. 55 N., R. 100 W., Bighorn Basin, Wyoming.

Ectoganus cf. *E. copei bighornensis*: AMNH 86852, left M_3 and canine fragments (Pl. 35: fig. 19): from middle Clarkforkian? strata of the "lower variegated beds" (McKenna 1980a, p. 330), Togwotee Pass area, Purdy Basin, northwestern Wyoming.

Diagnosis. Small *Ectoganus* with relatively low-crowned and shallow-rooted cheek teeth; cusps on upper premolars smaller and not as well developed as in *E. c. copei.*

Taxonomic Distinctions in *Ectoganus*

As here revised, *Lampadophorus* Patterson, 1949a, is considered to be congeneric with *Ectoganus* Cope, 1874. Patterson's (1949a, p. 42) original diagnosis of *Lampadophorus* reads as follows:

> *Canines rootless, enamel-free portions more compressed than in* Psittacotherium. *Cheek teeth with cement at bases of crowns, roots with vestiges of former divisions; crowns higher than in* Psittacotherium, *lower than in* Ectoganus*; little or no tendency toward development of enamel-free bands on anterior and posterior faces.* P^{1-2} *smaller than in* Ectoganus*; ridges running externally from protocones of* P^{3-4} *as in*

Ectoganus, *more crenulated than in* Psittacotherium. M^3 *wider than in* Psittacotherium, *hypocone less isolated than in* Ectoganus. P^{3-4} *with independent talonid crests.*

None of these characters serve clearly to distinguish *Lampadophorus* from *Ectoganus* and each point is addressed below.

Rootless canines with relatively compressed enamel-free parts are common to both *Ectoganus* and *Stylinodon.* Whether cement is preserved at the base of the enamel on the cheek teeth appears to be an artifact of preservation. Many specimens of *Ectoganus* (sensu Patterson) have cement at the base of the enamel: USNM 1017 (Pl. 32: figs. 2, 12), the type specimen of *Calamodon arcamaenus* Cope, 1874, is an example. Furthermore, this character is preserved on neither the type specimen of *L. expectatus* (FMNH P 26083, Pl. 35: figs. 1, 2) nor on the type specimen of *L. lobdelli* (AMNH 22234, Pl. 32: figs. 1, 11).

The type specimen of *L. expectatus* does not include the roots of any of the cheek teeth. However, they are present on Patterson's referred specimens (Pl. 35: figs. 3–18) and on the type specimen of *L. lobdelli,* and do not differ from the roots of previously accepted specimens of *Ectoganus* (e.g., USNM 1017). The "vestiges of former divisions" of the roots mentioned by Patterson (see quote above) are variable, but seem to be no better developed in Patterson's *Lampadophorus* than in previously accepted specimens of *Ectoganus* (cf. Pls. 32, 35).

Crown height also appears to be extremely variable in *Lampadophorus–Ectoganus.* This may be partly due to the fact that crown height of the cheek teeth in *Ectoganus* increases anteriorly (i.e., P^1_1 generally is highest crowned and M^3_3 lowest crowned) and often it is difficult to position isolated teeth in a tooth row accurately. Thus, alleged crown height differences can be largely an artifact of comparing teeth which are from different positions in the tooth row. Furthermore, whereas the crowns of Patterson's type and referred specimens of *Lampadophorus* are higher than those of *Psittacotherium,* they are not demonstrably lower than all specimens of *Ectoganus* (sensu Patterson: cf. Pls. 32, 36, 37, 41, 45).

Anterior and posterior enamel-free bands are best developed on the anterior cheek teeth of *Ectoganus* (P^{1-2}_{1-2}). Patterson, however, did not have the anterior cheek teeth of *Lampadophorus* (see list of his referred specimens for *Lampadophorus* above). The posterior cheek teeth which he did have show a definite "tendency toward development of enamel-free bands" (cf. Pl. 35: figs. 4, 6, 14, 18). Although enamel-free bands are better developed (along with increased hypsodonty) in some specimens of *Ectoganus,* the development of enamel-free bands here is considered an extremely variable character and worthy only of subspecific recognition.

It is impossible to say how Patterson determined that P^{1-2} of *Lampadophorus* are smaller than in *Ectoganus*; P^{1-2} are not preserved in the type specimen or in the referred specimens of *L. expectatus.* The alveoli for P^{1-2} on FMNH P 26083 are incomplete, distorted and unmeasurable. Furthermore, as P^{1-2} of *Ectoganus* erupt, their dimensions change.

P_{3-4} of *Ectoganus* have independent talonid crests. The type specimen of *Lampadophorus lobdelli* (AMNH 22234) is here identified as a right M^3 (Patterson 1949a considered it to be a P^4). The posterointernal cusp ("hypocone") is less isolated on AMNH 22234 than the same cusp on the M^3 of FMNH P 26083, the type specimen of *L. expectatus.* However, given the general variability of M^3s (Gingerich 1974; Gingerich and Schoeninger 1979; Gingerich and Winkler 1979), I would not judge this character to be of much taxonomic value. The M^3 of

FMNH P 26083 does not differ significantly from the M^3 of AMNH 16771 (Pl. 36: fig. 17), an upper dentition of *Ectoganus* from the Wasatchian of the Bighorn Basin, Wyoming.

As Patterson already noted (1948b, p. 251), the only other cheek teeth preserved in the type specimen of *Lampadophorus expectatus,* the P^{3-4}, agree "almost cusp for cusp and groove for groove" with the P^{3-4} of *Ectoganus* (AMNH 16771, Pl. 36). Thus, FMNH P 26083 and AMNH 16771 are morphologically indistinguishable from one another and must be placed in the same species.

The comparable parts of AMNH 16771 and USNM 1137 (Pl. 32: figs. 5–10, 16–21, 24–33), the type specimen of *Ectoganus gliriformis,* dP^{3-4}, a damaged M^1 or M^2, and incisor and canine fragments, are indistinguishable. The upper molar of USNM 1137 is crushed and broken, but it is a bilophodont tooth bearing cuspidate, transverse, anterior and posterior crests like those of AMNH 16771. The enamel distribution and degree of hypsodonty appear to be identical in the left M^1 or AMNH 16671 and the upper molar of USNM 1137. Considering the crushed nature of USNM 1137, these molars also appear to be identical in size, and are both larger than the M^{1-2} in *Ectoganus copei.*

The dP^{3-4} of USNM 1137 are also indistinguishable from those of AMNH 16771. However, the deciduous teeth of *Ectoganus* do not appear to be diagnostic at the specific level. As Gazin (1936) noted, the dP^4_4 of USNM 1137 are indistinguishable from the dP^4_4 of USNM 12714 as well (see Table 31), the type specimen of *Ectoganus copei* (Pl. 45: figs. 1–4). A lower molar trigonid and talonid of USNM 1137 are also larger than those of the lower molars of *E. copei.*

Taxonomic problems within the genus *Ectoganus* are similar to those encountered with *Psittacotherium* (see earlier discussion). Many specimens of *Ectoganus* are fragmentary, isolated and heavily worn teeth. Taxonomic decisions based on these specimens cannot be made with any degree of confidence. However, *Ectoganus* is better represented by well-preserved specimens than is *Psittacotherium,* and thus finer taxonomic distinctions can be made.

I formally recognize two species, each composed of two subspecies, to encompass most known *Ectoganus* material. The decision was made to recognize subspecies on the basis of characters which are variable (forming a seemingly continuous grade) but recognizable in over 75% of the specimens (cf. Simpson 1943, 1961, on subspecies).

At the specific level, I recognize large (*Ectoganus gliriformis*) and small (*Ectoganus copei*) species of *Ectoganus* (cf. Gazin 1936 and Guthrie 1967, p. 23, who also recognized a large and a small species). As demonstrated above, the type specimens of *Ectoganus gliriformis* (USNM 1137), ?*Psittacotherium lobdelli* (AMNH 22234) and *Lampadophorus expectatus* (FMNH P 26083) all belong to the large species of *Ectoganus* (Table 7). Cope also described three other species of *Ectoganus* (= *Calamodon*): *Calamodon simplex,* based on a left P^4 and canine fragments (USNM 1012; Pl. 32: figs. 3, 13, 22, 23); *Calamodon arcamaenus,* based on a right M_2, canine and dentary fragments (USNM 1017; Pl. 32: figs. 2, 12); and *Calamodon novomehicanus,* based on a right P^2 (USNM 1102; Pl. 32: figs. 4, 14, 15). When Gazin (1936) described USNM 12714 (Fig. 8; Pls. 43, 44), a skull of *Ectoganus,* he noted that Cope's three types appear to belong to a single species. Cope based his species on distinctions between teeth which he believed to occupy the same positions in the tooth row. However, by comparison with the complete dentition of USNM 12714, Gazin recognized that these teeth occupy different positions. Gazin (1936) considered the type of *E. gliriformis* to represent the same, dentally small species, as USNM 12714. He also recognized that there might be a second, larger species of *Ectoganus,* which he provisionally

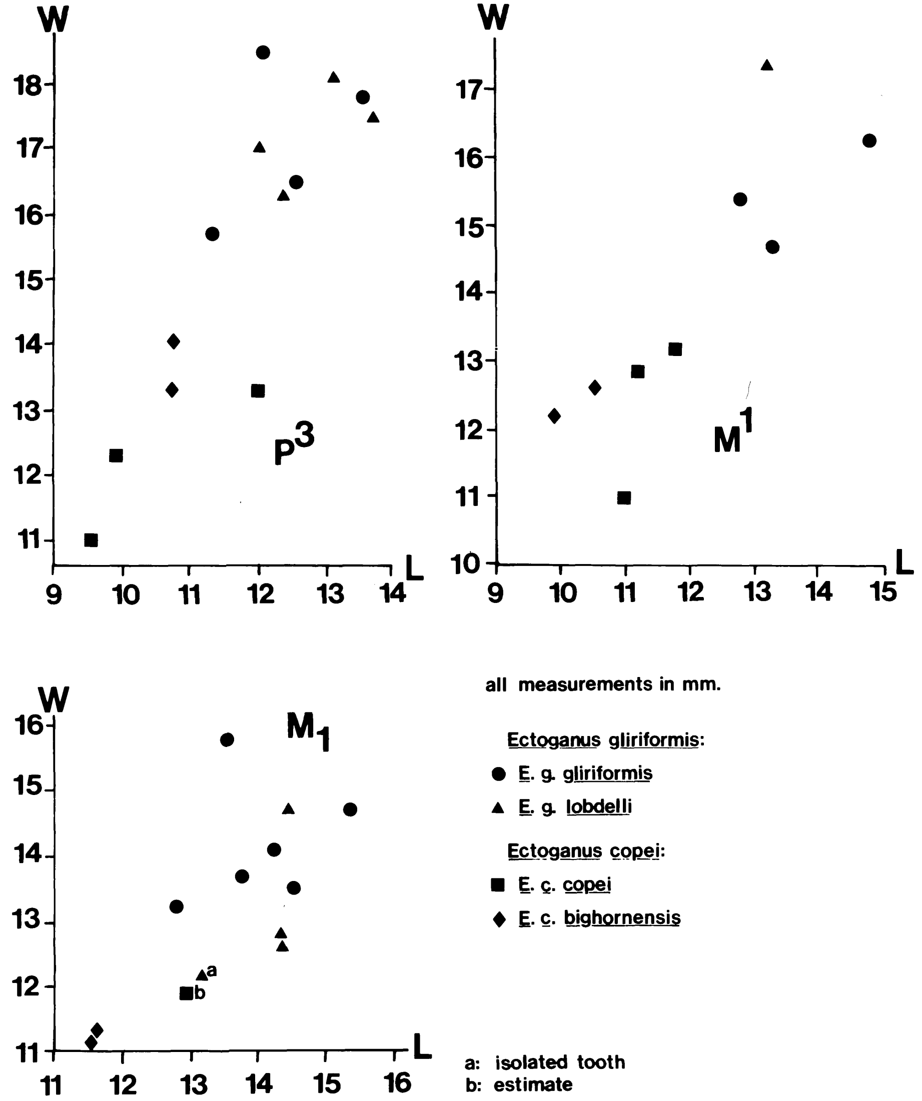


FIG. 24. Bivariate plots of P^3 width vs. P^3 length (*top left*), M^1 width vs. M^1 length (*top right*) and M_1 width vs. M_1 length (*bottom*) of specimens of *Ectoganus* listed in Tables 29 and 30. (Footnotes: *a*, measurements of an isolated tooth that is questionably an M_1; *b*, approximate measurements of a damaged tooth.)

called *Ectoganus simplex* (Gazin 1936, p. 611). However, he also tentatively subsumed all four of Cope's names under *Ectoganus gliriformis*.

As demonstrated above, USNM 1137, the extremely fragmentary type specimen of *Ectoganus gliriformis* also pertains to the large species of *Ectoganus*. Thus, the correct name for the large species is *Ectoganus gliriformis* (= *Calamodon simplex*). USNM 12714 pertains to a distinct small species of *Ectoganus, E. Copei* (Table 30), which at present is distinguished from *E. gliriformis* only by its smaller size. The type specimen of *Dryptodon crassus* (YPM 11100; Pl. 42: figs. 3–5) is an incomplete mandible with heavily worn teeth that falls in the size range of *E. gliriformis* (Table 29). As Gazin noted (1936), it is indistinguishable from Cope's *Ectoganus* and thus *D. crassus* is a junior subjective synonym of *E. gliriformis*.

Ectoganus gliriformis and *E. copei* are easily recognizable visually. When coefficients of variation are calculated for P^3, M^1 and M_1 (Table 32, Fig. 24; the only teeth for which there is enough reliable information for both species: P_2 is difficult to measure and changes shape with eruption), they vary from 8.5 to 15.8 for the pooled data, which is higher than expected for a single species (cf. Simpson and others 1960). In contrast, for *E. gliriformis* alone they range from 5.4 to 8.3 and for *E. copei* alone they range from 3.7 to 9.1. From the fragmentary material known, *Ectoganus copei* also appears to have had a relatively smaller skull (and body, presumably) than *Ectoganus gliriformis.* Thus, USNM 12714 (*E. copei*) and FMNH P 26083 (*E. gliriformis*) are both skulls of young individuals of comparable age, yet not only do they differ in the size of their teeth, but the size of FMNH P 26083 is relatively larger; e.g., the length from the anterior face of the canine to posterior M^2 is 88 mm in USNM 12714, and approximately 105 mm in FMNH P 26083. However, sexual dimorphism cannot be ruled out, so I do not attach much taxonomic significance to these differences in size.

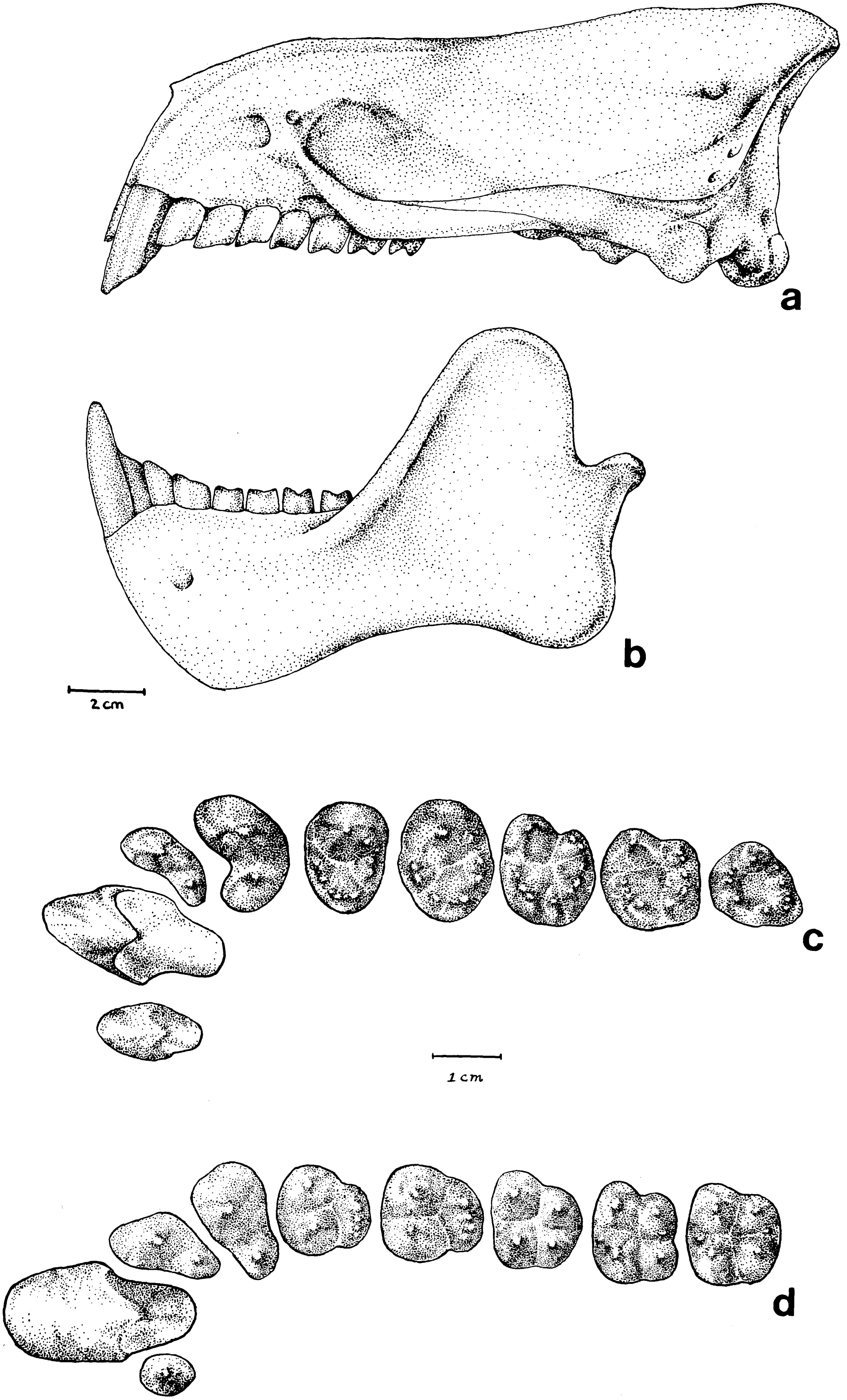
Within each species, I recognize two subspecies: *E. gliriformis* is divided into *E. g. gliriformis* and *E. g. lobdelli*; *E. copei* is divided into *E. c. copei* and *E. c. bighornensis.* Subspecific distinctions are made on the basis of the variable characters of degree of hypsodonty, relative root development and overall crown morphology (cf. Simpson 1943, 1961, on subspecific distinctions). Patterson (1949b) recognized and tried to use differences in some of these characters to make a case for the validity of *Lampadophorus.*

E. g. lobdelli differs from *E. g. gliriformis* in having relatively less hypsodont teeth, with the exception of the canine which is evergrowing in both forms. The incisors of *E. g. gliriformis* approach a totally rootless condition and are relatively smaller in length and width than those of *E. g. lobdelli* which are less deeply rooted (cf. Pl. 35: figs. 9, 10; Pl. 36: figs. 3, 4 and Pl. 32: figs. 35). P^2_2 in *E. g. lobdelli* (P^1_1 are unknown in *E. g. lobdelli*), although much more hypsodont and more deeply rooted than in *Psittacotherium,* are less so than in *E. g. gliriformis* (cf. Pl. 32: figs. 4, 14, 15; Pl. 36: figs. 7, 8, Pl. 39: figs. 4–6, 16–18 and Pl. 40: figs. 1, 2). In *E. g. lobdelli* the roots of P^2_2 are shorter and the internal and external bands of enamel are relatively wider anteroposteriorly and do not extend as far up and down the roots. In contrast, the P^{1-2}_{1-2} of *E. g. gliriformis* are deeply rooted with long, thin internal and even longer, thin external bands. The posterior cheek teeth of *E. g. lobdelli* also are less hypsodont than those of *E. g. gliriformis* with shallower, more compressed roots that sometimes form narrow points. The posterior cheek teeth of *E. g. gliriformis* are generally more hypsodont than those of *E. g. lobdelli* and have thicker, blunter roots. The P^{3-4} crowns of *E. g. lobdelli* are usually simpler than those of most *E. g. gliriformis,* lacking well-defined metacones and hypocones and having less cuspidate, or smaller cusps, on the transverse crests. The lower P_3–M_3 of *E. g. lobdelli* are relatively bulbous and globose compared to the corresponding teeth of *E. g. gliriformis* and bear small, but distinct paraconids. P_3–M_3 of *E. g. gliriformis* are less bulbous than those of *E. g. lobdelli* and lack paraconids, or at best these cusps are minute.

E. c. bighornensis differs from *E. c. copei* in having less hypsodont cheek teeth that are more shallowly rooted. The cusps of the upper premolars are larger and better developed in *E. c. copei* than in *E. c. bighornensis* (Pl. 45).

Description of *Ectoganus*

The upper incisors of *Ectoganus* (Fig. 25) mimic the canines by having enamel confined to an anterior band, and the posterior enamel-free part is compressed laterally. USNM 12714, a skull of *Ectoganus copei,* and USGS 3838, left and right premaxillae and a left maxilla of *E. copei,* both bear only one upper incisor


a
b
2 cm
c
1 cm
d

(here designated I^3) on either side and do not show any trace of I^2. USNM 1137, the holotype of *Ectoganus gliriformis*, and AMNH 16771, a principal referred specimen of *Ectoganus gliriformis*, both include a pair of upper incisors which presumably are I^3s. In addition, both specimens include a smaller (?)upper incisor which may be an inner incisor (Pls. 32 and 36) comparable to the small pair of upper inner incisors of *Stylinodon* (Pl. 48: fig. 3). PU 18954, here referred to *E. gliriformis*, also includes two relatively low-crowned and shallow-rooted incisors. One incisor of PU 18954 is much larger than the other, but it cannot be determined whether these incisors are uppers or lowers. Thus, there is some evidence that *Ectoganus gliriformis* possessed two upper incisors on either side. Alternatively, the small incisors of USNM 1137 and AMNH 16771 may be deciduous incisors (both USNM 1137 and AMNH 16771 are the dentitions of young individuals that retain deciduous premolars), or lower incisors, or they may be teeth of a different individual. Both USNM 1137 and AMNH 16771 consist of only isolated, but associated teeth which are presumably from one individual. At present, I suggest that the smaller incisors are deciduous incisors which may have been retained for some time after the eruption of the permanent incisors. Both the larger incisors and the smaller incisor of AMNH 16771 show definite signs of wear. The upper incisors of USNM 12414 may have been rootless, whereas those of AMNH 22235 and FMNH P 241 represent rooted incisors of *Ectoganus*.

The lower incisors of *Ectoganus gliriformis* are known with certainty to consist of one peglike incisor on either side, placed lingual to the anterior margin of the canines (AMNH 4286; Pl. 42: fig. 2). The lower incisors are not known for *E. copei*.

The upper and lower canines of *Ectoganus* are similar to those of *Psittacotherium* and *Stylinodon*. Enamel is limited to the anterior face and the posterior enamel-free part is laterally compressed. Anteriorly the canines of *Ectoganus* functioned in cutting and posteriorly they functioned in grinding. The canines of *Ectoganus* are rootless and evergrowing.

Both species of *Ectoganus* have seven cheek teeth on either side above and below and the morphology of the canines and cheek teeth is very similar in both species (cf. Pls. 32, 35–45).

P^1_1 are triangular in cross section and enamel is limited to labial and postero-internal bands. The crown structure of P^1_1 is unknown. On P^1_1 the labial band is longer anteroposteriorly and extends farther down the side of the tooth than the posterolingual band. The anterolingual enamel-free part of P^1_1 complements and is labial to the posterolabial enamel-free part of the canine. Thus, the labial enamel of C^1_1 and P^1_1 form a continuous surface, broken only by a small gap between the teeth.

P^2_2 are similar to P^1_1, but more ovoid in cross section and transversely set in the jaw. The unworn crown of P^2_2 bears two cusps, a higher labial and slightly anterior cusp, and a lower lingual, slightly posterior cusp. Except around the unworn crown, enamel bands on P^2_2 are limited to the labial and lingual sides of the teeth. The labial band is slightly longer anteroposteriorly and extends down

←

FIG. 25. Restoration of the skull and mandible of *Ectoganus copei* and the dentition of *Ectoganus gliriformis*. Skull based primarily on USNM 12714; dentition based primarily on AMNH 4286, AMNH 4287, AMNH 15633, AMNH 16244, AMNH 16345, AMNH 16771 and AMNH 48001. *a*) Left lateral view of skull. *b*) Left lateral view of mandible. *c*) Occlusal view of upper left dentition in essentially unworn condition. *d*) Occlusal view of lower right dentition in essentially unworn condition.

the tooth farther than the lingual band. The distribution of enamel on P^2_2 complements P^1_1 just as the enamel on P^1_1 complements C^1_1.

P^{3-4} are subequal in size, and it is nearly impossible to distinguish between them on the basis of isolated teeth. Both bear a large, high paracone anterolabially and a variably developed though small metacone posterolabially. Lingually, they bear small and low, subdistinct to fused protocones and hypocones. On the basis of their position, these two cusps appear to be homologous to the single lingual protocone of the corresponding teeth in *Psittacotherium*. Between the protocone–hypocone and paracone–metacone is a deep valley bounded anteriorly and posteriorly by minutely cuspidate transverse crests that connect the apex of the hypocone to the base of the metacone. These transverse crests are highest lingually and decrease in height labially. P^{3-4} are hypsodont, with enamel extensions labially and lingually and enamel-free parts anteriorly and posteriorly. The enamel extends farther lingually than labially.

M^{1-3} are transversely bilophodont teeth. Each is approximately square in cross-section and anteriorly bears a large transverse crest formed by a large protocone and smaller paracone connected by a minutely cuspidate transverse ridge. The posterior crest is slightly lower and is not as wide as the anterior crest; it is composed of the large hypocone and smaller metacone connected by a minutely cuspidate transverse crest. Whereas the hypocone is placed directly posterior to the protocone, the metacone is placed slightly posterolingual of the paracone. Posteriorly, M^{1-3} decrease in size, in degree of hypsodonty and in the relative size of the posterior crest. The enamel extends farther lingually than labially on the upper molars.

P^{3-4} are of similar morphology, subequal in size, and difficult to distinguish from one another. P_{3-4} are bilophodont and bear wide and high trigonids and lower, narrower, lingually placed talonids. The trigonids bear large, conical protoconids and slightly smaller and lower metaconids, connected to the protoconids by minutely cuspidate transverse crests. In *E. gliriformis* there are often small paraconids at the anterolabial bases of the metaconids. The talonids bear large hypoconids and small, low entoconids, both connected by minutely cuspidate transverse crests. P_{3-4} are hypsodont with enamel extending farther down the teeth labially than lingually.

M_{1-3} are transversely bilophodont teeth of morphology similar to P_{3-4}, except that the talonids are wider and higher and the entoconids are about the same size as the hypoconids. M_{1-3} are square in cross-section. Their trigonids are compressed anteroposteriorly and bear large protoconids and metaconids which fuse to form transverse lophs. In *Ectoganus gliriformis* there often are small protoconids at the anterolabial bases of the metaconids. The talonids of M_{1-3} are also compressed anteroposteriorly. In *E. copei* the talonids bear subequal hypoconids and entoconids that fuse to form posterior transverse lophs. The talonids of *E. gliriformis* also bear subequal hypoconids and entoconids, and hypoconulids or cuspidate transverse ridges occur between them to form posterior transverse lophs. Variably, mesoconids or entoconulids or both on the talonids are present in *E. gliriformis*. M_{1-3} decrease in size and hypsodonty posteriorly, and enamel extends farther labially than lingually on the lower molars.

Skull

The skull of *Ectoganus* is known principally from two specimens: FMNH P 26083, an incomplete and badly crushed skull of *E. g. lobdelli* (Pl. 33: figs. 1, 2) and USNM 12714, a fairly complete and only slightly distorted skull of the smaller form, *E. c. copei* (previously described and discussed by Gazin 1936: Fig.

25; Pls. 43, 44). These two skulls are generally similar to each other, although FMNH P 26083 is much larger and more robust and appears to have a shorter, deeper face, especially anterior to the anterior border of the orbit. In this respect it is similar to *Psittacotherium multifragum* and *Stylinodon inexplicatus.* USNM no number, a specimen referred to *E. g. gliriformis,* also includes a partial edentulous left maxilla; what remains of it is even larger and more massive than FMNH P 26083. Likewise, USGS 3838, a specimen referred to *E. c. copei,* includes a poorly preserved left maxilla that is small and relatively gracile, like USNM 12714. Posteriorly, the small skull of *E. c. copei* (USNM 12714) includes a high, well-developed sagittal crest as in *S. mirus.* In contrast, FMNH P 26083 does not have so well developed a sagittal crest and in this respect is more similar to *P. multifragum* and *S. inexplicatus.*

The nares of *Ectoganus* are terminal. The nasals are primitively broad and extend posteriorly to a point above M^{1-2}, where they end abruptly. The posterior part of the dorsal surface of each nasal bears four to seven foramina. The premaxillae bear the two central incisors and extend as thin wedges between the nasals and maxillae to a point above P^{3-4}. As Gazin (1936, p. 598) noted, in the young individual represented by USNM 12714 the upper canines may not have been completely covered by bone laterally or by only a very thin sheath of bone. The premaxilla and maxilla are extremely thin on either side of the canine and, although broken along their margins, may not have met over the canine. In FMNH P 26083 they fully meet over the canine, as they also appear to do in USGS 3838.

The maxillae are short and massive in *E. gliriformis,* but relatively slender in *E. copei.* The anterior margins of the orbits are above P^{3-4} and there is a small but distinct postorbital process above M^1. The anterior root of the zygomatic arch is thick and massive in *E. gliriformis,* but relatively slender in *E. copei.* It arises from the maxilla above P^4. The infraorbital foramen is moderate-sized and placed above P^3. Above P^{3-4} there is a knoblike process for the origin of the maxillolabialis musculature, as in *Stylinodon.* Dorsally the maxillae extend posteriorly between the nasals and frontals to a point approximately above M^1.

The sutures between the bones forming the dorsal aspect of the skull of *Ectoganus* are not distinct in the known specimens. Dorsally the supraorbital ridges are slight, joining in the midline of the skull approximately above M^2 and continuing posteriorly as the distinct sagittal crest. The temporal fossa, formed by the parietal and squamosal, is large and smooth. Posteriorly, it is bounded by a well-developed lambdoidal crest which extends ventrally and anteriorly to become continuous with the zygomatic arches. A large foramen pierces the skull in the middle of the parietal and a series of about five foramina lie along the posterior margin of the temporal fossa.

The posterior root of the zygomatic arch is moderate in size in *E. copei,* but unknown in *E. gliriformis.* In *E. copei* the zygomatic arches are of moderate size and robustness, as in *Stylinodon.* The suture between the zygomatic portions of the squamosal and jugal extends far anteroposteriorly.

The mastoid processes are large and extend far laterally. The occiput is high, wide and triangular-shaped in posterior view with an inion which is prominent and extends backwards. The occipital condyles are large and relatively set off posteriorly from the rest of the skull.

Ventrally, the glenoid fossae are smooth, shallow and relatively transverse. Posterointernally they are bound by relatively strong and medial-set postglenoid processes. Directly behind the postglenoid processes, separating them from the mastoid processes, are transverse grooves for the audital tubes.

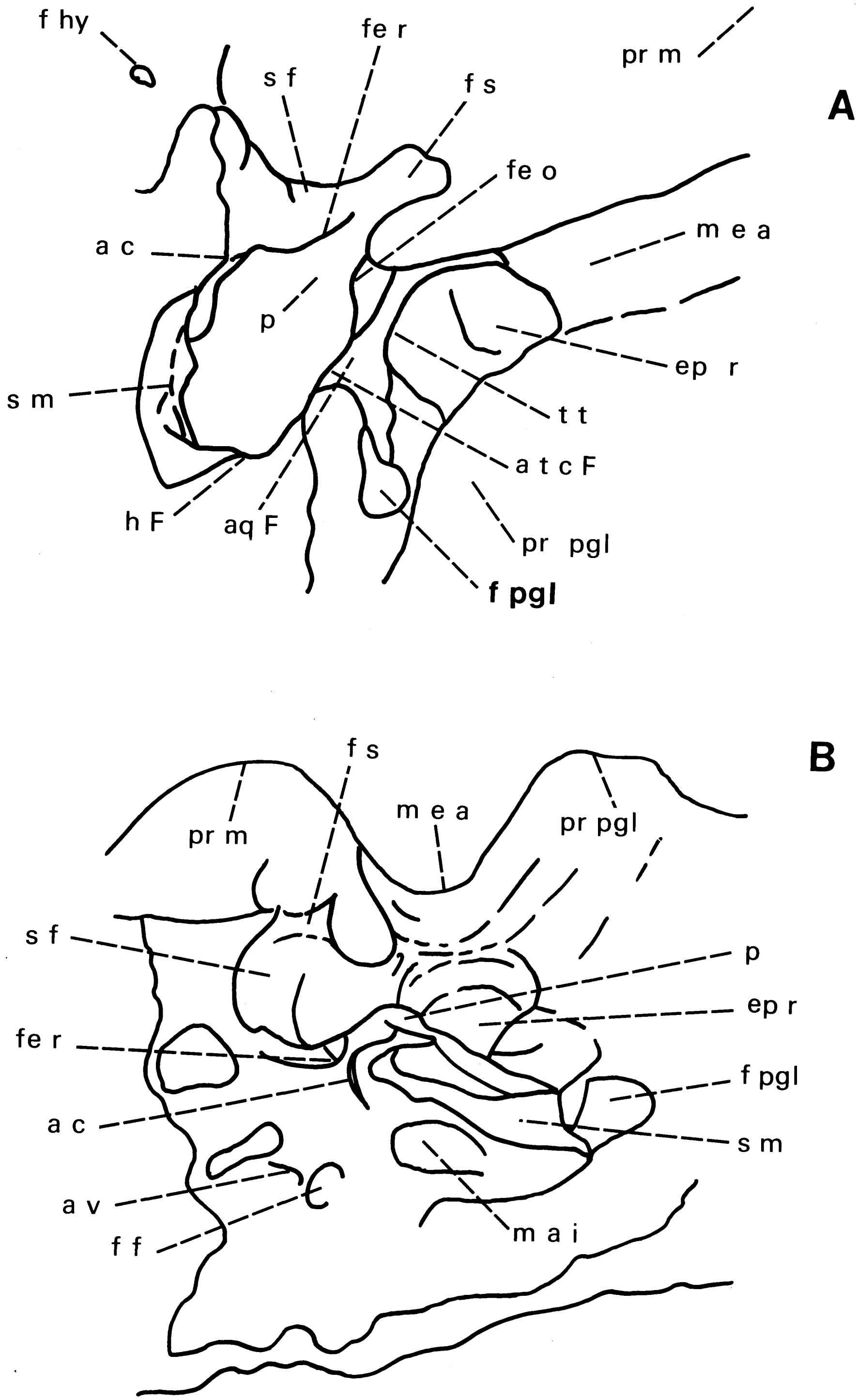


FIG. 26. The periotic region of *Ectoganus copei,* USNM 12714. Drawings after Gazin (1936, figs. 1, 2). *a*) Camera lucida drawing of ventral surface of periotic region on right side of skull. Lateral is to the right, posterior (back of the skull) is to the top. *b*) Camera lucida drawing of medial view of periotic region on right side of skull. Anterior is to the right.

Abbreviations: ac = aqueductus cochleae (= canaliculus cochleae); aq F = open part of aqueduct of Fallopius or facial canal (for nerve VII, facial nerve); atcF = outer or tympanic aperture for canalis

The periotic region of USNM 12714, described and illustrated in detail by Gazin (1936), is similar to that known for *Stylinodon* and is further described and discussed below.

Mandible

The mandible of *Ectoganus* is intermediate in morphology between that of *Psittacotherium* and that of *Stylinodon,* although somewhat closer to the condition seen in *Stylinodon.* In *E. copei* (e.g., USNM 12714) the mandible is relatively small and gracile whereas in *E. gliriformis* (e.g., AMNH 4286) it is large and massive and close to the size and robustness of the mandible of *Stylinodon mirus.* The mandible of *Ectoganus* is extremely short and deep anteriorly, with a massive, heavily fused symphysis that extends posteriorly to under P_4 in *E. copei* and to under M_1 in *Ectoganus gliriformis.* Posteriorly, the mandible shallows and is most shallow under M_{2-3}. Anteriorly and internally there is a large, well-developed pit for the genioglossus muscle. Externally, there are one to three mental foramina positioned under P_{1-2}. The ascending ramus is large and broad, but not recurved posteriorly; it arises from a point external to M_2. The coronoid process is relatively high and triangular in shape when viewed laterally. The angle is moderately well developed, rugose and slightly inflected in AMNH 4286. The condyles are smoothly convex dorsoventrally, extremely elongated transversely and set at, or just above, the level of the tooth row.

The Periotic Region of *Ectoganus* and *Stylinodon*

The ear region of the Taeniodonta (Fig. 26) is known only for *Ectoganus* and *Stylinodon.* It is best preserved in USNM 12714, the type specimen of *Ectoganus copei* (Gazin 1936). The periotic region is also moderately well known for *Stylinodon mirus* (UW 2270, FMNH PM 3895, YPM 11096) and *S. inexplicatus* (PU 16012, described in Schoch and Lucas 1981d). In all three of these species what is known of the ear region is effectively identical.

Gazin (1936) described and illustrated the ear region of USNM 12714 and little can be added to his description. In fact, since Gazin described USNM 12714, the separated pieces of the cranium and ear region have been glued and plastered together such that many of the details that Gazin was able to observe are now partially obscured. In particular, the medial view illustrated by Gazin (1936, fig. 2) is no longer accessible and the dorsal process separating the stylomastoid foramen from the channel for the auditory tube has been broken off and lost. Therefore, the following description, although based on original observations made on all of the skulls listed above, relies heavily on Gazin's (1936) work; Figure 26 is redrawn from Gazin's (1936, figs. 1, 2) camera lucida drawings of the ear region of USNM 12714 with only minor additions.

←

Fallopii; av = aqueductus vestibuli (for endolymphatic duct of membranous labyrinth of ear); ep r = epitympanic recess; fe o = fenestra ovalis (or vestibuli: perforation in wall of petrosal for foot-plate of stapes); fe r = fenestra rotunda (or cochleae: foramen in petrosal leading into cochlea); ff = probably the floccular fossa; f hy = hypoglossal foramen (= condylar or condyloid foramen: for emergence of the hypoglossal nerve, XII, from the cranial cavity); f pgl = postglenoid foramen (transmits internal facial nerve from superior petrosal sinus); fs = stylomastoid foramen (indicates course of facial nerve as it exits auditory region ventrally); hF = hiatus Fallopii; mai = internal auditory meatus (openings for facial, VII, and auditory, VIII, nerves); mea = channel for external auditory meatus; p = promontorium; pr m = mastoid process; pr pgl = postglenoid process; sf = possible location of stapedial fossa; sm = sulcus medialis (for medial branch of internal carotid artery and inferior petrosal sinus); tt = tegmen tympani.

For general references on ear regions, see especially McDowell 1958; MacIntyre 1972; Archibald 1977; Novacek 1977; MacPhee 1981; and Cifelli 1982.

The periotic region and mastoid are separated from the anterior glenoid fossa and postglenoid process by the smooth, transverse groove for the auditory tube that formed the roof of the external auditory meatus laterally. In *Ectoganus* and *Stylinodon* there is no indication that either the auditory bulla or the auditory tube was ossified. At the medial extremity of the groove for the auditory tube is the large, subcircular, epitympanic recess. This is separated from the anteromedially directed facial canal (aqueduct of Fallopius) by a partition, the tegmen tympani. Medial to the postglenoid process, anterolateral to the facial canal and anteromedial to the epitympanic recess, is a postglenoid foramen that may have communicated with the foramina venosae of the squamosal and parietal.

The almond-shaped petrous part of the periotic projects anteromedially and contains the inner ear. In USNM 12714 it measures approximately 18 mm by 8.5 mm. The inner ear communicated with the middle ear through the fenestra rotunda, which faces posteriorly, and the fenestra ovalis, which faces anterolaterally toward the medial end of the channel for the unossified auditory tube. These two fenestrae are separated by a small, laterally projecting spur. A slight bone prominence, the ?stapedial promontory (for origination of part of the stapedial muscle), lies just anterior to the fenestra rotunda, and medial to the projecting spur, presumably above the cochlea.

On the mediodorsal aspect of the petrous part is the prominent internal auditory meatus. Through the internal auditory meatus passed, among other things, cranial nerve VII (the facial nerve), which passed through the open aqueduct Fallopii and thence posterolaterally through the stylomastoid foramen (in *Ectoganus* and *Stylinodon* formed merely by a notch in the anteromedial margin of the ventral surface of the periotic). On the medial and anterior margin of the petrous part of the periotic is a distinct groove which may have carried, in part, the entocarotid artery and which may also have served as a venous sinus (Gazin 1936, p. 601). There is a small foramen at the anterolateral end of this groove which may be the hiatus Fallopii, transmitting the superficial petrosal nerve. Medial to the facial canal and on the lateral face of the petrous part of the periotic is the "outer or tympanic aperture" (Gazin 1936, p. 600) for the canalis Fallopii.

Medially, Gazin (1936) was able to observe several apertures and fossae which are no longer clearly visible because the skull (USNM 12714) has been glued and plastered together. Just medial to the fenestra rotunda Gazin (1936, p. 603) observed a small opening, presumably to the aqueductus cochlea and posterointernal to the internal auditory meatus Gazin (1936, p. 603) observed "the anteroventrally directed slit-like aperture of the aqueductus vestibuli." There is a fossa anterolateral to the aqueductus vestibuli that Gazin (1936, p. 603) identified as probably for the floccular lobe of the cerebellum.

Before USNM 12714 was glued and plastered together, Gazin (1936, p. 603) was also able to observe that "a large depression on the medial surface of the periotic near the ventral margin and posterior to the position of the foramen lacerum posterius appears to be a part of a more general cavity opening posteriorly into the condyloid sinus. The condyloid sinus in the exoccipital is doubled anteriorly and appears to be entirely separate from the hypoglossal foramen."

Endocranial Cast of *Ectoganus*

The holotype skull of *Ectoganus copei* Schoch, USNM 12714, was used to prepare an endocranial cast. This cast is described, discussed and illustrated in Schoch (1983a).

Postcrania of *Ectoganus*

The postcrania of *Ectoganus* are known from several partial skeletons including FMNH P 26083 (the type specimen of *Lampadophorus expectatus* but now referred to *E. g. lobdelli*); USGS 3838, a fragmentary skeleton of *E. c. copei* USNM 1001, forelimb fragments of *E. g. gliriformis* and other isolated bones. All of these specimens are of similar general morphology and will be described together, but vary in such parameters as size (Tables 10–21) and degree of robustness. This is due to such factors as that two species and three subspecies are represented (*E. g. lobdelli, E. g. gliriformis* and *E. c. copei*) and that the individuals represented are of varying ages. When appropriate, differences between individuals and taxa will be noted below.

Vertebral Column

In USGS 3838 the centra of various vertebrae are preserved; these appear to represent ?thoracic, lumbar and caudal vertebrae. However, all of these specimens are crushed, have all of the processes broken off and are heavily encrusted with an impregnable ironstone concretion. The most that can be said is that it appears that *Ectoganus* had a heavy vertebral column and a long, thick tail similar to that of *Stylinodon* (see below).

Pectoral Girdle and Forelimb

Scapula

A left scapula of *Ectoganus* is preserved in FMNH P 26083 (Pl. 33: figs. 3, 4) and a small distal portion of the scapula showing only a part of the glenoid surface is preserved in USNM 1001. FMNH P 26083 is heavily encrusted in an impregnable ironstone concretion and the perimeter of the blade and all of the processes have been broken off. Furthermore, the glenoid surface is obscured. The neck is short and wide. The missing acromion and coracoid processes appear to have been relatively large. The spine is low and only extends a little over half the length of the scapula, unlike in *Stylinodon* where it extends approximately three-fourths the length of the scapula. This may be due to the immaturity of the individual represented, as may the small size of the scapula compared to that of *Stylinodon.*

Humerus

The humerus of *Ectoganus* is especially well preserved in YPM 27201 and FMNH P 26090 (Fig. 27; Pl. 38: figs. 21, 22). It is very similar to the humerus of *Stylinodon,* although in general slightly less stout and robust, and also very similar to what is known of the humerus of *Psittacotherium.* In many ways, the humerus of *Ectoganus* gives the appearance of a scaled-up version of Gregory's (1910, p. 249) "primitive fossorial type." Overall, it is relatively robust with a broad distal end and well-developed muscular crests.

Proximally, the head is of moderate size, hemispherical and positioned well posteriorly. The greater tuberosity is large, heavily rugose and extends higher than the head of the humerus proximally. Distally, it runs into the deltopectoral crest (deltoid ridge) which extends for over half the length of the shaft, is flattened dorsoventrally and broadened mediolaterally. The lesser tuberosity is also prominent, but confined to the proximal end of the humerus. Medially, in the middle of the shaft, is the teres eminence. The teres eminence varies from a slight protuberance in YPM 27201 to being extremely well developed and recurved such that it points posteriorly in FMNH P 26090.

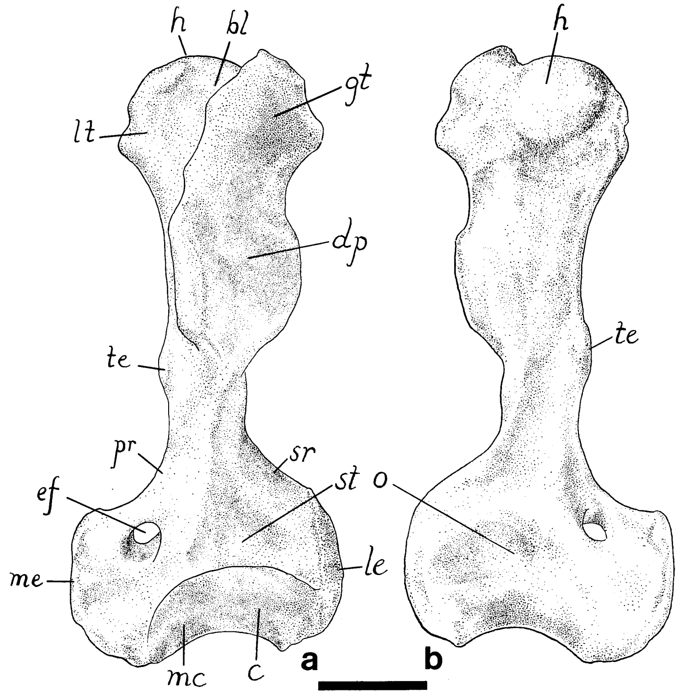


FIG. 27. A left humerus of *Ectoganus,* YPM 27201. *a*) Anterior view. *b*) Posterior view.
Abbreviations: c = lateral condyle (= capitulum); bl = bicipital groove; dp = deltopectoral crest; ef = entepicondylar foramen (= supracondyloid foramen); gt = greater tuberosity; h = head; le = lateral epicondyle; lt = lesser tuberosity; mc = medial condyle (= trochlea); me = medial epicondyle; o = olecranon fossa; pr = pronator ridge; sr = supinator ridge; st = supratrochlear fossa; te = teres eminence.
Scale is 4 cm long.

Distally, the humerus is extremely broad with an enlarged medial epicondyle. Above this is a large, circular entepicondylar foramen which, as in *Psittacotherium,* is enclosed by a massive internal condyloid (pronator) ridge. The lateral epicondyle is also prominent, but not so large as the medial epicondyle. The supinator ridge is also well developed and slightly recurved anteriorly. Anteriorly, there is a shallow supratrochlear fossa above the capitulum. Posteriorly, the olecranon fossa is relatively small, but deep. Mediolaterally, the trochlea is smoothly concave and the capitulum smoothly convex. The medial trochlear crest is moderately developed and extends slightly farther distally than the surface of the capitulum.

Ulna

Several partial ulnae are preserved, most notably in USNM 1001, FMNH P 26083 (Pl. 34: figs. 3, 4) and USGS 3838 (Pl. 46: fig. 9). Unfortunately, all of these ulnae are rather fragmentary and in none of them is the distal end preserved.

As in other taeniodont genera, the olecranon is large, rugose, extends far distally and is inflected slightly medially. The olecranon and shaft of the ulna are heavy, deep dorsoventrally but flattened (compressed) transversely. The shaft is most compressed along its length in the middle and is slightly wider dorsally and ventrally, such that it appears to bear external and internal grooves. The semilunar and radial notches are broad and shallow; the radial notch is almost flat and positioned well dorsally (anteriorly) rather than more laterally. The coronoid process is low whereas the olecranon process (sensu Greene 1935, i.e., the most proximal and anterior edge of the semilunar notch) is higher.

Radius

An isolated right radius is preserved in USNM 1001, and YPM 39805 is an isolated left radius from the San Jose Formation, New Mexico, here referred to *Ectoganus* (Pl. 46: figs. 3, 4). While USNM 1001 is a fairly gracile radius, YPM 39805 is much more heavily rugose, with large muscular attachments. YPM 39805 is extremely similar in gross morphology to the radius of *Stylinodon* and is of about the same length. However, the radius of *Stylinodon* is much more stout and massive. The head and shaft of the radius of *Stylinodon* is one and a half to two times as wide as the shaft of the radius of *Ectoganus*.

The proximal head is oval in shape (seen proximally), with the long axis elongated mediolaterally and the far lateral side flattened. The articular surface for the capitulum of the humerus is smoothly concave in both directions. Posteriorly, the head bears an articular surface for the radial notch of the ulna. The neck is relatively thin and there is no distinct tuberosity, although posteriorly there is a shallow fossa just distal of the head.

Distally the shaft of the radius is greatly expanded both mediolaterally and dorsoventrally. Toward the distal end, the shaft is almost square in cross-section. Distally, the styloid process is broad, blunt and positioned anteriorly and slightly medially. The distal surface bears a large, suboval, shallowly concave facet which articulated primarily, or solely, with the lunar as in *Stylinodon*. Posteriorly, on the distal end of the radius, there are two small, rather flat, facets separated by a slight depression, which may have articulated with the ulna. Two distinct ridges run proximally from these raised prominences to meet in the middle of the posterior surface of the shaft.

Manus

The manus of *Ectoganus* is almost completely unknown. A right magnum is preserved in USNM 1001, a specimen of *E. g. gliriformis* (described and illustrated by Cope 1877, p. 168–69, pl. 43: fig. 12 as a "magnum," but called a "cuboid" in his table of measurements on p. 169). The magnum of *Ectoganus* is only slightly larger than the magnum of *Psittacotherium* and similar to that of *Onychodectes* and *Psittacotherium,* rather than being enlarged and modified as in *Stylinodon* (see below).

In dorsal view, the magnum is relatively small (a primitive feature, cf. Matthew 1937, p. 263) and five-sided; ventrally, the magnum is relatively expanded. Proximally, there is a narrow (mediolaterally) lunar facet that is slightly concave dorsally, but proximally expanded ventrally, forming a dorsoventrally convex knoblike subhemispherical surface that articulated with the distal surface of the overlying lunar. Proximomedially there is a relatively large, dorsoventrally concave facet for a fair-sized centrale. Medially, there is a slight facet for the trapezoid. Laterally, there is a small, rather flat facet for the unciform. Distally, the magnum bears a large facet that is smoothly concave dorsoventrally and smoothly convex mediolaterally. This facet evidently articulated with the central part of the proximal articular surface of metacarpal three as in *Onychodectes* and *Psittacotherium*.

Fragments of a few metapodials are preserved in USGS 3838; however, none is complete and it is uncertain which of these pertain to the manus and which pertain to the pes. They are relatively long and slender as compared to *Stylinodon* (in this respect resembling *Psittacotherium,* but perhaps also slightly more slender than those known for *Psittacotherium*). Distally, the articular surfaces are squared-off, strongly convex dorsoventrally, and bear strong ventral median keels or ridges in contrast to the metapodials of *Psittacotherium,* in which the median keels are poorly developed, and to *Stylinodon,* in which median keels are virtually absent.

A few medial or proximal phalanges and several unguals of the manus are preserved in USGS 3838 (*E. copei*: Pl. 46: figs. 7, 8) and FMNH P 26083 (*E. gliriformis*: Pl. 33: figs. 5–8). In both of these specimens these elements are heavily encrusted with an ironstone concretion, but they do not appear to differ in morphology from the same elements in *Psittacotherium* and *Stylinodon.* They are approximately intermediate in size between these two genera. The proximal and medial phalanges are little more than "wedges," as in *Stylinodon.* The unguals of the manus bore large, high, laterally compressed and recurved claws with large ventral processes proximally.

Pelvic Girdle and Hindlimb

Pelvis

The ?right acetabular part of the pelvis of *Ectoganus* is preserved in USGS 3838; however, it is heavily encrusted with an impregnable ironstone concretion and less of it remains than does the same part which is preserved of *Stylinodon* (USNM 16664, Pl. 59: figs. 10, 11). In USGS 3838 the acetabulum is relatively deep, as in *Stylinodon,* but the diameter across the acetabulum of USGS 3838 is only about four-fifths that of USNM 16664.

Femur

Fragments of the femur of *Ectoganus* are preserved in FMNH P 26083 and USGS 3838, and a complete left femur, missing only the neck and head, is preserved in USNM no number (Pl. 46: figs. 1, 2). The following description is based primarily on USNM no number.

The femur of *Ectoganus* is remarkably similar to that of *Psittacotherium,* but is slightly longer. As in *Psittacotherium,* the shaft is flattened dorsoventrally and narrowed mediolaterally in its central part. The distal, and especially proximal, ends are greatly expanded transversely. As in the femur of *Psittacotherium,* the femur of *Ectoganus* gives the impression of being top-heavy due to this proximal expansion.

Apparently the neck was wide as in *Psittacotherium* and carried a spherical head. The greater trochanter is large, high, and wide. The lesser trochanter is set fairly high and is expanded medially such that it is prominent both in anterior and posterior views of the femur. Laterally, there is a moderately large (larger than in *Psittacotherium*) third trochanter, which is set high on the shaft and slightly inflected anteriorly. The digital fossa is extremely broad and shallow.

Distally, the condyles are large and well developed. Their convex articular surfaces form an arc through 180 degrees or more. The medial condyle is larger and extends farther distally than the lateral condyle. The condyles are separated posteriorly by a deep intercondyloid fossa. Anteriorly, the articular surface for the patella is wide and smoothly concave transversely, but does not extend up the shaft so far proximally as in *Psittacotherium.* The internal and external tuberosities are prominent.

USNM no number has been broken in half in the middle of the shaft and, although poorly preserved, shows the gross internal morphology of the femur of *Ectoganus* in cross-section. The compact bony tissue is thick relative to the cancellous bone in the center. Around the edge, the compact bone is 7 to 11 mm thick, whereas in cross-section the cancellous internal bone forms a mediolaterally elongated oval with the principal axes measuring 22 mm and 11 mm.

Tibia

Both tibiae are preserved in FMNH P 26083 (Pl. 34: figs. 7, 8) and fragments of what may be the tibia are preserved in USGS 3838. The tibiae in FMNH P 26083 are badly crushed dorsoventrally and the extremities are missing. Likewise, the material in USGS 3838 is so fragmentary that little can be said about the tibia of *Ectoganus* beyond that it was apparently relatively short and stout.

Pes

The proximal (anterior) part of the left calcaneum of *E. copei* is preserved in USGS 3838 (Pl. 46: figs. 5, 6). This specimen is somewhat distorted, but preserves a moderately large, proximodistally elongated and convex astragalocalcaneal facet and a smaller medial calcaneal sustentacular facet. The calcaenum as a whole is slightly compressed mediolaterally and deepened dorsoventrally, but not to the same extent as is seen in USNM 18425 (the hindfoot of *Stylinodon,* see below). The calcaneum is more comparable to what is known of that of *Psittacotherium* (TMM 41364-1) although somewhat smaller than TMM 41364-1. Distally, USGS 3838 bears an ovoid cuboid facet that is slightly concave in both directions.

Also preserved with USGS 3838 is a left ectocuneiform of *E. copei,* which is virtually identical in morphology, and only slightly larger in size than the ectocuneiform preserved in AMNH 16560, a partial left pes of *Psittacotherium multifragum*. It is quite unlike the ectocuneiform of *Stylinodon* (discussed below). In dorsal view the ectocuneiform is rectangular in outline. It is deep ventrally, especially proximally, and bears a distinct proximoventral process as in *Psittacotherium*. Proximally, it bears a relatively flat facet for articulation with the navicular. Distally, it bears a large, dorsoventrally concave facet for articulation with the third metatarsal. On the medial face, proximally there is a rather flat facet, which is short proximodistally, but elongated dorsoventrally, for articulation with the mesocuneiform. On the distal edge of the medial face of the ectocuneiform there are two small, relatively flat facets, one placed dorsally and the other placed ventrally, which evidently articulated with the proximolateral edge of the second metatarsal as in *Psittacotherium*. Laterally and proximally, the ectocuneiform bears a slightly concave, ovoid (with the long axis oriented dorsoventrally) facet for articulation with the cuboid.

Several metapodials are preserved with USGS 3838, but those of the manus are not surely distinguishable from those of the pes and are discussed above with the manus.

A fragment of an ungual of the pes of *Ectoganus* is preserved in USNM 1001. It is short, stout, and not laterally compressed. Morphologically, it is identical to the hindlimb unguals of *Psittacotherium* and *Stylinodon* and intermediate in size.

Ectoganus sp. cf. *E. gliriformis*
(Pl. 41: figs. 13–27)

Referred Specimen. UW 1823, right $P^{4(?)}$, left $P_{4(?)}$, left $M_{1(?)}$ and canine fragments (Pl. 41: figs. 13–27): from Wasatchian strata of the Willwood Formation, Little Sand Coulee, S ½ of Sec. 26, T. 56 N., R. 102 W., Bighorn Basin, Wyoming.

Discussion. The teeth of UW 1823 here interpreted as a right P^4 and a left M_1 are indistinguishable from the corresponding teeth of *Ectoganus gliriformis.* However, the crown morphology of the tooth here interpreted as a left P_4 is aberrant. It bears two tall, centrolabially placed conids (the ?protoconid and ?metaconid), a large, cuspidate posterolingual "cingulid" (the ?talonid) and a slightly smaller anterolingual cingulid (perhaps incorporating the paraconid). This may be the tooth of an aberrant individual, it may represent a distinct taxon or I may have wrongly interpreted it as a P_4.

Ectoganus sp.
(Figs. 27, 47)

Ectoganus sp.: Lucas, 1982, p. 19.

Referred Specimens. UNM GE-097, fragmentary right humerus (Fig. 47): from Wasatchian strata of the lower part of the Galisteo Formation, Cerrillos local fauna, SE ¼, SE ¼, Sec. 16, T. 14 N., R. 8 E., Santa Fe County, New Mexico.

YPM 27201, left humerus (Fig. 27): from Wasatchian strata of the Willwood Formation, Bighorn Basin, Wyoming.

Discussion. The humerus of derived taeniodonts is highly distinctive (cf. Cope 1877; Marsh 1897; Patterson 1949b; Wortman 1897b; the humerus of *Stylinodon,* Pl. 55: figs. 1, 2). It is short and robust with extremely well-developed muscular crests. The greater and lesser tuberosities are both well developed, and the deltopectoral crest extends over half the length of the shaft. The teres eminence is large and centered medially at the midlength of the shaft and points backwards. The humerus is extremely broad distally, with large, well-developed internal and external condyles, a well-developed supinator ridge, and a large, subcircular entepicondylar foramen. The distal articular surface (capitulum and trochlea) is broad and smoothly curved. The olecranon fossa is of moderate size. YPM 27201, a left humerus, and UNM GE-097, a right humerus (Fig. 47; Lucas 1982), are identical to the humeri of FMNH P 26083, FMNH P 26090 and USNM 1001 and are referable to *Ectoganus.*

Ectoganus sp. or *Stylinodon* sp.

Referred Specimens. FMNH P 15602, tips of canines; FMNH PM 336, canine fragment: both from Wasatchain strata of the Wasatch Formation ("Rifle Member of the DeBeque Formation"), Garfield County, Colorado.

Discussion. Although generically indeterminate, these apparently rootless canines document the presence of an advanced stylinodontid.

Stylinodon Marsh, 1874

Stylinodon Marsh, 1874, p. 531.
Calamodon: Cope, 1881c, p. 184.
Calamodon: Cope, 1884c, p. 192 (in part).

Type Species. *Stylinodon mirus* Marsh, 1874 (= *Calamodon cylindrifer* Cope, 1881c).

Included Species. The type species and *Stylinodon inexplicatus* Schoch and Lucas, 1981d.

Distribution. Late Wasatchian of Colorado and Wyoming, Bridgerian of Colorado and Wyoming, Uintan of Utah and Bridgerian or Uintan of western Texas.

Revised Diagnosis. Taeniodonts with the dental formula I^2_1, C^1_1, P^4_4, M^3_3; all of the teeth evergrowing and rootless; moderately worn teeth without enamel entirely around their perimeter; posterior premolars and molars with only thin strips of enamel labially and lingually after moderate wear.

Stylinodon mirus Marsh, 1874

(Tables 22, 33; Figs. 28, 30–40; Pls. 47–50; Pl. 52: figs. 3–13; Pls. 53–55, 59, 62–65)

Stylinodon mirus Marsh, 1874, p. 531.
Calamodon cylindrifer Cope, 1881c, p. 184.
Calamodon cylindrifer: Cope, 1884c, p. 192.
Stylinodon mirus: Marsh, 1897, p. 137.
Stylinodon mirus: Wortman, 1897b, p. 93.
Stylinodon cylindrifer: Wortman, 1897b, p. 92.
Stylinodon cylindrifer: White, 1952, p. 193.
Stylinodon sp.: Robinson, 1966, p. 44.
Stylinodon cylindrifer: Guthrie, 1971, p. 66.
Stylinodon mirus: Schoch and Lucas, 1981d, p. 176 (in part).

Type Specimen. YPM 11095, right and left dentary fragments with partial right P_3–M_1, left P_3 and alveoli for right P_2, $M_{2\text{-}3}$ and left P_2, P_4–M_1; labial enamel fragment of left P_1 (Pl. 47: figs. 4–6).

Horizon and Locality of the Type. Collected by Sam Smith in 1873 from Bridgerian strata of the Bridger Formation, near Millersville, Bridger Basin, Wyoming.

Referred Specimens. AMNH 4810, $M^{3(?)}$, fragments of enamel from the upper canine(?), and fragments of the skull (Pl. 50: figs. 11–22; the type of *Calamodon cylindrifer*); AMNH 14743–14745, canine and tooth fragments: all from late Wasatchian strata of the Wind River Formation, Wind River Basin, Wyoming.

USNM 18440, cheek tooth: from late Wasatchian strata of the Wind River Formation, east side of Big Horn River and north side of Birdseye Creek, Boysen Reservoir area, SW ¼, Sec. 5, T. 39 N., R. 94 W., Wind River Basin, Wyoming.

MCZ 3477, canine tip: from late Wasatchian strata of the Wind River Formation, Muddy Creek, Wind River Basin, Wyoming.

UW 2270, edentulous complete skull, mandible and partial skeleton (Pls. 62–65): from Bridger "A" beds, Bridger Formation, E ½, SE ¼, Sec. 33, T. 22 N., R. 113 W., Lincoln County, Wyoming.

USNM 16664, mandible with partial right and left C_1–P_1, partial right $P_{2\text{-}3}$, M_3, alveoli for right and left I_3, left $P_{2\text{-}3}$, right and left P_4–M_1, right M_2, isolated cheek teeth, vertebrae, acetabular part of the pelvis, shaft of the femur, patella, ungual of the pes, and other bone fragments (Pl. 50: figs. 1–10; Pl. 52: figs. 3–13; Pl. 59: figs. 10, 11): from Bridger "C" beds, Bridger Formation, Sage Creek Basin, ("Greater Bridger Basin"), Uinta County, Wyoming.

AMNH 107954, partial skull with left C_1, right M^2, roots of right C^1, M^1, M^3, alveoli for right and left I^{2-3}, right P^{1-4}, mandible with right and left I_3–P_4, left M_{1-3}, isolated teeth, skull fragments, miscellaneous vertebrae and ribs (Pl. 48; Pl. 59: figs. 1–6, 8, 9, 12, 13): from Bridger "D" beds, Bridger Formation, SW ¼, NW ¼, Sec. 20, T. 13 N., R. 113 W., Green River Basin ("Greater Bridger Basin"), Uinta County, Wyoming.

FMNH PM 3895, skull and mandible with complete dentition and partial skeleton (Fig. 40): from late Bridgerian strata, lower part of the Adobe Town Member, lower part of the Washakie Formation, along Manuel Road, SSE of Haystack Mountain, Sweetwater County, Wyoming [(Turnbull 1972, 1978); this specimen will be described by William D. Turnbull].

YPM 11096, left dentary fragment with alveoli for C_1, P_3–M_3, occiput of skull, left scapula, humerus, ulna, radius and partial manus, seven cervical vertebrae, first thoracic vertebra, right and left first ribs and partial sternum (Figs. 32–40: Pls. 53–55; Pl. 59: fig. 7): from late Bridgerian(?) strata of the Washakie Formation, lower green sand at Haystack Mountain, Washakie Basin, Wyoming.

AMNH 17525, molariform tooth fragment: from late Wasatchian strata of the lower Huerfano Formation, Garcia Canyon region, Huerfano Basin, Colorado.

AMNH 17451, (?)upper canine: from early Bridgerian strata of the upper Huerfano Formation, Sand Draw, 3.2 km NW of Gardner, Huerfano Basin, Colorado.

YPM 14616, (?)lower canine: from late Wasatchian or early Bridgerian strata of the Huerfano Formation, "south of Hausero's Ranch" (Robinson 1966, p. 44), Huerfano Basin, Colorado.

FMNH P 12185, palate and partial skull with left C^1, M^{2-3}, and alveoli for right C^1, right and left P^1–M^1, right M^{2-3} (Pl. 47: figs. 1–3): from Uintan strata, Horizon B, Wagonhound Member, Uinta Formation, Coyote Basin, Uintah County, Utah.

DNHM V-25, skull with complete right and left C^1, alveoli for right and left I^{2-3}, P^1–M^3, lower jaw with complete right and left M_2, right and left roots of I_3–M_1 and M_3 (Pl. 49): from the center of Sec. 24, T. 8 S., R. 24 E., Uintan strata, Horizon B, Wagonhound Member, Uinta Formation, Coyote Basin, Uintah County, Utah.

Revised Diagnosis. Largest species of *Stylinodon*; approximately twice as large as *Stylinodon inexplicatus* (Table 33).

Stylinodon inexplicatus Schoch and Lucas, 1981d
(Table 33; Fig. 29; Pl. 51; Pl. 52: figs. 1, 2)

Stylinodon inexplicatus Schoch and Lucas, 1981d, p. 178.

Type and Only Known Specimen. PU 16102, skull with complete and unerupted right and left M^3, roots of right and left I^2–C^1, left P^{1-3}, right and left P^4–M^2, associated vertebrae, rib and indeterminate bone fragments (Pl. 51; Pl. 52: figs. 1, 2).

Horizon and Locality of the Type. Bridgerian strata ("Washakie A") of the Washakie Formation, Sec. 11, T. 16 N., R. 96 W., Washakie Basin, Wyoming.

Diagnosis. Smallest known species of *Stylinodon*; approximately half as large as *Stylinodon mirus* (Table 11).

Stylinodon sp.

Stylinodontine: West, 1973, p. 125.
Stylinodon mirus: Schoch and Lucas, 1981d, p. 175 (in part).
Stylinodon sp.: West, 1982, p. 11.

Referred Specimens. FMNH PM 15198–15200, 15590, tooth and enamel fragments: from late Wasatchian–early Bridgerian strata of the Wasatch Formation, Sublette County, Wyoming.

TMM 41444-3, TMM 41443-291, cheek tooth fragments: from late Bridgerian or early Uintan strata of the Pruett Formation, basal Tertiary conglomerate in the Aqua Fria area, Whistler Squat local fauna, Trans-Pecos, Texas (see West 1982; J. A. Wilson 1974; A. E. Wood 1973).

Eaton (1980) has reported *Stylinodon* sp. from Bridgerian–Uintan(?) strata of the Wiggins Formation, Carter Mountain area, southeastern Absaroka Range, Wyoming.

Discussion. Although specifically indeterminate, these rootless cheek tooth fragments document the presence of *Stylinodon* in these areas.

Undetermined Stylinodont, cf. *Stylinodon mirus*
(Figs. 41, 42; Pls. 56–58)

Undetermined Stylinodont: Gazin, 1952, p. 26.

Referred Specimens. USNM 18425, partial hind- and forelimbs and miscellaneous vertebral fragments (Figs. 41, 42; Pls. 56–58): from late Wasatchian strata of the Wasatch Formation (upper "Knight Formation"), 19.3 km north of Big Piney, west side of US Highway 189, La Barge fauna, SW ¼, Sec. 33, T. 32 N., R. 111 W., Sublette County, Wyoming.

CM 37474, partial hindfoot: from Bridgerian strata of the Washakie Formation, east end of Haystack Mountain near the base, Sweetwater County, Wyoming.

Description and Discussion of *Stylinodon*

Schoch and Lucas (1981d) revised the genus *Stylinodon* and described the unique holotype of *S. inexplicatus*. Schoch and Lucas (1981d) also discussed the dentition of *Stylinodon* and the reader is referred to that paper. However, I here briefly summarize pertinent facts about the dentition of *Stylinodon*. The dental formula of *Stylinodon mirus* is known with certainty to be: I^2_1, C^1_1, P^4_4, M^3_3; that of *S. inexplicatus* is $I^2_?$, $C^1_?$, $P^4_?$, $M^3_?$.

The M^3 crown of the holotype of *S. inexplicatus* is the only unworn cheek tooth of any *Stylinodon* known. The crown of M^3 bears two transverse, cuspidate lophs. The anterior loph is broad, slightly convex anteriorly, and bears large cusps, one on the extreme labial edge and the other on the extreme lingual edge. Between these two cusps is a series of six smaller cuspules. The posterior loph is similar, but is lower, narrower, and convex posteriorly. Between the two lophs is a deep, circular valley. All other known teeth of *Stylinodon* are extremely well worn and lack any details of crown morphology.

All of the teeth of *Stylinodon* are rootless and evergrowing. The incisors are of moderate size and peglike. The canines are the largest teeth; they are laterally compressed and free of enamel posteriorly, as in *Ectoganus*. P$^1_1$ are L-shaped teeth that complement the shape of the canines. P^2 is short anteroposteriorly but wide transversely; in contrast, the remaining cheek teeth are round to square pegs of subequal size. On all of the cheek teeth (except for the unworn M^3 of *S. inexplicatus* noted above) enamel is limited to the labial and lingual aspects of the teeth, where it forms parallel bands.

Skull of *Stylinodon mirus*

The skull of *S. mirus* (Figs. 28, 30; Pls. 49, 62, 63, Pl. 64: fig. 1) is extremely similar to that of *S. inexplicatus* (Fig. 29; Pl. 51, described in Schoch and Lucas 1981d) in terms of its bony elements and their mutual relationships. The primary differences lie in the relative size of the skulls (Table 10) and the generally more massive and robust appearance of the skull of *S. mirus*. The skull of *S. mirus* is roughly twice the size of *S. inexplicatus* in linear dimensions throughout. Furthermore, in *S. mirus* the sagittal crest is high and well developed and the temporal fossae are large, broad, and deep as compared to *S. inexplicatus*. This may largely be due to allometry: the larger skull of *S. mirus* possessed comparatively larger temporal muscles that could not be accommodated solely by the roof of the skull without the development of a median sagittal crest. Here, the skull of *S. mirus* will be described insofar as it differs from that of *S. inexplicatus,* or adds to our knowledge of the genus.

The nasals of *S. mirus,* as in all other taeniodonts, are broad, narrowing only slightly posteriorly where they tuck between the frontal bones. The nares are terminal. In the area of the nasal–frontal suture there is a massive bony buildup, the postorbital ridges, which in dorsal view form a V with the apex directed posteriorly. The apex of the V is situated approximately above the M^2 and marks the anteromost point of the sagittal crest.

The face of *S. mirus* is short, deep and massive. In anterior view it presents a squared-off boxlike appearance. The lateral sides of the face are parallel to each other and perpendicular to the palate and dorsal surface. The nares are terminal and form a large, round opening. The large canines project ventrally out of the anterolateral corners of the mouth. In ventral view the tooth rows are straight, but converge posteriorly such that the maximum width across the palate of *Stylinodon* is positioned far anteriorly across the canines. The posterior border of the palate extends to slightly behind M^3. The pterygoid flanges in *S. mirus* are relatively small and stout. The glenoid fossae are broad and shallow with only slight, internally set, postglenoid processes. The mastoid processes and occipital condyles are large and massive. The periotic region does not differ, as far as is known, from that of *S. inexplicatus* or *Ectoganus.*

The occiput of *S. mirus* is high, triangular and heavily rugose for strong, tendinous muscle attachments. The sutures between many of the bones forming the skull roof (e.g., maxilla–frontal, frontal–parietal and parietal–occipital sutures) are heavily fused and obscured in all known specimens of *S. mirus*; however, from what can be made out, the bony elements and their relationships appear to have been essentially the same in *S. mirus* and *S. inexplicatus.* The skull of *S. mirus* bears the same arrangement of foramina venosae seen in *Ectoganus* and *S. inexplicatus.* The zygomatic arches of *S. mirus* arise anteriorly from a point above P^4 and are massive anteriorly. Posteriorly, they flare out smoothly, but the middle parts of the zygomatic arches themselves are relatively thin in comparison to the overall massiveness of the skull. Posteriorly, the zygomatic arches join the large, broad squamosals.

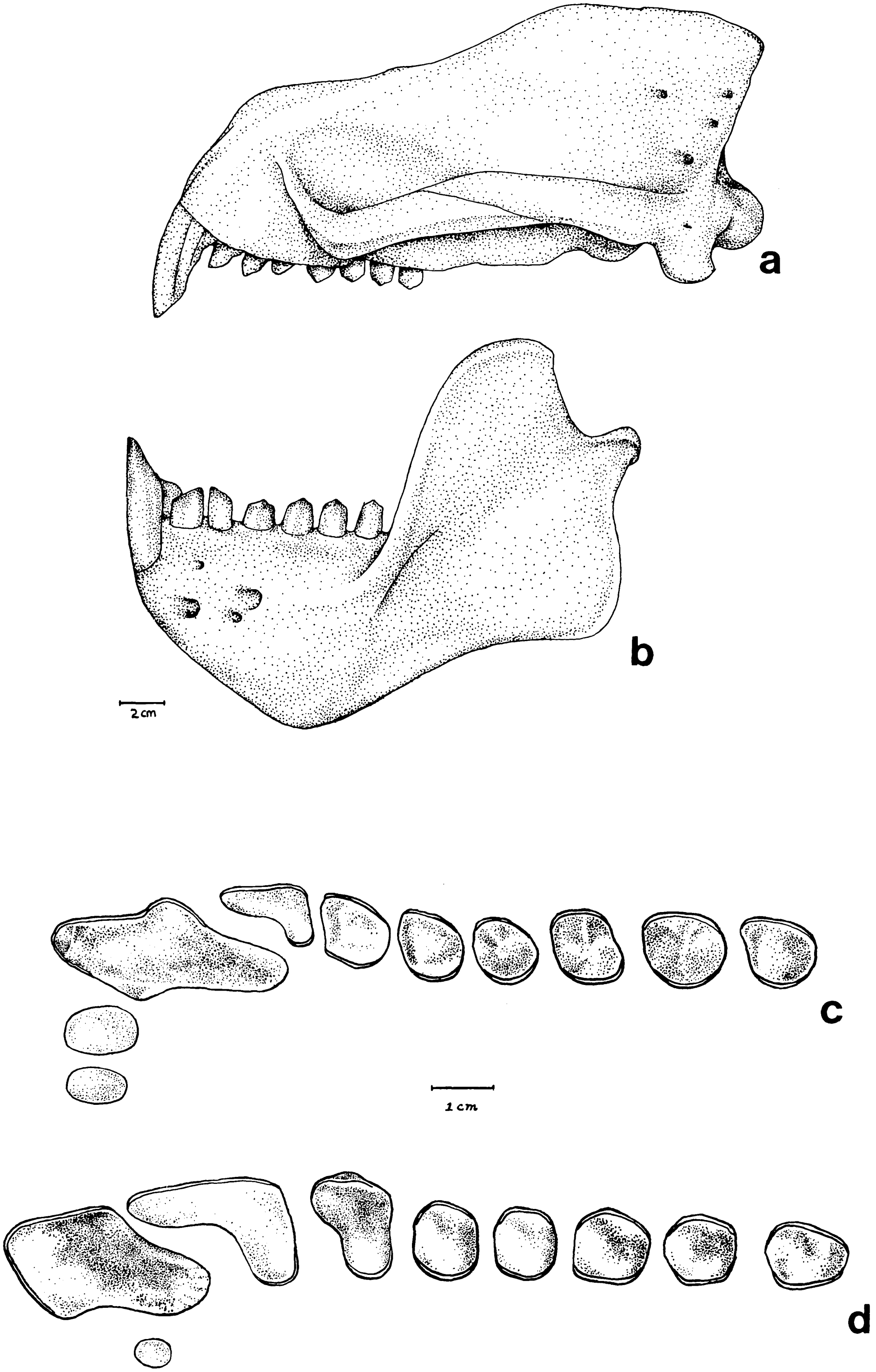


FIG. 28. Restoration of the skull, mandible and dentition of *Stylinodon mirus*, based primarily on AMNH 107954, DNHM V-25 and UW 2270. The teeth are shown worn (unworn teeth of *Stylinodon mirus* are not known). *a*) Left lateral view of skull. *b*) Left lateral view of mandible. *c*) Occlusal view of upper left dentition. *d*) Occlusal view of lower right dentition.

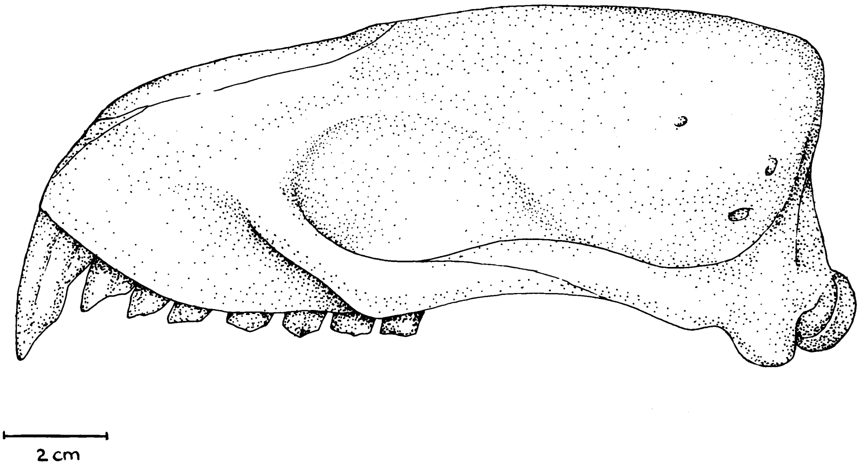


FIG. 29. Restoration of the skull of *Stylinodon inexplicatus* based on PU 16102: left lateral view.

Mandible

The mandible of *S. mirus* is fairly well known from numerous specimens (Fig. 28; Pl. 48: figs. 5, 6; Pl. 49: fig. 2; Pl. 53: figs. 1, 2; Pl. 62: figs. 2, 3) but that of *S. inexplicatus* is wholly unknown. The following discussion is therefore based only on the mandible of *S. mirus.*

The mandible of *S. mirus* is extremely large and massive, short and deep with an extremely heavily fused symphysis anteriorly which extends to under P_4–M_1 (depending on the individual). Posteriorly, the mandible shallows and is shallowest under M_{2-3}. Anteriorly and internally there is a large, well-developed circular pit which extends anteriorly in the middle of the symphysis. Presumably this provided the attachment for a powerful genioglossus muscle for the large, well-developed tongue of *Stylinodon.*

Externally, there are variably two to four mental foramina situated under P_{1-3}. The ascending ramus arises from a point external to M_2 and forms a large, broad, moderately high coronoid process which may be slightly recurved posteriorly. The angle of the mandible is moderately well developed and internally rugose. The condyles are smoothly convex dorsoventrally, extremely elongated transversely, and set slightly above the level of the tooth row. Overall, the morphology of the mandible of *S. mirus* is remarkably similar to that of *E. gliriformis.*

Axial Skeleton

Atlas

The atlas of *Stylinodon* (Fig. 32a–c; Pl. 53: figs. 3, 4) is short and broad. It is most noteworthy for its extremely large neural canal, which takes both the spinal cord dorsally and the odontoid process of the axis ventrally. The transverse processes are small and stout and are pierced by small, ovoid foramina. Dorsally, the rudiment of the neural spine and ventrally, the hypapophysial tubercle are only moderately developed. On either side dorsally, behind the anterior processes, are distinct transverse foramina. The anterior articular surfaces are large and deeply concave and bore the occipital condyles of the skull. The posterior articular surfaces are smaller and shallower, and articulated with the anterior articular surface of the axis.

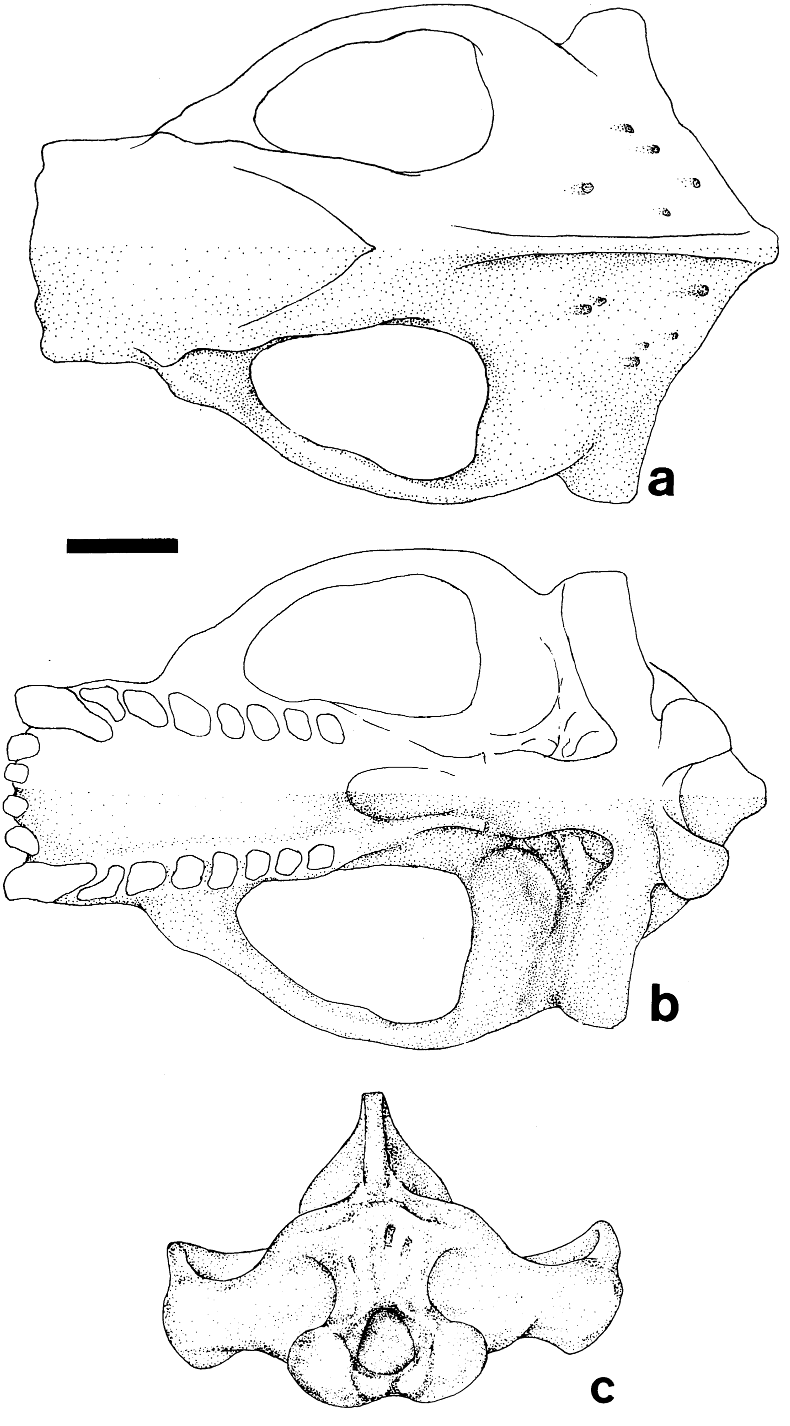


FIG. 30. Restoration of the skull of *Stylinodon mirus*, based primarily on AMNH 107954, DNHM V-25 and UW 2270. *a*) Dorsal view. *b*) Ventral view. *c*) Occipital view.

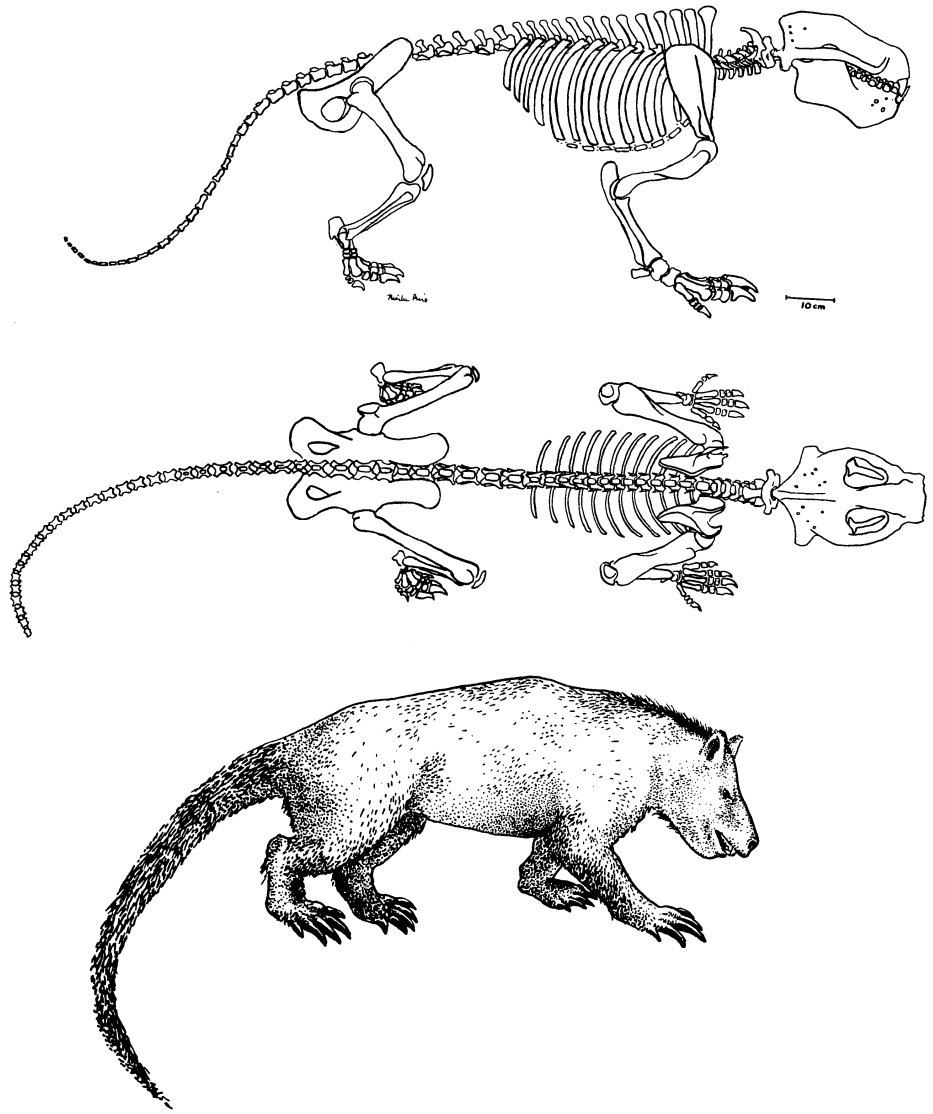


FIG. 31. Reconstructed skeleton and life restoration of *Stylinodon mirus* based on specimens described and illustrated in the text and plates. *Top:* right lateral view of the reconstructed skeleton. *Middle:* dorsal view of the reconstructed skeleton. *Bottom:* life restoration.

Axis

The axis of *Stylinodon* (Figs. 32d, 34; Pl. 53: fig. 5; Pl. 54: fig. 3) is short and stout, as are the other cervical vertebrae. The odontoid process is short, stout and slightly bifid cranially (anteriorly). The anterior articular surface is large and smoothly convex. The small, weak transverse processes are pierced by foramina forming the vertebral canals. The neural spine of the axis rises high above the rest of the cervical column and is directed posteriorly. Posteriorly, it broadens transversely. The anterior part of the neural spine is not preserved (YPM 11096); Marsh (1897, p. 140, fig. 3) illustrated it as being directed anteriorly and meeting the dorsocaudal aspect of the atlas, but it is not clear if it was present when Marsh studied the specimen or if it is his reconstruction (the break appears to

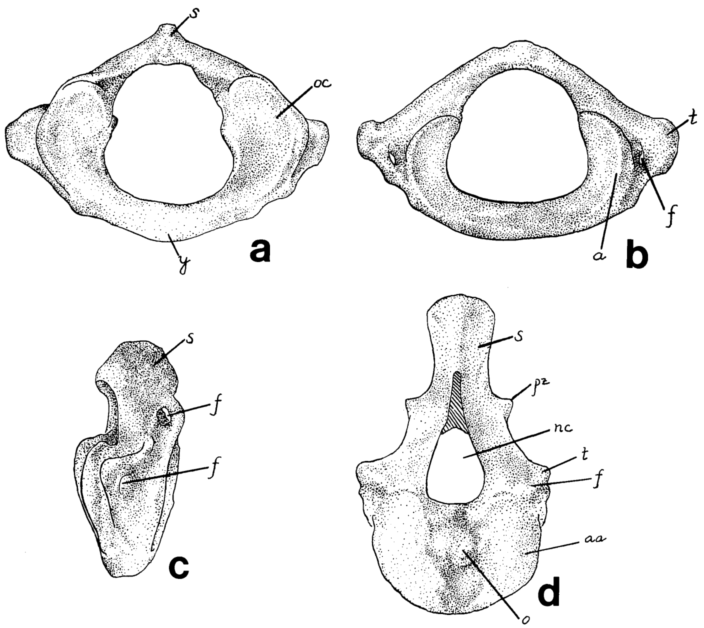


FIG. 32. The atlas and axis of *Stylinodon mirus,* YPM 11096. *a*) Anterior view of atlas. *b*) Posterior view of atlas. *c*) Right lateral view of atlas. *d*) Anterior view of axis.

Abbreviations: a = articular surface for axis; aa = anterior articular surface; f = foramen; nc = vertebral canal; o = odontoid process; oc = articular surface for occipital condyles; pz = posterior zygapophysis; s = neural spine; t = transverse process; y = hypapophysial tubercle.

Scale is 4 cm long.

be fairly recent in YPM 11096). The posterior articular surfaces are of moderate size, smoothly convex, and face relatively ventrally.

Cervical Vertebrae Three through Seven

Overall, the neck of *Stylinodon* was extremely short, thick, stout and massive (Fig. 34; Pl. 53: fig. 5; Pl. 54: fig. 3). The third through seventh cervical vertebrae of *Stylinodon* are very similar to each other, but increase in size posteriorly. They are most notable for their greatly flattened (anteroposteriorly) and enlarged (dorsoventrally and mediolaterally) centra. The anterior and posterior articular surfaces of the centra are rather flat. The transverse processes are relatively small, but pierced by large, circular foramina forming the vertebral canal. The neural canal is relatively large; the neural spines are relatively small and short, but thick. The pre- and postzygapophyses face well craniad and caudad. Their articular surfaces are relatively flat.

Postcervical Vertebrae

The thoracic vertebrae (or what might remain of them) of FMNH PM 3895 have not been fully prepared. Fragments of the vertebral column are preserved in USNM 16664 (Pl. 52: figs. 3–13), UW 2270, AMNH 107954 (Pl. 59: figs. 3, 4, 12, 13) and PU 16102 (Pl. 52: fig. 2). However, in all of these specimens the material is incomplete, crushed and poorly preserved. Thus, only the general outlines of the postcervical vertebral column can be reconstructed.

As stated in the discussion of the ribs (see below), the thoracic (dorsal) vertebrae probably numbered from thirteen to fifteen. The thoracic vertebrae are

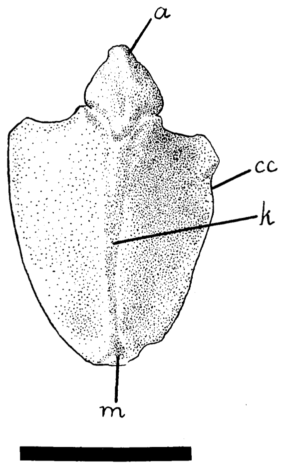


FIG. 33. Anterior view of the manubrium of *Stylinodon mirus,* YPM 11096.
Abbreviations: a = anterior tip; cc = facet for costal cartilage; k = keel; m = facet for first mesosternum.
Scale is 4 cm long.

large, massive, relatively short and decrease in length (anteroposteriorly) posteriorly. They bear the large, high vertical spines which decrease in size posteriorly. The spine of the first dorsal vertebra rises vertically to a height above that of the occiput of the skull. It is flattened transversely and elongated anteroposteriorly. Its dorsal tip is even further expanded anteroposteriorly. The spines of the following thoracic vertebrae quickly decrease in size posteriorly and are angled posteriorly rather than standing relatively vertically. The thoracic vertebrae bear large, concave, dorsally placed capitular articular surfaces. The central vertebral canal is large and subcircular in shape. The metapophyses, anapophyses, and anterior and posterior zygapophyses all appear to be relatively large and well-developed. The centra of the posterior thoracics in AMNH 107954 appear to be deeper dorsoventrally than they are wide transversely. The more anterior thoracic vertebrae are short and wide transversely and less deep than wide. The proximal surfaces of the vertebrae are slightly convex and the distal surfaces are slightly concave.

No lumbar or sacral vertebrae of *Stylinodon* have been identified positively. Matthew (1937, pl. 64) reconstructed *Psittacotherium* with seven lumbar vertebrae based on AMNH 2455, which has since been referred to *Pantolambda* (see above). It would appear reasonable that *Stylinodon* would have five to seven lumbar vertebrae (the primitive number, cf. Gregory 1910). The number of sacral vertebrae is also unknown.

A number of isolated caudal vertebrae, consisting of centra with the processes broken off, are preserved in USNM 16664 and UW 2270. Matthew (1937, pl. 64) reconstructed the tail of *Psittacotherium* with twenty-eight vertebrae. Apparently, the anterior caudal vertebrae had relatively long transverse processes and neural spines. The distal caudal vertebrae are small, featureless centra, slightly elongated anteroposteriorly. All of the caudal vertebrae are stout and massive and only slightly elongated anteroposteriorly. The ends of the centra are relatively concave in the anterior part of the tail and flatten toward the end of the tail. Judged from the large size of the known proximal caudal vertebrae, *Stylinodon* had a fairly long, heavy tail which may have contained about thirty vertebrae.

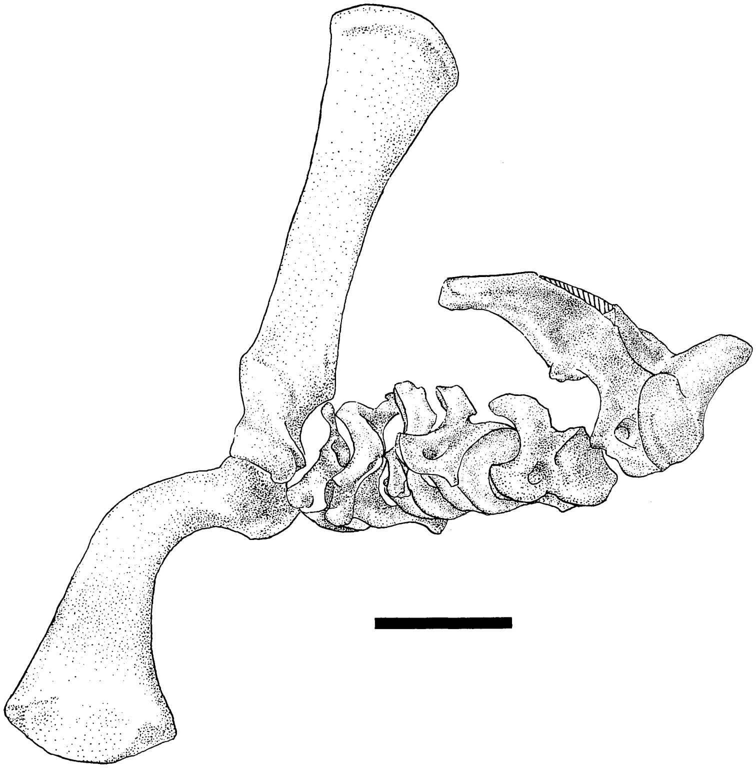


FIG. 34. Right lateral view of axis, next five cervical vertebrae, neural spine of first thoracic vertebra and right first rib of *Stylinodon mirus,* YPM 11096.
Scale is 4 cm long.

Manubrium and First Ribs

The manubrium and first ribs are preserved articulated in YPM 11096 (Figs. 33, 34; Pl. 53: fig. 5; Pl. 54: fig. 3). The manubrium is greatly thickened, enlarged and deepened dorsoventrally with a high ventral keel that extends for the entire length of the manubrium. Dorsally, it is slightly concave transversely. The lateral facets for the caudal cartilages are large. The anterior tip forms a large protuberance and an epiphysislike structure fused to the main body of the manubrium. Posteriorly there is a triangular facet for the first mesosternebra.

The first rib is stout, quite wide transversely, flattened dorsoventrally and strongly curved. Proximally, there is no true neck; the capitulum and tubercle are both large and closely appressed together forming one large, continuous prominence which is transversely concave anteriorly. Distally, the first rib is transversely broadened and forms an anteroposteriorly elongated surface for the cartilaginous attachment to the lateral border of the manubrium.

Posterior Ribs

By my count, a minimum of eleven ribs posterior to the first rib are preserved in various specimens of *Stylinodon* [e.g., AMNH 107954 (Pl. 59: figs. 5, 6, 8, 9), FMNH PM 3895, UW 2270 and PU 16102 (Pl. 52: fig. 1)]. Matthew (1937, pl. 64) reconstructed *Psittacotherium* with thirteen thoracic (dorsal) vertebrae which would have borne ribs. It appears reasonable to assume that *Stylinodon,* and probably all other taeniodonts, had thirteen to fifteen thoracic vertebrae and ribs, as is frequent among "primitive" mammals (Gregory 1910, p. 431).

The ribs of *S. mirus* are relatively strong, thick, long and wide. They decrease in size and robustness posteriorly. The necks are short and stout. The capitulae are large, well-developed and broadly convex. They bear two faint facets, for articulation with the two vertebrae that each rib contacts, one anteriorly and the other posteriorly. The tuberclae lie almost directly behind the capitulae (heads) and form slightly convex facets. The shafts of the ribs are flat, slightly expanded ventrally and bear large articular surfaces for the costal cartilage. The upper (dorsal) half of the ribs bear roughened external surfaces for the costal muscles. The more anterior ribs are sharply angled; in the posterior ribs the angle decreases. The ribs of *S. inexplicatus* are morphologically similar to, but much smaller than, those of *S. mirus*.

Pectoral Girdle and Forelimb

Scapula

The scapula of *Stylinodon* (Fig. 35; Pl. 54: fig. 3) is robust and relatively squared-off in outline. Dorsally, the vertebral border forms approximately right angles with the anterior and posterior (axillary) borders. The neck is thick and the scapular notch is shallow. A high, thick spine runs approximately three-fourths to four-fifths the length of the scapula, but does not meet the vertebral border. The glenoid cavity is large with a well-developed, overhanging coracoid process. The large and robust acromion process extends far ventrally. The metacromion process is large, robust and oriented posteriorly, reaching to a point level with the axillary border. The infraspinous fossa is only slightly larger than the supraspinous fossa. The subscapular fossa is shallow.

Humerus

The humerus of *Stylinodon* (Pl. 55: figs. 1, 2) is extremely similar, if not nearly identical, to the humerus of *Ectoganus,* although somewhat shorter and stouter.

Proximally, the head is of moderate size (but very slightly larger than that of *Ectoganus*), hemispherical, and positioned well posteriorly. The greater tuberosity is large, heavily rugose and extends proximally higher than the head of the humerus. Distally, it turns into the deltopectoral crest (deltoid ridge) which extends for over half the length of the shaft, is flattened dorsoventrally and broadened mediolaterally. The lesser tuberosity is also prominent, but is confined to the proximal end of the shaft. In the middle of the shaft is a small to moderate-sized teres eminence which points slightly posteriorly.

The humerus is broad distally with well-developed medial and lateral epicondyles. Medially, there is a large, circular entepicondylar foramen that is enclosed by a massive internal condyloid (pronator) ridge as in *Psittacotherium* and *Ectoganus.* The lateral epicondyle is also prominent and proximally from it runs a well-developed supinator ridge, which is slightly recurved anteriorly. Anteriorly there is a shallow supratrochlear fossa above the capitulum and posteriorly a relatively small olecranon fossa. As in *Ectoganus,* the trochlea is smoothly concave and the capitulum is smoothly convex mediolaterally. The medial trochlear crest is moderately developed and extends slightly further distally than the surface of the capitulum.

Ulna

The ulna of *Stylinodon* (Fig. 36; Pl. 55: figs. 5, 6) is stout, thickened, and extremely robust. The olecranon is large, expanded, heavily rugose, and slightly inflected medially. The shaft is deep dorsoventrally but compressed transversely.

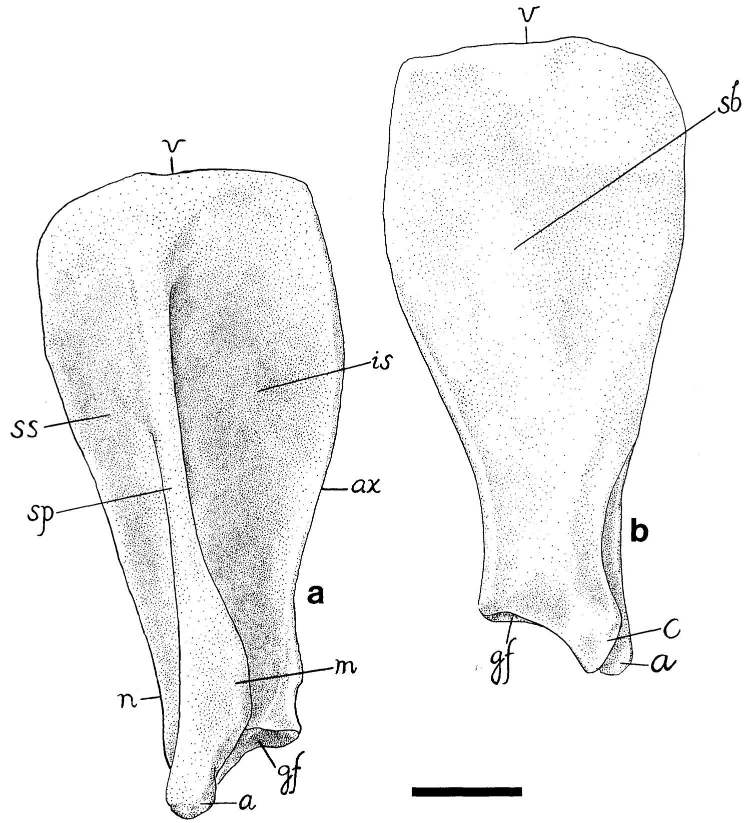


FIG. 35. The left scapula of *Stylinodon mirus,* YPM 11096. *a*) Lateral view. *b*) Medial view. Abbreviations: a = acromion; ax = axillary border; c = coracoid process; gf = glenoid fossa; is = infraspinous fossa; m = metacromion; n = neck; sb = subscapular notch; sp = spine; ss = supraspinous fossa; v = vertebral border.
Scale is 4 cm long.

The semilunar notch is broad mediolaterally and shallow, as is the radial notch, which is almost flat. The radial notch is positioned well dorsad (anteriorly) rather than more laterally. The coronoid process is relatively low, whereas the olecranon process (sensu Greene 1935) is raised slightly higher above the shaft. The distal end is slightly expanded and bears a well-developed, posteriorly-set styloid process. This bears an anterodistally facing facet that is very slightly concave dorsoventrally for articulation with the cuneiform, and medially a triangular-shaped facet, which is slightly convex in both directions, for articulation with the pisiform.

Radius

The radius of *Stylinodon* (Fig. 37; Pl. 55: figs. 3, 4) is similar to and about the same length as that of *Ectoganus,* but much more robust. The proximal head is oval in shape (seen proximally) with the long axis elongated mediolaterally. The posterior (ventral) facet, which articulates with the radial notch of the ulna, is rather flat and of moderate size. The articular facet for the capitulum of the humerus is smoothly concave in both directions. The neck is stout and there is no distinct tuberosity. Distally, the shaft of the radius is expanded both mediolaterally and dorsoventrally. The styloid process is broad, blunt and positioned

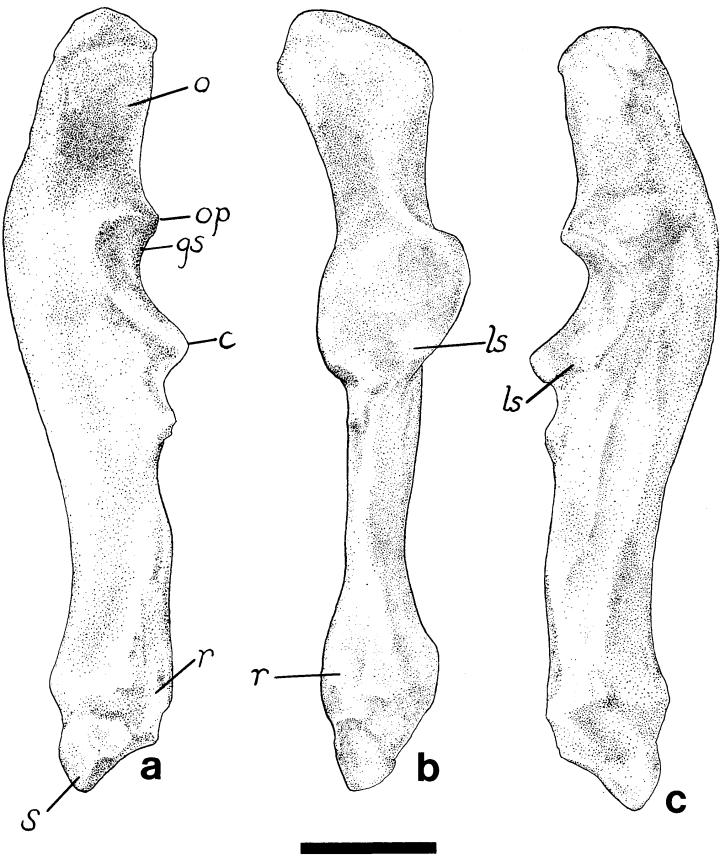


FIG. 36. The left ulna of *Stylinodon mirus,* YPM 11096. *a*) Medial view. *b*) Anterior view. *c*) Lateral view.

Abbreviations: c = coronoid process; gs = semilunar notch (= greater sigmoid cavity); ls = radial notch (= lesser sigmoid cavity); o = olecranon; op = olecranon process; r = surface for radius; s = styloid process.

Scale is 4 cm long.

anteriorly and slightly medially as in *Ectoganus.* The distal articular surface is large, circular to pear-shaped, shallowly concave in both directions, and appears to have articulated primarily with the lunar.

Manus

A fairly complete left manus is preserved in FMNH PM 3895; however, the elements are still embedded in matrix. This specimen is currently being prepared further and will be described by Dr. William D. Turnbull (FMNH). A partial left manus is preserved in YPM 11096 (Figs. 38–40: Pl. 59: fig. 7); this includes the third and fourth metacarpals, their proximal and medial phalanges, the lunar, magnum and unciform. Preserved in USNM 18425 are also a few elements of the left manus: the unciform, metacarpals four and five, the distal portion of metacarpal three and the phalanges of digits three and four (Pl. 56: figs. 9, 10, 13, 14). Also preserved are a ?left pisiform and what Gazin (1952, p. 26–27) identified as the ?right scaphoid (Pl. 56: figs. 7, 8, 11, 12). FMNH PM 3895 and YPM 11096 are of approximately the same size, but in USNM 18425 the elements are much smaller and less robust. This may be due to various factors such as sexual dimorphism, age differences or simply individual variation be-

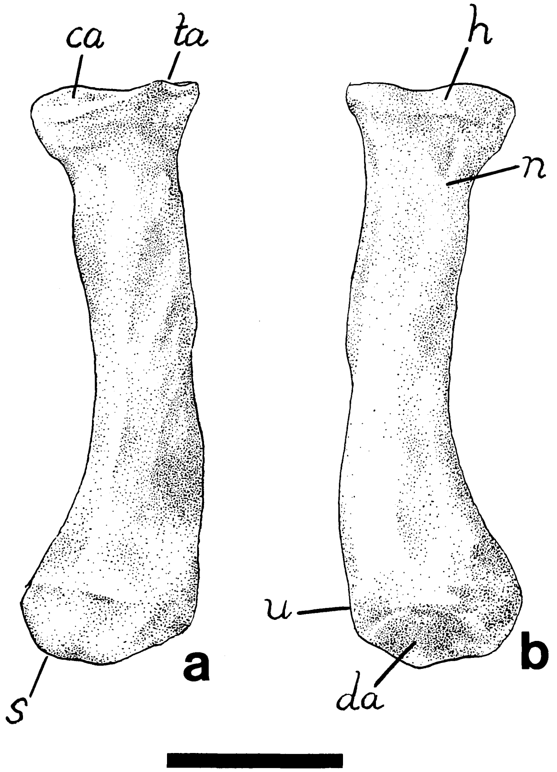


FIG. 37. The left radius of *Stylinodon mirus,* YPM 11096. *a*) Anterior view. *b*) Posterior view.
Abbreviations: ca = articular surface for capitulum of humerus; da = distal articular surface for carpals; h = head; n = neck; s = styloid process; ta = articular surface for trochlea of humerus; u = surface for ulna.
Scale is 4 cm long.

tween the individuals represented. It may also be possible that late Bridgerian stylinodontids were, on the average, larger and more robust than the late Wasatchian stylinodontids.

The general characters of the manus of *Stylinodon* have been described previously by Gazin (1952) and Patterson (1949b). The three middle digits are stout and robust with greatly enlarged, transversely compressed, recurved claws. The proximal and medial phalanges are little more than short, squat wedges. Metacarpal five is reduced to vestigial in both USNM 18425 and FMNH PM 3895. In neither specimen is it clear that the phalanges of the fifth digit were present. They are not preserved in USNM 18425, and only a small, spherical, circular bony element (sesamoid?) that may have articulated with the fifth metacarpal is preserved in FMNH PM 3895. Likewise, the first metacarpal (and thus, the digit) was probably greatly reduced or vestigial, but is not preserved in any of the specimens. Distally and ventrally the three central metacarpals bear pairs of large, ovoid sesamoids.

Lunar

Seen dorsally, the lunar is elongated mediolaterally and five-sided. The distal facets for the magnum and unciform are set at an angle of approximately thirty degrees to one another. Proximally, it bears a large, ovoid, smoothly convex (in both directions) articular facet for articulation with the distal end of the radius.

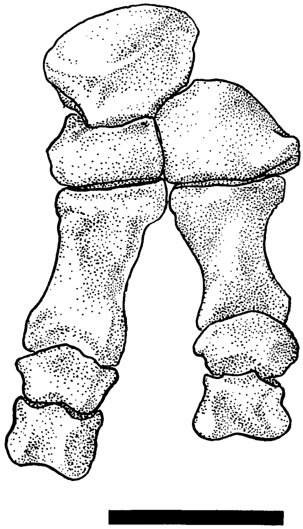


FIG. 38. Anterior (dorsal) view of a partial left manus (lunar, magnum, unciform, third and fourth metacarpals and their proximal and medial phalanges) of *Stylinodon mirus,* YPM 11096.
Scale is 4 cm long.

The lunar is compressed and elongated distally and ventrally from this facet. Distally, the lunar bears two thin, dorsoventrally deep facets for articulation with the magnum medially and the unciform laterally. The articular facet for the magnum is wider mediolaterally than that for the unciform and is slightly concave transversely. Running dorsoventrally, dorsally it is strongly convex and ventrally it is strongly concave. The facet for the unciform is similar, but narrower transversely. It too is slightly concave mediolaterally, strongly convex dorsally and deeply concave ventrally. However, when viewed distally, the facet for the unciform, especially its ventral half and far ventral edge, is much higher than the facet for the magnum. Laterally, the lunar bears a large, dorsoventrally elongated and concave facet for articulation with the cuboid. Medially and dorsally, it bears a moderate-sized, triangular shaped facet that is concave in both directions for articulation with the scaphoid.

Magnum

The magnum of *Stylinodon* is enlarged relative to those of *Onychodectes* and *Psittacotherium.* In dorsal view it forms a rectangle that is elongated transversely. Proximally, the magnum bears one large articular facet that contacts the lunar exclusively, unlike in *Onychodectes* and *Psittacotherium* where medially the proximal face of the magnum also contacts the centrale. The dorsal half of this facet is rather flat dorsoventrally but high and strongly convex ventrally. This raised convex surface articulates with the corresponding concave depression of the lunar. The distal face of the magnum forms one large facet that covers the entire proximal surface of the third metacarpal. This distal face is dorsoventrally concave, but rather flat transversely. Laterally and dorsally the magnum bears a square, flat facet, which is oriented at about ninety degrees to the dorsal face, for articulation with the mediodorsal portion of the unciform. Ventral to this facet is a shallow depression, along the proximal border of which is also a thin, smooth facet that contacted with the corresponding edge of the unciform. Medially, the magnum bears a small, triangular facet situated dorsodistally. This facet is concave dorsoventrally and apparently articulated with the trapezoid.

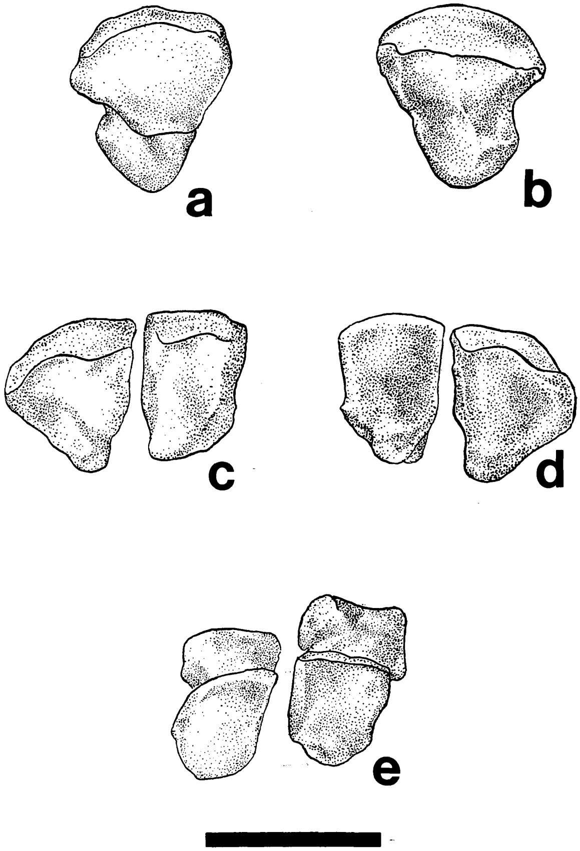


FIG. 39. Carpals and metacarpals of *Stylinodon mirus,* YPM 11096. *a*) Proximal view of lunar. *b*) Distal view of lunar. *c*) Proximal view of magnum and unciform. *d*) Distal view of unciform and magnum. *e*) Proximal view of fourth and third metacarpals.
Scale is 4 cm long.

Unciform

The unciform is larger than the magnum. Seen dorsally, it is five-sided. Proximally, it bears a moderate-sized, triangular facet that is concave dorsoventrally and articulates with the corresponding convex facet of the lunar. Distally, it bears a large, shallowly concave (dorsoventrally) and flat (transversely) facet for articulation with the entire proximal surface of the fourth metacarpal. Lateral to this facet and on the dorsal edge of the unciform is a minute, flat facet for articulation with the reduced fifth metacarpal. Medially and dorsally is a large, flattish facet whose proximal articular surface extends as a prong ventrally along the medial border of the unciform. This facet articulates with the lateral face of the magnum. Ventral to this facet is a shallow depression. Along the distomedial edge of the unciform is a long, dorsoventrally concave facet for articulation with the third metacarpal. The unciform bears a large, distolaterally facing facet that is smoothly convex proximally and smoothly concave distally. This facet articulated with the relatively large cuboid.

Scaphoid

What appears to be a small right scaphoid is preserved in USNM 18425. The proximal surface bears a large, smoothly convex (in both directions) facet for the radius. Distally, it bears a smaller, pear-shaped facet for articulation with the

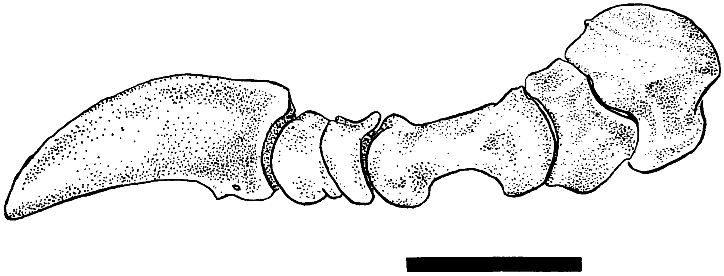


FIG. 40. Lateral view of lunar, magnum, metacarpal three, proximal and medial phalanges (YPM 11096) and ungual phalanx (FMNH PM 3895) of *Stylinodon mirus*.
Scale is 4 cm long.

trapezoid or trapezium. This facet meets the proximal facet dorsally (anteriorly). Laterally there is a smaller, ovoid shaped and rather flat facet for articulation with the lunar. This facet is set at an angle of about ninety degrees to the distal facet, but the angle formed between it and the proximal facet when viewed dorsally is only about seventy degrees.

Pisiform

A left pisiform is preserved with USNM 18425. The pisiform is relatively large and expanded both dorsoventrally and proximodistally. Laterally and dorsally it bears a deep depression with a large protuberance behind. Anteriorly (dorsally), it bears a large, transversely concave facet for articulation with the ulna. Medially and distally (ventrally) it bears a medial projection with a smaller facet for articulation with the cuneiform.

Metacarpals

Metacarpals two through four are short, stout and robust bones. Metacarpal three is the longest, metacarpals two and four are slightly shorter, and five, and presumably also one, are much reduced. The metacarpals do not overlap one another as in *Onychodectes* and *Psittacotherium* and the third metacarpal rests only against the magnum; it has lost its contacts with the unciform and trapezoid.

Metacarpal three bears a large facet that is obliquely oriented and faces proximomedially. This facet is subrectangular, rather flat transversely and slightly convex dorsoventrally. The proximal end is deepened ventrally. Medially and laterally it bears deep and narrow, flat to slightly convex (proximodistally) articular facets for the proximal ends of metacarpals two and four. The distal end of metacarpal three is expanded and squared-off. The articular surface for the proximal phalanx is large, cylindrical, smoothly convex dorsoventrally and rather straight mediolaterally. Ventrally, it is slightly concave transversely and the medial and lateral edges of the articular surface extend further proximally than the central articular surface. There is no posterior median keel or spine.

The fourth metacarpal is stout and robust, but overall shorter and smaller than the third metacarpal. Proximally, it is deepened dorsoventrally and bears a large facet for articulation with the unciform. The dorsal half of this facet is rather flat, whereas the ventral half is slightly convex dorsoventrally. Medially, it bears a deep, flat facet, which is perpendicular to the proximal facet, for articulation with the third metacarpal. Laterally, there is a moderate-sized, ovoid facet that is slightly convex proximodistally, for articulation with the fifth metacarpal. The distal end is expanded and virtually identical to the distal end of the third metacarpal, although somewhat smaller.

The fifth metacarpal is short, flat and widened transversely. Proximally it bears a large, lateral protuberance and a smaller, medial protuberance. The proximal end bears a relatively small facet, which is slightly convex transversely, for articulation with the unciform, and medially a larger, flat to slightly concave (proximodistally) facet for articulation with the fourth metacarpal. Distally, the end is much reduced, with a poorly developed articular facet for the first phalanx.

Phalanges

The proximal and medial phalanges of the second through fourth digits are extremely short (proximodistally), but broad transversely and deep dorsoventrally. The proximal articular surfaces are concave dorsoventrally, rather straight transversely, and bear slight median keels dorsally. The distal surfaces are saddle-shaped, being convex dorsoventrally and concave mediolaterally. The distal articular surface for the large unguals are much better developed, are more distinctly convex (the proximal and distal articular surfaces almost meet at the dorsal and ventral edges) and concave, and extend further dorsally and ventrally on the medial phalanges than on the proximal phalanges. The ventral surfaces of the proximal and medial phalanges are concave transversely.

The unguals on digits two through four form greatly enlarged, deep (dorsoventrally), laterally compressed, unfissured and recurved claws. The claw is largest on digit three. These claws bear large ventral processes proximally. Their proximal articular surfaces are deeply concave dorsoventrally and bear median keels to complement the saddle-shaped distal articular surfaces of the medial phalanges. Dorsally and ventrally the unguals extend far proximally around the distal articular surface of the medial phalanges. The claws of *Stylinodon* follow the same general pattern, but carry the trend further, as in the claws of *Wortmania, Psittacotherium* and *Ectoganus.*

Pelvic Girdle and Hindlimb

Pelvis

The ?right acetabular part of the pelvis of *Stylinodon mirus* is preserved in USNM 16664 (Pl. 59: figs. 10, 11). This specimen indicates that the acetabulum is relatively deep and well-developed, but little else can be determined from this fragment.

Femur

The femur of *Stylinodon* (Pl. 57: figs. 1, 2; Pl. 65: figs. 1–4) is similar to that of *Psittacotherium* and *Ectoganus.* It is relatively short, robust, "top-heavy" and somewhat flattened anteroposteriorly (USNM 18425 is badly crushed mediolaterally). The head is large, hemispherical and set upon a thick, stout neck. The pit for the ligamentum teres is directed medially and slightly posteriorly. The greater trochanter is stout and wide, rising to a height at about the middle of the head. The lesser trochanter is well developed and prominent in both anterior and posterior views. The digital fossa is moderately shallow. There is no third trochanter. Distally, the condyles are well developed and similar to those of *Psittacotherium* and *Ectoganus* in that the internal condyle extends slightly farther distally than the lateral condyle. The internal and external tuberosities are moderately developed. The intercondyloid fossa is narrow and deep. The surface for the patella is wide and extends far proximally on the anterior surface of the femur.

Tibia

The tibia (Pl. 57: figs. 3, 4; Pl 65: figs. 5, 6) is shorter than the femur, stout, and similar to that of *Psittacotherium.* Proximally, it is slightly expanded and bears large internal and external condyles for the femur. The internal condyle is larger than the external. The internal, external and medial tuberosities and cnemial crest are all broad and blunt. The intercondyloid fossa is small and shallow. Posteriorly, there is a prominent ridge which is thin transversely, flares out posteriorly and extends distally a short distance (approximately 36 mm) from the top of the internal (medial) condyle (not the external condyle as reported by Gazin 1952). The head of the fibula is tucked under the expanded external posterior part as in most generalized mammals. The distal end of the tibia is slightly expanded and bears a large internal malleolus which covered the medial side of the astragalus. There is no well-defined descending process. Laterally, there is a well-developed facet for the distal end of the fibula. The astragalar trochlea faces distally and is strongly concave anteroposteriorly. There is a slight keel in the middle which fits the corresponding fossa of the trochlear surface of the astragalus. In all of these features, the distal end of the tibia is extremely similar to that of *Psittacotherium.*

Fibula

The fibula of *Stylinodon* (Fig. 41; Pl. 57: figs. 5, 6; Pl. 65: figs. 5, 6) is relatively short and robust in UW 2270, but thinner shafted in USNM 18425 with enlarged extremities. The shaft is slightly curved with the concave face anterior and flattened transversely. Proximally, it is broad anteroposteriorly and articulates with the tibia in the usual manner. Distally, it is expanded in both directions and bears a prominent external malleolus with a large, slightly concave facet that faces medioventrally and slightly posteriorly for articulation with the anterolateral side of the astragalus.

Patella

A patella is preserved in USNM 16664 (Pl. 50: figs. 9, 10). It is semicircular in anterior view, coming to a slight point distally. Posteriorly, the articular surface is smoothly convex transversely and slightly concave proximodistally.

Pes

Parts of both the right and left pes of *Stylinodon* are preserved in USNM 18425 and UW 2270 (Fig. 42; Pl. 58: figs. 1–3; Pl. 64: figs. 2, 3). USNM 18425 has previously been described by Gazin (1952, p. 27–32). The pes is composed of the usual elements in unreduced number, i.e., astragalus, calcaneum, navicular, three cuneiforms, cuboid, five metatarsals and three phalanges on each of the five digits, except the first which bears two phalanges. As Gazin (1952) noted, the distal tarsals and metatarsals articulate such that they recurve ventrally (posteriorly) and the first and fifth digits approach each other on the plantar surface. The metatarsals were close to perpendicular to the ground when *Stylinodon* was standing; the majority of the weight borne was by the distal ends of the metatarsals and associated sesamoids. The proximal and medial phalanges are short and stout, while the unguals bore large claws.

Astragalus

The astragalus is obscured in the left foot of USNM 18425 and slightly crushed mediolaterally in the right foot, but the general morphology is clear enough to be observed as similar to that of *Onychodectes* and *Psittacotherium*. The proximal body and distal head are separated by a distinct neck. The trochlear crests are distinct, more so than in *Psittacotherium* and in this respect more nearly similar to *Onychodectes*. The lateral trochlear crest is slightly longer proximodistally, and is slightly higher, than the medial trochlear crest. The articular surface of the trochlea extends through an angle of 180 degrees, the trochlear fossa is relatively shallow and a superior astragalar foramen is absent. The tibial and fibular facets are vertical.

Ventrally, the astragalus of *Stylinodon* bears a large proximomedioventral tuberosity as in *Psittacotherium*. The calcaneoastragalar and sustentacular facets are both elongated proximodistally, are both concave proximodistally and are parallel to each other. They are separated by a wide and deep interarticular sulcus.

Laterally, the head of the astragalus bears a small, smoothly convex (in both directions) facet for articulation with the cuboid. Medial to this is a large, convex (in both directions) facet for articulation with the navicular. As in *Onychodectes*, this facet is broadest laterally, and tapers medially, and then proximally.

Calcaneum

The tuberosity or tuber calcis of the calcaneum of USNM 18425 is relatively narrow transversely (this appears to be real, although extenuated by crushing), but extremely deep dorsoventrally. Ventrally, this expansion projects forward forming a "hook" shape. As Gazin (1952, p. 30) noted, this may have served in part for attachment of the flexor brevis digitorum. These characters are not so well-developed in the calcaneum of UW 2270, which is similar to that of *Psittacotherium*.

Dorsally, the calcaneum bears a large astragalocalcaneal facet. Just distal (anterior) to this facet and meeting its upturned distal margin is a transversely elongated and concave facet, which faces distally and medially, for the cuboid. Lateral to the distal projection of this facet the calcaneum is thickened and well-developed for the support of the cuboid. The distal part of the calcaneum, which bore the calcaneal sustentacular facet, is missing in USNM 18425.

Navicular

The navicular is greatly elongated transversely; the navicular tuberosity is pronounced and wraps far proximally around the head of the astragalus. Proximally, the astragalonavicular facet is elongated transversely and deeply concave in both directions. Ventrally, there is a prominent tuberosity as in *Psittacotherium*; Gazin (1952, p. 30) suggests that this "may well represent a sesamoid commonly found in certain groups of mammals on the tibial side of the tarsus, which has become co-ossified with the navicular." Laterally, the moderate-sized, flat facet for the cuboid is perpendicular to both the astragalonavicular facet and the facet for the ectocuneiform. Distally, the three facets for the cuneiforms are arranged in a semicircle along the dorsal edge of the navicular. The largest facet, for the ectocuneiform, faces distally and is very slightly concave dorsoventrally. The facet for the mesocuneiform is about half as large, rather flat and faces distally and very slightly dorsally. The facet for the entocuneiform is slightly convex dorsoventrally, set proximally relative to the other facets, and faces distomedially.

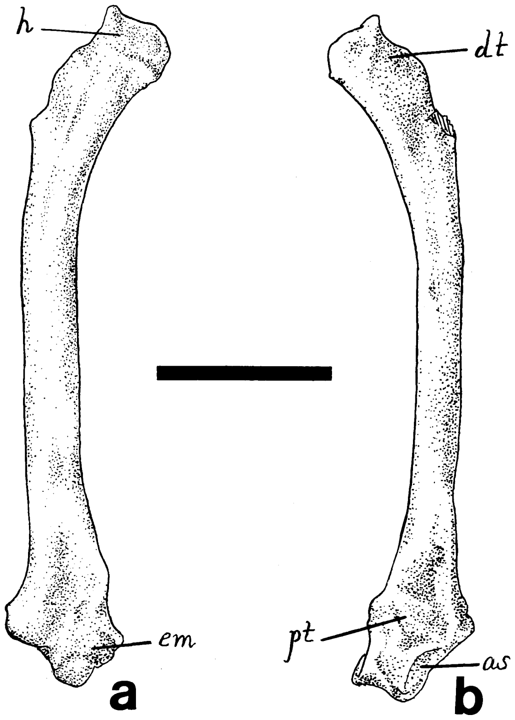


FIG. 41. The right fibula of cf. *Stylinodon mirus,* USNM 18425. *a*) Lateral view. *b*) Medial view. Abbreviations: as = astragalar facet; dt = distal tibial facet; em = external malleolus; h = head; pt = proximal tibial facet.
Scale is 4 cm long.

Entocuneiform

The entocuneiform is only partially preserved in USNM 18425 and was further reconstructed by Gazin (1952). It is more than twice the size of either of the other two cuneiforms. The proximal surface is broad and deeply concave for articulation with the first metatarsal. Laterally, it articulates with the mesocuneiform.

Mesocuneiform

The mesocuneiform is a small, somewhat cube-shaped bone which is rectangular in dorsal view. Medially and laterally it bears rather flat facets for articulation with the entocuneiform and ectocuneiform respectively. Proximally, it bears a very slightly concave facet for articulation with the navicular. Distally, it bears a fairly flat facet that is primarily for articulation with the second metatarsal, but overlaps slightly onto the third metatarsal laterally.

Ectocuneiform

The ectocuneiform is similar in size and shape to the mesocuneiform but slightly larger, whereas the proximal and distal ends are more triangular in shape. Medially and laterally it bears relatively flat surfaces for articulation with the mesocuneiform and cuboid respectively. Proximally, it bears a large, slightly concave facet for articulation with the navicular. Distally, it bears a large, flat surface for articulation with the third metatarsal. On the distolateral edge there is a

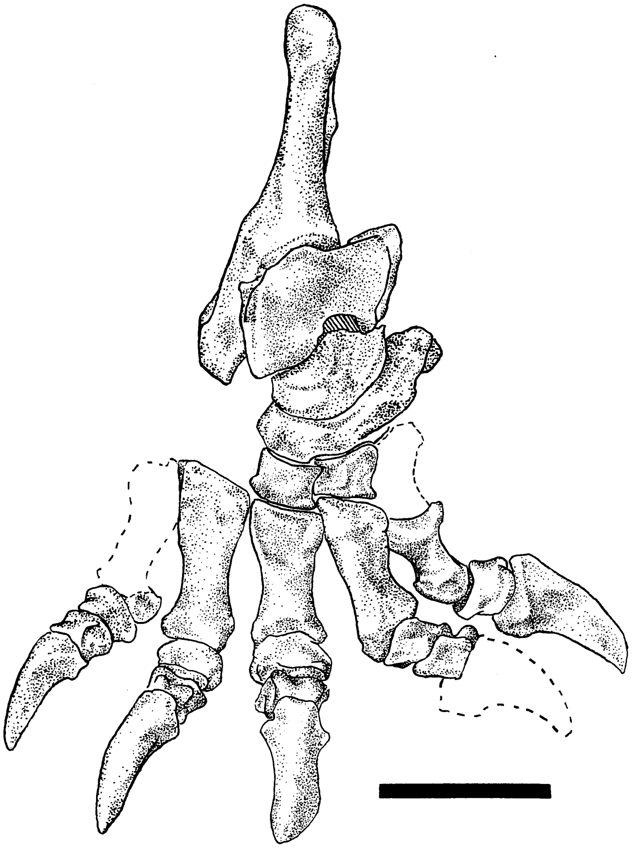


FIG. 42. Anterior (dorsal) view of the partial right pes of cf. *Stylinodon mirus,* USNM 18425. Scale is 4 cm long.

small, slightly convex facet where the ectocuneiform overlaps onto the fourth metatarsal.

Cuboid

The cuboid is missing from the right foot of USNM 18425 and extremely poorly preserved in the left foot. However, it was apparently of relatively large size. Proximally, it articulated with the calcaneum, astragalus and navicular, as noted above. Medially, it articulated with the ectocuneiform. Distally, it was broad and articulated with the fourth and fifth metatarsals.

Metatarsals

The metatarsals of *Stylinodon* are shorter, with flatter, more constricted shafts and expanded extremities, compared to the metatarsals of *Psittacotherium.* The distal ends of all of the metatarsals of *Stylinodon* are squared-off and bear strongly convex (dorsoventrally) articular surfaces that are only slightly convex to very slightly concave transversely and are not obliquely set. Ventrally, the distal articular surface is slightly concave transversely with only the slightest hint of the median spine seen in *Onychodectes* and to a lesser extent in *Psittacotherium.*

The first metatarsal is the shortest bone in the series; it is slightly shorter than the fifth metatarsal. The proximal end is greatly expanded. It bears a large facet that is slightly concave in both directions, and longer dorsoventrally laterally than medially, for articulation with the entocuneiform. Ventrally, the far proximal end bears two protuberances placed medially and laterally. The middle of the shaft of metatarsal one is flattened dorsoventrally and slightly constricted. The distal end is expanded, squared-off and slightly concave mediolaterally, with no trace of a median spine or keel. As Gazin (1952, p. 31) noted, the second metatarsal apparently did not articulate with the first.

The second, third, and fourth metatarsals are subequal in length and flattened dorsoventrally. Metatarsal two is wider mediolaterally than any of the other metatarsals. In both the left and right pes of USNM 18425 the proximal end of metatarsal two is missing; however, the proximal end apparently bore a rather large, flattish facet which articulated with the distal end of the mesocuneiform and perhaps also with part of the entocuneiform medially. Proximolaterally, it apparently had a facet for articulation with the third metatarsal. Distally, the second metatarsal is slightly expanded and bears a large, strongly convex (dorsoventrally) facet for articulation with the first phalanx. This surface is elongated laterally, but narrows considerably medially. It is slightly convex transversely on the distolateral side and slightly concave transversely on the distomedial side. Ventrally, the distal end is concave transversely.

The third metatarsal is not so flattened dorsoventrally as the second, fourth, or fifth. The proximal end is slightly expanded and bears a large, quadrilateral, slightly convex (transversely) facet for articulation primarily with the ectocuneiform. Medially and laterally there are small, rather flattish facets for articulation with the second and fourth metatarsals. These two facets are triangular-shaped as seen medially and laterally, with the proximal and dorsal sides at right angles to each other. The distal end of the third metatarsal is expanded, squared-off, deeply convex dorsoventrally and bears a slight hint of a median keel.

The fourth metatarsal is similar to the third in general proportions, although the shaft is somewhat flattened. Proximally, it bears a large, flattish, triangular-shaped facet for articulation with the cuboid. Medial to this facet and facing somewhat medioproximal is a slightly concave facet for articulation with the ectocuneiform. Mediodistal to this facet is a facet for articulation with metatarsal three. On the lateral side of the proximal end is a fairly flat, triangular-shaped facet for articulation with the fifth metatarsal. Distally, the end of the fourth metatarsal is expanded, squared-off, and virtually identical to the distal end of the third metatarsal, except for being somewhat shallower ventrally just proximal to the articular surface.

The fifth metatarsal is very slightly longer than the first, but less robust and greatly flattened dorsoventrally. The proximal part bears a large, external flare or protuberance, the middle part is constricted and the distal end is expanded. The ventral surface of the fifth metatarsal is broadly concave in both directions. Proximally, it bears a large, slightly concave articular surface for the cuboid, and perpendicular to this surface, a slightly convex (proximodistally) medial articular facet for the fourth metatarsal. Distally, the articular surface for the proximal phalanx is squared-off and slightly convex transversely, bears a small median spine on the ventral surface, and is extremely similar to the distal ends of metatarsals three and four. However, laterally on the distal end of the fifth metatarsal is a marked protuberance not seen in the other bones of the series.

Phalanges

The proximal and medial phalanges of the pes of *Stylinodon* are greatly shortened such that they are wider than they are long. As in most primitive mammals, the first digit apparently had only two phalanges whereas digits two through five had three.

As Gazin (1952, p. 32) noted, the proximal phalanges are wedge-shaped, thinning ventrally. Their proximal surfaces are slightly concave dorsoventrally, whereas their distal surfaces are rather flat. Ventrally, on the proximal edge, they bear medial and lateral protuberances.

The medial phalanges bear somewhat flat articular surfaces proximally, and distally bear dorsoventrally convex, saddle-shaped (with a median groove) articular surfaces for the ungual phalanges.

All five digits bear large, stout, unfissured claws similar to those of the pes of *Psittacotherium,* but larger. The claws are slightly recurved, but not high and laterally compressed as are those of the manus. Their dorsal surfaces are smooothly convex transversely, whereas their ventral surfaces are flat. Their proximal articulations are strongly concave dorsoventrally and bear a median ridge which fits into the saddle-shaped distal surface of the medial phalanges. Proximally and ventrally the claws bear well-developed plantar prominences.

OTHER SUPPOSED OCCURRENCES OF TAENIODONTS

At present, taeniodonts are known only from western North America and South Carolina. Several supposed taeniodonts have been reported from outside of North America. These reports are:

1. Rütimeyer (1890, 1891) reported and described a new species of "*Calamodon*" (= *Ectoganus*), "*C.*" *europaeus,* from the middle Eocene Egerkingen deposits of Switzerland. Rütimeyer thought his specimen, a lower right incisor (Pl. 60: figs. 6, 7), was a lower canine of *Ectoganus.* Rütimeyer also reconstructed a left dentary fragment (Pl. 60: figs. 4, 5) to look like the mandible of *Ectoganus* (Pl. 42). Schlosser (1894) and Cope (1894) were both aware of these specimens and believed that they did extend the range of "*Calamodon*" into Europe. However, in his revision of the Eocene faunas of Switzerland, Stehlin (1916) thoroughly redescribed and discussed "*Calamodon*" *europaeus,* demonstrating beyond doubt that it only superficially resembles a taeniodont. Stehlin (1916) thus referred "*Calamodon*" *europaeus* to "*Amphichiromys* (=*Heterohyus*: Saban, 1958), a genus of Insectivora (sensu lato). Among other features which exclude "*Calamodon*" *europaeus* from being a taeniodont are: its relatively small size; the distribution of enamel on its tusk which occurs primarily on the labial and anteroexternal sides, rather than equally on the anterointernal and anteroexternal faces as in taeniodonts; and the fact that the posterior enamel-free portion of the tusk is not laterally compressed as in taeniodonts.

Simpson (1947b, p. 618) and Kurtén (1966, p. 3; citing Simpson 1947b) have listed *Ectoganus* as occurring in the early Eocene of Europe. This report may possibly be based on Rutimeyer's "*Calamodon.*" According to Russell (1968), despite these reports, *Ectoganus* is not known in Europe.

2. Ameghino (1891) described *Entocasmus heterogenidens* on the basis of a premolar and incisor (Pl. 60: figs. 1, 2) from the Tertiary of Patagonia and believed it to be a new genus and species of "Ectoganidae." However, Ameghino (1902) later reassigned it to the Notoungulata, synonymizing "*Ectocasmus heterogenidens*" with *Notohippus toxodontoides.*

3. Chow (1963a) described a new genus and species, *Chungchienia sichuanica* from the middle (?) or upper Eocene of southern Henan, China. This taxon was based on what Chow claimed was a right mandibular ramus (Pl. 60: fig. 3) with a single cheek tooth in place, a partial alveolus for a second tooth behind and an internal, horizontally oriented alveolus for a "chisel-like 'incisor' of rodent or taeniodont type" (Chow 1963a, p. 1891). D. E. Savage (1971) suggested that *Chungchienia* may represent a Chinese taeniodont. However, in his original description, Chow (1963a) rejected the notion that *Chungchienia* is a taeniodont and instead referred it to the Xenarthra (Edentata). I concur with Chow's judgment that *Chungchienia* probably is not a taeniodont, although I do not consider it to be an edentate, due to the constricted band of thick enamel which the cheek tooth bears. *Chungchienia* shares with taeniodonts the characters of evergrowing cheek teeth with restricted bands of enamel and a large "tusk." However, *Chungchienia* has a large diastema between the incisorlike tooth and what is evidently the first cheek tooth; this is not a feature seen in any known taeniodonts. The enamel on the only known tooth of *Chungchienia* is limited to the anteroexternal face, whereas in all derived taeniodonts, enamel is lost anteriorly and posteriorly on the cheek teeth, but remains as thin bands both internally and externally. Therefore, I here exclude *Chungchienia* from the Taeniodonta, although the taxonomic position of *Chungchienia* must remain uncertain until more complete material is known.

4. Chow (1963b) also described a gliriform tooth (Pl. 61: figs. 9, 10) which he originally referred to "Tillondontia, gen. indet. sp. 2" from the late Eocene of Shandong, China. Later, Chow and others (1973) suggested that this specimen is a lower canine of a taeniodont and should be referred to "?*Stylinodon* sp." However, Chow's (1963b) original identification of this specimen as the I_2 of a tillodont appears to be correct. In both stylinodontid taeniodont canines and trogosine tillodont second incisors the enamel is limited to the labial portion of the tooth as in IVPP V. 2766 (Patterson 1949b; Gazin 1953). However, in taeniodont canines the enamel-free part is laterally compressed posteriorly (cf. Pl. 48), unlike the second incisors of tillodonts which are not compressed (Gazin 1953). In IVPP V. 2766 the enamel-free part is not laterally compressed as in taeniodonts, but rather resembles the Tillodontia in having subparallel internal and external sides. Therefore, I refer IVPP V. 2766 to the Tillodontia, genus indet.

5. West and others (1977), West (1978) and McKenna (1980b) have reported a stylinodontid taeniodont from the upper portion of the Eocene Eureka Sound Formation of Ellesmere Island, North-West Territories, Canada. This occurrence is based on a single enamel fragment (MPM 30848, Pl. 61: figs. 6–8). Examination of this fragment suggests that it may be the enamel fragment of a tillodont lower incisor. The enamel of MPM 30848 shows the slightly beaded pattern often seen in trogosine tillodonts (cf. Pl. 61: fig. 5; an incisor fragment of *Trogosus*), and the preserved part of enamel-free dentine is in the same plane as the enamel-covered part. It does not show any evidence that the posterior enamel-free part was laterally compressed as in taeniodonts. Therefore, it is possible that MPM 30848 represents a tillodont rather than a taeniodont, but the material is too incomplete to permit a definitive identification. Trogosine tillodonts were large, herbivorous extinct mammals (Gazin 1953), and if MPM 30848 is a tillodont, it would still have the same paleoclimatic implications as would a taeniodont (cf. McKenna 1980b).

6. Dehm and Oettingen-Spielberg (1958) described *Basalina basalensis* as a new genus and species of stylinodontid taeniodonts from the middle Eocene Kuldana Formation near Ganda Kas, Pakistan. *Basalina basalensis* is based on a left dentary fragment with one preserved cheek tooth (Pl. 61: figs. 1–4). *Basalina* has recently been reviewed thoroughly and reinterpreted as a tillodont (Lucas and Schoch 1981a) in accord with earlier suggestions by Gingerich and Gunnell (1979) and West (1980). The preserved cheek tooth of *Basalina,* originally described as an M_1 (Dehm and Oettingen-Spielberg 1958), appears to be a molariform, bunoselenodont P_4 closely comparable to the P_4 of *Esthonyx* and other tillodonts (Gazin 1953). It is unlike the hypsodont, transversely bilophodont cheek teeth of derived taeniodonts.

4. THE GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION OF THE TAENIODONTA

INTRODUCTION

All unequivocally known taeniodonts come from the Rocky Mountain early Tertiary intermontane sedimentary basins of western North America (Figs. 43, 44; Table 1: see Foreword for one exception to this statement), which were formed or rejuvenated during the Laramide orogeny. The major areas where taeniodonts occur are, from north to south: the Crazy Mountain Field (south-central Montana), Bighorn Basin (north-central Wyoming), Togwotee Pass area (northwestern Wyoming), Wind River Basin (central Wyoming), Green River/Bridger Basin (southwestern Wyoming), Washakie Basin (south-central Wyoming), Uinta Basin (northeastern Utah), Huerfano Basin (south-central Colorado), San Juan Basin (northwestern New Mexico and southwestern Colorado) and Tornillo Flat area (western Texas). Here I place special emphasis on the San Juan Basin (Fig. 45), from which the early Puercan to middle Wasatchian taeniodonts are best known. The history of study and nomenclature of the Tertiary strata of the San Juan Basin (Fig. 46) has been discussed and reviewed in numerous papers, including Baltz and others (1966), Gardner (1910), Granger (1914), Kues and others (1977), Lucas (1981), Lucas and others (1981), Matthew (1937), Reeside (1924), Simpson (1948, 1959, 1981), Sinclair and Granger (1914), Tsentas (1981) and H. E. Wood and others (1941).

PUERCAN-TORREJONIAN

Taeniodonts of Puercan and Torrejonian age occur in the Paleocene Nacimiento Formation at several localities in the southwestern and south-central San Juan Basin (Fig. 45; Table 1). The Nacimiento Formation is composed of red and green, buff and gray clay-shales and siltstones, black clay-shales and lenticular arkosic and quartzose sandstones (Baltz and others 1966; Tsentas and Lucas 1980; Tsentas and others 1981). In the upper part of the Nacimiento Formation a northern facies of relatively high energy fluvial deposits (with a greater overall percentage of sandstone) and a southern facies of lower energy fluvial and swamp deposits is recognizable (Tsentas and others 1981). This distribution of facies suggests a northern source area for much of the upper part of the Nacimiento Formation (Baltz 1967; Tsentas and others 1981).

The Puercan strata of the Nacimiento Formation have been subdivided into two "zones," a lower *Ectoconus* zone (also known as the *Hemithlaeus* zone: Van Valen 1978) and an overlying *Taeniolabis* zone (formerly known as the "*Polymastodon*" (=*Taeniolabis*) "zone": Lindsay and others 1978; Matthew 1937; Osborn 1929; Sinclair and Granger 1914). Localities in Betonnie Tsosie Wash and Kimbeto Wash are in the *Ectoconus* zone whereas localities in De-na-zin Wash and Alamo Wash include both zones. These zones have been considered to represent superposed biostratigraphic units well separated temporally. Alternately, they have been thought to represent different facies or to reflect collecting biases (Matthew 1937). Previously, *Onychodectes tisonensis* has been thought to occur throughout the Puercan in both zones whereas *O.* "*rarus*" and *Wortmania otariidens* were restricted to the *Taeniolabis* zone (Russell 1967). Here *O.* "*rarus*" is considered a junior subjective synonym of *O. tisonensis* at the specific level and *Wortmania otariidens* is now known from the *Ectoconus* zone in Betonnie Tsosie

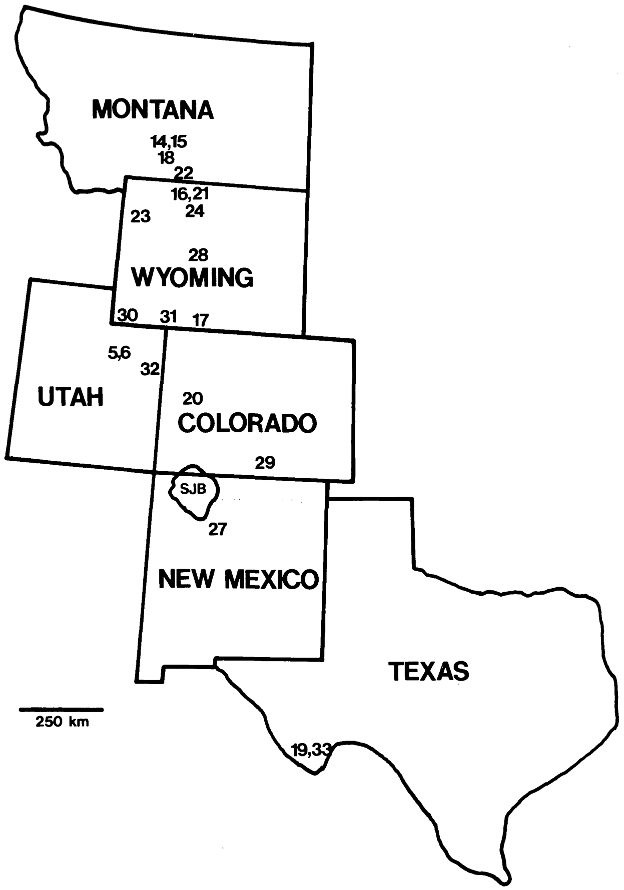


FIG. 43. Localities at which taeniodonts have been found. Numbers correspond to localities listed in Table 1. For localities in the San Juan Basin (SJB), see Figure 45. Not shown is the St. Stephen, South Carolina, locality.

and Kimbeto Washes. However, as far as is known, *O. t. tisonensis* does occur in both zones while *O. t. rarus* is known only from the *Taeniolabis* zone. Thus, better knowledge of the Puercan taeniodonts reduces the distinctiveness of these zones and does not strongly support the idea that they are separated by a significant span of time.

Both *O. tisonensis* and *W. otariidens* are restricted to the Puercan. The occurrence of *O. tisonensis* in the Wagonroad local fauna of the upper part of the North Horn Formation of east-central Utah supports the correlation of this locality with the Puercan-aged strata of the Nacimiento Formation (Robison and Lucas 1980).

The Torrejonian strata of the Nacimiento Formation have also been divided into two zones on the basis of mammalian faunas (Lindsay and others 1978; Matthew 1937; Osborn 1929). The presumably lower *Deltatherium* zone occurs in Kutz Canyon, Torreon Wash and Kimbeto Wash, whereas the overlying *Pantolambda* zone is well known from Torreon Wash and University of Kansas New Mexico Locality 15 as well as the areas southeast of Kimbeto and just south of Cedar Hill (R. W. Wilson 1956; Tsentas 1981). These zones also have been thought to represent superposed biostratigraphic units separated by a significant length of time (Lindsay and others 1978; Taylor and Butler 1980). Alternatively, it has been suggested that the differences between the faunas of

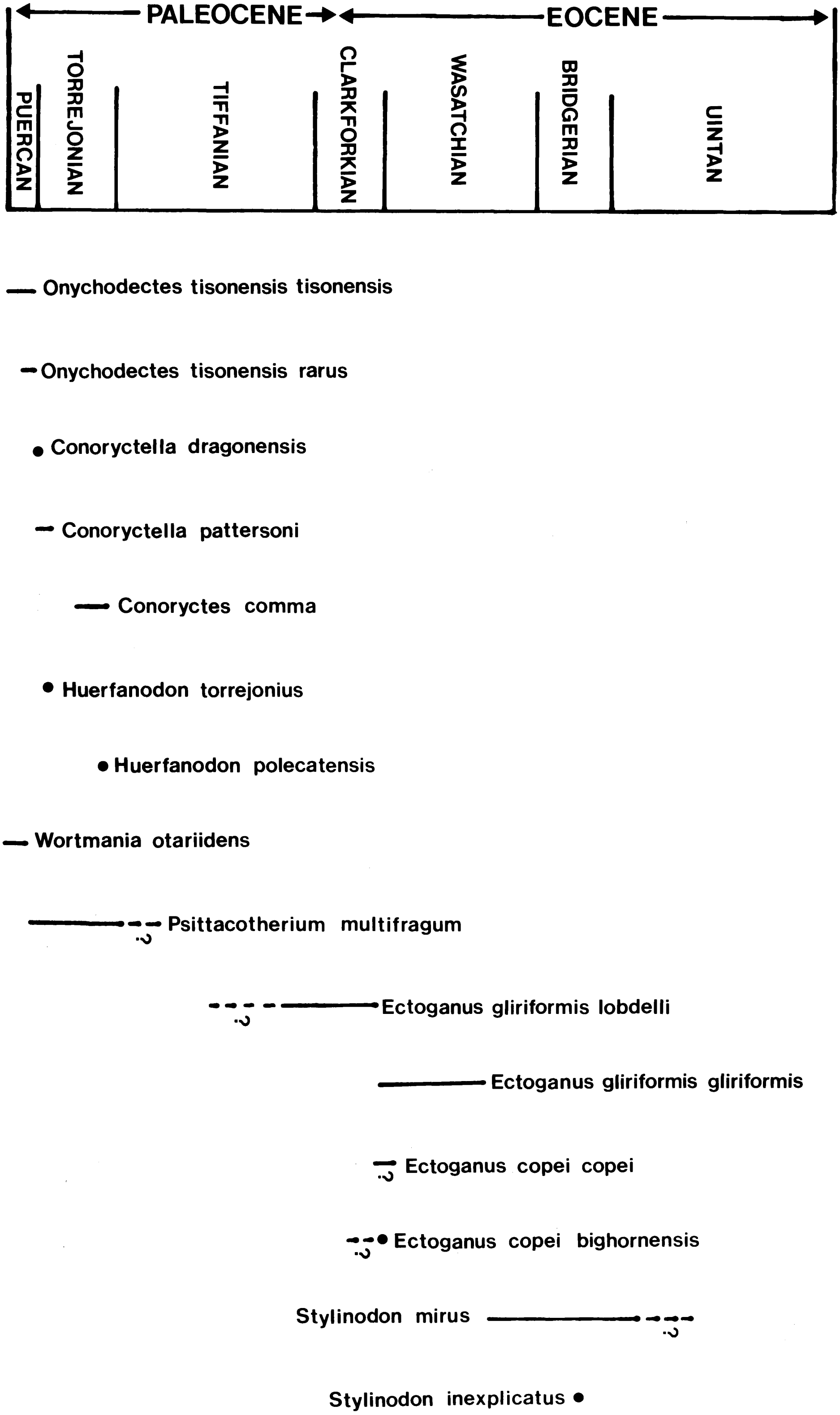


FIG. 44. The biostratigraphic distribution of the Taeniodonta.

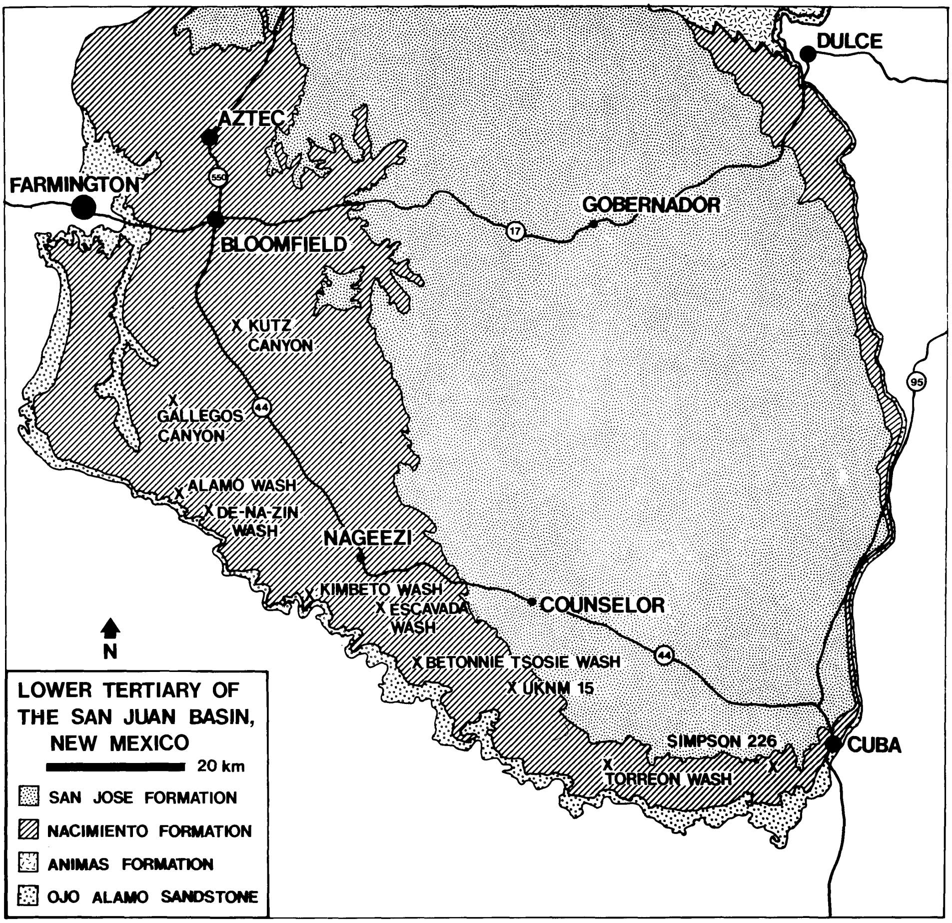


FIG. 45. Geologic map of the lower Tertiary strata of the San Juan Basin, New Mexico, showing the major Paleocene localities which have produced taeniodont fossils. For lower Eocene localities in the San Juan Basin, see figures 2 and 3 in Lucas and others (1981). See also Table 1; geology modified after Fassett and Hinds 1971, pl. 1.

the two zones reflect facies differences or collecting biases (Matthew 1937; Tsentas 1981; R. W. Wilson 1956). Recently, a specimen of *Pantolambda* was found in a *Deltatherium* zone horizon in Kutz Canyon, supporting the idea of collecting biases (Lucas and O'Neill 1981). *Conoryctes comma* is known with certainty only from the *Pantolambda* zone. The specimens reported by Taylor (1981) as *Conoryctes comma* from a *Deltatherium* zone horizon in Kutz Canyon are here assigned to *Conoryctella* (Schoch and Lucas 1981c). However, because it is relatively rare, I do not stress the possible biostratigraphic significance of the absence of *C. comma* in the *Deltatherium* zone.

Huerfanodon torrejonius is presently known in the San Juan Basin only from the *Deltatherium* zone in Kimbeto Wash (Schoch and Lucas 1981b). *Huerfanodon polecatensis* is known from the Rock Bench Quarry of the Polecat Bench Formation, Bighorn Basin (Schoch and Lucas 1981b), and ?*Huerfanodon* sp. is known from Silberling Quarry, Lebo Formation, Montana. Both Rock Bench and Silberling Quarries are considered to be in the late Torrejonian (*Pantolambda* zone) (Gingerich and others 1980). Although *Huerfanodon polecatensis* may appear to be slightly more "advanced" (and perhaps younger?) than *Huerfanodon torrejo-*

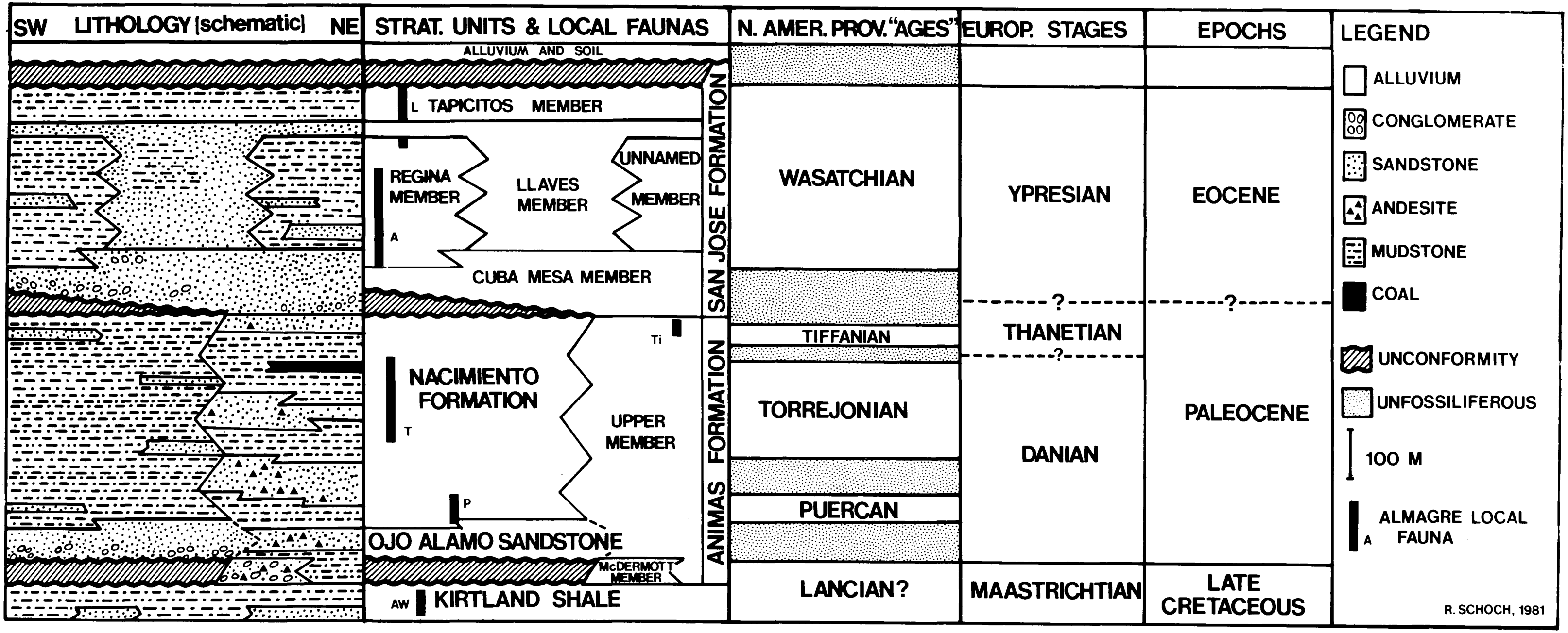


FIG. 46. The stratigraphy of the lower Tertiary strata of the San Juan Basin. Lithologies are schematic. Stratigraphic units after Baltz (1967). Local faunas after Sinclair and Granger (1914), Matthew (1937), Simpson (1935a, b, c) and Lucas and others (1981). North American land mammal "ages" after H. E. Wood and others (1941). Correlation of North American "ages" with European stages after Berggren and others (1978).

Abbreviations for faunas are: A = Almagre local fauna, AW = Alamo Wash local fauna, L = Largo local fauna, P = Puerco fauna, T = Torrejonian fauna, Ti = Tiffany fauna.

nius, it is unwise to try to hypothesize that one species is the ancestor of another and then base the relative correlation and dating of the strata in different basins on such hypothetical lineages (contra Gingerich 1976). Rather, the occurrence of *Huerfanodon* in New Mexico, Wyoming and Montana suggests that these strata are all approximately the same age.

Tomida (1981) has recently described a typical Torrejonian faunal assemblage in the San Juan Basin in sediments that can be magnetostratigraphically correlated with the Dragon local fauna of the North Horn Formation, Utah (Tomida and Butler 1980), the type locality of the "Dragonian" land mammal "age" (H. E. Wood and others 1941). These sediments are also stratigraphically below a *Deltatherium* zone horizon and suggest the presence of a third, earliest Torrejonian zone. *Conoryctella pattersoni* occurs in Tomida's (1981) Dragonian zone in the San Juan Basin, in the Kutz Canyon *Deltatherium* zone (R. W. Wilson 1956) and in the Dragon local fauna of Utah (Schoch and Lucas 1981c). Thus, these occurrences of *Conoryctella* suggest that all three localities do not significantly differ temporally. The Dragon local fauna can thus be correlated with the "lower" Torrejonian strata of the Nacimiento Formation.

Psittacotherium is a far-ranging genus, both geographically and temporally. It occurs throughout the Torrejonian strata (all three zones) of the Nacimiento Formation. It may also occur in the Dragon local fauna, and, if substantiated, this would further support a Torrejonian age for that fauna. *Psittacotherium* is present in the Torrejonian Swain Quarry, Fort Union Formation, Wyoming and in the late Torrejonian–early Tiffanian strata of Montana (Gidley, Lebo and Douglass Quarries) and Texas (Tornillo Flat, Black Peaks Formation).

TIFFANIAN-UINTAN

In the northeastern San Juan Basin the Nacimiento Formation grades laterally into the upper part of the Animas Formation and the Ojo Alamo Sandstone grades into the lower Animas (McDermott Member: Baltz 1967; Barnes and others 1954; Reeside 1924). The type locality of the Tiffanian land mammal age (H. E. Wood and others 1941), Mason Pocket, is in the Animas Formation in southern Colorado, but has not produced any taeniodonts (Barnes and others 1954; Simpson 1935a, b, c). *Psittacotherium multifragum* does occur in early Tiffanian strata of Montana (Melville Formation: Simpson 1937) and Texas (Black Peaks Formation: Schiebout 1974).

"*Lampadophorus lobdelli*" and "*L. expectatus*" are junior subjective synonyms of *Ectoganus gliriformis. Ectoganus gliriformis lobdelli* occurs in late Tiffanian–Clarkforkian strata of Colorado in the Clarkforkian of the Bighorn Basin, Wyoming, and in upper Paleocene strata of South Carolina (see Foreword). *E. gliriformis gliriformis* occurs in the Clarkforkian strata of the Togwotee Pass area, but otherwise is restricted to the early–middle Wasatchian of Wyoming and New Mexico. Except for a single specimen of *Ectoganus* cf. *E. copei bighornensis* from the Clarkforkian of the Togwotee Pass area, both *E. copei copei* and *E. copei bighornensis* are restricted to the early Wasatchian of the Bighorn Basin, Wyoming. Rose (1977) has used "*Lampadophorus,*" in part, to support the validity of the Clarkforkian land mammal age; the revised taxonomy of *Ectoganus* eliminates "*Lampadophorus*" as a distinctive Clarkforkian, or even latest Paleocene, genus.

The San Jose Formation ("Wasatch" of early workers), a series of variegated continental mudstones and sandstones (Simpson 1948), unconformably overlies

TABLE 1. Summary of the stratigraphic and geographic distribution of the Taeniodonta

	LOCALITY	FORMATION	AGE	TAXA
1	Betonnie Tsosie Wash	Nacimiento	Puercan	*Onychodectes tisonensis tisonensis* *Wortmania otariidens*
2	Kimbeto Wash	Nacimiento	Puercan	*O. t. tisonensis* *W. otariidens*
3	De-na-zin Wash	Nacimiento	Puercan	*O. t. tisonensis* *O. t. rarus* *W. otariidens*
4	Alamo Wash	Nacimiento	Puercan	*O. t. tisonensis* *O. t. rarus* *W. otariidens*
5	Wagonroad Ridge	North Horn	Puercan	*O. t. tisonensis* stylinodontine indet.
6	Dragon Canyon	North Horn	Torrejonian	*Conoryctella dragonensis* *Conoryctella pattersoni* ?*Psittacotherium* sp. or ?*Wortmania* sp.
7	Kutz Canyon	Nacimiento	Torrejonian	*C. pattersoni* *Psittacotherium multifragum*
8	Kimbeto Wash	Nacimiento	Torrejonian	*Huerfanodon torrejonius* *P. multifragum*
9	Torreon Wash	Nacimiento	Torrejonian	*Conoryctes comma* *P. multifragum*
10	UK NM Locality 15	Nacimiento	Torrejonian	*C. comma* *P. multifragum*
11	Gallegos Canyon	Nacimiento	Torrejonian	*P. multifragum*
12	Escavada Wash	Nacimiento	Torrejonian	conoryctine indet. *P. multifragum*
13	Simpson's Locality 226	Nacimiento	Torrejonian	*P. multifragum*
14	Gidley Quarry	Lebo	Torrejonian	conoryctine indet.
15	Silberling quarry	Lebo	Torrejonian	?*Huerfanodon* sp. *P. multifragum*
16	Rock Bench Quarry	Polecat Bench	Torrejonian	*Huerfanodon polecatensis*
17	Swain Quarry	Fort Union	Torrejonian	*P. multifragum*
18	Douglass Quarry	Melville	Tiffanian	*P. multifragum*
19	Tornillo Flat	Black Peaks	Tiffanian	*P. multifragum*
20	Plateau Valley	Wasatch ("DeBeque")	Tiffanian–Clarkforkian	*Ectoganus gliriformis lobdelli*
21	Polecat Bench	Polecat Bench	Clarkforkian	*E. g. lobdelli*
22	Bear Creek	Fort Union	Clarkforkian	*E. g. lobdelli*
23	Togwotee Pass Area	"Lower variegated beds"	Clarkforkian	*E. g. gliriformis* *E.* cf. *E. copei bighornesis*
24	Bighorn Basin	Willwood	Wasatchian	*E. g. gliriformis* *E. copei copei* *E. c. bighornesis*
25	Almagre Arroyo	San Jose	Wasatchian	*E. g. gliriformis*
26	Gobernador	San Jose	Wasatchian	*E. g. gliriformis*
27	Cerrillos	Galisteo	Wasatchian	*Ectoganus* sp.
28	Wind River Basin	Wind River	Wasatchian	*E. g. gliriformis* *Stylinodon mirus*
29	Huerfano Basin	Huerfano	Wasatchian–Bridgerian	*S. mirus*
30	Green River/Bridger Basin	Bridger	Bridgerian	*S. mirus*
31	Washakie Basin	Washakie	Bridgerian	*S. mirus* *Stylinodon inexplicatus*
32	Uinta Basin	Uinta	Uintan	*S. mirus*
33	Brewster County, Texas	Pruett	Bridgerian–Uintan	*Stylinodon* sp.
34	St. Stephen, South Carolina	"Black Mingo"	Late Paleocene	*E. g. lobdelli*

References for localities. 1) Simpson 1959; Sinclair and Granger 1914. 2) Simpson 1959; Sinclair and Granger 1914. 3) Sinclair and Granger 1914. 4) Sinclair and Granger 1914. 5) Robison and Lucas 1980. 6) Gazin 1941; Schoch and Lucas 1981c. 7) Granger 1917; Schoch and Lucas 1981c;

the Nacimiento Formation and is in the structural center of the San Juan Basin. Granger (1914) distinguished two Wasatchian facies in the San Jose: the lower variegated "Almagre beds" exposed in Almagre and Blanco Arroyos near the present town of Regina, and the upper red "Largo beds" exposed near Lindrith and Gavilan (see Simpson 1948). Cope's specimens of *Ectoganus* and "*Calamodon*" as well as Marsh's "*Dryptodon*" almost surely came from the Almagre fauna, as have most taeniodonts since then (Lucas 1977; Lucas and others 1981). Recently (1977) a specimen of *Ectoganus* was collected from rocks stratigraphically equivalent to the Almagre beds near Gobernador (UNM B-970/971/973; Pl. 38: figs. 5–20).

Baltz (1967) defined and mapped four formal members of Simpson's San Jose Formation. The Cuba Mesa Member is the lowest and is essentially unfossiliferous (Lucas 1977); the overlying Regina Member includes the Almagre fauna and the lower part of the Largo fauna; the Llaves Member is essentially unfossiliferous (Lucas 1977) and either overlies the Cuba Mesa Member or the Regina Member, or grades into and intertongues with the Regina Member. The Tapicitos Member is the youngest member and either overlies or laterally grades into the Llaves Member; it includes the majority of the Largo fauna (Lucas 1977).

The only taeniodont known from the San Jose Formation is *Ectoganus gliriformis gliriformis*. Although the vast majority of specimens of *Ectoganus* have come from the Almagre local fauna, *E. gliriformis gliriformis* is also known from the Largo local fauna. AMNH 16245, a lower jaw fragment of *E. g. gliriformis* (Pl. 36: fig. 13) was collected by Granger in 1912 from the "west branch of Almagre Arroyo, upper beds." This locality corresponds to the lower part of the Largo of Granger (1914) and is in the upper part of the Regina Member of the San Jose Formation.

The Wasatchian land mammal "age" is usually divided into three "subages," the Graybullian, Lysitean and Lostcabinian, from oldest to youngest (Granger 1914; H. E. Wood and others 1941; Lucas and others 1981). *Ectoganus gliriformis gliriformis* (= *Ectoganus* "*simplex*": Schankler 1980, p. 104) occurs in Graybullian and Lysitean strata of the Willwood Formation, Bighorn Basin, Wyoming, but not in the Lostcabinian strata of the Willwood. Likewise, in the Wind River Formation of the Wind River Basin, Wyoming, the type area of the Lysitean and Lostcabinian, *E. g. gliriformis* occurs only in the Lysitean strata and is superseded by the taeniodont *Stylinodon mirus* in the Lostcabinian (Guthrie 1967, 1971). Thus, *Ectoganus* is not known from strata younger than the Lysitean. The presence of *E. g. gliriformis* in the Almagre fauna suggests a Graybullian or Lysitean rather than a Lostcabinian age for that fauna (contra Lucas 1977) and the occurrence of *E. g. gliriformis* in the lower part of the Largo would suggest that that horizon of the Largo (Granger 1914) in the Regina Member of the San Jose Formation is of Graybullian or Lysitean age. Nevertheless, the majority of the Largo fauna, which occurs stratigraphically higher in the Tapicitos Member, may be of Lostcabinian age (Lucas 1977).

←

R. W. Wilson 1956. 8) Schoch and Lucas 1981b. 9) Matthew 1937; Tsentas 1981. 10) R. W. Wilson 1956. 11) Sinclair and Granger 1914. 12) Kues and others 1977. 13) Simpson 1959. 14) Simpson 1937. 15) Simpson 1937. 16) Gingerich and others 1980. 17) Rigby 1980. 18) Douglass 1908; Simpson 1937. 19) Schiebout 1974; J. A. Wilson 1967. 20) Patterson 1936, 1949a; Sloan and others 1980. 21) Gingerich and others 1980. 22) Simpson 1929a, b. 23) McKenna 1972, 1980a. 24) Bown 1980; Schankler 1980. 25) Granger 1914; Simpson 1948. 26) Kues and others 1977. 27) Lucas and Kues 1979; Lucas 1982. 28) Granger 1910; Guthrie 1967, 1971. 29) Robinson 1966. 30) West 1972a. 31) Turnbull 1972, 1978. 32) Black and Dawson 1966. 33) J. A. Wilson 1972, 1974. 34) See Foreword of this monograph.

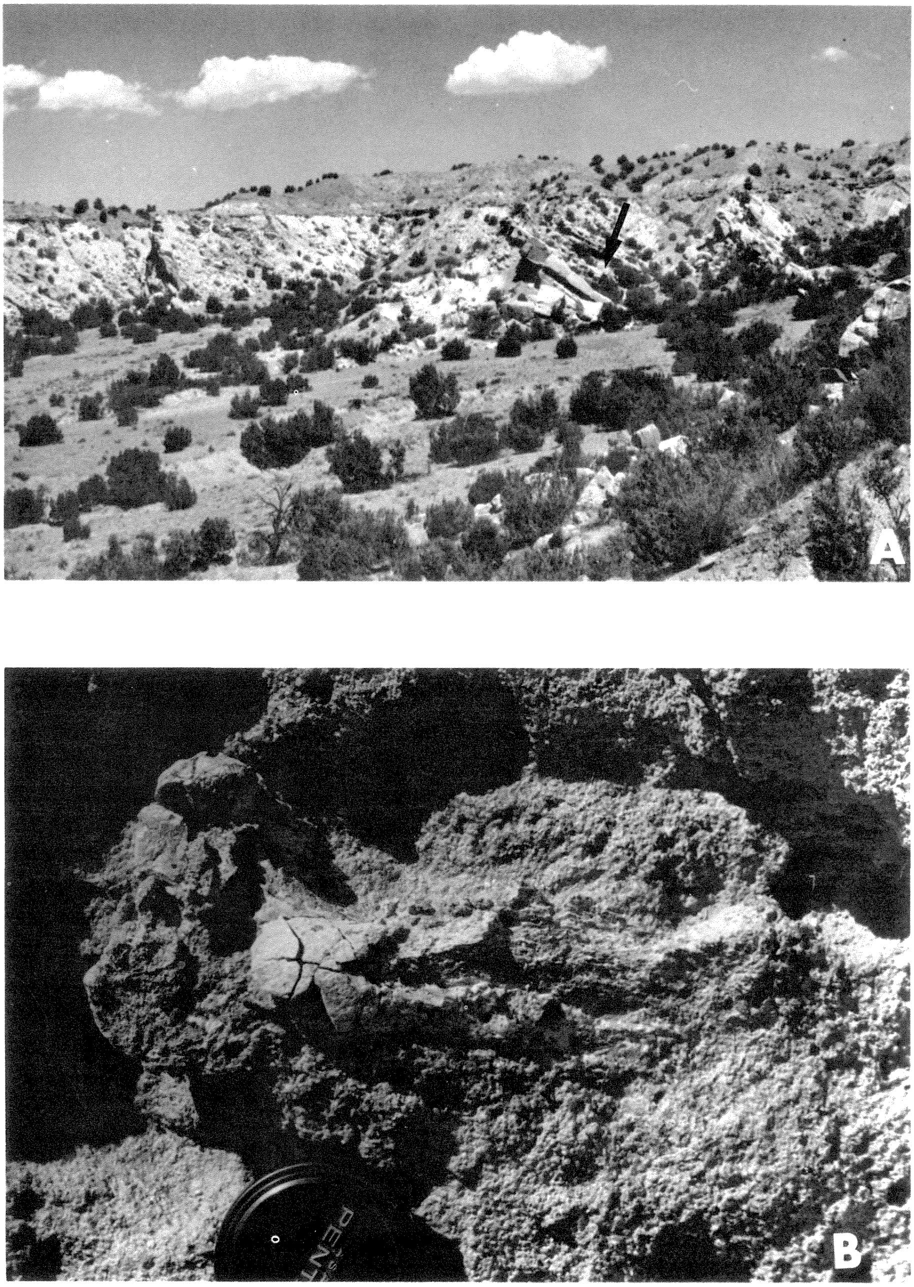


FIG. 47. UNM GE-097, fragmentary right humerus of *Ectoganus* sp. from Wasatchian strata of the lower part of the Galisteo Formation, Cerrillos local fauna, SE ¼, SE ¼, Sec. 16, T. 14 N., R. 8 E., Santa Fe County, New Mexico. *A,* Photograph showing the locality, arrow points to where the humerus was found. *B,* The humerus in situ, anterior view, the distal end is to the left. Lenscap is 5.5 cm in diameter.

Southeast of the San Juan Basin in north-central New Mexico in the Wasatchian Cerrillos local fauna of the Galisteo Formation (Lucas and Kues 1979; Lucas 1982), a humerus of *Ectoganus* sp. has recently been found (Fig. 47: Lucas 1982), supporting the assignment of a pre-Lostcabinian Wasatchian age to the Cerrillos local fauna.

The earliest occurrence of *Stylinodon mirus* is in the late Wasatchian (Lostcabinian) strata of the Wind River Basin, Wyoming. It also occurs in the late Wasatchian–early Bridgerian of Colorado, in the Bridgerian of the Green River/Bridger and Washakie basins of Wyoming and in the middle Uintan ("Horizon B") of the Uinta Basin, Utah. *Stylinodon inexplicatus* is known from only one specimen of Bridgerian age in the Washakie Basin. Two specimens of *Stylinodon* sp. are known from late Bridgeria- or early Uintan–aged strata of the Pruett Formation, Trans-Pecos, west Texas (Schoch and Lucas 1981d). The presence of *Stylinodon,* therefore indicates a Lostcabinian–Uintan age.

CONCLUSIONS

The early to middle Paleocene conoryctids (*Onychodectes, Conoryctella, Conoryctes, Huerfanodon*) appear to have the most potential for high-resolution dating and biostratigraphic correlation. The species and subspecies of stylinodontids (*Wortmania, Psittacotherium, Ectoganus, Stylinodon*) are either known only from a few specimens or are so broadly distributed geographically and of such long durations temporally that at present they are not useful except for very general correlations no more refined than the level of land mammal ages.

5. FUNCTIONAL MORPHOLOGY OF THE TAENIODONTA

INTRODUCTION

In this section I attempt to reconstruct the functional morphology of the Taeniodonta. In a previous section (Chapter 3) I have described the osteology of all of the known elements of the various genera of taeniodonts. In summary (Table 2), among the conoryctids, *Onychodectes* is known from two skulls and a moderate amount of skeletal material. *Conoryctella* is virtually unknown except for the ulna, mandible and dentition. Likewise, *Conoryctes* and *Huerfanodon* are known from little more than a few skulls and a partial manus. *Wortmania* is known from one incomplete skeleton and a few teeth. *Psittacotherium* is known from a moderate amount of material. *Ectoganus* is known from fragments of many scattered specimens. *Stylinodon* is best known; virtually the complete skull and skeleton can be composited from several known partial skeletons.

Stylinodon is the most derived, and in this sense the most "typical" taeniodont, i.e., it appears to have carried out the taeniodont specialization most completely (see Chapter 7 below). In all known morphological features the cranium and skeleton of *Psittacotherium* and *Ectoganus* are very similar to, or clearly foreshadow, the condition seen in *Stylinodon.* Most of these features, as far as are known, are also foreshadowed in the scanty remains of the more primitive (generalized) *Wortmania.* Furthermore, all three genera are roughly subequal in size; the main differences between them are seen in the jaws and dentitions as described above. Therefore, the descriptions and interpretations given below for the stylinodontids are based primarily on *Stylinodon,* but in general are also applicable in large part to *Ectoganus* and *Psittacotherium,* and to a lesser degree to *Wortmania.* Cranially and postcranially, *Onychodectes* is considered to be both representative of the primitive, generalized taeniodont morphotype and of the conoryctid condition. What little is known postcranially of the other conoryctids is not widely different from the condition seen in *Onychodectes.*

The functional morphology described here is based on study of articular surfaces, the study of the general shape and detailed morphology of bone elements, the interpretation of preserved muscle attachments, manipulation of actual specimens and analogy with other mammals. For the appendicular skeleton in particular, the normal stance or habitual stationary position of the animal is based on the angles that the skeletal elements of the limb bones form with one another when their corresponding articular surfaces are most nearly in apposition (cf. Jenkins 1971a and references cited therein; Prins and Schoch 1983). Muscle and ligament reconstructions are based on such standard works as Wake (1979), Mivart (1881), Flower (1876b), Coues (1872), Ellseworth (1976), Schumacher (1961), Windle and Parsons (1901, 1903), Murie (1872), Hiiemae and Jenkins (1969), Hildebrand (1974), Miller (1952), Slijper (1946), J. G. Savage (1957), Davison (1917), and Gregory (in Osborn 1929). It must be kept in mind that the muscle descriptions and reconstructions are my interpretation based on preserved morphologies and analogy with extant mammals.

Reconstruction of the limb posture of taeniodonts indicates that the limbs were not vertically oriented or moved in parasagittal planes; rather, taeniodonts were noncursorial (cf. Jenkins 1971b) and the many biomechanical models developed for cursorial mammals (cf. Manter 1938; Barclay 1953; Ottaway 1955) are not directly applicable. Furthermore, it has been well demonstrated (e.g., Grant 1973) that use of an instantaneous center of rotation in biomechanical modeling may lead to significantly different results from those obtained using a fixed axis

TABLE 2. Known taeniodont specimens (partial specimens in parentheses)

CONORYCTIDAE				STYLINODONTIDAE			
Onychodectes	*Conoryctella*	*Conoryctes*	*Huerfanodon*	*Wortmania*	*Psittacotherium*	*Ectoganus*	*Stylinodon*
Skull	(Skull)	Skull	Skull	(Skull)	(Skull)	Skull	Skull
(Scapula)	—	—	—	—	—	(Scapula)	Scapula
Humerus	—	(Humerus)	—	—	(Humerus)	Humerus	Humerus
(Ulna)	(Ulna)	(Ulna)	—	(Ulna)	Ulna	(Ulna)	Ulna
(Radius)	—	(Radius)	—	Radius	Radius	Radius	Radius
Carpals	—	Carpals	—	—	Carpals	—	Carpals
Mc III	—	Mc III	—	—	Mc III	—	Mc III
(Femur)	—	—	—	(Femur)	Femur	(Femur)	Femur
(Tibia)	—	(Tibia)	—	Tibia	(Tibia)	—	Tibia
—	—	—	—	—	(Fibula)	—	Fibula
Tarsals	—	—	—	—	Tarsals	—	Tarsals
Mt III	—	—	—	—	Mt III	—	Mt III

of rotation. At present, the continuously moving instantaneous center of rotation can only be determined with any degree of accuracy for extant animals which can be observed moving naturally. Thus, any simplistic biomechanical modeling of fossils may, at best, be coarse approximations.

The nature of the known taeniodont material makes it necessary to be extremely typological at this stage. Any single element, if known at all, is often only known from one, or at most a few, individuals, and is usually not known from more than one or two species (Table 2). Furthermore, the material is often incomplete or damaged, making accurate measurements difficult or impossible. For these reasons, statistical analysis of large amounts of metric data, useful in studying some groups, is not possible for study of the Taeniodonta as presently known. Rather, here the emphasis is placed on nonmetric morphology of elements and qualitative size relations. [These remarks also hold for other studies, such as Jenkins (1971a) on the postcranial skeleton of African dicynodonts.] Accordingly, I have tried to present these data through description supplemented by numerous illustrations (photographs and drawings) of specimens in the descriptive osteology section above, along with tables of representative measurements of various elements (see Appendix I).

In the remainder of this section I present and discuss a proposed muscular and postural reconstruction of *Stylinodon,* arbitrarily starting at the anterior of the head (face) and working toward the tail; I discuss the functional morphology (including biomechanics) of *Stylinodon* and the other stylinodontids; and I discuss the reconstructed anatomy and functional morphology of the conoryctids as exemplified by *Onychodectes.*

FUNCTIONAL ANATOMY AND RECONSTRUCTION OF *STYLINODON* AND THE STYLINODONTIDS

Facial Musculature in *Stylinodon*

Beneath the masseter and anterior to it along the alveolar margins of the jaws probably lay the buccinator. Around the mouth lay the orbicularis oris. From the front of the zygomatic arch below the orbit arose the zygomaticus which connected to the orbicularis oris at the angle of the mouth. The orbicularis palpebrarum would have surrounded the eye and attached to the inner margin of the orbit. Slightly anterior to the margins of the orbits on either side of the skull above P^{2-3} are small knoblike processes which probably served as the sites of attachment for a well-developed maxillolabialis which attached to a movable upper lip. A relatively large nasolabialis originated near the nasal-maxillary border and inserted on the surface of the upper lip. The massive, blunt, heavy construction of the face, along with the large nasal cavities and solid areas for muscle attachments of the labial muscles suggest that *Stylinodon* may have had a strong set of prehensile lips and a keen sense of smell (also suggested by the large nasal cavities and olfactory bulbs in the morphologically similar *Ectoganus*).

Inside the lower jaw is a prominent pit or depression in the mandibular symphysis, as noted in the description above. From this arose the large genioglossus (geniohypoglossus) muscle which inserted beneath the tongue. The large size of this pit in *Stylinodon* (and in the other stylinodontids as well) indicates a large, powerful tongue superficially analogous to that of the parrot (cf. Patterson 1949b, p. 265; Cope 1882b, p. 157).

Masticatory Apparatus and Occlusal Relationships in *Stylinodon*

The jaw-closing musculature in all mammals is comprised of three major muscle groups: the masseter group (including the M. zygomaticomandibularis), the temporalis group, and the pterygoideus group (Becht 1953; Turnbull 1970). There is one major jaw-opening muscle group, the digastric group (Turnbull 1970). The areas of origin and insertion of these general muscle groups can be recognized on the skull of *Stylinodon* (Fig. 48).

The temporalis group originated on the large, broad temporal fossa and inserted on the coronoid process of the mandible. The masseter group originated from the strong zygomatic arch and inserted on the lateral and posteroventral border of the mandible. The pterygoideus group originated from the pterygoid flanges and inserted on the internal posteroventral border of the mandible from the angle to below the condyle. The digastric group arose from the back of the skull on the anterior part of the mastoid processes and inserted on the flattened ventral border of the mandible just behind the symphysis.

Judged from the size of the areas of muscle origins and insertions, all of these muscles appear to have been large and powerful. The temporalis group was probably the heaviest, filling most of the area within the large temporal fossa and rising up the sagittal crest. The masseter was next in size with the pterygoideus group close behind. The digastric shows a large area of insertion on the ventral border of the mandible and was also of considerable size.

The transverse condyle of *Stylinodon* is set only very slightly above the tooth row. When moment arms in a parasagittal plane (after the manner of Smith and Savage 1959) are calculated for the three major jaw-closing muscle groups, they are seen to be subequal in length (Fig. 49f): no significant differences are readily detected between the moment arms, and *Stylinodon* does not readily fit into either Smith and Savage's (1959) "carnivore" or "herbivore" category, but rather seems to be intermediate between the two (as is also the case for the manus of *Stylinodon,* see below). Primitively the temporalis group is the dominant muscle group (Smith and Savage 1959; Turnbull 1970), with a large moment arm. The condyle is low and the coronoid is high. This arrangement is retained in many carnivores, whereas in many herbivores the masseter or pterygoideus group, or both, is enlarged, the moment arm of the masseter group is increased over that of the temporalis, the condyle is raised high above the tooth row (perhaps primarily to insure simultaneous occlusion of the upper and lower tooth rows [Greaves 1974]) and the coronoid process rises only slightly higher than the condyle. In *Stylinodon*

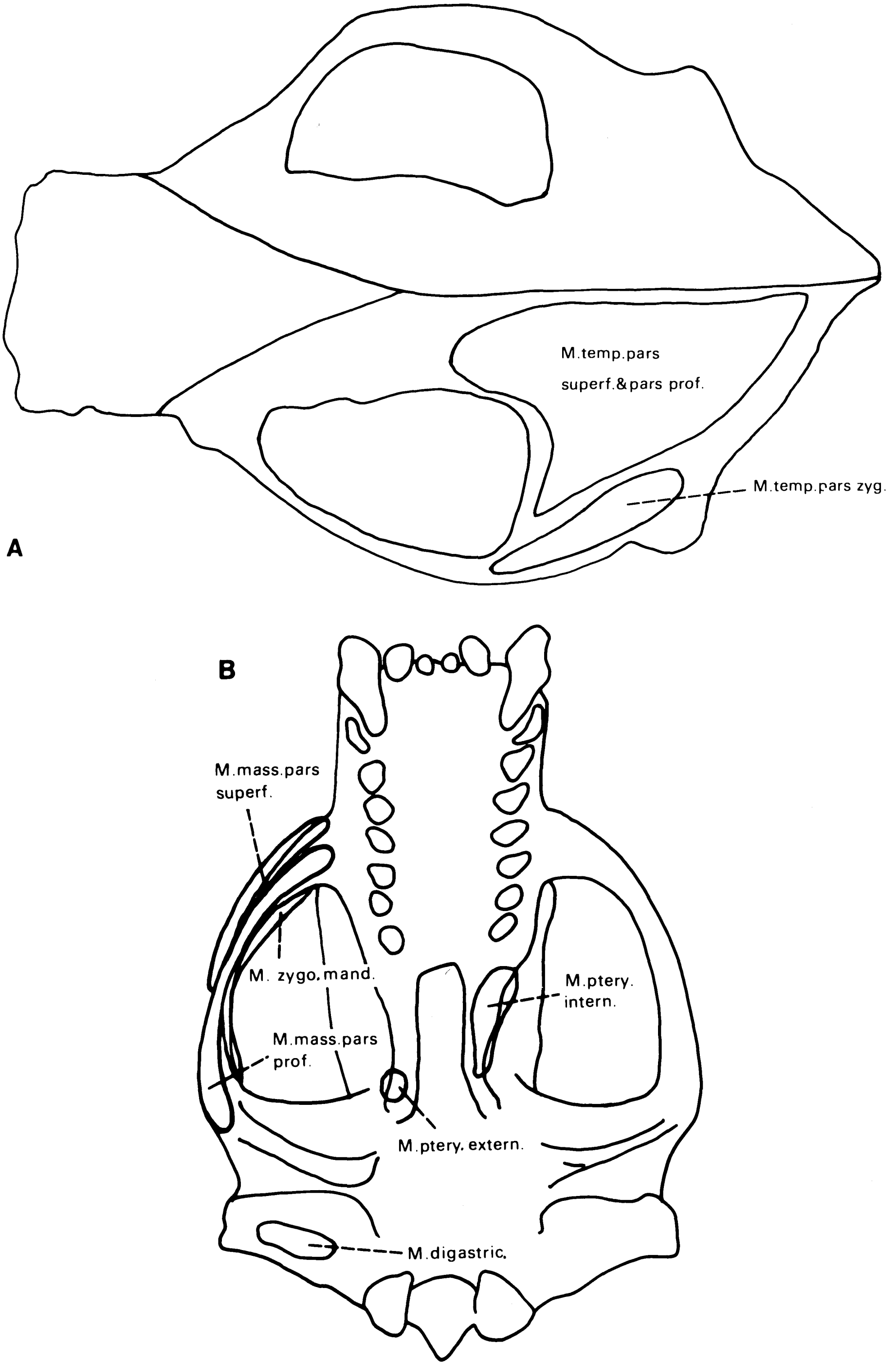


FIG. 48. Sketch maps showing the general areas of origin and insertion of the major muscles of the masticatory apparatus of *Stylinodon mirus*. *a*) Dorsal view of skull. *b*) Ventral view of skull. *c*) Left lateral view of skull. *d*) Labial view of mandible. *e*) Lingual view of mandible. *f*) Occlusal view of mandible.

Muscles represented: M. temporalis pars superficialis; M. temporalis pars profunda; M. temporalis pars zygomatica; M. masseter pars superficialis; M. masseter pars profunda; M. pterygoideus internus; M. pterygoideus externus; M. zygomaticomandibularis; M. diagastricus; M. genioglossus.

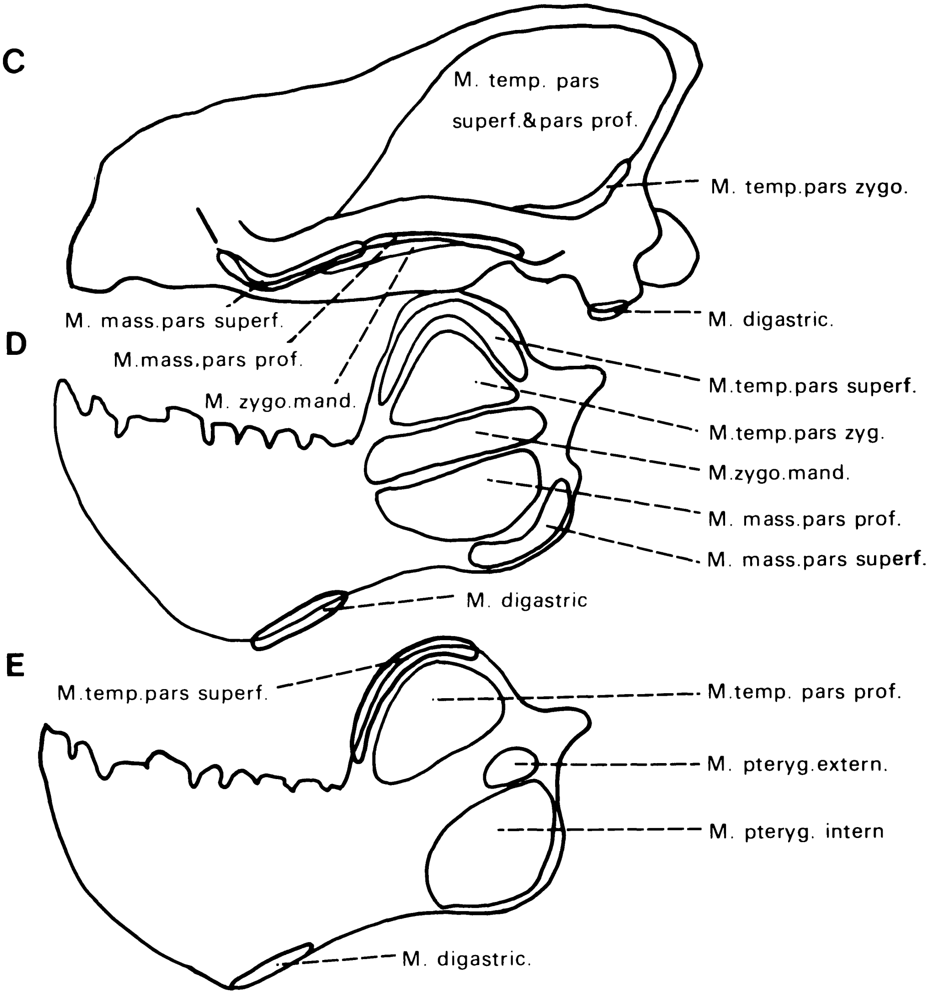


FIG. 48.—*Continued.* See legend on p. 135.

the temporalis group is still large and the condyle is still relatively low. However, the masseter and pterygoideus groups are also large and the moment arms of all three groups are subequal.

The ratio of the moment arm of the temporalis muscle group to that of the masseter muscle group is a measure of the relative development and importance of these muscle groups in the jaw-closing apparatus of a mammal (cf. Smith and Savage 1959). In both clades of taeniodonts, the conoryctids and the stylinodontids, this ratio decreases in later and progressively more derived forms (Fig. 49) indicating the increasing importance of the masseter complex relative to the temporalis group. Thus, this ratio is approximately 1.5 in *Onychodectes,* 1.2 in *Conoryctes,* 1.4 in *Wortmania,* 1.3 in *Psittacotherium* and 1.1 in *Ectoganus* and *Stylinodon.*

The mandibular condyles of *Stylinodon* are elongated transversely and articulate in the shallow glenoid fossae; thus the condyles were free to slide over the flattened squamosal surface and allowed the jaws to move mediolaterally to a limited degree and also anteroposteriorly, as in some extant herbivores (Smith and Savage 1959). Apparently this is a modification of a primitive (i.e., carni-

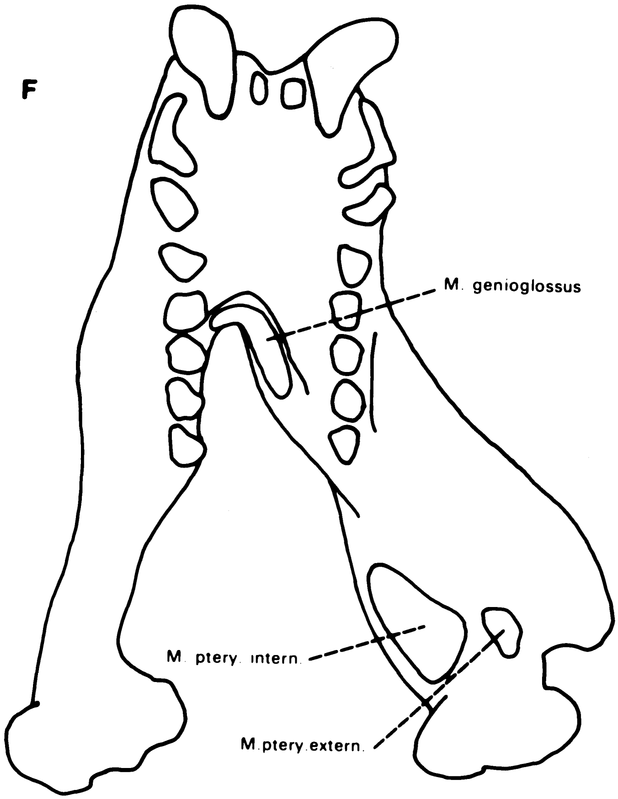


FIG. 48.—*Continued.* See legend on p. 135.

vorelike) condition. In *Stylinodon,* as in *Ailuropoda* (Davis 1964, p. 51), the glenoid fossa is shallow and somewhat expanded transversely to allow some side-to-side motion of the teeth, whereas the postglenoid processes are medially set, allowing the condyles to pivot around them laterally (such that, when pivoted, the sagittal axis of the mandible was at an acute angle to the sagittal axis of the skull). However, these adaptations in *Stylinodon* appear to be poorly developed and perhaps were fairly inefficient.

The biomechanics of the jaw-closing mechanism of *Stylinodon* can be analyzed using the bifulcral model of Bramble (1978). In this model (Fig. 50), the bite point is considered an independent occlusal fulcrum along with the traditional joint fulcrum, and under analysis the lower jaw is considered to rotate about this point as well as about the craniomandibular joint. Thus, there are vertical rotational forces at the bite point (B) and also secondary rotational forces at the condyle of the jaw (r). Whereas the forces applied at the bite point by the jaw musculature are always positive (i.e., they drive the jaws together), at the craniomandibular joint they may be positive (i.e., driving the condyle against the glenoid fossa), negative (driving the condyle away from the glenoid fossa) or zero. There are also horizontal translational components to the forces generated by the jaw-closing muscle groups. These forces may be positive (driving the mandible anteriorly), negative (driving the mandible posteriorly) or zero.

The external morphology of the craniomandibular joint in *Stylinodon* consists of a relatively heavy bony roof vertically above the mandibular condyle and a relatively small postglenoid process. There is no postglenoid "hook," as found in some carnivores (see Bramble 1978) and used to passively resist negative rota-

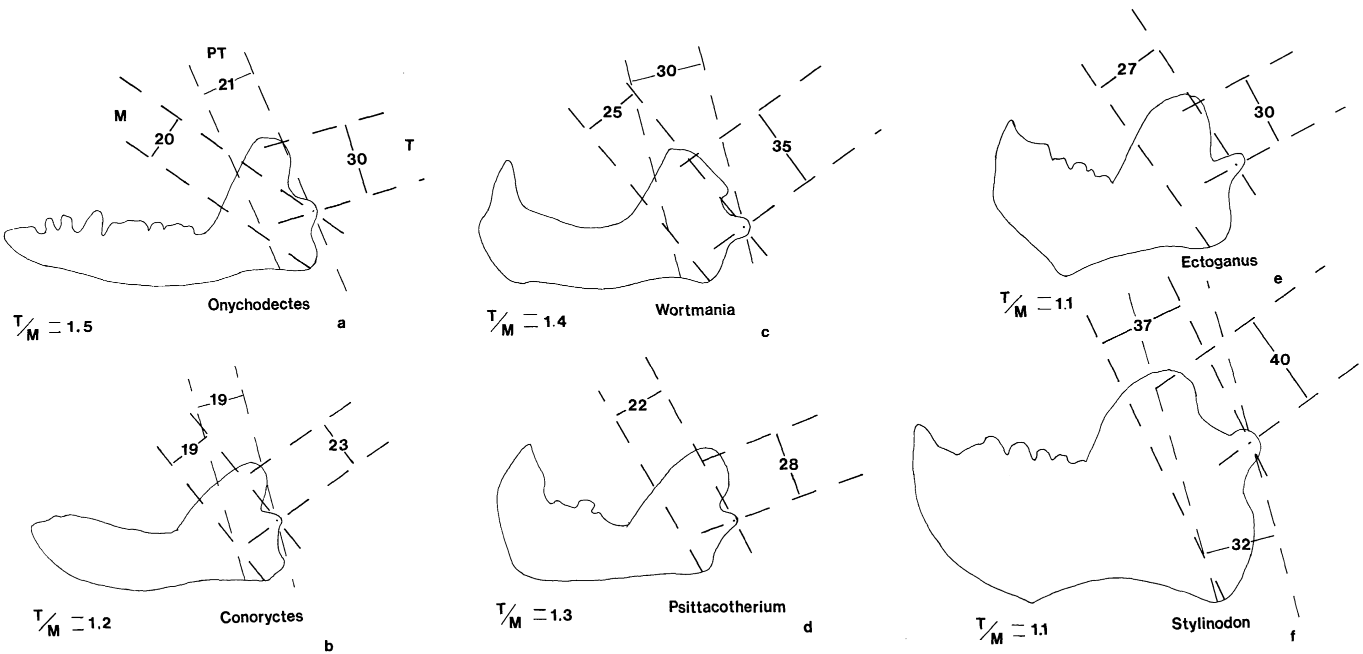


FIG. 49. Diagrams of the lower jaws of taeniodonts showing the moment arms for the temporalis (*T*), masseter (*M*) and pterygoideus (*PT*) muscle groups. *a*) *Onychodectes tisonensis*. *b*) *Conoryctes comma*. *c*) *Wortmania otariidens*. *d*) *Psittacotherium multifragum*. *e*) *Ectoganus gliriformis*. *f*) *Stylinodon mirus*.

tional displacement. Thus the gross morphology of the craniomandibular joint in *Stylinodon* is indicative of moderately strong positive rotational values (+r) and translational values (t) which are slightly positive to zero. This is the condition seen in most generalized mammals (Bramble 1978). Furthermore, positive *r* values are correlated with the use of the more anterior dentition, and it is the anterior dentition in particular which is enlarged and specialized in *Stylinodon.*

A simple vector analysis of the jaw-closing muscles of *Stylinodon,* after the manner of Bramble (1978), leads to similar conclusions. Thus, when the bite point is at the most anterior point of the jaw (at the tips of the canines), the displacement of the condyle is predominantly upward in a nearly vertical direction (Fig. 50). As the bite point is moved posteriorly, the force applied to the bite point increases and the secondary rotational value decreases to zero at approximately the second molars, and then becomes negative posterior to the tooth row (Fig. 50; Table 3).

The gape of *Stylinodon* must also be considered, i.e., whether it could open its mouth wide enough to clear the canines. Herring (1975) and Herring and Herring (1974) have studied adaptations to gape in mammals. Using their formula as applied to *Stylinodon* (Fig. 51 and explanation thereof), a stretch factor of 1.20–1.30 for the superficial masseter would be involved in opening the jaws by 25–35 degrees; this would be enough to clear the canines. The upper limit, involving a stretch factor of 1.40 (Herring and Herring 1974 consider 1.3–1.4 a probable maximum stretch factor for tendinous masticatory muscles), may have given a gape of approximately 50 degrees in *Stylinodon.*

The occlusal relationships of the upper and lower teeth are such that when the jaws are at rest and centered one upon the other, the upper inner pair of incisors occlude with the single pair of lower incisors. The large outer incisors occlude with the posterior (grinding) parts of the lower canines. The anteromesial edges of the upper canines occlude with anterodistal edges of the lower canines. The posterolingual parts of the upper canines occlude with the anteroposteriorly elongated lower first premolars. The posterolingual parts of the upper P^1s occlude with the anterolabial parts of the P_2s. Anterior P^2 occludes with posterior P_2 and posterior P^2 occludes with anterior P_3. This situation proceeds for the length of the rest of the dentition posteriorly, ending with the anterior M^3 occluding with posterior M_3. The lower tooth rows are set closer together than the upper tooth rows.

In analogy with peccaries (Tayassuidae; Kiltie 1981), it is suggestive that the somewhat interlocking canines of the stylinodontids served as occlusal guides and also acted to resist forces during mastication that would tend to dislocate the lower jaw. As Kiltie (1981, p. 467) comments concerning pigs vs. peccaries, "If canines function to buttress the jaw and guide occlusion, I would not expect sexual dimorphism in canine size because the benefit would presumably be as important to females as to males. In contrast to most pigs, peccaries are not dimorphic in body size or in cranial traits." Likewise, I have not detected any sexual dimorphism within the Taeniodonta.

The teeth of *Stylinodon* have been described in a previous section. The cheek teeth wear such that on the cheek teeth the labial and lingual bands of enamel form sharp, high, anteroposteriorly elongated ridges with dentine valleys between. Seen from the side, the posterior cheek teeth wear such that the tips are triangular in shape. The anterior and posterior parts are worn lower, leaving an apex in the middle. All of the teeth are well spaced and do not occlude interstitially. The canines are loosely interlocking such that side-to-side motion was possible.

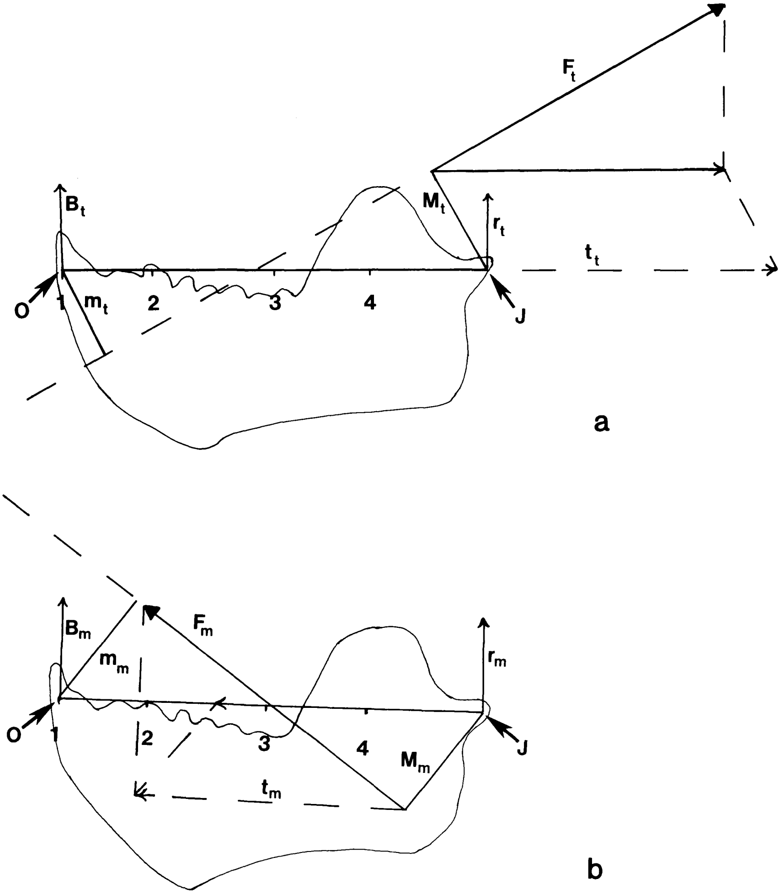


FIG. 50. A simple biomechanical analysis of the jaw mechanics of *Stylinodon mirus,* using the bifulcral model of Bramble (1978). *a*) Stick figure showing the action of temporalis (shown for bite point at 1, anterior tip of canine). *b*) Stick figure showing action of masseter (shown for bite point at 1, anterior tip of canine).

Abbreviations: B_m, B_t = Primary rotational or bite force for masseter (B_m) or temporalis (B_t); F_m, F_t = Muscular force of masseter (F_m) or temporalis (F_t); J = Joint fulcrum at jaw articulation; M_m, M_t = Primary moment arm of F_m or F_t; m_m, m_t = Secondary moment arm of M_m or F_t; O = Occlusal fulcrum of bite point; r_m, r_t = Secondary rotational force for masseter (r_m) or temporalis (r_t); t_m, t_t = Translational component of F_m or F_t; 1 = Bite point at the anterior tip of canine; 2 = Bite point at the middle of the premolar series; 3 = Bite point at the second molar (neutral point); 4 = Bite point posterior to the tooth row.

All numbers in the accompanying Table 3 are in arbitrary units. The muscular force generated by the temporalis = masseter was arbitrarily set at 100. Note that the translational forces generated by the temporalis and masseter remain constant (are independent of the bite point) and approximately cancel out one another. For calculated values of B_t, B_m, r_t and r_m at points 1 through 4, see Table 3.

On most specimens of taeniodonts, wear striations are not clearly visible, even under high magnification. This may be due to the shallow, fine nature of the striations which are easily obscured during fossilization. In general the teeth are worn smooth, with highly polished dentine/enamel occlusal surfaces. In a few unusual specimens, for example the lower jaw of AMNH 107954, extremely thin, faint striations are preserved on the dentine surfaces; more often only a few deeper striations or grooves will be seen preserved on the enamel ridges, whereas the dentine centers have a smooth to slightly pitted appearance.

When striations are preserved on the canines and cheek teeth they are nu-

TABLE 3. Values of bite forces and secondary rotational forces generated along the mandible of *Stylinodon mirus* (see Fig. 50). All numbers are in arbitrary units for comparative purposes.

POINT	DISTANCE OF O FROM J	B_t	B_m	R_t	R_m
1	130	25.4	30.0	23.1	28.5
2	102	33.3	35.3	17.6	22.5
3	65	52.3	55.0	0.0	0.0
4	36	94.5	100.0	−41.7	−44.4

merous, thin, parallel and transverse (oriented perpendicular to the length of the tooth row). This further corroborates side-to-side jaw motion for *Stylinodon* as suggested below (cf. Costa and Greaves 1981). The wear surfaces on the lower incisors of AMNH 107954 bear small, parallel striations running approximately anteroposteriorly, suggesting that perhaps *Stylinodon* was pulling vegetation through its mouth between the canines and incisors. The general lack of wear striations may also indicate a large crushing-puncturing functional component to the teeth of taeniodonts which would tend to wear down the teeth relatively quickly without producing striations (Crompton and Hiiemae 1970). The dominant side-to-side motion postulated for taeniodont mastication would also have an anteroposterior component which would produce a slight circular or oval grinding pattern. This could produce the smooth to slightly pitted surface usually seen on the dentine surfaces of taeniodont teeth. The slight pitting may be extenuated by the fossilization process in many cases, further obscuring any original striations. This discussion applies to the conoryctids as well as to the stylinodontids. I have observed a similar pattern of wear (including the relative lack of distinct striations) on the teeth of the wombat.

Based on the morphology of the teeth, the occlusal relationships of the teeth in centric occlusion, wear patterns seen on the teeth, and manipulation of actual specimens, an occlusal sequence can be postulated for *Stylinodon mirus*. This is diagrammatically illustrated and explained in Figure 52.

This evidence indicates that *Stylinodon* used its posterior cheek teeth to puncture, crush, slice and grind by moving the jaw up vertically, initially puncturing and crushing, accompanied by some jaw movement anteroposteriorly and more from side to side. The dominant grinding movement was from side to side. The anteroposteriorly elongated enamel ridges are at right angles to the side-to-side movement. The pattern of fit between the upper and lower cheek teeth (Fig. 52) acted as guiding ridges for the lateral grinding movement. *Stylinodon* chewed on one side at a time, as the uppers and lowers cannot occlude simultaneously on both sides.

The action of the major muscle groups during side-to-side chewing must be considered in plan view. As Smith and Savage (1959) have pointed out for *Strepsiceros,* the lateral motion on either side is brought about by a slight rotation of the whole jaw that can be produced by contraction of the masseter and pterygoid muscles on the occluded side or by contraction of the temporalis on the opposite side. Furthermore, Smith and Savage (1959) noted that if the temporalis is responsible for a large component of this movement, large stresses are imposed on the lower jaw across the symphysis, whereas if the masseter and pterygoid muscles are primarily responsible for the movement, only a small region of the mandible, where the active chewing is taking place, will be stressed. The latter is therefore more efficient and has evolved in most advanced ungulates. In *Stylinodon,* the temporalis group is large, as are the masseter and pterygoideus

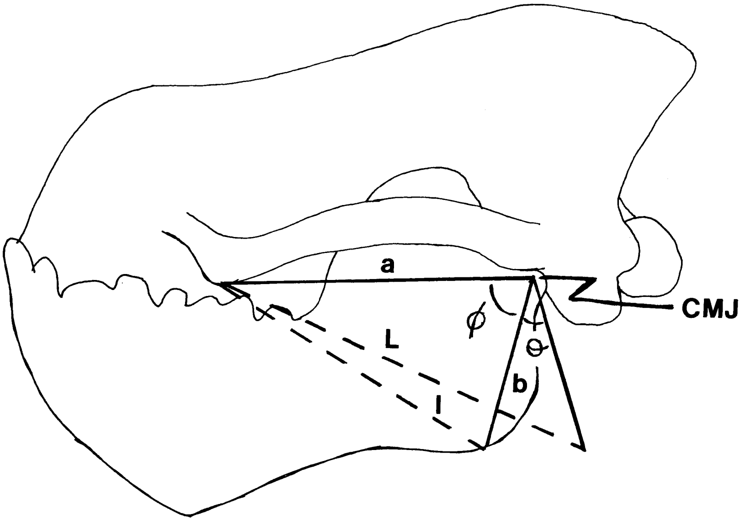


FIG. 51. A simple biomechanical analysis of the gape of *Stylinodon mirus* using the model of Herring and Herring (1974). In the figure, a and b are the distances of the origin and insertion of the superficial masseter, respectively, from the craniomandibular joint (CMJ) and ϕ is the angle between them. The l represents the length of the muscle in closed position and L represents the length of the muscle in open position when the jaw is rotated through the angle θ. The stretch factor $\frac{L}{l}$ is the positive square root of:

$$\left(\frac{L}{l}\right)^2 = \frac{a^2 + b^2 - 2ab\cos(\theta + \phi)}{a^2 + b^2 - 2ab\cos\phi}$$

Based on the figure (in arbitrary units), $a = 7.5$, $b = 4.3$, $\phi = 73$ degrees. Thus, if $\theta = 50$ degrees, $\frac{L}{l} = 1.40$, if $\theta = 35$ degrees, $\frac{L}{l} = 1.30$, if $\theta = 25$ degrees, $\frac{L}{l} = 1.22$.

groups. The symphysis of the mandible of *Stylinodon* is extremely heavy and thick as well. This suggests that in *Stylinodon* the temporalis was responsible for a large component of the side-to-side chewing, and the stresses generated, in part, were responsible for the massive symphysis in *Stylinodon*. The internally set postglenoid processes could possibly have acted as pivots for a transverse, arclike motion. This may have been a relatively inefficient way to process food, and may have contributed to the eventual extinction of the taeniodonts. All three groups of muscles acting together, but in differing directions, may have helped to keep the jaw from disarticulating.

The canines and anterior cheek teeth are greatly enlarged in *Stylinodon*. These teeth, and the incisors, may have served a crushing/grinding function. Occlusion between the upper and lower canines and P_1 may also have performed a cutting or slicing scissorlike function. Lastly, the enlarged canines may have, in part, been used in active digging, rooting or some other activity in which the upper canines, in particular, hit an especially hard surface. In several known specimens of *Stylinodon* (e.g., FMNH P 12185, FMNH PM 3895) an upper canine has had the tip partially broken off and an anteriorly directed chip of enamel removed. Subsequently, during the individual's lifetime through continued use of the canine, this facet became well worn. In other specimens of *Stylinodon* the canines are well-worn posteriorly, but retain sharp tips and a full enamel covering anteriorly.

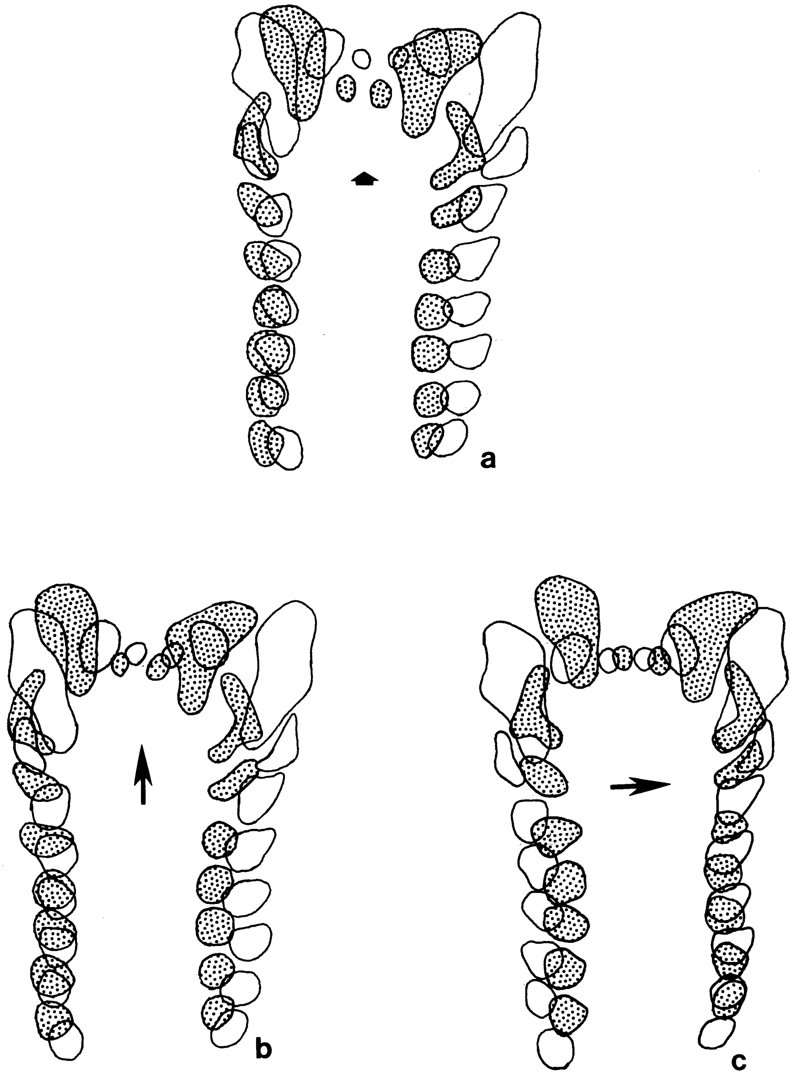


FIG. 52. Postulated occlusal pattern in *Stylinodon mirus* as the mandible is brought up to occlude with the upper jaw; the major chewing stress is on the left side in the sequence. Arrows indicate the predominant motion of the lower jaws in a horizontal plane relative to the uppers. *a*) The lower jaws, which are initially slightly left of center and placed relatively posterior to the uppers, are brought up vertically and slightly forward to begin to occlude with the upper jaws. *b*) Tooth to tooth occlusion (contact) begins, first at the canines and then progressively posteriorly, and the lower jaws are moved relatively anteriorly. *c*) With a short, powerful transverse stroke the lower jaws are moved from left to right of center and the right condyle might pivot laterally around the right postglenoid process.

Masticatory Apparatus of Other Stylinodontids

It appears, based on the close similarity between the morphologies of the jaws of *Stylinodon* and those of *Ectoganus* and also *Psittacotherium,* that the latter two had a jaw musculature extremely similar to that of *Stylinodon.* As described previously, the unworn posterior cheek teeth of *Ectoganus* bear bilophodont, transversely cuspidate ridges. As the upper and lower jaws of *Ectoganus* occluded, the anteroposterior motion of the jaws would produce a certain amount of shear between the transverse ridges of the upper and lower teeth. However, these crests, even when unworn, are relatively low, blunt and uneven, and they rapidly wore off completely; thus it appears that they were used primarily in a crushing/puncturing capacity. Unworn, the transverse crests may have acted to a certain extent as guides for side-to-side motion. The same may also have been true for the unworn, presumably bilophodont dentition of *Stylinodon*. However, extremely worn teeth of *Ectoganus* do not come to trihedral points as in *Stylinodon*; this suggests that side-to-side chewing motion was not as well developed in *Ectoganus* as in *Stylinodon*. In *Psittacotherium* and *Wortmania* there may have been greater emphasis on vertical, puncturing and crushing movements as opposed to side-to-side movement of the jaws relative to one another.

Occiput and Neck Posture and Musculature in *Stylinodon*

As noted previously, *Stylinodon* had a short, thick neck. The posterior cervical vertebrae are thin, wide and deep with short spines and small transverse processes. The atlas is relatively large, but thin anteroposteriorly and could easily rotate (i.e., twist on the vertebral axis) through approximately 25 degrees to either side. When the axis, atlas and skull are articulated, even taking into account the separation of these bones from each other due to loss of intervening soft tissue (cartilage, etc.), the odontoid process of the axis runs through the entire length of the anteroposteriorly shortened atlas and slightly protrudes into the foramen magnum between the posteroventral and medial (internal) surfaces of the occipital condyles. The occipital condyles have large, distinct facets for articulation with the odontoid process. This could have provided a stable and powerful joint, particularly for resisting lateral stresses placed on the head.

The occipital condyles are large, project backwards from the occiput, are deeply convex both dorsoventrally and transversely and fit deeply into the atlas such that the occipital condyles almost made contact with the transverse articular surface of the axis. This again indicates an extremely strong and stable joint. It appears that the skull (using the zygomatic arches as a horizontal plane) was usually carried at an angle of 160–70 degrees to the axis of the cervical series. However, the head could be moved from an angle of about 10 degrees above the cervical series to 40 degrees below the cervical series. The longitudinal axes of the cervical vertebrae are horizontal or only very slightly oblique, indicating that the head was probably carried at about the level of the body.

The first dorsal vertebra of *Stylinodon* bears a large, high, massive spine which rises vertically to a height slightly above the occiput. This spine is flat transversely and wide anteroposteriorly. Its dorsal end is further anteroposteriorly and heavily rugose dorsally. The rest of the thoracic vertebrae bear similar spines that are directed slightly posteriorly and decrease in size and height posteriorly. The apex of the high, vertical, triangular occiput bears a roughened surface for the insertion of the ligamentum nuchae, which helped hold the massive skull of *Stylinodon* in a horizontal position. Deep to this tendon, the depressions seen in the middle of each side of the occiput may have taken, in part, the M. rectus capitis posticus group from the occiput to the atlas–axis. The lateral occipital ridges are roughened and probably took the complexus group attaching to the posterior cervical vertebrae and, superficial to it, the splenius inserting onto the outer lambdoidal ridge and arising from the anterior thoracic (dorsal) neural spines and middle of the neck. These muscles helped to keep the large head of *Stylinodon* erect.

The mastoid processes of *Stylinodon* are extremely large and almost as broad as the neck is long. They probably served as attachments for an enlarged sternomastoid and large cleidomastoid which attached to the massive manubrium and clavicle respectively (a large clavicle is postulated for *Stylinodon* based on analogy with *Psittacotherium* and the large acromion process of *Stylinodon* to which the clavicle probably attached). These muscles served both to depress the head and to move it from side to side. The enlargement of these muscles, as indicated by their areas of attachment, suggest that *Stylinodon* could have used its head, snout and canines in digging, grubbing, or rooting (see below).

Forelimb Posture in *Stylinodon*

In *Stylinodon,* the proximal surfaces of the metacarpals (the three enlarged ones, two through four, which are functionally important) are relatively flat. That of metacarpal three is slightly convex dorsoventrally and that of metacarpal four is slightly concave dorsally and slightly convex ventrally. This indicates that little flexion or extension took place between the distal carpal series and the metacarpals. The illustration by Patterson (1949b, p. 253, fig. 4C) suggests that the proximal surfaces of the metacarpals were flush with one another and presented a smooth surface to the distal surface of the carpals which likewise was relatively smooth and transversely convex. This would suggest that the manus of *Stylinodon* was capable of a relatively significant amount of radial–ulnar deviation between these two series. However, this is not the case. In actuality, the proximal surfaces of the distal carpals are not flush, but slightly stepped. Thus, the proximolateral edge of the third metacarpal contacts the mediodistal edge of the unciform. This arrangement would greatly limit radial–ulnar movement of this joint.

The carpal series of *Stylinodon* is significantly modified from that seen in *Onychodectes* or *Psittacotherium.* The carpal arrangement is much more serial in aspect, rather than alternating. The carpals have become large, stout, and thick. The magnum especially is enlarged; the lunar rests firmly against it and the unciform. The centrale is reduced or lost. The large proximal surface of the lunar rests against almost the entire distal surface of the radius. This arrangement appears to be an adaptation to having relatively heavy stress placed on the manus.

Between the proximal and distal carpal series, a fair amount of flexion but little, if any, extension or hyperextension appears to have been possible. The proximal surfaces of the distal carpal series dorsally are slightly concave (dorsoventrally) to nearly flat and convex ventrally. The distal surface of the proximal carpal series matches this shape. Thus, whereas the manus between these two joints could be flexed 30 to 45 degrees, little if any hyperextension was possible. The lunar (and presumably also the scaphoid) has developed a ventral "heel" (see Yalden 1971, p. 482, fig. 15C, D). Distally, the convex articular surfaces of the unciform and magnum have shifted ventrally to articulate in this concave heel. Proximally, the large, convex articular surface of the lunar rests in the concave distal articular surface of the radius and was capable of both moderate hyperextension and a considerable amount of flexion. This joint may have been capable of moving through an angle of approximately 50 degrees total. When flexed, the heel of the lunar could rock on the flexor lip of the radius and allow further flexion. The flexion hinges described here for *Stylinodon* are intermediate between those described by Yalden (1970, 1971) for Carnivora, in which a large amount of flexion is possible (but little extension), and those for most ungulates in which a large amount of flexion is still possible, but a more stable joint and firmer base are also formed. The distal surface of the radius and the large styloid process of the ulna formed a large, transversely concave articular surface in which the proximal carpals articulated and allowed radial–ulnar movement through perhaps 40 degrees at this joint.

The articular surfaces of the distal ends of the metacarpals extend far anteriorly and posteriorly (dorsally and ventrally) and allowed great extension and flexion of the proximal phalanges. The squared-off outline, however, reduced mediolateral movement to a minimum. Movement was limited between the proximal and medial phalanges. The distal surfaces of the medial phalanges are saddle-shaped and extend far anteriorly and posteriorly. These were matched by the articular surfaces of the unguals bearing median keels and greatly limited mediolateral movement. However, the claws (borne by the unguals) could be hyperextended and flexed through perhaps 100 degrees. Extension was limited by the proximodorsal borders of the ungual phalanges and flexion was limited by the proximoventral protuberances of the unguals.

In the articulated manus of *Stylinodon,* the metacarpals form an angle of 40–45 degrees to the horizontal when the proximal articular surface of the lunar is facing straight up. Usually, the ulna and radius probably were directed posteriorly (cf. Jenkins 1971b) and likewise the proximal surface of the proximal carpus would be directed relatively posteriorly. Therefore, the manus of *Stylinodon* was probably plantigrade to subplantigrade.

The olecranon process (sensu stricto, cf. Greene 1935) of the ulna fits into the olecranon fossa of the humerus when the elbow is fully extended. In this position the humerus and ulna–radius form an angle of approximately 140 degrees. The elbow could be flexed to a point such that the ulna–radius and humerus formed an angle of approximately 40 degrees. At an angle of 90 degrees the articular surfaces of the radius and ulna completely cover the distal articular surface of the humerus; it can be postulated that this may have been the position (or perhaps slightly more flexed) in which the humerus and radius–ulna were often held.

When the humerus is articulated with the scapula, the two bones fit together most easily when at an angle of approximately 90–100 degrees to each other and with the distal end of the humerus oriented slightly laterad at an angle of approximately 25 degrees to a parasagittal plane. The humerus and scapula could probably articulate with each other (seen in a parasagittal plane) through angles from 60 to 180 degrees. Likwise, seen in dorsal or ventral view, the humerus could probably have been moved with ease through 50 degrees either side of the parasagittal plane.

The above analysis suggests that the usual stance and posture for *Stylinodon* was a slight variation of that of a "typical" noncursorial mammal, as has been described by Jenkins (1971b, typified by *Didelphis*).

Forelimb Musculature in *Stylinodon*

The scapula of *Stylinodon* is large, broad and slightly longer than the humerus; this in itself indicates an extremely powerful, if slow, forearm. Referring to the scapula, Smith and Savage (1956, p. 606) state that "in fossorial types the spine is usually high and long and carries an elongated acromion process, often extending a great distance beyond the glenoid." This describes the scapula of *Stylinodon.* In contrast, though, other features often seen in the scapulae of advanced fossorial animals, such as a backward prolongation, ventral curvature and secondary spines (cf. Smith and Savage 1956) are absent in the scapula of *Stylinodon.* However, this may only indicate that *Stylinodon* is not as derived or specialized toward the fossorial condition as some extant mammals.

The acromiotrapezius originated from the neural spines of the cervical and first thoracic vertebrae and inserted on the large spine and metacromion process of the scapula, drawing the scapula dorsad and holding the scapulae on either side together. Originating on the atlas and occipital and inserting also on the metacromion process was the levator scapulae ventralis which moved the scapula craniad.

The large infraspinous fossa of the scapula was occupied by the infraspinatus which inserted on the greater tuberosity of the humerus and abducted the humerus. The smaller supraspinous fossa was occupied by the supraspinatus which inserted on the greater tuberosity of the humerus medial to the insertion of the infraspinatus and held the shoulder joint (Davis 1949) and also extended the humerus.

The rhomboideus originated from the neural spines of the cervical and first thoracic vertebrae and inserted along the vertebral border of the scapula; it served to both raise the head and draw the scapula toward the head.

The large teres major originated from the posterodorsal border of the scapula and inserted on the medial surface of the humerus along the middle of the shaft at the large, slightly recurved teres eminence. It rotated and retracted the humerus. The latissimus dorsi probably also inserted at this point, originating from the last thoracic and lumbar vertebrae, and also retracted the humerus. The spinodeltoid originated along the spine of the scapula and the acromiodeltoid originated on the acromion process; both inserted on the deltopectoral crest of the humerus and served to retract and abduct the humerus.

As Smith and Savage (1956, p. 607) note, in digging the manus of fossorial animals "passes through an ellipse, enabling the arm to avoid the earth scooped out in the previous movement." Thus in the scapulae of fossorial animals a large acromion process is often developed (as is seen in *Stylinodon*) for attachment of muscles to produce powerful abduction and adduction, as well as extension–flexion, of the forelimb.

Medially and ventrally, the subscapular fossa was occupied by the subscapularis which inserted on the lesser tuberosity of the humerus and pulled the humerus medially. Dorsal to the subscapularis, the serratus inserted. It originated from the transverse processes of the posterior cervical vertebrae and the middle and anterior ribs. It could draw the scapula craniad or ventrad and also helped to support the trunk.

The long head of the triceps originated on the posteroventral (glenoid) border of the scapula. The lateral head of the triceps originated from the greater tuberosity and deltopectoral crest of the humerus. The medial head of the triceps must have arisen from somewhere along the shaft of the humerus, but its exact origin is unclear. All three parts of the triceps inserted on the olecranon of the ulna and were powerful extensors of the forearm.

The large pectoralis major inserted on the enlarged deltopectoral crest of the humerus and originated from the sternum (which, as indicated by the preserved manubrium, was greatly enlarged in *Stylinodon*). The large pectoralis minor also originated from the sternum and inserted on the ventral side of the humerus. Likewise, the pectoantibrachialis originated from the manubrium and probably inserted on the fascia of the forearm. These muscles primarily served for adduction and retraction of the forelimb.

The biceps brachii originated from the upper margin of the glenoid cavity (coracoid process) of the scapula and inserted on the anteroproximal portion of the radius. As in titanotheres (cf. Gregory in Osborn 1929, p. 715), the facets between the proximal radius and ulna are moderately flattened, and whereas the radius could be rotated on the ulna to a limited degree, full supination may not have been possible. Likewise, in *Stylinodon,* as in titanotheres, the tubercle of the radius was reduced and no longer served as the chief insertion point of the biceps. In *Stylinodon* the biceps brachii was primarily a powerful flexor of the forearm. The brachialis probably originated on the middle of the lateral side of the shaft of the humerus and passed medially along the anterodistal aspect of the humerus to insert on the ulna medial and slightly distal to the coronoid process. The brachialis also flexed the forearm.

The forearm of *Stylinodon* bore the usual extensors (largely on the lateral surface) and flexors (largely on the medial surface) found in most mammals. The brachioradialis (supinator longus) originated slightly distal to the middle of the humerus on the lateral side and inserted on the outer side of the distal end of the radius. It rotated the manus to a supine position. From the area of the large supinator ridge and lateral epicondyle originated a set of powerful extensors (e.g., extensor digitorum lateralis, extensor digitorum communis, extensor carpi radialis, extensor carpi ulnaris), which inserted on the metacarpals and extended the manus and digits. Originating from the medial surface of the forearm and medial epicondyle, the pronator teres inserted on the mediodistal aspect of the radius and rotated it to a prone position. Originating from the strong pronator ridge and medial epicondyle of the humerus, and in some cases also from the ulna, were a powerful set of flexors (e.g., flexor carpi radialis, palmaris longus, flexor carpi ulnaris, flexor digitorum profundus) which inserted on the metacarpals and had the general function of flexing the metacarpals and digits.

The relatively large scapula with well-developed spine, acromion and metacromion processes; the large manubrium and clavicle; the short, stout humerus with a large deltopectoral crest, pronator and supinator ridges and a wide distal end; the stout ulna and radius with a large olecranon on the ulna, and the shortened and thickened carpals and metacarpals all indicate that *Stylinodon* had an extremely strong and powerful, if slow moving, forelimb. The relatively wide distal end of the humerus and long, well-developed olecranon are suggestive of a burrowing/digging adaptation in *Stylinodon* (Goldstein 1972). In *Stylinodon* strength and force of the forelimb were selected at the expense of rapid motion. The forelimb of *Stylinodon* is the opposite extreme of the gracile limbs seen in extant cursorial forms (e.g., cats, horses) and rather shows similarities to fossorial forms (e.g., *Orycteropus*; see discussion below).

Using my reconstruction of the forelimb posture of *Stylinodon* (Fig. 31), the ratio of the length of the moment arm (l) of the M. teres major about the fulcrum of the forelimb at the glenoid fossa to the perpendicular distance to the ground (h) is approximately ⅓ in *Stylinodon*. This compares well with the ratio of ¼ given for the fossorial *Dasypus* by Smith and Savage (1956) and indicates a slow, powerful movement of the forelimb. In contrast, the same ratio in the cursorial *Equus* is $\frac{1}{13}$ (Smith and Savage 1956). The ratio of the length of the olecranon (from its tip to the middle of the sigmoid notch) to the length of the forearm and manus is a measure of the mechanical advantage of the triceps muscle (Smith and Savage 1956). In *Stylinodon* this ratio is 8.0 cm/32.4 cm = .25, a value which falls into the "aquatic, fossorial and graviportal types" of Smith and Savage (1956, table 1). Contraction of the M. teres major by one-third to one-fifth would rotate the humerus through 30 to 50 degrees.

Gambaryan (1974, p. 250–52) has noted that some bears actively dig for roots and tubers with the forelimbs, as well as using them for overturning stones and climbing. The manus of the bear is subplantigrade and bears relatively large claws, as did the manus of *Stylinodon*. Furthermore, the forelimb of the bear is characterized by powerful flexors of the digits and elbow, as suggested for *Stylinodon*. Gambaryan (1974) also points out that when bears run/gallop they generate much of the thrust with their forelimbs as compared with their hindlimbs. The forelimbs stay in contact with the ground longer than the hindlimbs. *Stylinodon,* characterized by more powerful fore- than hindlimbs, may have run or galloped in a similar manner. This mode of fast locomotion contrasts with that of most cursorial mammals in which the greater part of the thrust is provided by strong, powerful hindlimbs.

The brachial index (100 × length of radius/length of humerus) is 66 for *Stylinodon,* which is rather low (Gregory 1912; Howell 1944) and again indicates that the forelimb of *Stylinodon* was adapted for slow/powerful movements at the expense of speed.

Hindlimb Posture in *Stylinodon*

In *Stylinodon* the tarsals and metatarsals have medial and lateral articular surfaces (described above) that are set at angles such that when articulated, they formed a strong arc (through 180–210 degrees) that curved posteriorly, bringing the first and fourth digits together on the plantar surface of the foot. Thus, the metatarsals stood at an angle nearly perpendicular to the ground (probably 70–90 degrees to the horizontal plane) and the main weight of the animal was carried through the length of the metatarsals and large plantar sesamoids and thus to the ground. The small, wedge-shaped proximal and medial phalanges and large, stout unguals probably bore a minimum of weight, but rather had a stabilizing and bracing influence on the hindlimb. Whereas the weight of force passed through the central metatarsals and thus to the ground, the digits bearing the unguals could flex slightly, digging or locking into the substrate and preventing the limb from slipping, shifting or otherwise moving around. The tarsals, especially the cuneiforms, are small, stout, serially arranged bones with rather flat articular surfaces which likewise would form good weight-bearing elements. The distal end of the navicular lay solidly on the proximal ends of the underlying tarsals.

The head of the astragalus was fully rotatable in both directions on the proximal surface of the navicular. It is between these two surfaces that the majority of movement within the pes took place. However, it appears that the usual position of the astragalus would have its proximodistal axis (parallel to the neck) approximately 70 degrees (with the acute angle facing posteriorly) to 90 degrees to the horizontal. The medial and lateral sides of the trochlea of the astragalus bear distinct facets for articulation with the internal and external malleoli of the tibia and astragalus. Whereas the tibia–fibula and astragalus could easily articulate with each other through an angle of approximately 50 degrees (determined by manipulating the actual skeletal material), these facets show that the tibia-fibula and astragalus (using the proximodistal axis parallel to the neck as a reference line for the astragalus) were frequently oriented at an angle of approximately 110 degrees.

The proximal articular surface of the tibia is long anteroposteriorly and the articular surfaces of the condyles of the distal end of the femur extend far proximally on the posterior side. Furthermore, the medial (internal) condyle extends slightly further distally than the lateral condyle. Thus, the long axis of the tibia and femur appear to have most frequently formed an angle of 90 degrees, although they could articulate through perhaps as much as 125 degrees (60 to 185 degrees when hyperextended). Also, when the femur rested upon the proximal end of the tibia, it did not sit vertically (seen anteriorly or posteriorly), but rather angled approximately 10 degrees laterally. The angle of the head and neck of the femur indicates that when held horizontally (seen dorsally or ventrally) the long axis of the femur was frequently carried at an angle from about 15 to 50 degrees to a parasagittal plane of the animal, rather than swinging in a parasagittal plane.

Based on this analysis, a hindlimb posture used frequently by *Stylinodon,* which minimized muscle stress (i.e., stance or habituary stationary position: Jenkins 1971a, p. 132) can be diagrammatically represented as in Figure 31. This posture agrees well with the posture observed in extant noncursorial mammals (e.g., Jenkins 1971b). It may have been this hindlimb posture that *Stylinodon* took when actively digging or burrowing (analogous to Jenkins' [1971b] Phase III, propulsion thrust), whereas at rest (sitting position) it may have relatively flexed the pes, brought the tibia-fibula into a more nearly vertical position and the femur into a more horizontal position, perhaps even with the distal end of the femur higher than the proximal end. The same analysis also appears to hold for *Psittacotherium* and *Ectoganus*.

Hindlimb Musculature in *Stylinodon*

Unfortunately, the pelvis of *Stylinodon* is virtually unknown; only small fragments are preserved, most notably a part preserving the acetabulum in USNM 16664. The acetabulum is deeply concave and apparently provided a strong joint which was not easily dislocated when under heavy stress.

The large gluteus medius inserted on the greater trochanter of the femur of *Stylinodon*. It would have originated from the crest and lateral surface of the ilium as well as from the transverse processes of the last sacral and proximal caudal vertebrae. The gluteus medius served to abduct the thigh. Partially covering and set slightly posterior to the gluteus medius was the thin gluteus maximus. This inserted along the proximolateral side of the femur. In *Wortmania, Psittacotherium* and *Ectoganus* there is a small to moderately developed, but high-set, third trochanter on which the gluteus maximus inserted in part. The third trochanter is lost in *Stylinodon*. This may indicate a relative reduction in size of the gluteus maximus (corresponding with an increase in the size of the gluteus medius). Alternatively, it may indicate that the point of insertion of the gluteus maximus migrated up the shaft until it primarily inserted on the greater trochanter along with the gluteus medius. The gluteus maximus originated from the transverse processes of the last sacral and first caudal vertebrae and also served to abduct the thigh.

The biceps femoris would have originated from the ischium and inserted on the stout patella and anteroproximal part of the tibia. It acted to abduct the thigh and flex the crus. Serving the same function was the caudofemoralis which would have originated from the transverse processes of the proximal caudal vertebrae and also inserted on the patella.

On the posteroproximal surface of the femur within the area of the shallow digital fossa probably inserted the gemelii, obturator internus and externus and the quadratus femoris. These originated primarily from the ischium, but also perhaps from the ilium and pubis to a certain extent. They served to abduct, retract and rotate the thigh.

The psoas, originating from the transverse processes of the lumbar vertebrae, and the iliacus, originating from the ilium, probably inserted on the lesser trochanter. The adductor muscle group and pectineus arose from the pubic symphysis, pubis and ischium and inserted along the posterodistal surface of the femur and perhaps also in the area of the medial epicondyle. These served as powerful adductors of the thigh.

In the proximal and middle part of the anterior aspect of the femur originated the vastus muscle group, which inserted on the patella and extended the crus. The rectus femoris originated on the ilium near the acetabulum, inserted on the patella and also served to extend the crus.

The sartorius arose from the ventral border of the ilium and inserted on the internal tuberosity of the tibia and patella. It served to adduct, flex and rotate the thigh. The gracilis arose from the area of the pubic symphysis, inserted on the proximomedial aspect of the tibia posterior to the sartorius and also served to flex the hind leg.

The gastrocnemius formed a large muscle running along the posterior surface of the crus. It originated primarily from behind the condyles of the femur, ran the length of the crus, and inserted on the calcaneum as the tendon of Achilles. The gastrocnemius served as a powerful ventroflexor of the pes. The popliteus originated on the large lateral epicondyle of the femur and inserted on the proximolateral aspect of the tibia. It served to flex and rotate the crus. The soleus arose from the proximoposterior aspect of the fibula and inserted on the calcaneum along with the gastrocnemius, serving much the same purpose. The plantaris arose, along with part of the gastrocnemius, from the patella and passed by the ventral surface of the calcaneum to divide and insert on the ventral surfaces of the digits. It served to flex the digits.

Originating from the proximal anterolateral side of the crus, and also from the lateral epicondyle of the femur, were a series of extensors (e.g., tibialis anterior, extensor digitorum longus, peroneus muscle group). These inserted primarily on the metatarsals and digits and served to extend (dorsiflex) the pes and digits.

Originating from the posteromedial side of the crus were the powerful extensors, some of which have already been discussed above (gastrocnemius, soleus, plantaris, popliteus). The tibialis posterior and flexors of the digits (e.g., flexor brevis digitorum, flexor longus digitorum, flexor longus hallucis) inserted on the ventral (plantar) aspects of the tarsals, metatarsals and digits. As previously noted by Gazin (1952, p. 28), these flexor muscles appear to have been extremely powerful. The unusual process (described in Chapter 3) which appears on the medial side of the proximoventral aspect of the tibia, the well-developed postero-internal margin of the navicular and the ventrointernal prominence of the navicular appear to have served as muscle attachments for these powerful ventroflexors of the pes and digits.

The lengths of the femur, tibia, and pes of *Stylinodon* expressed as percentages of the total hindlimb length are 41%, 32% and 27% respectively. Thus, the relative lengths of these elements of the hindlimb of *Stylinodon* decrease distally, as is seen in graviportal types (Smith and Savage 1956, table 2). Gambaryan (1974, p. 75, fig. 61) has demonstrated that shortening of the foot and tibia leads to a drecrease in the force moments of the talocrural joints and thus allows them to bear more weight. Gambaryan (1974, p. 75) states that "naturally, with very large increases of body mass or of the forces developed by the limb, one of the changes of the ratios in the limb levers must be a decrease in the relative size of the distal segments." This statement applies well to *Stylinodon* and suggests that the hindlimb of *Stylinodon* was under considerable stress. I suggest that *Stylinodon* used its hindlimbs as a powerful, stable support while digging with its forelimbs, somewhat analogous to the manner in which *Orycteropus* and other extant fossorial forms dig. It is also interesting to note in this connection that Gambaryan (1974, p. 54, fig. 47) has suggested that the parasagittal positioning of the hindlimbs and the asymmetrical gait of mammals indicates that the ancestor of the mammals primitively dug to obtain its food.

When the index of slenderness [= (length of leg)squared/100 × cross-sectional area of the femur: see Smith and Savage 1956] is calculated for the femur of *Stylinodon,* it is approximately 4.0 for USNM 16664 and 5.29 for USNM 18425. These indices are extremely low, indicating a strong, robust femur, and fall within the graviportal range of Smith and Savage (1956, table 3). This further supports the hypothesis that *Stylinodon* used its hindlimbs as a powerful support or brace. The cross-sectional areas of the tibia-fibula and pes of USNM 18425 appear to be smaller than those of the femur, i.e., the limb is tapered distally. However, this is common to all mammals (cf. Smith and Savage 1956) and just how much the limb of USNM 18425 was truly tapered distally, and how much of this is due to crushing of the specimen, is unknown.

The crural index (100 × length of tibia/length of femur) is 79 in *Stylinodon.* This low value again supports the thesis that the hindlimb of *Stylinodon* was adapted for strength and power at the expense of speed. The intermembral index (100 × humerus plus radius length/femur plus tibia length) is 85 for *Stylinodon.* This value is approximately the same as that of *Solenodon* (Novacek 1980) and may be a primitive retention of a relatively generalized mammalian trait.

Trunk and Tail Posture and Musculature in *Stylinodon*

From what little is known of the vertebral column and ribs (described above), it appears that *Stylinodon* had a relatively stout, strong, only slightly arched and rather nonflexible vertebral column. This is indicated by the large, medially placed zygopophyses and slightly interlocking (convex anteriorly–concave posteriorly) centra of the thoracic vertebrae. It is assumed that the trunk and tail muscles were generally similar to those of extant mammals, but various muscles cannot be individually identified in *Stylinodon.*The ribs do bear heavily rugose, roughened external surfaces for strong costal muscles. The tail vertebrae are strong and stout. The anterior caudal vertebrae may have had strong, short transverse processes and poorly developed zygopophyses whereas the posterior caudal vertebrae are relatively featureless. Again, a stout, moderately long tail is indicated for *Stylinodon.*

FUNCTIONAL ANATOMY AND RECONSTRUCTION OF *ONYCHODECTES* AND THE CONORYCTIDS

In most features, the skeleton of *Onychodectes* is characteristic of that of a primitive, generalized mammal (using *Didelphis* and *Solenodon* as representative in many ways of the primitive therian morphotype: see Gregory 1910; Matthew 1937; Novacek 1980, 1982; B. F. Taylor 1978). The osteology of *Onychodectes,* as far as is known, has been described above. *Onychodectes* was approximately the size of *Tamandua,* but lacked the many specializations of the anteater and in general morphology and proportions *Onychodectes* was similar to the generally smaller *Didelphis.* Accordingly, the muscular anatomy of *Onychodectes* was probably very similar to that described for *Didelphis* by Coues (1872) and a hypothetical muscular reconstruction of *Onychodectes* as presented above for *Stylinodon* is unnecessary. Rather, here certain features of *Onychodectes* will be discussed from a functional aspect and contrasted with *Didelphis* and the supposed primitive mammalian morphotype as advocated primarily by Gregory (1910) and Novacek (1980).

As Matthew (1937, p. 241) noted, the skull of *Onychodectes* is "strikingly insectivore-like," i.e., it is relatively long, narrow and unspecialized. Primitive features that are seen in the skull of *Onychodectes* (cf. Novacek 1980, table 5) include terminal nares; nasals broadly expanded posteriorly; relatively large premaxillae; absence of postorbital processes; origin of temporalis muscles extending anteriorly over the frontals; occiput not greatly expanded posteriorly; lower jaw relatively shallow and long anteroposteriorly; postglenoid fossa moderately developed; anterior border of the coronoid process inclined slightly posteriorly and condyle not greatly transverse, only slightly above the tooth row and lower than the coronoid process.

Most features of the forelimb of *Onychodectes* are also remarkably similar to *Didelphis* and are shared primitive characters retained from the ancestral therian morphotype (cf. Novacek 1980, table 3). These features of the forelimb include: large metacromion process (postulated from the broken base of this process in AMNH 3576a); deltoid and pectoral crests of the humerus strong and converging to a high tuberosity; greater and lesser tuberosities of the humerus moderately large; entepicondylar foramen present and oval in shape; supinator ridge distinct; supracapitular and olecranon fossae shallow; capitulum relatively spindle-shaped; ulna robust with moderately long olecranon; deep semilunar notch; radius fully rotatable on ulna; manus with seven alternating carpals (scaphoid and lunar unfused, centrale present); digit number unreduced (i.e., five digits present); and small, unfissured claws on the manus. The manus of *Onychodectes* indicates a plantigrade to subplantigrade forefoot that was capable of a wide degree of flexion–extension and also radial–ulnar deviation with a slightly divergent and perhaps slightly opposable pollex. Digits one and five of the manus are slightly reduced relative to two, three and four, but only slightly more so than is seen in *Didelphis*. The forelimb of *Onychodectes* is definitely indicative of a noncursorial, perhaps even arboreal, mammal. In all probability, the forelimb posture of *Onychodectes* was similar to that of *Didelphis* as described by Jenkins (1971b). The incomplete nature of the known limb material of *Onychodectes* does not lend itself to the type of postural analysis done above for *Stylinodon*.

The hindlimb, except for the incomplete hind foot, is even more poorly known than the forelimb. The partial ilium of *Onychodectes* bears a deep acetabulum. What is known of the femur indicates a relatively flattened shaft with the following primitive features (cf. Novacek 1980, table 3, fig. 14): greater trochanter large and higher than the head of the femur; third trochanter moderately developed and high on the shaft; and digital fossa distinct. The femur of *Onychodectes* differs from that of *Didelphis* primarily in having a flattened shaft and a distinct third trochanter. The tibia and fibula were apparently separate in *Onychodectes*. Present knowledge of the tibia of *Onychodectes* shows no distinctive characters other than the articular surface for the astragalus which is discussed next.

The pedal elements, especially the astragalus and calcaneum, are the most distinctive postcranial elements of *Onychodectes*. Metatarsals and digits two through four are slightly elongated, and metatarsals and digits one and five are relatively reduced. The ungual phalanges are relatively small and unfissured. The astragalar-calcaneum proximal tarsal complex is of the leptictimorph morphotype (as previously noted by Matthew 1937; Szalay 1977). The pes of *Onychodectes* was subplantigrade to subdigitigrade and the metatarsals were probably often held slightly elevated off the substrate, although they may have been variably held from fully plantigrade to fully digitigrade. The leptictimorph foot seen in *Onychodectes* allows a great amount of flexion-extension at the tibial-astragalar joint (Szalay 1977). The trochlear arc is well-developed proximodistally, whereas the relatively sharp medial and lateral crests of the trochlea increase stability. The large, greatly convex navicular facet of the astragalus also suggests that a great amount of movement was possible between the proximal and distal tarsal elements both in a dorsoventral and transverse plane. Again, the hindlimb of *Onychodectes* suggests a generalized, noncursorial mammal whose general hindlimb posture may have been similar to that of the opossum (cf. Jenkins 1971b).

The pes of *Onychodectes* suggests a scansorial, perhaps partly arboreal, active mammal.

As noted in the description, *Onychodectes* may have had a relatively short neck. Very little can be said about the trunk of *Onychodectes,* although the lumbar vertebrae appear to have been large and strong; they bear large transverse processes. The tail of *Onychodectes* was extremely long and heavy. As in *Didelphis,* the more proximal and medial caudal vertebrae were large with distinct anterior and posterior transverse processes, whereas in the posterior caudal vertebrae these processes are greatly reduced and the vestigial zygapophyses do not contact between one vertebra and the next. It is thus possible that the tail of *Onychodectes* was prehensile to a certain degree.

Masticatory Apparatus of *Onychodectes*—Muscular Restoration

The lower jaw of *Onychodectes* is relatively long and slender with a long (extending to under P_3) but shallow and weak symphysis. The coronoid process is moderately high and the angle of the jaw is distinct. The condyle is set just above the tooth row, slightly transverse, and moved relatively freely in the shallow glenoid fossa. The zygomatic arches appear to have been relatively weak; the temporal fossae are moderately well developed. In overall appearance, the jaw of *Onychodectes* is similar to that of a carnivore (cf. Smith and Savage 1959), although this is probably due to retained primitive features. In *Onychodectes* the temporalis muscle group was the largest, followed in size by the masseter, pterygoideus and digastric groups. In *Onychodectes,* the moment arm of the temporalis is relatively the largest of any taeniodont (the ratio of the moment arms of the temporalis to the masseter is 1.5, the highest of any taeniodont). This agrees well with the postulated diet (see below) for *Onychodectes,* based on tooth morphology, which contained (probably primitively retained) a large carnivorous component. As Smith and Savage (1959) have pointed out, the larger temporalis (e.g., in carnivores) is mainly used in capturing prey, whereas all three muscle groups (temporalis, pterygoideus and masseter) are used in slicing and grinding in carnivorous forms. The digastric of *Onychodectes* was probably of moderate size and inserted on the ventral border of the mandible under the posterior cheek teeth as in *Canis* (Scapino 1976).

Simple biomechanical analysis of the jaw-closing mechanism of *Onychodectes* using the bifulcral model of Bramble (1978; Fig. 53), suggests that the temporalis group was used primarily for generating bite force on the canines and anterior dentition; here the primary function of the masseter may have been to prevent dislocation of the jaw (cf. Smith and Savage 1959). Posteriorly, in the area of the molars, force was generated by the temporalis and masseter. While biting and chewing, whether with the anterior dentition or with the more posterior dentition, primarily positive rotational loads, combined with some posterior translational motion, were applied to the craniomandibular joint.

Masticatory Apparatus of *Onychodectes*—Occlusal Relationships

The labial borders of the upper cheek teeth of *Onychodectes* are set slightly farther apart than the labial borders of the lower cheek teeth; however, as the upper cheek teeth are wider than the lowers, the lingual borders of the upper and lower cheek teeth are set at about an equal distance from each other in the palate and mandible. The cheek teeth are set in rows which are generally straight, but labially are very slightly convex posteriorly. The mesial (anterior) border of the upper canine occludes with the distal (posterior) border of the lower canine and the upper canine fits between the lower canine and first premolar. The subsec-

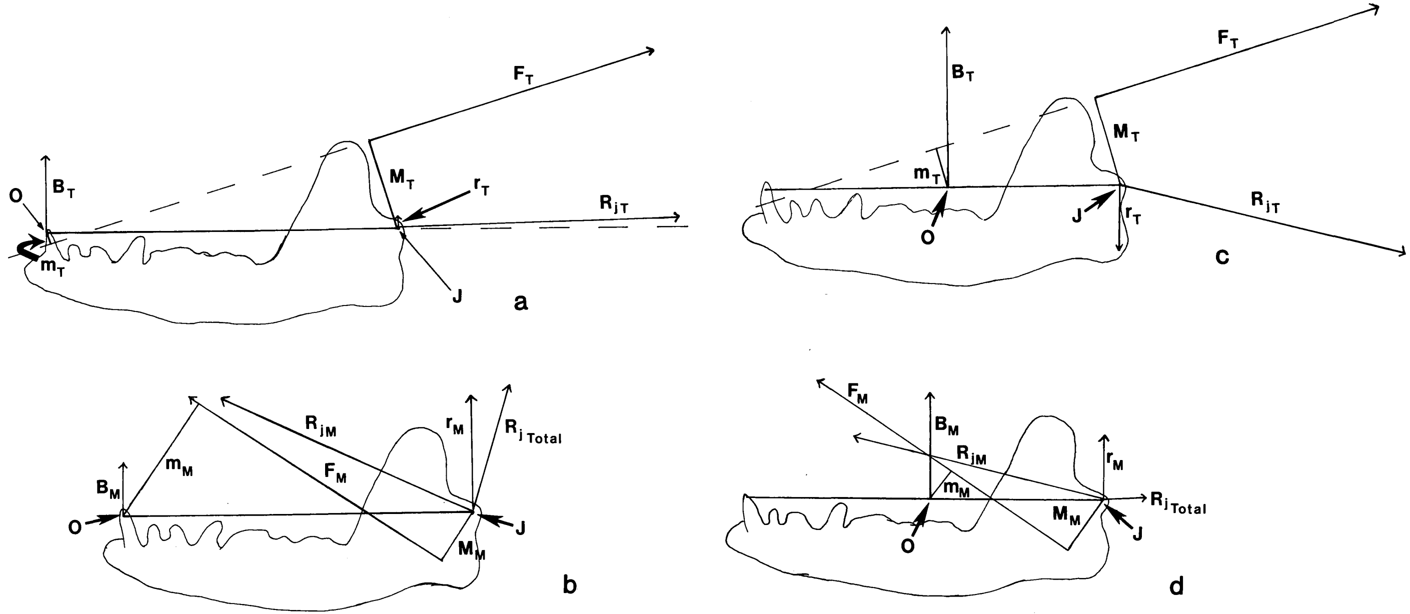


FIG. 53. A simple biochemical analysis of the jaw mechanics of *Onychodectes t. tisonensis* using the bifulcral model of Bramble (1978). *a*) Stick figure showing the action of the temporalis with bite point at the canine. *b*) Stick figure showing the action of the masseter with bite point at the canine. *c*) Stick figure showing the action of the temporalis with bite point above M_{2-3}. *d*) Stick figure showing the action of the masseter with bite point above M_{2-3}.

Abbreviations: B_M, B_T = Primary rotational or bite force for masseter (B_M) or temporalis (B_T); F_M, F_T = Muscular force of masseter (F_M) or temporalis (F_T) (arbitrarily set equal to each other); J = Joint fulcrum at jaw articulation; M_M, M_T = Primary moment arm of F_M or F_T; m_M, m_T = Secondary moment arm of F_M or F_T; O = Occlusal fulcrum at bite point; r_M, r_T = Secondary rotational force for masseter (r_M) or temporalis (r_T); R_{jM}, R_{jT} = Resultant joint force for masseter (R_{jM}) or temporalis (r_{jT}); R_{jTotal} = Combined resultant forces for masseter and temporalis with bite point at the canine (*b*) or with bite point above M_{2-3} (*d*).

torial premolars are well separated and do not occlude interstitially. The P^1 fits between the P_1 and P_2, the P^2 between the P_2 and P_3, and the P^3 between the P_3 and P_4. The P^3 has begun to develop a small, internal "protocone" which occludes with the incipient posterior heel (talonid) of P_3. P^4 of *Onychodectes* bears a small, internal protocone which occludes with the small talonid of P_4 The distal (posterior) edge of P^4 also occluded with the mesial (anterior) face of the trigonid of M_1. Likewise, the protocones of M^{1-3} fit into the talonid basins of M_{1-3} during occlusion. The mesial faces of M^{1-3} occluded with the distal faces of the trigonids of M_{1-3} and the distal faces of M^{1-2} occluded with the mesial faces of M_{2-3}. Thus, during full occlusion with the protocones of the upper molars resting in the talonids of the lower molars, the labial paracones and metacones of the upper molars lay labial to the labial faces of the lower molars. During occlusion and use, the protocones, trigon basins, and talonid basins (especially their labial edges) wore first. This was countered by the typical taeniodont rolling eruption in which enamel extended far lingually on the upper cheek teeth and continued eruption of the teeth on their lingual aspects caused an "outrolling" of the upper cheek teeth. Likewise, the lower cheek teeth are characterized by enamel which extends far labially and continued eruption caused an "inrolling" of the teeth. Next to wear were the trigonids (and protoconids of the lower premolars) of the lower molars and lastly the labially appressed protocones and metacones of the upper cheek teeth.

During mastication, it appears that *Onychodectes* fully occluded its teeth on one side only, and then moved the lower jaw laterally toward the other side (Fig. 54). This dragged the lower cheek teeth in a lingual direction across the upper cheek teeth (cf. Mills 1966; Crompton and Hiiemae 1970). The lower molar trigonids, which are slightly compressed anteroposteriorly and widened transversely [these features are better developed in the later (more derived) conoryctids], fit between the mesial and distal edges of the upper molars and acted as the guiding ridges. In the unworn upper molars of *Onychodectes* the protocones are high, sharp, far appressed lingually and slightly recurved labially. Likewise, the paracones and metacones are subequal in size, high, sharp, far appressed labially and slightly recurved lingually. The conules and internal trigon basins are set distinctly lower than the labially and lingually flanking paracones, metacones, and protocones. During wear this morphology was further extenuated with the paracone and metacone forming an anteroposteriorly elongated labial crest, and the protocone and lingual edge of the trigon forming an anteroposteriorly elongated lingual crest. The central trigon basin was deeply excavated with wear. These crests formed the main cutting, shearing, grinding crests of the posterior dentition of *Onychodectes.* The unworn lower molar talonids bear conids that are slightly punctate, slightly bulbous, but relatively low (compared to insectivores and the primitive mammalian morphotype). The trigonids are only slightly higher than the talonids. With continued wear, the lower molars became relatively smooth surfaces with any discrepancy in height between the trigonids and talonids becoming negligible. Evidently, the primary function of the lower molars was merely to provide a surface (roughened when unworn or slightly worn, but essentially smooth when worn) for the upper molars, with the moderately developed grinding ridges, to occlude against.

The incisors and canines are sharp and punctate, and the premolars, especially the more anterior premolars, are sectorial to subsectorial. These are primitive retentions, but functionally indicate that whereas *Onychodectes* was developing a grinding dentition in the posterior cheek teeth adapted to a more omnivorous/herbivorous diet, the more anterior cheek teeth, canines and incisors may have

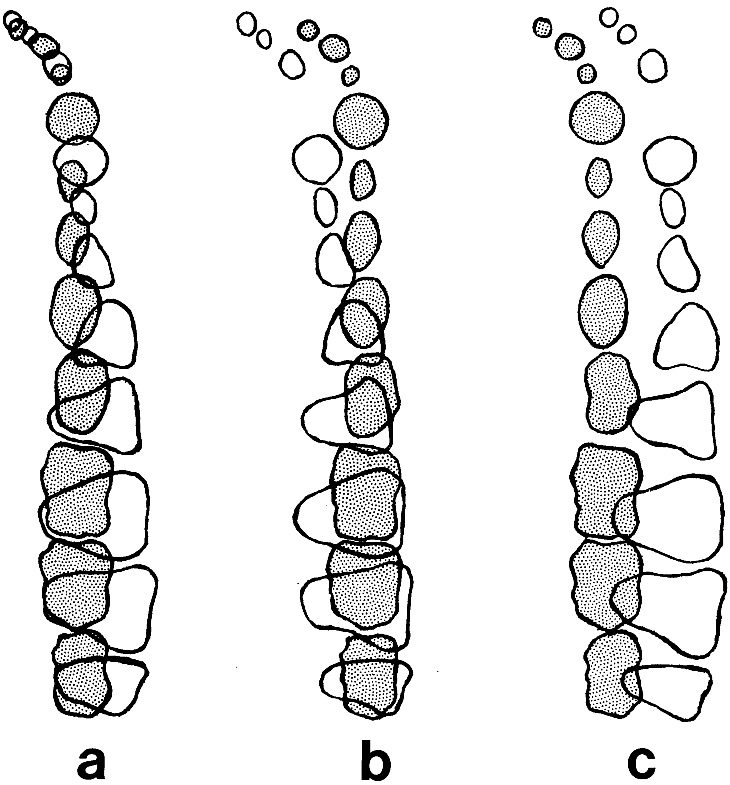


FIG. 54. Occlusion diagrams for *Onychodectes tisonensis*: shown only for the right side; the lower teeth are stippled. *a*) Teeth shown in centric occlusion. *b*) Occlusion at the beginning of the chewing stroke. *c*) Relative positions of the tooth rows at the end of the chewing stroke.

been used in a more carnivorous manner. Thus, *Onychodectes* may have hunted and eaten insects, small vertebrates, birds' eggs and perhaps rarely even larger vertebrates, possibly up to near its own body size.

Opossums (*Didelphis* sp.), which in many respects are morphologically similar cranially and postcranially to *Onychodectes,* although sometimes smaller, may form a good extant analogue for *Onychodectes.* However, the posterior cheek teeth of *Didelphis* are not as well adapted to a grinding function as those of *Onychodectes.* Approximately 80% of the diet of *Didelphis* is divided equally between insects and mammals, with the remaining 20% consisting of birds, birds' eggs, other small vertebrates, fruits, and seeds (Sandidge 1953). Taking the increased grinding function of its teeth into account, *Onychodectes* may have been more truly omnivorous: it may have split its diet about equally between carnivorous prey items (e.g., insects, small vertebrates, eggs) and herbivorous items (fruits, seeds, foliage, possibly tubers).

The later conoryctids progressively molarized the premolars and put increasingly more emphasis on herbivory. Yet, the more derived conoryctids never really changed or improved the basic bauplan seen in *Onychodectes*; they merely increased slightly the size and degree of crown hypsodonty of the posterior cheek teeth and extended molarization to fully include P^4_4 and P^3_3 to a certain extent (in *Huerfanodon*). This may not have been a particularly efficient way to approach a herbivorous mode of life. For most of the life of a typical individual that lived to a moderately old age, the cheek teeth were worn nearly flat and essentially consisted of a central dentine core surrounded by a band of enamel. The conoryctids may eventually have been outcompeted in one sector by their larger cousins, the stylinodontids (if conoryctids also dug roots and tubers at times) and in another sector by animals their own size, but with a more sophisticated system of grinding crests adapted to a herbivorous mode of existence. Contemporaries of the conoryctids which may have competed with them and were more successful carnivores include the miacids and perhaps some arctocyonids. Periptychids, other condylarths and pantodonts developed more efficient dentitions for a herbivorous mode of life than did conoryctids. As the conoryctids and stylinodontids converged and progressively adapted to the same "niche," the conoryctids of Torrejonian times may easily have been outcompeted by the abundant Torrejonian *Psittacotherium.*

6. TAENIODONT AUTECOLOGY AND LIFE RESTORATIONS

ONYCHODECTES AND THE CONORYCTIDS

Onychodectes had a skull length of approximately 11.5 cm, and based on my reconstruction (Fig. 2) stood about 17–18 cm high at the shoulder and had a head and body length of approximately 58 cm (Table 4). Using Jerison's (1973) formula [body weight in gm = 0.050 (heavy habitus) or 0.025 (light habitus) × (head and body length in cm) cubed] for estimating body weight from the head and body length, *Onychodectes* weighed 4.88 kg (light habitus) to 9.76 kg (heavy habitus). The average of these two is 7.32 kg (or about 16 lbs). The skeleton of *Onychodectes* is about the size of the extant *Tamandua* (cf. Matthew 1937), which weighs about 5 kg (Grzimek 1975); this agrees well with body weight estimates made for *Onychodectes* using Jerison's formula. Thus, *Onychodectes* was a medium-sized, small animal, about the size of a large house cat or small dog, whereas the other conoryctids were of similar proportions, but slightly larger (Table 4). *Onychodectes* had a long, strong tail and considering that it lived in a fairly warm climate (see below), probably had a fairly short-haired coat.

To summarize the preceding descriptions and discussions, cranially and postcranially, the conoryctids are relatively primitive, generalized mammals (using *Didelphis* and *Solenodon* as representative in many respects of the primitive mammalian morphotype; see Gregory 1910). The skull of *Onychodectes* is long and narrow and quite insectivorelike (Matthew 1937) with a long muzzle, long nasal bones, large premaxillae, a low sagittal crest, absence of postorbital processes, a long shallow dentary, a moderately large coronoid process, and a condyle set just above the tooth row. In more advanced conoryctids (such as *Conoryctes*) the face was shorter and deeper and the mandible was more robust.

The postcranial skeleton of conoryctids is also relatively primitive with few specializations. The limb bones are moderately long and robust. The femur bears three trochanters and the tibia and fibula are unfused. The humerus approaches what Gregory (1910, p. 249) termed the "primitive fossorial type," which is broad distally and retains an entepicondylar foramen, whereas the deltoid crest is well developed, but not flattened, and projects anteriorly. The olecranon of the ulna is relatively large and robust. The ulna and radius were not fused so the radius could rotate on the ulna. The tail of *Onychodectes* was long and heavy.

The carpals and tarsals of the conoryctids are unreduced, unfused and alternating. Both the fore- and hindfeet bear five digits, but the medial and lateral digits (one and five) are somewhat reduced. The metatarsals are somewhat elongated relative to the metacarpals. The astragalar-calcaneal complex of *Onychodectes* is of the leptictimorph morphotype characterized by modifications for extreme plantar–flexion (Szalay 1977, p. 354). The unguals of the manus and pes of the conoryctids are relatively small, unfissured claws.

The cheek teeth of the conoryctids are characterized by crown hypsodonty with the enamel extending far labially on the lower cheek teeth and far lingually on the upper cheek teeth. The cusps of the molars are relatively low and easily lost with wear, forming broad grinding surfaces. Conoryctid premolars are sectorial teeth separated in the jaw such that the upper and lower teeth mesh tightly with each other. The canines of *Onychodectes* are of moderate size, but the canines increased in relative size during conoryctid evolution.

In terms of its general morphology, *Onychodectes* is quite similar to, although larger and more robust than, *Didelphis marsupialis*. Thus, the opossum can pro-

TABLE 4. Estimated skull lengths, skull and body lengths (tip of snout to base of tail) and body weights for various taeniodonts. Body weight estimates calculated according to the method of Jerison (1973): lower weight value assumes a "light habitus" for the animal; higher weight value assumes a "heavy habitus."

TAXON	SKULL LENGTH (CM)	SKULL AND BODY LENGTH (CM)	WEIGHT (KG)
O. tisonensis	11.5	58.0	4.9–9.8
Conoryctella sp.	Intermediate between *O. t.* and *C. c.*		
C. comma/ Huerfanodon sp.	15.0	67.5	7.7–15.4
W. otariidens	18.5	83.3	14.4–28.8
P. multifragum	25.0	112.5	35.6–71.2
E. gliriformis	Intermediate between *P. m.* and *S. m.*		
E. copei	20.0	90.0	18.2–36.4
S. mirus	29.0	130.0	54.9–109.0
S. inexplicatus	14.5	65.3	7.0–13.9

vide a living analogue for *Onychodectes*. On this basis, *Onychodectes,* like the opossum (McManus 1970), was a noncursorial, plantigrade mammal which may also have been reasonably adept at climbing. The humeri and femora probably functioned in a position held more nearly horizontal than vertical and at an angle to the parasagittal plane (cf. Simpson and Elftman 1928; Jenkins 1971b). The humeral–ulnar morphology indicates that the forearm was relatively powerful and the morphology of the manus may have allowed relatively precise movements and some grasping abilities.

The skull and dentition of *Onychodectes* and *Didelphis* are also superficially/functionally similar. Thus, in both animals the snout and mandible are relatively long and the condyle is set only slightly above the tooth row. Both have a set of small incisors, sharply pointed, tall canines, and well-separated sectorial premolars. However, the cheek teeth of all of the conoryctids exhibit well-developed crown hypsodonty, and the molars provide a large, low-relief grinding surface. Therefore, *Onychodectes* and the later conoryctids may have fed on a diet which included some of the types of food eaten by *Didelphis,* but also a large component of coarser vegetation/plant matter. Insects and small mammals appear to be the most important component of the opossum's diet (82% by weight) with birds and plant matter (primarily fruits) composing the rest (Sandidge 1953). In analogy, conoryctids may have eaten a fair-sized component of insect, mammal and bird matter. But, taking the increased grinding function of their molars into consideration, they may also have eaten a large amount of plant matter; i.e., conoryctids may have been general omnivores. Furthermore, their heavy forelimbs and claws may have allowed them to harvest subsurface food items. Again, in analogy to extant forms of a size similar to *Onychodectes,* such as the common raccoon, *Procyon, Onychodectes* may have had a lifespan of two to ten years.

STYLINODON AND THE STYLINODONTIDS

The skull length of *Stylinodon* was approximately 29 cm and based on my reconstruction (Fig. 31) the head and body length was approximately 130 cm and *Stylinodon* stood about 62 cm high at the shoulder. Using Jerison's (1973) formula for estimating body weight from head and body length, *Stylinodon* may have weighed between 54.9 kg (light habitus) to 109.9 (heavy habitus), the average of which is 82.4 kg (181.3 lbs; Table 4). Postcranially, the aardvark, *Orycteropus,* is similar morphologically to and about the same size as USGS 3838, a partial skeleton referred to *Ectoganus copei,* and can be used as an extant analogue for some stylinodontids (cf. McKenna 1980b). *Orycteropus* weighs approximately 60–70 kg (Walker 1975) which is in the same general range (by order of magnitude) as, but somewhat heavier than, *Ectoganus copei* based on USNM 12714 (a skull), using Jerison's (1973) formula (Table 4).

Thus, *Stylinodon* was a medium-to-large animal, although not particularly large for its time; contemporaneous animals that were larger than *Stylinodon* include uintatheres, pantodonts, brontotheres, and achaenodonts. However, the Torrejonian *Psittacotherium* was only slightly smaller than *Stylinodon* (53.4 kg using the same calculations; Table 4) and was one of the largest animals of its time (cf. Matthew 1937). *Stylinodon* bore a large, massive, piglike or wombatlike head on a body that superficially resembles that of an aardvark with strong limbs, large claws and a long, heavy tail. Considering that *Stylinodon,* and the stylinodontids in general, lived in a fairly warm, temperate-to-tropical climate (see below), they may have had relatively short fur. It is also possible that they bore short manes (shown in Fig. 31) as do many extant African mammals.

To summarize the preceding descriptions and discussions, stylinodontids are characterized by large heads with short, deep faces and mandibles, a shortened and widened snout, large mastoid processes, a prominent sagittal crest and a wide, high, triangular-shaped occiput. The mandible was deep and extremely robust with a well-fused mandibular symphysis, a large, heavy coronoid process, a rugose, slightly inflected jaw angle (primarily for attachment of the M. pterygoideus) and a large internal shelf or pit behind the symphysis for the origin of the tongue musculature (M. genioglossus). The main emphasis of the stylinodontid dentition was on the incisors, canines and anterior premolars.

The canines and upper incisors became greatly enlarged, rootless and subgliriform with enamel limited to the anterior part of the teeth, the posterior part being enamel-free. Thus the canines were chisel-like teeth with an anterior cutting surface and a posterior crushing and grinding surface. The anterior premolars complemented the canines as cutting blades whereas the posterior premolars became rootless and evergrowing pegs for grinding, with bands of enamel limited to their lingual and labial faces. (The taeniodonts are the first known mammals in North America to have truly hypsodont teeth [White 1959; Webb 1977]). The crowns of the posterior premolars and molars were transversely bilophodont, but with moderate wear the cusps were obliterated and dentine pegs with incomplete bands of enamel around their perimeters remained. This evidently was the condition in which the teeth were used for the majority of an individual animal's life.

The stylinodontid skeleton is a modified version of the generalized, primitive skeleton of *Onychodectes.* Major modifications include increased size, plus the development of an extremely squat, robust skeleton and powerful forelimbs with large, laterally compressed and recurved claws on the manus. The neck is short and stout. The humerus is large and robust with a prominent deltopectoral crest, supinator ridge and teres eminence, and large epicondyles. The radius and ulna are short and robust and the radius could rotate around the ulna. The olecranon is large and robust suggesting the presence of powerful flexors for retraction of the forelimb. The femur, tibia, and fibula are all moderately stout and robust and the tibia and fibula are unfused. The tail is long and heavy.

The stylinodontid manus bears large, laterally compressed and recurved claws on short, robust metacarpals and phalanges. The medial and lateral digits (one and five) are greatly reduced on the manus. The articular surfaces of the metacarpals and phalanges allowed a high degree of extension and flexion, but minimized medial-lateral movements. The carpus is alternating in more primitive stylinodontids (such as *Psittacotherium*) whereas in more advanced forms (e.g., *Stylinodon*) the carpus is more nearly serial. The magnum is greatly enlarged in *Stylinodon*. The large third metacarpal proximally rests fully against the distal surface of the magnum; the proximal surface of the magnum in turn rests against the distal surface of the lunar. A large component of the stress placed on the manus may have passed directly through these three bones.

The stylinodontid pes bears five well-developed digits arranged in an arc. The tarsus is serial and the metatarsals are short and thick. Most of the stress placed on the pes passed through the serial tarsus, the short metatarsals and associated sesamoids and onto the substrate. The short digits bear large, broad and only slightly recurved claws. This arrangement provided a firm support for the stylinodontid hindfoot.

There are many functional similarities between the morphology of the postcranial skeletons of stylinodontids and *Orycteropus* that suggest that stylinodontids were active diggers like the aardvark. *Orycteropus* also is characterized by powerful, robust limb bones, especially those of the forelimb. The humerus of *Orycteropus* is broad distally and bears a prominent deltopectoral crest and supinator ridge; the ulna bears a large olecranon and the radius is short and robust (Colbert 1941; Patterson 1975) as in stylinodontids. Aardvarks dig up and feed on ants and termites, although they have also been recorded eating wild cucumbers, probably to obtain moisture (Melton 1976). They also dig large, extended labyrinthian burrows to live in (Roberts 1923; Melton 1976). East African warthogs (*Phacochoerus aethiopicus*) also make active use of large underground burrows in which they seek refuge from predators and inclement weather, pass the nights and give birth to their young. It is believed that *Orycteropus* digs the initial holes used by the warthogs (Bradley 1971).

In digging, the body weight of *Orycteropus* is supported by the hindlimbs and heavy tail while the forelimbs are used for the actual digging (Melton 1976). In a similar manner, stylinodontids may have supported their weight on the hindlimbs and tail and used their powerful forelimbs and claws to dig for food and perhaps to dig out burrows. *Myrmecophaga* and *Tamandua* (anteaters: B. F. Taylor 1978) and *Manis* (pangolin: Cuvier, 1821–24; Roberts 1923) also have similar digging adaptations, and in these forms the central, especially third, digits of the manus are greatly enlarged and the forelimb carries large, laterally compressed and recurved claws (Walker 1975) as in the stylinodontids. All of these forms, however, have reduced dentitions and relatively slender jaws as an adaptation to a myrmecophagous diet (cf. Patterson 1975). In contrast, stylinodontids progressively increased in size and robustness of the skull, mandible and anterior dentition (especially the canines). This suggests that they were eating something besides ants and termites, although they may have eaten these also. I suggest that stylinodontids may have been feeding on tough vegetable matter, which they could rip and tear with their powerful claws, skulls and dentitions. In particular, their powerful, thick jaws with deep mandibles and heavy, blunt anterior dentition appear to have been suited to massive crushing and chopping of hard plant food, but not adapted to shredding high fiber leaves and stems (cf. Bakker 1980, p. 368). Furthermore, they probably actively dug for roots, tubers and other succulent subsurface food items, using their powerful claws and canines for this purpose. In analogy to the skull and canines of stylinodontids, pigs, hogs and peccaries (such as *Potamochoerus, Sus, Phacochoerus, Hylochoerus, Babyrousa* and *Tayassu*) use their powerful snouts and protruding canines if present, to dig and grub for roots, tubers and other underground vegetable matter (Stegeman 1938; Leister 1939; Dorst 1969; Field 1970; Grzimek 1975; Walker 1975).

The common African warthog (*Phacochoerus aethiopicus*) is 65 cm tall at the shoulder and weighs 75–100 kg (Field 1970; Walker 1975), about the height and weight of *Stylinodon mirus* (see estimates above and Table 4), and like *Stylinodon* has a short, stout neck (Field 1970) which aids in withstanding stresses generated when using the snout for digging for food. In order to reach the surface with the snout and also to dig below the surface, warthogs will kneel on their forelegs (Field 1970). *Stylinodon* was capable of a good deal of flexion in all of the limbs, especially the forelimb (see discussion above on the posture of *Stylinodon*) and would have been able to kneel, bringing the body and face low to the ground. However, *Stylinodon* probably dug primarily with its forelimbs, as does the aardvark (Melton 1976) rather than primarily or exclusively with its head and snout as does the warthog.

Ewer (1958) has noted that whereas the bushpig (*Potamochoerus koiropatamus*) and the warthog (*Phacochoerus africanus*) greatly overlap in their feeding habits, when each is in its preferred habitat the bushpig is primarily "an omnivore, in which digging with the snout constitutes an essential element in the method of obtaining food" (Ewer 1958, p. 136) and the warthog may be characterized as "a highly selective grass plucker" (Ewer 1958, p. 139). These differing modes of feeding have left their mark on the musculature, skulls and dentition of these suids (Ewer 1958). Thus, the bushpig has relatively larger premolars and more bunodont cheek teeth as compared to the warthog, in which the premolars are reduced and the large molars, especially M_3, are hypsodont, multicusped, and more adapted to shredding fibrous grasses. In the bushpig as compared to the warthog, the temporal and digastric muscles are larger and the superficial masseter slopes backwards from the origin to insertion, rather than being oriented relatively vertically. The snout of the bushpig is elongated, but does not slope downward anteriorly as in the warthog such that the nasals in the bushpig are nearly horizontal. The snout of the bushpig is also less rounded and the side walls are nearly vertical. The mandible of the bushpig is deeper and heavier, with an elongated symphysis, as compared to the warthog. The forest hog, *Hyloechoerus meinertzhangeni,* shows a mixture of features and specializations, some of which are shared by the bushpig and some of which are shared by the warthog (Ewer 1958, 1970). In all of the functional differences between the bushpig and the warthog cited above, *Stylinodon* and the stylinodontids in general more nearly resemble the bushpig; this further suggests that stylinodontids were diggers.

The wombat (*Vombatus ursinous* = "*Phascolomys*" *ursinous*) can provide another stylinodontid analogy. The wombat feeds mainly on grass and roots, using the claws on its forefeet to grasp, dig and forage (Walker 1975); the hindlimbs act as a stable, resistant support and also may be used to pass earth backwards when digging (Elftman 1929). The skull of the wombat (YPM Osteology Collection 237) is massive, short and wide with a broad, moderately high (but squared) occiput. The mandible is short and deep with a thick, well-fused symphysis. In all of these features the skull is broadly similar to that of *Stylinodon*. *Vombatus* also has a pair of large, evergrowing incisors above and below, analogous to the canines of stylinodontids, and the cheek teeth of *Vombatus* are transversely bilophodont, rootless teeth which erupt by a rolling eruption, the uppers outrolling and the lowers inrolling, as in all taeniodonts.

The large amount of grit which is inevitably part of a diet composed of underground vegetable matter could account for the substantial wear typical of most stylinodontid teeth. Furthermore, feeding on roots and tubers would have provided a relatively stable and constant food resource and may have freed stylinodontids from always being fairly near water (cf. Hatley and Kappelman 1980 on use of underground food resources by pigs, bears and hominids). In analogy, the fringe-eared oryx (*Oryx beisa*) of Africa has been observed by Root (1972) to search and dig up tubers during droughts in order to obtain its necessary nourishment and moisture. *Phacochoerus* and *Sus* will also occasionally eat carrion, *Potamochoerus* will supplement its principal diet of roots, berries and wild fruit with reptiles, eggs and young birds, and *Tayassu* is known to eat snakes and other vertebrates occasionally (Walker 1975). Again in analogy, there seems to be no reason why the stylinodontids might not have utilized their powerful masticatory apparatus to take advantage of carrion and other animal nourishment if they happened to stray across it (Schoch 1981a).

Thus, stylinodontids may have been primarily open-country, upland forms, perhaps one of the first upland radiations of mammals. This may help to explain their general rarity in the fossil record (as noted by Patterson 1949b; see further discussion below) because they did not generally live on riverine floodplains where sediments were being actively deposited, so their remains would not have been readily fossilized and preserved.

It should also be noted that stylinodontids were probably not truly fossorial (Shimer 1903) as moles (cf. Yalden 1966; Puttick and Jarvis 1977) might be considered; based on the digging/burrowing adaptations seen in the stylinodontids, I would term these forms "subfossorial." Shimer (1903) lists a number of external and skeletal modifications commonly seen in fossorial mammals. Those which apply to the stylinodontids include: 1. "Limbs short and stout"; 2. "Manus broad and stout, with long claws"; 3. "Fore feet and hind feet have undergone divergent specialization"; 4. "Bones of fore limb strong, tuberosities prominent"; 5. "Bones of hind limb not so strongly developed as those of the fore limb." However, unlike many truly fossorial forms (Shimer 1903), the bodies of stylinodontids were not fusiform, the tail was not shortened and vestigial, the skull was not narrow and triangular, and the vertebrae were not heavily fused. Also, many truly fossorial forms, such as the moles (e.g., Chrysochloridae and Talpidae) are small forms with extreme modifications and specializations of the forelimb (see Yalden 1966; Puttick and Jarvis 1977; and references cited therein). The relatively large body size developed by the stylinodontids may have excluded them from adopting completely fossorial habits.

Stylinodontids were relatively small-brained (see discussion of the endocranial cast of *Ectoganus copei* in Schoch 1983a) but physically powerful forms. All of the modifications of their skulls, dentitions and postcrania appear to be toward elaboration of their food gathering and processing functions. None of the modifications appear to be for social interactions. Thus, stylinodontids did not develop any display objects such as horns, antlers or sexually dimorphic canines; there are no features which are clearly sexually dimorphic in any taeniodonts. This suggests that stylinodontids were not particularly gregarious animals, but rather may have been rather solitary as are extant aardvarks (Melton 1976). From the small orbits and large nasal cavities of *Stylinodon,* we can hypothesize that these forms may have been relatively more dependent upon their sense of smell than sight, as is the aardvark (Melton 1976). *Orycteropus* is primarily nocturnal and travels (walks) approximately 10 km a night while foraging, but follows a circuitous route such that an individual may often end the night close to where it began (Melton 1976); we can suggest that the stylinodontids may have followed a similar pattern. *Orycteropus* usually bears a single offspring at a time and captive aardvarks have been known to live for ten years (Walker 1975). Extant suids and tayassuids may bear from one to twelve offspring in a litter and may potentially live ten to twenty years (Walker 1975). By analogy we can hypothesize that stylinodontids produced one or a few offspring at a time, and lived for ten years or more. It is interesting to note that many stylinodontid individuals may have lived to fairly old ages, as shown by the extremely worn condition of their preserved teeth. Alternatively, the extremely worn teeth typical of stylinodontid specimens may simply be due to their coarse, gritty diet.

SEDIMENTARY ENVIRONMENTS IN WHICH TAENIODONTS HAVE BEEN FOUND

The general lithologies of two of the major formations in which taeniodonts have been found (the Nacimiento and San Jose Formations of the San Juan Basin) have been described briefly in the biostratigraphy section (see above, Chapter 4). Lithologies in the Bighorn Basin are discussed by various authors in Gingerich (1980); those in the Washakie Basin are covered by various authors in West (1972b) and likewise the lithologies of other taeniodont localities are variously described in the references cited for Table 1.

The mammal-producing early Tertiary sedimentary deposits of the Rocky Mountain intermontane basins are considered to generally represent freshwater, fluviatile, riverine, floodplain, and swamp deposits (e.g., Sinclair and Granger 1914; Simpson and Elftman 1928; Hickey 1980; Tsentas and others 1981; Lucas and Schoch 1981b). The sediments and preserved flora and fauna generally indicate an equitable, moist, warm temperate to subtropical-tropical, heavily forested lowland environment (Van Houten 1945; Hickey 1980; Bown 1980; Wing 1980; Webb 1977; Black 1967) with few indications of long-term aridity. The paleofloras of the Rocky Mountain region of western North America during the Paleocene–Eocene document "a subtropical forest of broad-leafed angiosperms" (Webb 1977, p. 357; see also Brown 1962; Wolfe 1978; Hickey 1980). Plants which are known to occur as fossils in Paleocene–Eocene sediments of western North America include elm, oak, hickory, conifers, palms, breadfruit (Gingerich 1976), walnut, mulberry, fig, laurel, honeysuckle, willow, and others (see Brown 1962; Hickey 1980; Wing 1980; Tidwell, Ash and Parker 1981; and references cited therein for flora lists and references to other works). Based on leaf margin data, during middle to late Paleocene times there was a general cooling trend in western North America from what may have been a Puercan subtropical climate to a late Torrejonian–Tiffanian warm temperate climate. In Clarkforkian times this trend was reversed and the climate progressively warmed throughout the Eocene, returning to a subtropical climate (Wolfe and Hopkins 1967; Wolfe 1978; Hickey 1981). Of course, within any one basin or through any one formation or local vertical section, there may be geographic, temporal, or ecologically controlled changes in the sediments and the specific environments they represent, causing the local absence of certain taxa (Schankler 1981).

As noted above, the taeniodonts are extremely rare in all of the deposits in which they are found, comprising at most under 7% (Tables 5, 6) of the mammalian fauna (in terms of numbers of specimens) in any local fauna. This may be due not so much to the rarity of taeniodonts, per se, but to the conditions under which mammalian fossils of the early Tertiary were usually preserved. A similar suggestion was made by Simons (1960, p. 68) to explain the general rarity of large pantodonts in the Paleocene record. Many depositional processes

TABLE 5. Relative abundances of taeniodonts (both families). Values are in percentages of total numbers of specimens.

Single localities		
1	UK NM Loc. 15 (9)	6.52
2	Swain Quarry (6)	less than 1.00
3	Rock Bench Quarry (5)	0.22
4	Polecat Bench (Silver Coulee) (5)	0.46
5	Plateau Valley local fauna (5)	6.66
Multiple localities		
1	Puerco fauna (5)	3.35
2	Dragon local fauna (5)	1.39
3	Torrejon fauna (5)	2.48
4	Kutz Canyon local fauna (8)	2.71
5	Nacimiento Formation (4)	1.96
6	Crazy Mountain Field (7, 8)	0.96
7	Willwood Formation (1)	less than 1.00
8	San Jose Formation (4)	3.57
9	San Jose Formation (5)	3.09
10	Lysite (2)	0.30
11	Lostcabinian (3)	0.54
12	Bridger (5)	0.07
13	Uinta (5)	0.10

References. 1) Bown 1980. 2) Guthrie 1967. 3) Guthrie 1971. 4) Kues and others 1977. 5) Patterson 1949b. 6) Rigby 1980. 7) Simpson 1937. 8) Taylor 1981. 9) R. W. Wilson 1956.

which would tend to concentrate smaller bones and teeth would exclude larger specimens such as the large taeniodonts. Indeed, the smallest taeniodont, *Onychodectes,* is the most common form of taeniodont in sediments where it occurs and most specimens of the larger taeniodonts consist of isolated teeth. Furthermore, as suggested elsewhere, taeniodonts may not have been frequently preserved because they represent a relatively upland radiation and they generally lived away from the riverine floodplains where sediments were being actively deposited.

Unfortunately, the majority of taeniodont specimens were collected fifty to one hundred years ago and detailed lithologic information (i.e., what facies, e.g., clay-shale vs. siltstone, etc.) is not available for most specimens. Thus at present it is impossible to determine if there are any consistent associations between certain taeniodont taxa and certain rock types. However, a few observations are possible. Virtually all taenidont specimens recovered are surface finds as opposed to recoveries in quarries. For example, Princeton Quarry (of Tiffanian age in the Bighorn Basin, Wyoming: Gingerich and others 1980) has produced no taenidonts out of a sample of 541 specimens, although remains of *Ectoganus* have been found on the surface in the vicinity of Princeton Quarry. Swain Quarry (of Torrejonian age, Carbon County, Wyoming: Rigby 1980) has produced 28,000 fossil mammal specimens (mostly isolated teeth and jaw fragments), yet the Taeniodonta are only represented by two isolated teeth of *Psittacotherium multifragum.*

Both Simpson (1937, p. 62–63) and Van Houten (1945, p. 443) have suggested that two major faunal facies are represented in many Paleocene–Eocene collections. As Van Houten states for the early Eocene (1945, p. 443): "Members of an arboreal forest facies are concentrated in local pockets in drab layers, while large terrestrial mammals that lived in the savannahs are preserved as 'surface' faunas sparsely scattered throughout the Early Eocene deposits." Thus, taeniodonts would form a component of the latter faunal facies (cf. also Webb 1977, p. 357–58) and this further supports the hypothesis expressed above, based on

TABLE 6. Relative abundances of Conoryctids versus Stylinodontids. Data as in Table 5; also see Table 5 for references.

	CONORYCTIDS	STYLINODONTIDS
Single localities		
1 UK NM Loc. 15 (9)	2.17	4.35
2 Big Pocket (8)	0.96	1.60
3 Rock Bench (5)	0.22	0
Multiple localities		
1 Puerco fauna (5)	2.81	0.54
2 Dragon local fauna (5)	1.11	0.28
3 Torrejon fauna (5)	0.70	1.78
4 Crazy Mountain Field (7, 8)	0.77	0.23

the functional morphology of their dentitions and skeletons, that taeniodonts were primarily terrestrial, open-country forms.

In the Willwood Formation of the southern part of the Bighorn Basin, Bown (1979, 1980) has distinguished two facies: the Sand Creek facies and the Elk Creek facies. To quote Bown (1980, p. 129):

> *The Sand Creek facies is typified by relatively thin mean thicknesses of colored mudstones, a predominance of purple and gray mudstones (22% and 21%, respectively), paler mudstone colors, paucity of calcium carbonate cement in sandstones, absence of calcium carbonate nodules, abundance of iron and manganese oxyhydrate nodules and concretions, and dominance of sandstones of shoestring and apron-channel cross-sectional geometries (Bown, 1979). The Elk Creek facies, on the other hand, is characterized by relatively thick deep-colored mudstone bands, predominance of orange and red mudstones (41%), abundance of calcium carbonate cement in sandstones, abundance of calcium carbonate nodules, relative paucity of iron and manganese oxyhydrate nodules and concretions, and dominantly apron-channel sandstones. (Bown, 1979)*

Bown has postulated that the Elk Creek facies was deposited under drier conditions with more seasonal rainfall, whereas the Sand Creek facies was deposited under moister conditions with rainfall more equally distributed throughout the year. *Ectoganus* is a rare component of the Elk Creek facies, but is entirely absent from the Sand Creek facies (Bown 1980, table 1). Likewise, uintatheres and dermopterans are known only from the Elk Creek facies, and perissodactyls, artiodactyls, the condylarth *Phenacodus,* mesonychids and carnivores are more common in the Elk Creek facies than in the Sand Creek facies. These all suggest a more terrestrial, open-country, upland assemblage.

RARITY OF TAENIODONTS IN THE FOSSIL RECORD

Taeniodonts are relatively rare in the early Tertiary fossil assemblages in which they occur (Tables 5, 6; Simpson 1937; Patterson 1949b; Bown 1980; Gingerich and others 1980; Schoch 1981a, b; Schoch and Lucas 1981e; Taylor 1981). This rarity does not result from taeniodont fossils either being missed in the field or not recognized in the museum. Taeniodonts are relatively large; their fossils are readily spotted during collecting and are easily identifiable as those of taeniodonts (Patterson 1949b). Thus, taeniodont fossils are genuinely rare in the deposits in which they have been found. Patterson (1949b, p. 270) suggested "the possibility that the group [taeniodonts] may have been abundant in areas in which sediments did not accumulate or from which they have subsequently been removed by erosion requires consideration." However, he rejected this alternative because the early Tertiary deposits in which taeniodonts have been found include fossils of mammals from a variety of habitats. Patterson (1949b, p. 272) concluded that the successive populations of the stylinodontids "were certainly not large but were at most of medium size (sensu Wright) throughout the greater part of the history of the group." He extended this interpretation to include the other family of taeniodonts, the Conoryctidae.

According to Patterson, a single mutation was the starting point for the stylinodontid adaptive type. This single mutation, "the development of large, laterally compressed claws," (Patterson 1949b, p. 273) was a quantum shift followed by rapid evolution of the stylinodontids facilitated by their small to medium population sizes (cf. Wright 1949). The conoryctids, not blessed with this new mutation, remained in the ancestral taeniodont adaptive zone; however, their small population sizes also aided in their supposed relatively rapid evolution, although little speciation occurred. The story of quantum evolution in taeniodonts seemed so convincing that Simpson (1953) used it as an example of quantum evolution on the penultimate page of his *Major Features of Evolution* and it has not been seriously challenged since.

The scenario of small population sizes and the relatively rapid evolution of taeniodonts espoused by Patterson (1949b) is based primarily on negative evidence, i.e., the lack of abundant taeniodont fossils in the early Tertiary sediments of North America. In contrast, I propose an alternative explanation for the rarity of taeniodont fossils. My explanation is based on the positive evidence of the autecology of taeniodonts as inferred from the morphology of their preserved remains. Thus, I propose that taeniodonts are rare in the fossil record because they primarily inhabited areas away from the riverine floodplains where most sediments were deposited and therefore their remains were only infrequently incorporated into these sediments and subsequently fossilized.

The functional morphology of the stylinodontids (see above) suggests that they may have been diggers, grubbers and rooters. Underground plant organs may form an important food resource for some mammals. This resource has been used to advantage by suids, ursids, and hominids (Hatley and Kappelman 1980), and I suggest that the stylinodontids may also have subsisted in large part on subsurface food items. Roots, tubers and other underground storage organs often contain large reserves of water, carbohydrates and protein (Noy-Meir 1973). Thus, feeding on roots and tubers frees an animal from total dependence on perennial water resources and associated aboveground vegetation, allowing it to inhabit drier and seasonally arid regions. The smaller conoryctids may have used underground food resources to a certain extent, but if they also actively hunted or scavenged and completely utilized their kill (i.e., ate almost the entire animal, including crushing and grinding bones to get at marrow), they too may have been freed from total dependence on perennial water resources by deriving the majority of moisture needed from tubers and other animals' flesh.

Taeniodonts may have formed an important element of the early Tertiary North American "protosavanna." This protosavanna (as opposed to the contemporaneous subtropical forest) is suggested by the association of red-banded mudstones, perhaps denoting relative aridity, or at least seasonality of rainfall (Bown 1980) and certain large vertebrates which may have been adapted to more open country (Webb 1977). Other early Tertiary mammals, besides taeniodonts, which might have formed important elements of this biota include larger terrestrial periptychids, phenacodontids, arctocyonids, pantodonts and uintatheres (Simpson 1937; R. W. Wilson 1951; Simons 1960; Webb 1977).

Taeniodonts may represent one of the first inland and upland radiations of the Mammalia. They lived in highlands and other areas of denudation away from streams and waterways where most sediments were deposited and subsequently preserved. Thus, the relative rarity of taeniodonts is not due to their small population sizes, but to ecology. Taeniodonts primarily inhabited regions away from the riverine floodplains and the fossil record is naturally biased against preserving their remains.

7. PHYLOGENY AND EVOLUTION OF THE TAENIODONTA

PHYLOGENY RECONSTRUCTION AS APPLIED TO THE TAENIODONTA

Taeniodonts are a relatively rare order of animals (i.e., their fossils are not particularly common), as are many fossil vertebrates (the incredible incompleteness of the sedimentary record is well known: Schopf 1981; Schoch 1982c), and I do not hope to find direct ancestors and their descendants, much less be able to recognize them (cf. Englemann and Wiley 1977). At best, it appears that it might be possible to reconstruct the relative recency of common ancestry, or cladistic branching sequence, of the known taxa (cf. Hennig 1965, 1966). Through a monophyletic, evolving lineage lasting 20 million years, as Patterson (1949b) and Wortman (1897b) hypothesized for taeniodonts, if there were ten distinct, semicontemporaneous populations over every span of one million years, nine of which went extinct without descendants, and one-tenth of the populations were randomly preserved in the fossil record (which was fully recovered), the probability of sampling an ancestor and its descendant of a million years later would at best be $\frac{1}{10} \times \frac{1}{10} = 0.01$. The chances of doing this over a period of three million years would be $\frac{1}{10}$ cubed = 0.001; over twenty million years it would be $\frac{1}{10}$ raised to the twentieth power. In reality we are dealing with from one specimen to at best a few tens or hundreds of specimens for any taxon (these taxa represent conglomerates of populations). Furthermore, during any small time interval there may have been many more than ten populations, the majority of which neither left descendants nor were preserved in the fossil record. The chances of merely recovering a sample (i.e., one or more individuals) of a population which was both fossilized and left descendants seems rather small, much less actually finding an ancestor and its descendant, and then doing this repeatedly through a lineage. Presumably actual ancestors and descendants have been found, but if so they are unrecognizable as such (the ancestor being completely primitive relative to the descendant).

If a form is considered completely primitive relative to another form, one might ask "Why not call it an ancestor of such and such?" However, this is not a demonstrated ancestor; it is simply a primitive form which conveniently serves as an ancestral morphotype (structural ancestor). If this assumption is kept in mind, it may be convenient to discuss "ancestor–descendant" relationships (vs. sister-group relationships hypothesized in a purely cladistic analysis) and propose hypothetical phylogenetic trees, perhaps also taking the temporal sequencing of forms into account, as opposed to cladograms. Such phylogenetic trees may be useful and heuristic in helping to visualize and grasp the general patterns of evolution in a group; however, it must always be remembered that in all likelihood most of the supposed "ancestors" may actually be sterile side-branches which may be later demonstrated by the collection of more material, or by the restudy of old material, revealing previously unknown autapomorphies of the taxa involved. In the particular case of the Taeniodonta, in the majority of taxa, with the notable exception of the poorly known *Wortmania,* I have identified what I believe to be autapomorphies. Furthermore, any true ancestors would never be demonstrable. In the rest of this paper this is the sense in which I will use "ancestor" and "descendant." Thus, I may suggest that a species of *Psittacotherium* (perhaps unknown) is in some way ancestral to *Ectoganus,* but I certainly do not believe that I have a recognizable sample of a population which actually led to *Ectoganus,* much less the *Ectoganus* I have represented by samples of fossils. On the contrary, the *Psittacotherium* I have studied appears to be excluded from being ancestral to *Ectoganus.* It is purely a convention to speak of *P. multifragum* as ancestral to or evolving into *E. gliriformis,* just as it is a convention to speak of *E. g. lobdelli* evolving into *E. g. gliriformis* even though I consider these to be temporally successive subspecies, recognizable on the basis of morphology, of a single species. In the same vein, Van Valen (1978, p. 45) noted in discussing early condylarth phylogenies "the phylogenies are merely permissive" (cf. also Simpson 1961, on the meaning of subspecies as not incipient species and Borissiak 1945, p. 678, on phylogeny reconstruction in chalicotheres).

The above argument would apply to populations evolving and being fossilized in a closed sedimentary basin. The problem of recognizing true ancestors and descendants becomes all the more hopeless when one takes migrations and other movements of mammal populations into account. For these reasons, too, rates of evolution, whether calculated as taxonomic rates or morphologic rates (e.g., darwins), are also rather meaningless except in a sense in sympathy with the above discussion.

In the following discussion I attempt to reconstruct the phylogeny of the taeniodonts, i.e., to determine the relative degrees of relatedness between the known taxa. This is done using cladistic methodology (Hennig 1965, 1966; see also McKenna and others 1977; Eldredge and Cracraft 1980; and many recent articles in the journal *Systematic Zoology*). I advocate the position that phylogeny reconstruction must be based solely on morphology, and not on extrinsic data (Hecht 1976; Hecht and Edwards 1976; Schaeffer and others 1972; McKenna and others 1977; Lillegraven and others 1981). Thus the stratophenetic methodology (Gingerich 1976), which relies on extrinsic data for phylogeny reconstruction, is flatly rejected. Once a hypothesis of relationships is posited, however, it is important to compare it to the stratigraphic and geographic distribution of the taxa involved (cf. Szalay 1977). Finally, taking the above discussion into account, after a cladistic analysis and consideration of extrinsic data, we may vaguely and informally speak of ancestors and descendants.

RELATIONSHIPS WITH OTHER GROUPS AND SHARED-DERIVED CHARACTER-STATES OF THE TAENIODONTA

Astragalar-Calcaneal Complex

Although *Onychodectes* is not here considered primitive relative to all other taeniodonts (its dentition shares derived character-states with the rest of the conoryctids, see below), its astragalar-calcaneal complex may be taken as an approximation of the primitive morphotype of these elements in the Taeniodonta. As Szalay (1977) has pointed out (and also Matthew 1937, before him), *Onychodectes* shares the derived astragalo-calcaneal morphology of *Cimolestes, Procerberus, Gypsonictops* and other "leptictids" sensu lato. These derived features include the complete obliteration of the astragalar foramen, increase in neck length of the astragalus, increase of the trochlear arc, increased sharpness of the lateral border of the tibial trochlea, reduction of the fibular facet of the calcaneum, and obliteration of the groove for the plantar calcaneocuboid ligament (Szalay 1977). Thus, Szalay (1977) has formally united the taeniodonts with the Leptictidae (including the Palaeoryctinae) and the Pantolestidae as the order Leptictimorpha.

Ear Region

The only well-preserved and described periotic region of a taeniodont is seen in USNM 12714, the holotype skull of *Ectoganus copei* (see description above). Apparently neither the bulla nor the auditory tube were ossified, and in general configuration it appears to be relatively primitive although somewhat closer to the "ferungulate" rather than the "unguiculate" ancestral morphotype (MacIntyre 1972). Thus, the mastoid processes are large (a character which may also be confounded by functional considerations), the tympanic process is apparently vestigial or absent, and the promontorium is low in profile and bears an uneven surface as in the ferungulate morphotype proposed by MacIntyre (1972). This scanty evidence of the basicranium corroborates leptictimorph affinities based on the calcaneal-astragalar morphology.

Recently Dr. M. C. McKenna (AMNH) has pointed out to me that taeniodonts may share a number of derived character-states of the ear region and basicranium with pantolestids. This hypothesis is based on undescribed, and still only partially prepared, pantolestid skulls currently under study by McKenna. Here it should be noted that pantolestids and "palaeoryctids" may be closely related, as suggested by Szalay (1977, see discussion therein). Thus, a fairly close relationship between pantolestids and taeniodonts does not necessarily exclude a fairly close relationship between palaeoryctids (such as *Cimolestes-Procerberus* and allies) and taeniodonts as hypothesized below.

Dental Evidence

On the basis of the astragalar-calcaneal complex and the ear region, *Procerberus-Cimolestes* and allied leptictimorph forms can be considered the sister-group of the taeniodonts. However, it is at present unclear if the palaeoryctids (sensu lato; see Van Valen 1966; Lillegraven 1969; Clemens 1973) form a symplesiomorphic sister-group of the Taeniodonta, or if at least some of these forms are distinguished by apomorphies which would exclude them from a direct ancestral relationship with the Taeniodonta. Lillegraven (1969, p. 69; see also McKenna 1969, 1975; Kielan-Jaworowska and others 1979) has stated that a large species of *Procerberus* (represented by a specimen from Mantua Lentil) might be ancestral to the Taeniodonta. There are also several undescribed specimens known from the earliest Paleocene of the Tullock Formation, Wyoming (W. Clemens, Jr., personal communication, 1981), the Denver Formation, Colorado (M. Middleton, personal communication, 1980) and the Polecat Bench Formation, Wyoming (W. Clemens, Jr., personal communication, 1981) which superficially appear to be transitional between a *Procerberus*-like form and a primitive taeniodont morphotype (as closely approximated by *Onychodectes*). These specimens probably represent several new genera and species (some of which may ultimately prove referable to the Taeniodonta) and will be described in detail by Dr. W. A. Clemens, Jr. (University of California, Berkeley) and Mr. M. Middleton (University of Colorado, Boulder); for the purposes of this paper they will be referred to as the "*Procerberus*-like forms." The P^4_4s of *Procerberus* and the *Procerberus*-like forms are relatively molariform, i.e., they bear well-developed protocones and metacones (Sloan and Van Valen 1965; personal examination of specimens) in contrast to the species of *Cimolestes* in which P^4_4 and the anterior premolars are usually non- to submolariform (Clemens 1973). McKenna (1975, p. 37) has hypothesized that "the last premolar is primitively a nonmolariform P^4_4" for Tokotheria; when trends within the clades of taeniodonts are extrapolated backwards they indicate that primitively the ancestral taeniodont morphotype has a nonmolariform P_4^4 (a condition approached by *Onychodectes*) and anterior premolars of a relatively simpler pattern.

In upper molar characters the species of *Procerberus* mentioned by Lillegraven (1969) and the *Procerberus*-like forms approach the condition seen in taeniodonts relative to forms such as *Cimolestes*. Thus, as Lillegraven (1969, p. 69) noted, the molars of these specimens are narrowed labiolingually as in taeniodonts, the pre- and postcingula are relatively reduced, the stylar shelves are relatively narrow, the ectoflexi are shallow, and M^{1-2} are subequal in length and width. However, P^4 bears a large metacone (i.e., is molariform) and the upper molars are not characterized by the extreme lingual enamel extension seen in most taeniodonts (although this may be seen in an incipient form in *Cimolestes*, *Procerberus* and the *Procerberus*-like forms). Thus, to derive taeniodonts directly from a *Procerberus*-like form with a relatively molarized P^4 would mean unmolarizing the premolars (which were relatively molarized from a previous nonmolariform condition as seen in *Cimolestes*) and then molarizing the premolars again within the Taeniodonta (especially within the Conoryctidae): i.e., character reversal occurred. Evolutionary trends in which somewhat molariform posterior premolars in an ancestral stock were reduced have been hypothesized for some eutherians (see Van Valen 1969; Clemens 1973, p. 44). Alternatively, the *Procerberus*-like forms may be considered to be derived toward the taeniodont condition in molar characters, but the molariform premolars may be regarded as an apomorphy of these forms, excluding them from being directly ancestral to the Taeniodonta. This scheme would invoke convergence in the development of molariform premolars in the *Procerberus*-like forms and the conoryctids. At present the detailed data needed to choose between these alternatives is lacking or unpublished; however, both schemes suggest that the *Procerberus*-like forms are the sister-group of the taeniodonts relative to other known eutherians. Moreover, in either scheme the primitive taeniodont morphotype has nonmolariform posterior premolars and the internal relationships of the Taeniodonta (as here defined) are unaffected. At present I consider Node 1 of Figure 56 to correspond to the Taeniodonta, although once the *Procerberus*-like forms are described, some of these new forms may be best accommodated by also being formally included in the Taeniodonta.

Edentate-Taeniodont Ties

Early in the study of this group, Marsh (e.g., 1874) and Cope (e.g., 1877, 1897) both suggested edentate ties for the Taeniodonta. However, it was Wortman (1896a, b, 1897a, b) who strongly advocated edentate affinities for the Taeniodonta. Wortman believed that the stylinodontids gave rise to the ground sloths and that the conoryctids probably gave rise to the armadillos. However, Wortman's views were rejected by a number of workers (Scott 1905; Ameghino 1902, 1906a, b; Winge 1915, 1923; Simpson 1931; Matthew 1937) and gained at best a limited acceptance (cf. Matthew 1918, 1928; Schlosser 1911). Wortman's (1897b) argument for a close relationship between the Edentata and the Taeniodonta has been thoroughly reviewed and rejected by Simpson (1931). In summary, Wortman based his arguments on many superficial characters of the skull, dentition and postcrania, along with "a good deal of over statement" (Matthew 1918, p. 611). Many of the resemblances cited by Wortman are in the forelimb and related to a functional convergence based on a fossorial adaptation. Other characters cited are merely primitive retentions in both groups which do not indicate a close relationship. There do not appear to be any special (shared-derived) characters which unite the taeniodonts with the true, South American edentates; rather, as described above, the taeniodonts are united with the "Leptictimorpha" on the basis of astragalocalcaneal characters (Szalay 1977).

Taeniodont-Tillodont Ties

The taeniodonts were also early associated with the Tillodontia (e.g., Cope 1882b; Marsh 1875b; Osborn and Earle 1895). However, this was based primarily upon the superficial similarity between the deeply rooted to evergrowing incisors of tillodonts and the canines of taeniodonts (at first thought to be incisors). It was Wortman (1897b) who first demonstrated decisively that these teeth (the incisors of tillodonts and the canines of taeniodonts) are not homologous and therefore these groups are distinct. Moreover, the incisors of tillodonts, the canines of taeniodonts, and the cheek teeth in both groups have very different morphologies as described above and in Lucas and Schoch (1981a). In summary, the enamel-free posterior parts of the incisors of tillodonts are not transversely compressed posteriorly as are the canines of taeniodonts and the lower molars of tillodonts have a bunoselenodont crown morphology as opposed to the transversely bilophodont morphology seen in the lower molars of stylinodontid taeniodonts. On the basis of cranial, postcranial and dental characters, Gazin (1953), Van Valen (1963, 1978) and Szalay (1977) have proposed that the tillodonts are closely related to the arctocyonid condylarths. The tillodont astragalus and calcaneum much more closely resemble those of the primitive ungulate *Protungulatum* (cf. Gazin 1953, figs. 37, 38, and Szalay 1977, figs. 6–9) than it does that of *Procerberus* or those of the Taeniodonta.

THE ANCESTRAL TAENIODONT

By using both outgroup comparison (primarily primitive outgroups as discussed in the preceding section) to polarize morphoclines and by extrapolating backwards progressive trends seen in taeniodonts (see below), the primitive taeniodont morphotype can be hypothesized. As MacIntyre (1972, p. 276) pointed out, "When early members of diverse groups share characters that converge backwards in time to some common form, we can reasonably believe that to be the primitive form for all these groups." I have used this principle to arrive at my hypothesis as to what are primitive vs. derived features within the Taeniodonta and also between the Taeniodonta and other eutherians. However, I have tried, as far as possible, not to take the relative ages of specimens into account (the "early" of MacIntyre in the quote above) but rather to deal solely with morphoclines which when oriented (polarized) correctly, converge upon a common (presumed to be the primitive) form. As stated above, in my analysis I have tried to deal solely with the intrinsic morphology of the specimens so as to avoid circular reasoning and also be able to compare my hypothesis of relationships and morphoclines to the stratigraphic and geographic distribution of the taxa involved.

Based on backward extrapolations of progressive trends seen in taeniodonts and adopting Szalay's (1977) hypothesis that his "Leptictimorpha" (but excluding the taeniodonts) contains the sister-group of the Taeniodonta (perhaps *Procerberus* or a pantolestid) as discussed in the preceding section, the primitive taeniodont morphotype is hypothesized to be a small (primitive; "primitive" character-states are generally shared with *Procerberus*) eutherian with a complete dentition (primitive), generalized postcranial skeleton (primitive; see discussions above, Gregory 1910 and Novacek 1980 for discussions of features of the generalized, primitive eutherian skeletal morphotype); simple, nonmolariform, bladelike, sectorial lower premolars (primitive); simple (lacking protocones and metacones) upper premolars (primitive; as noted above, *Procerberus* may be independently derived in bearing a P^4 metacone); simple tritubercular upper molars lacking hypocones (primitive); lower molars with relatively large paraconids (primitive); upper molars and premolars relatively narrow as compared to *Procerberus* (derived character-state of taeniodonts: "derived" character-states are relative to *Procerberus*); upper molars with protocones, metaconules and paraconules lingually placed (derived); ectoflexi of upper molars reduced (derived); stylar shelves of upper molars narrow (derived); trigonids and talonids of all lower molars subequal in length and width (derived); molar trigonids only slightly higher than talonids (derived); protoconids and metaconids of molars subequal in height (derived); cingula on upper molars and cingulids on lower molars reduced (derived); incipient hypsodonty with labial extension of the enamel on the lower cheek teeth and lingual extension of the enamel on the upper cheek teeth (derived: crown hypsodonty is very rudimentary, if present at all, in *Wortmania*; thus, crown hypsodonty may better be considered convergent in stylinodontids and conoryctids); upper and lower molars subequal in size or decreasing in size posteriorly (derived), and a leptictimorph astragalocalcaneal complex (derived leptictimorph character-state, primitive relative to taeniodonts). Thus, relative to their "leptictimorph" sister group, the Taeniodonta are united as a monophyletic order by the complex of derived character-states cited above.

MORPHOCLINES WITHIN THE TAENIODONTA

Within the Taeniodonta (sensu stricto, exclusive of the *Procerberus*-like forms), there appear to be two monophyletic clades (Fig. 56), each characterized by unique shared-derived character-states and trends relative to the hypothesized ancestral taeniodont morphotype. These two clades are here referred to as the Conoryctidae (*Onychodectes, Conoryctella, Conoryctes* and *Huerfanodon*) and the Stylinodontidae (*Wortmania, Psittacotherium, Ectoganus* and *Stylinodon*). Each is characterized by its own dental trends from an ancestral morphotype with simple (essentially single-cusped) upper and lower premolars.

The conoryctids primitively retain anteroposteriorly elongated and transversely compressed, bladelike lower premolars which are progressively molarized (beginning with P_4) by the addition of distinct talonids posteriorly (seen in a rudimentary form even in *Onychodectes*) and the addition of metaconids and paraconids anteriorly. Likewise, the upper premolars are primitively simple, suboval to triangular in cross-section, narrow labiolingually, and become progressively molarized (beginning with P^4) by the addition of protocones and metacones (seen in rudimentary form in *Onychodectes*). Thus in *Onychodectes* P^4 bears a large paracone, moderate protocone and an incipient (variable) metacone and P_4 bears a small talonid heel. In *Conoryctella* these features are more strongly developed. In *Conoryctes* P^4 is fully molariform and bears a large and distinct protocone, paracone and metacone and P_4 bears a well-developed talonid. In *Huerfanodon* P^3 also bears a small, but distinct protocone and metacone as well as a large paracone, M^{1-3} have prominant mesostyles and P_4 may bear a large metaconid as well as a large protoconid and a well-developed talonid.

Other morphoclines seen in the conoryctids which corroborate the polarity of the morphocline from nonmolariform to molariform posterior premolars include: increasing crown hypsodonty of the cheek teeth, increasing size as reflected both in tooth, skull and overall body size, relative increase in size of the canines, and the development of a relatively short and deep face with a thick and deep mandibular ramus.

However, although *Onychodectes* is primitive relative to the other conoryctids in most features, the known P^4 of *Onychodectes* bears an incipient parastyle, stylocone, metastyle and metastylocone which may represent autapomorphies of the genus, perhaps excluding it from the direct ancestry of generally more derived conoryctids. Within the genus *Onychodectes, O. t. tisonensis* has relatively simpler-crowned premolars and molars than *O. t. rarus* and in all presently known features is totally primitive relative to *O. t. rarus.*

Conoryctella is generally primitive relative to *Conoryctes* and *Huerfanodon*; however, the known lower canine of *Conoryctella pattersoni* is triangular in cross-section and more deeply rooted than the canines in *Conoryctes* and *Huerfanodon.* These may represent autapomorphies of *Conoryctella.* Within the genus *Conoryctella, C. dragonensis* has a slightly more molariform P^4, and is slightly larger, than *C. pattersoni.* Thus, *C. dragonensis* appears to be derived relative to *C. pattersoni.*

Conoryctes is distinguished by the autapomorphy of reduced paraconids on the lower molars. *Huerfanodon* primitively retains large paraconids, but bears a more molariform P^3 and P_4 than *Conoryctes* and also an internal groove on the lower canine. Within *Huerfanodon, H. polecatensis* bears a slightly more molariform P_4, and is slightly larger, than *H. torrejonius* and thus appears to be derived relative to *H. torrejonius.*

In the primitive stylinodontids the upper and lower premolars are primarily simple, essentially unicuspid, suboval teeth which early on were set obliquely to transversely in the jaw. Thus, in *Wortmania* the lower premolars are all of similar morphology and subequal in size and bear single, large, high, labially set conids which are slightly recurved lingually. Posterolingually the lower premolars of *Wortmania* bear small cingulids. In *Psittacotherium* and *Ectoganus* P_{3-4} are molariform with well-developed trigonids and talonids, but in all of the stylinodontids P_{1-2} remain transversely set teeth with a large anteroexternal conid and a smaller posterointernal conid developed from the posterolingual cingulid seen on the P_{1-2} of *Wortmania.*

The upper premolars are poorly known in *Wortmania,* but appear to be simple, transversely set teeth, bearing only large paracones on P^{1-2} and large paracones and protocones on P^{3-4}. In *Psittacotherium* and *Ectoganus* (and presumably in *Stylinodon,* although unworn premolars are unknown) P^{1-2} remain relatively simple, bicuspid, transversely set teeth. P^{3-4} are elaborated by the addition of anterior and posterior transverse crests extending from the protocone to the paracone forming a bilophodont tooth, rather than by addition of a metacone and elaboration on a tritubercular pattern as seen in all of the conoryctids. Only slight metacones develop on the posterior face of the paracones of some P^{3-4}s of *Psittacotherium* and *Ectoganus.* In *Ectoganus* and perhaps also in *Stylinodon* (also foreshadowed in *Wortmania* and *Psittacotherium*) all of the molars bear two well-developed transverse lophs. In the lower molars these lophs are formed by the metaconid-protoconid and entoconid-hypoconid. In the upper molars these lophs are formed by the paracone-protocone and the metacone-hypocone (the hypocone develops by a splitting off from the protocone).

The stylinodontids also progressively elaborate on the crown hypsodonty of the teeth, which may be a derived character of all taeniodonts, and also develop root hypsodonty (White 1959). Thus in *Stylinodon* all of the teeth are evergrowing and rootless and the enamel is limited to thin labial and lingual strips on the cheek teeth after moderate wear.

Wortmania appears to be completely primitive relative to all other known stylinodontids. In most features *Psittacotherium* is primitive relative to *Ectoganus*; however, in *Psittacotherium* P_1 and the third trochanter of the femur are reduced relative to *Ectoganus*. These two features thus represent autapomorphies of *Psittacotherium*.

Within *Ectoganus, E. copei* appears to be slightly derived relative to *E. gliriformis* in generally having fewer traces of the paraconids on the lower molars. Possibly the small size of *E. copei* relative to *E. gliriformis* is also a secondarily derived feature. Within each species of *Ectoganus*, the subspecies with relatively higher crowned teeth (*E. g. gliriformis* and *E. c. copei*) may represent the derived condition relative to the subspecies with lower crowned teeth (*E. g. lobdelli* and *E. c. bighornensis*).

Although *Stylinodon* appears to be the most derived stylinodontid in almost all character-states (crown morphology, crown and root hypsodonty, cranial, mandibular and postcranial modifications, see below), there is one exception. *Stylinodon* is known from complete crania to definitely bear two upper incisors on either side: however, the known, admittedly fragmentary (with the exception of the holotype skull of *Ectoganus copei*) material indicates that both *Psittacotherium* and *Ectoganus* have only one upper incisor on each side. The known material of *Wortmania* is too incomplete to determine the incisor formula, but it is here assumed that *Wortmania* had at least two incisors above, following Wortman (1897b). Thus, it is here considered that *Stylinodon* is not a direct descendant of either *Psittacotherium* or *Ectoganus*, whereas all three genera form the sister-group of *Wortmania*.

Within the genus *Stylinodon, S. inexplicatus* may represent a derived, neotenous offshoot from the typical *S. mirus* (Fig. 55).

The stylinodontids are also united relative to the conoryctids by a number of shared-derived features of the crania and postcrania which are already well developed in *Wortmania*, such as the development of large, laterally compressed and recurved claws on the manus and less compressed, but large claws on the pes; relatively large and robust limb bones, especially of the forelimb, and a short and deepened face with a deep mandible and high occiput, a well-fused symphysis and a large pit for the genioglossus muscle of the tongue (cf. Patterson 1949b).

CLADOGRAM AND CLASSIFICATION OF THE TAENIODONTA

These above-mentioned morphoclines and the distribution of derived character-states can be set forth most conveniently in the form of a cladogram (Fig. 56) and an accompanying classification (Table 7) which represents a hypothesis of the evolutionary (cladistic) relationships (i.e., relative recency of common ancestry) of the taxa involved. Any cladistic analysis must be based only on morphological data, but once an hypothesis of relationships is posited, it is important and interesting to see how well it agrees with the temporal and zoogeographical distribution of the organisms under consideration.

The Taeniodonta is an order whose record is wholly limited to the Paleocene–Eocene sedimentary deposits of the Rocky Mountain intermontane sedimentary basins. At present, taeniodont fossils are too poorly known to determine if there are any trends in their geographical distribution. Thus, for example, the occur-

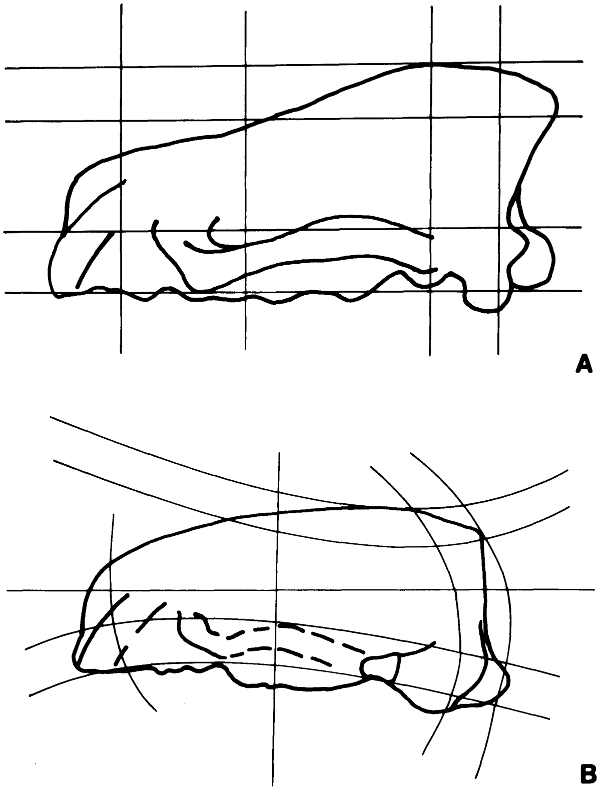


FIG. 55. Transform coordinates, after the manner of D'Arcy Thompson (1942), of *Stylinodon inexplicatus* (*b*) relative to *Stylinodon mirus* (*a*). The figure suggests that *S. inexplicatus* is a small, neotenous offshoot of *S. mirus* with differentially stunted growth. Whereas this suggestion may be tantalizing, its investigation is beyond the scope of the present paper. Furthermore, only one incomplete specimen of *S. inexplicatus* is known and an ontogenetic series is unknown for its presumed "ancestor," *S. mirus* (all known specimens of *S. mirus* are adults). Without more, especially the latter, data one can do little more than speculate that perhaps *S. inexplicatus* is a broadly paedomorphic form relative to *S. mirus* (cf. Roth 1982 for an interesting case study of paedomorphosis in a lineage of dwarf mammoths based on abundant skeletal material).

rence of *Wortmania* in only the San Juan Basin, New Mexico, and perhaps the Wagonroad or Dragon local faunas, Utah, may be wholly a result of the general rarity of earliest Paleocene deposits, confounded by the fact that *Wortmania* also appears to have been a particularly rare element of these faunas even when they are well known (i.e., in the San Juan Basin). In contrast, *Psittacotherium* is a far-ranging genus and this may simply correlate with the fact that there are more and better known Torrejonian–early Tiffanian faunas. However, the restriction of the Taeniodonta to western North America does appear to be real. It appears that enough deposits of Paleocene–Eocene age have been sampled in Asia, Europe and South America such that if taeniodonts existed on these continents, it is probable that they would have been found by now. Their restriction to western North America suggests that taeniodonts may have evolved in this area and never emigrated.

Kielan-Jaworowska (1980) has suggested that there was a one-way dispersal of mammals from Asia to western North America during the late Cretaceous. She suggests that the Eutheria and taeniolabidoid multituberculates originated in Asia and thence dispersed to North America, whereas the Marsupialia and

TABLE 7. A classification of the Taeniodonta

- Order TAENIODONTA Cope, 1876a, p. 39 (=GANODONTA Wortman, 1896a, p. 259; =STYLINODONTIA Marsh, 1897, p. 137; =TAENIODONTIDAE Szalay, 1977, p. 368).
  - Family CONORYCTIDAE Wortman, 1896a, p. 260.
    - Subfamily ONYCHODECTINAE Winge, 1917, p. 105 (Matthew, 1937, p. 238) (=ONYCHODECTINI Winge, 1917, p. 105).
      - *Onychodectes* Cope, 1888d, p. 317.
        - *Onychodectes tisonensis* Cope, 1888d, p. 318 (=*Onychodectes rarus* Osborn and Earle, 1895, p. 42).
          - *Onychodectes tisonensis tisonensis* Cope, 1888d, p. 317 (Schoch, 1981b, p. 938). E. Paleo.; NM, UT.
          - *Onychodectes tisonensis rarus* Osborn and Earle, 1895, p. 42 (Schoch, 1981b, p. 938). E. Paleo.; NM.
    - Subfamily CONORYCTINAE Wortman, 1896a, p. 260 (Schlosser, 1911, p. 414).
      - Tribe CONORYCTELLINI Schoch, 1982a, p. 470.
        - *Conoryctella* Gazin, 1939, p. 276.
          - *Conoryctella dragonensis* Gazin, 1939, p. 276. M. Paleo.; ?NM, UT.
          - *Conoryctella pattersoni* Schoch and Lucas, 1981c, p. 5. M. Paleo.; NM, UT.
      - Tribe CONORYCTINI Wortman, 1896a, p. 260 (Winge, 1917, p. 105).
        - *Conoryctes* Cope, 1881a, p. 829 (=*Hexadon* Cope, 1884a, p. 794; non *Hjexodon* Olivier, 1789, p. 1).
          - *Conoryctes comma* Cope, 1881a, p. 829 (=*Hexodon molestus* Cope, 1884a, p. 794). M. Paleo.; NM.
        - *Huerfanodon* Schoch and Lucas, 1981b, p. 683.
          - *Huerfanodon torrejonius* Schoch and Lucas, 1981b, p. 684. M. Paleo.; NM.
          - *Huerfanodon polecatensis* Schoch and Lucas, 1981b, p. 688. M. Paleo.; WY.
          - ?*Huerfanodon "heilprinianus"* (Cope, 1882b, p. 193) Schoch and Lucas, 1981b, p. 690, nomen dubium. Paleo.; NM.
  - Family STYLINODONTIDAE Marsh, 1875b, p. 221.
    - Subfamily WORTMANIINAE Schoch, 1982a, p. 470.
      - *Wortmania* Hay, 1899, p. 593.
        - *Wortmania otariidens* (Cope, 1885a, p. 492) Hay, 1899, p. 593. E. Paleo.; NM.
    - Subfamily STYLINODONTINAE Marsh, 1875b, p. 221 (Schlosser, 1911, p. 414).
      - Tribe ECTOGANINI Cope, 1876a, p. 39 (Schoch, 1983b, p. 205) (=ECTOGANIDAE Cope, 1876a, p. 39; =CALAMODONTIDAE Cope, 1876a, p. 39; =HEMIGANIDAE Cope, 1888d, p. 310; =PSITTCOTHERIINAE Matthew, 1937, p. 255; =PSITTACOTHERIINI Schoch, 1982a, p. 470).
        - *Psittacotherium* Cope, 1882b, p. 156 (=*Hemiganus* Cope, 1882e, p. 831).
          - *Psittacotherium multifragum* Cope, 1882b, p. 156 (=*Psittacotherium aspasiae* Cope, 1882c, p. 192; =*Hemiganus vultuosus* Cope, 1882e, p. 831; = *Psittacotherium megalodus* Cope, 1887b, p. 469). M. Paleo.; MT, NM, TX, ?UT, WY.
        - *Ectoganus* Cope, 1874, p. 592 (=*Calamodon* Cope, 1874, p. 593; =*Dryptodon* Marsh, 1876b, p. 401; =*Conicodon* Cope, 1894, p. 594; non *Calamodon* Amaral, 1935, p. 203; =*Lampadophorus* Patterson, 1949a, p. 41).
          - *Ectoganus gliriformis* Cope, 1874, p. 592 (see synonymies under the subspecies).
            - *Ectoganus gliriformis gliriformis* Cope, 1874, p. 592 (Schoch, 1981b, p. 938) (=*Calamodon simplex* Cope, 1874, p. 593; =*Calamodon arcamaenus* Cope, 1874, p. 593; =*Calamodon novomehicanus* Cope, 1874, p. 594; =*Dryptodon crassus* Marsh, 1876b, p. 403). ?L. Paleo.-E. Eoc.; NM, WY.
            - *Ectoganus gliriformis lobdelli* (Simpson, 1929b, p. 11) Schoch, 1981b, p. 938 (=?*Psittacotherium lobdelli* Simpson, 1929b, p. 11; =*Lampadophorus expectatus* Patterson, 1949a, p. 42). L. Paleo.; CO, MT, WY, SC.
          - *Ectoganus copei* Schoch, 1981b, p. 938.
            - *Ectoganus copei copei* Schoch, 1981b, p. 938. E. Eoc.; WY.
            - *Ectoganus copei bighornensis* Schoch, 1981b, p. 940. ?L. Paleo.-E. Eoc.; WY.
      - Tribe STYLINODONTINI Marsh, 1875b, p. 221 (Winge, 1917, p. 106).
        - *Stylinodon* Marsh, 1874, p. 531.
          - *Stylinodon mirus* Marsh, 1874, p. 531 (=*Calamodon cylindrifer* Cope, 1881b, p. 184). E.–M. Eoc.; CO, ?TX, UT, WY.
          - *Stylinodon inexplicatus* Schoch and Lucas, 1981d, p. 178. M. Eoc.; WY.

Abbreviations. CO = Colorado, E. = Early, Eoc. = Eocene, L. = Late, M. = Middle, MT = Montana, NM = New Mexico, Paleo. = Paleocene, SC = South Carolina, TX = Texas, UT = Utah, WY = Wyoming.

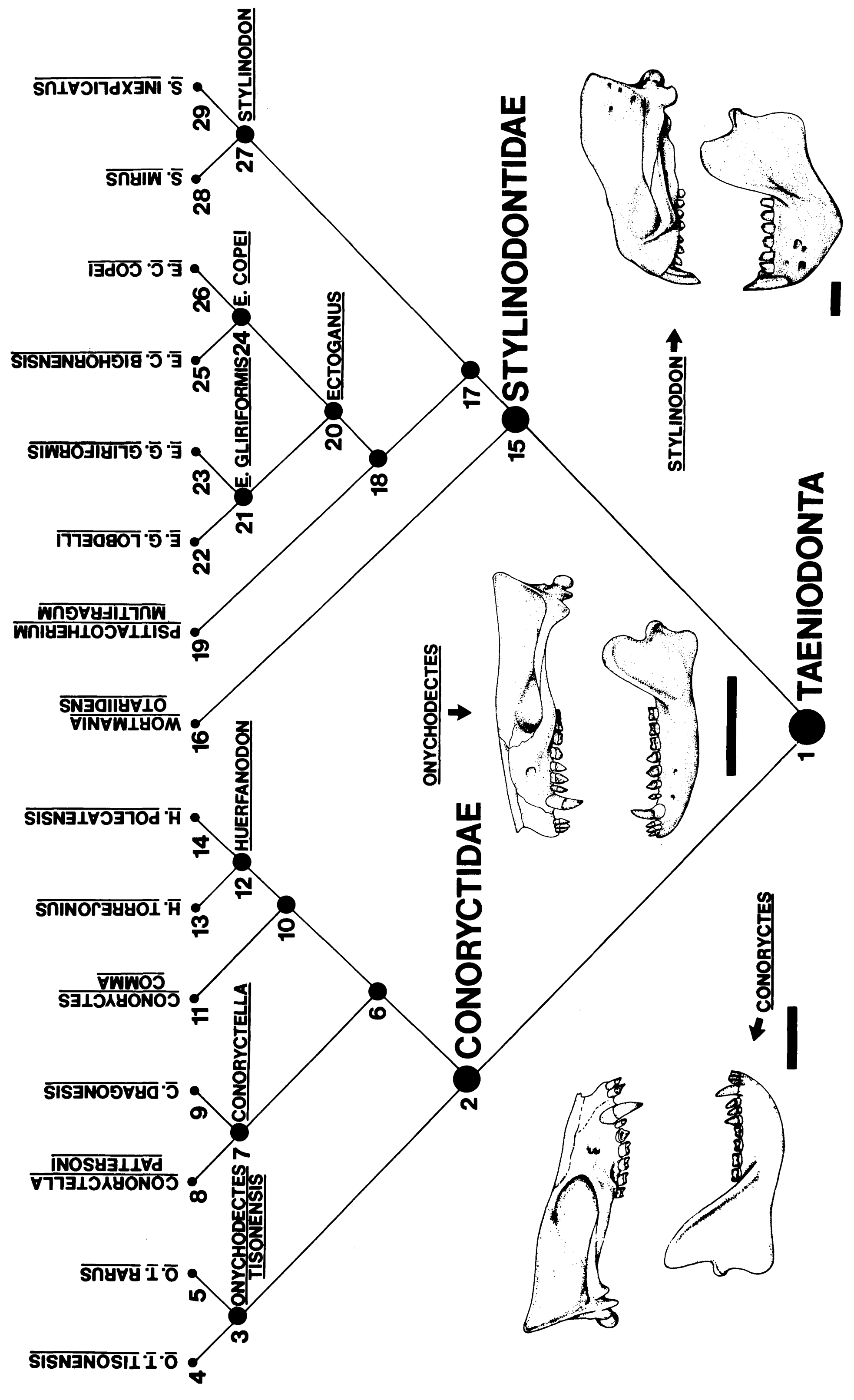

TAENIODONTA
1
CONORYCTIDAE
2
3
ONYCHODECTES TISONENSIS
4
O. T. TISONENSIS
5
O. T. RARUS
6
7
CONORYCTELLA
8
CONORYCTELLA PATTERSONI
9
C. DRAGONESIS
10
11
CONORYCTES COMMA
12
HUERFANODON
13
H. TORREJONIUS
14
H. POLECATENSIS
STYLINODONTIDAE
15
16
WORTMANIA OTARIIDENS
17
18
19
PSITTACOTHERIUM MULTIFRAGUM
20
ECTOGANUS
21
E. GLIRIFORMIS
22
E. G. LOBDELLI
23
E. G. GLIRIFORMIS
24
E. COPEI
25
E. C. BIGHORNENSIS
26
E. C. COPEI
27
STYLINODON
28
S. MIRUS
29
S. INEXPLICATUS
CONORYCTES
ONYCHODECTES
STYLINODON

FIG. 56. Hypothesis of the phylogenetic relationships of the Taeniodonta. Bars below the skulls are 4 cm long. Character–states [Asterisks (*) indicate convergences and question marks (?) indicate uncertain polarities.] corresponding to the node points are: *1,* Narrow upper molars with protocones, protoconules, and metaconules small and placed far lingually, paracones and metacones moderate-sized, punctate and placed far labially with reduced stylar shelves; pre- and postcingula lacking on upper molars; hypocone absent or developed by a splitting-off from the protocone; lower molars lack cingulids; trigonids and talonids of all molars subequal in size (length and width); trigonids bear subequal protoconids and metaconids; trigonids only slightly higher than talonids; molars subequal in size or decrease in size posteriorly; slight crown hypsodonty of the cheek teeth (characterized by lingual enamel extension on the uppers and labial enamel extension on the lowers) with an increased grinding function. *2,* Narrow, triangular-shaped P^{3-4}; well-developed crown hypsodonty*; P^4 with incipient metacone; P_4 with small talonid heel. *3,* P^4 with incipient parastyle, stylocone, metastyle and meta-stylocone (?). *4,* Plesiomorphous sister taxon of *O. t. rarus*. *5,* Anterior internal accessory cusp on P_4; M_{1-2} with external accessory cusp or cusps between the trigonid and talonid lobes. *6,* Paraconids somewhat reduced; molars very narrow. *7,* Lower canine triangular in cross-section and deeply rooted (known only for *Conoryctella pattersoni*). *8,* Plesiomorphous sister taxon of *C. dragonensis*. *9,* P^4 slightly more molariform; larger than *C. pattersoni*. *10,* Face and mandible short and deep*; P^1 absent; P^4_4 molariform. *11,* Very small paraconids. *12,* P^3 submolariform; mesostyles well-developed on M^{1-2}; lower canine with internal groove. *13,* Plesiomorphous sister taxon of *H. polecatensis*. *14,* P_4 bears large and distinct metaconid which approaches the protoconid in size. *15,* Premolars set obliquely to transversely; canines very large; skull and mandible very short and deep*; large, laterally compressed and recurved claws on the manus; large and robust limb bones. *16,* Plesiomorphous sister taxon of Stylinodontinae. *17,* Well-developed crown hypsodonty* and incipient root hypsodonty of the cheek teeth; canines subgliriform with enamel limited to the anterior faces and the posterior parts compressed transversely; skull and mandible extremely short and deep. *18,* A single upper incisor; P_{3-4} molariform. *19,* P_1 and third trochanter of the femur small (?). *20,* Canines rootless; crown and root hypsodonty of cheek teeth moderately well-developed; upper and lower molars bilophodont. *21,* Slightly larger in size (?). *22,* Plesiomorphous sister taxon of *E. g. gliriformis*. *23,* Crown and root hypsodonty of the cheek teeth extremely well developed*. *24,* Slightly smaller size (?); paraconids very small. *25,* Plesiomorphous sister taxon of *E. c. copei*. *26,* Crown and root hypsodonty of cheek teeth extremely well developed. *27,* All teeth rootless; anterior premolars large and well developed. *28,* Largest skull and body size; skeleton extremely massive and robust. *29,* Extremely small size.

ptilodontoid multituberculates originated in North America and never dispersed to Asia, although they survived in North America throughout the entire Paleocene–Eocene. Similarly, one might suggest that the eutherian ancestors of the Taeniodonta came from Asia in the late Cretaceous; the Taeniodonta originated in situ in western North America, and never emigrated from western North America again. Likewise, the marsupials appear to have originated and diversified in North America, but never migrated into Asia and only one lineage is known from the Paleogene of Europe (Clemens 1968; Lillegraven 1969; Marshall 1980). However, marsupials did extend to South America, Australia and Antarctica (Woodburne and Zinsmeister 1982). The taeniodonts' restriction to western North America even during the middle Paleocene to middle/late Eocene when faunal exchange did take place between Asia, North America and Europe may be due, at least in part, to a competitive inferiority of the Taeniodonta which did not permit them to readily expand their range and invade new territories. The Taeniodonta were an archaic order of relatively small-brained mammals ("Mesoplacentalia" in the terms of Osborn and Earle 1895, p. 3) which could not successfully compete against the introduction by immigration (Gingerich 1976, p. 87) or in situ evolution (Van Houten 1945, p. 440) of the mammals of more "modern aspect" ("Cenoplacentalia" of Osborn and Earle 1895) into western North America during the early Eocene and later times. At best, the Taeniodonta could only hold their own for a time.

Taeniodonts, in analogy with the aardvark (see above), may also have been rather solitary and not particularly mobile (for instance, there is no evidence of long distance travel or migration on the part of taeniodonts) with relatively restricted home ranges; whereas they may have made a circuit of 10 km radius while foraging, they may have often returned to the same burrow for shelter. Thus, these factors of the biology of taeniodonts may have greatly limited their dispersal ability and may be a primary reason why they did not get out of North America.

The temporal distribution of the taeniodonts is better known (Fig. 44) and in general agrees with the cladogram and the hypothesis of relationships that it represents. The *Procerberus*-like forms are all probably of earliest Paleocene age. Among the conoryctids, *Onychodectes* is a Puercan form, *Conoryctella* is an "early" Torrejonian form, *Conoryctes* is a "late" Torrejonian form and *Huerfanodon* is a Torrejonian form. Among the stylinodontids, *Wortmania* is a Puercan form, *Psittacotherium* is a Torrejonian–Tiffanian form, *Ectoganus* is a Tiffanian–middle Wasatchian form and *Stylinodon* is a late Wasatchian–Uintan form. Thus, in both clades what are here considered to be more derived forms generally occur later (stratigraphically higher in the rock sequence).

EVOLUTIONARY TRENDS AND ANCESTOR–DESCENDANT RELATIONSHIPS WITHIN THE TAENIODONTA

Based on the morphoclines seen within the taeniodonts and the cladistic analysis of the order, we can go a few steps further and speculate on evolutionary trends within the taeniodonts. Thus, we can imagine the primitive ancestral (first) taeniodont which gave rise to all later taeniodonts (as embodied in the ancestral morphotype hypothesized above). We can imagine a species that might be accommodated within the genus *Onychodectes,* which was completely primitive relative to, and truly ancestral to, a species of *Conoryctella,* which was likewise primitive and ancestral to a species of *Conoryctes* and *Huerfanodon.* Thus we might speak loosely of *Onychodectes* (stripped of autapomorphy) giving rise to *Conoryctella,* which likewise gave rise to *Conoryctes* and *Huerfanodon.* Among the stylinodontids we can speak easily of a *Wortmania* giving rise to a *Psittacotherium* giving rise to an *Ectoganus,* and also of a *Wortmania* eventually giving rise to a *Stylinodon* independently through a number of completely unknown intermediates. Furthermore, we can bring the stratigraphic and geographic data to bear on the problem (extrinsic data not permissible in a strict cladistic analysis) along with functional scenarios, when speculating on such a high level. That is, we can build an evolutionary story grounded in "fact" as we perceive it, but also frankly speculative.

Trends among the Conoryctids

Predominant trends which are discernible among the Puercan–Torrejonian conoryctids are increase in overall body size, increase in the relative size of the head with a shortening and deepening of the face and mandible, relative enlargement of the canines, slight increase in the degree of crown hypsodonty seen in the cheek teeth, and a tendency toward molarization of the posterior premolars (P^{3-4}_{3-4}) and a reduction of the anterior premolars (with P^1 apparently lost in *Conoryctes* and *Huerfanodon*).

When the length of the teeth of *Conoryctella, Conoryctes* and *Huerfanodon* are plotted on a graph as percentages of the lengths of the corresponding teeth in *Onychodectes* (Fig. 57) it can be seen that *Conoryctella* appears to be a slightly scaled-up version of *Onychodectes,* but with all of the teeth remaining in approximately the same proportions as in *Onychodectes.* (There is only a slight increase in the relative size of C_1; all other differences may be due to the small sample size for *C. pattersoni* on which Table 8 is based.) In contrast, *Conoryctes* and *Huerfanodon* are both absolutely larger than *Onychodectes* and there is also a relative increase in size of the canines and posterior premolars (P^{3-4}_{3-4}).

In *Conoryctes* the paraconids of the lower molars are reduced relative to *Onychodectes. Huerfanodon* primitively(?) retains distinct paraconids (of course there is the possibility that these are secondarily derived with the increasing molarization of P^{3-4}_{3-4}). Mesostyles, virtually absent on the upper molars of *Onychodectes* and *Conoryctella,* are variably developed in *Conoryctes* and well developed in *Huerfanodon.* The postcrania of the conoryctids are not well enough known to allow speculation about the evolutionary trends. As discussed in the previous section, all that can be said is that the later (younger) conoryctids were slightly larger in body size.

Trends among the Stylinodontids

The earliest known stylinodontid, *Wortmania,* is already a "good" stylinodontid in that it shows many of the derived traits which characterize the family. Thus, *Wortmania* is a relatively large, robust beast with a shortened, massive head, deep face and mandible, strong, powerful limbs, and large, laterally compressed and recurved unguals on the manus. While we can speculate on how the ancestor of *Wortmania* looked (see discussion of the ancestral taeniodont morphotype above), it probably did not bear a morphology particularly close to that of *Onychodectes.* Patterson (1949b) suggested that *Onychodectes* is very close to the ancestral condition for all taeniodonts, including *Wortmania* and the remaining stylinodontids. However, I suggest that *Onychodectes* and *Wortmania* had already diverged widely from each other. This is further corroborated by the fact that both genera are known from the earliest Puercan strata of the Nacimiento Formation, San Juan Basin. As discussed above, the premolar crown configuration of *Wortmania*

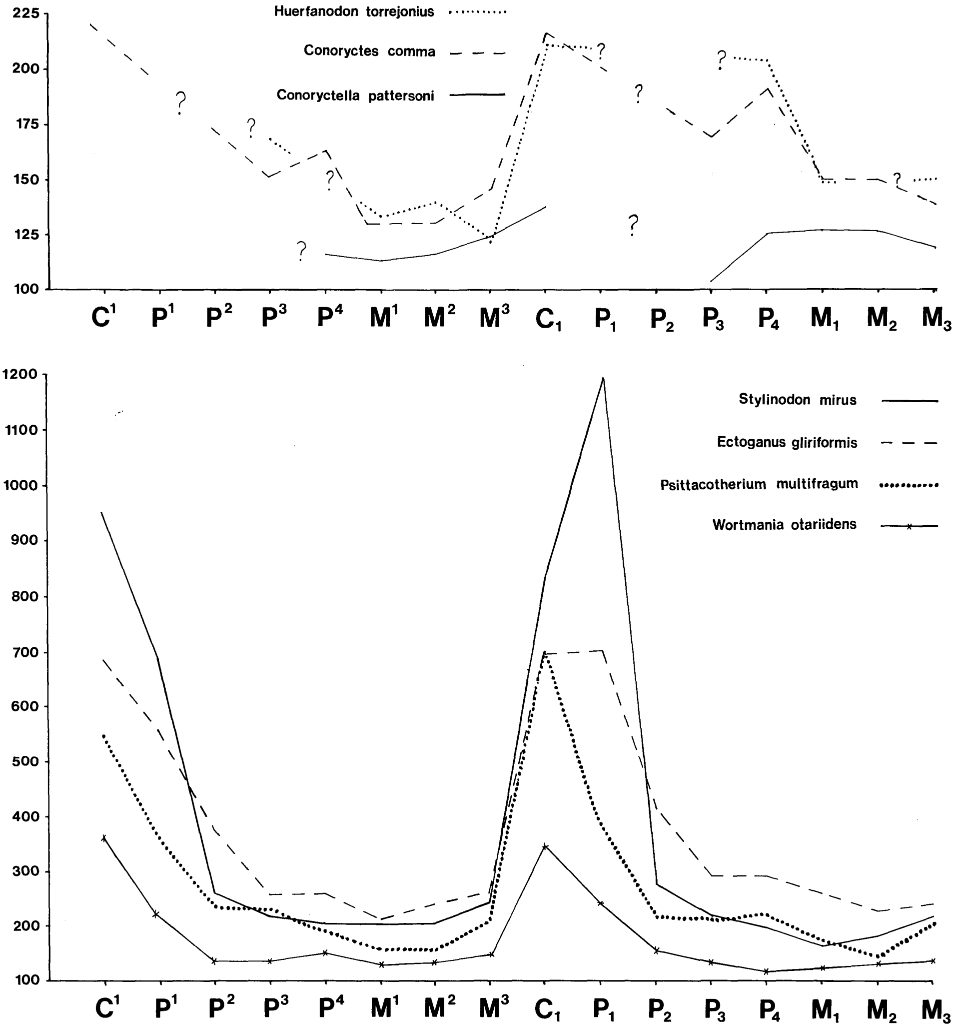


FIG. 57. Lengths of the teeth of various taeniodont species plotted as a percentage of the lengths of the corresponding teeth in *Onychodectes tisonensis*. Data upon which these graphs are based are presented in Table 8.

appears in some respects more primitive (e.g., lacking a well-developed talonid heel on P_4) than *Onychodectes* and in other respects derived in a different direction and towards the later, more advanced stylinodontids (e.g., in having transversely set premolars, with P_{1-4} bearing well-developed lingual cingulids). Also, significantly, *Wortmania* is the most primitive taeniodont in terms of the development of crown hypsodonty. Whereas *Onychodectes* has an extremely well-developed crown hypsodonty, in *Wortmania* this character-state (which is better developed in *Psittacotherium* and fully developed in *Ectoganus* and *Stylinodon*) is seen only in an incipient state. Thus, I suggest that whereas incipient hypsodonty was a character-state of the earliest ancestral taeniodont, it was independently elaborated upon in the conoryctids and stylinodontids. It is also interesting that whereas *Wortmania* is a much larger and more robust animal overall as compared to *Onychodectes* (cf. Tables 10–21), it does not intuitively seem that an animal of the size and proportions of *Onychodectes* would have given rise to *Wortmania*.

TABLE 8. Lengths of taeniodont teeth expressed as a percentage of those in *Onychodectes*

	Wortmania	*Psittaco-therium*	*E. g. gliriformis*	*S. mirus*	*C. pattersoni*	*C. comma*	*H. torrejonius*
C^1	362.5	548.3	687.5	950.8	—	220.0	—
P^1	—	362.5	560.4	687.5	—	—	—
P^2	131.7	234.4	378.0	262.2	—	—	—
P^3	131.9	229.1	262.3	223.4	—	150.6	168.1
P^4	151.1	194.4	264.4	203.8	115.3	161.0	—
M^1	127.6	167.7	214.6	203.9	113.4	130.2	133.9
M^2	131.9	155.8	240.6	203.8	116.4	131.0	138.7
M^3	—	214.5	264.8	243.2	129.5	145.5	122.7
C_1	346.3	699.3	696.3	832.5	137.5	215.0	210.0
P_1	242.2	—	700.8	1178.3	—	—	—
P_2	152.9	213.9	407.3	275.6	—	—	—
P_3	135.1	—	285.9	219.8	104.8	167.9	—
P_4	120.8	219.0	281.7	201.1	125.0	191.1	204.7
M_1	125.0	173.8	205.6	169.1	127.9	150.3	148.5
M_2	130.4	146.3	227.3	181.2	127.2	150.7	—
M_3	—	202.2	241.9	220.7	119.0	135.3	150.0

For example, metacarpal two of *Wortmania* is only slightly larger (longer) than that of *Onychodectes*, yet much wider and more robust (cf. Figs. 5 and 14). Intuitively, one might expect that a direct ancestor of *Wortmania* would bear a metacarpal two shorter than that of *Onychodectes*, yet more robust, i.e., of similar relative proportions to that of *Wortmania*, even if absolutely smaller.

Among the stylinodontids the major evolutionary trends have already been outlined. These include: an increase in overall size, increasing crown hypsodonty of the teeth, the development and elaboration of root hypsodonty of the teeth, emphasis shifted to the anterior dentition, bilophodonty of the molars elaborated, shortening and deepening of the face and jaw, enlargement of the unguals, and modifications of the manus and pes.

In terms of overall size and relative body proportions, the advanced stylinodontid condition was reached in the Torrejonian with *Psittacotherium* (Tables 10–21). Further modifications were concerned with the elaboration of the teeth, skull, manus and pes, all tending towards increased massiveness and robustness. The carpal and tarsal elements were arranged into a stronger, more powerful, serial arrangement (as described and discussed above). Once the stylinodontid morphotype was well established with *Psittacotherium*, it appears to have been modified and elaborated, but not radically changed by later species. That is, with *Psittacotherium* (or perhaps even *Wortmania*), the stylinodontids appear to have entered a niche which they never left or expanded significantly. One exception might be the unusual and extremely rare *Stylinodon inexplicatus*. Although of Bridgerian age and congeneric with *S. mirus*, the largest and most "advanced" stylinodontid, *S. inexplicatus* is the smallest stylinodontid known. It may have been a neotenous offshoot from the mainstream *Stylinodon*, which attempted to exploit a different niche but failed. Or, more likely, I would suggest that as *S. inexplicatus* bears the same basic morphological modifications as its large relative, *S. mirus*, it tried to exploit the same niche as an animal in a smaller size class, but failed (insofar as the species is at present known from only one specimen). *Ectoganus copei* is slightly smaller than *E. gliriformis* and *Psittacotherium multifragum* and may represent a similar experiment (i.e., smaller species offshoot) in *Ectoganus* during the early Wasatchian.

As far as is presently known, *Wortmania* is completely primitive relative to all other stylinodontids, occurs earlier, and thus could be ancestral to any or all other

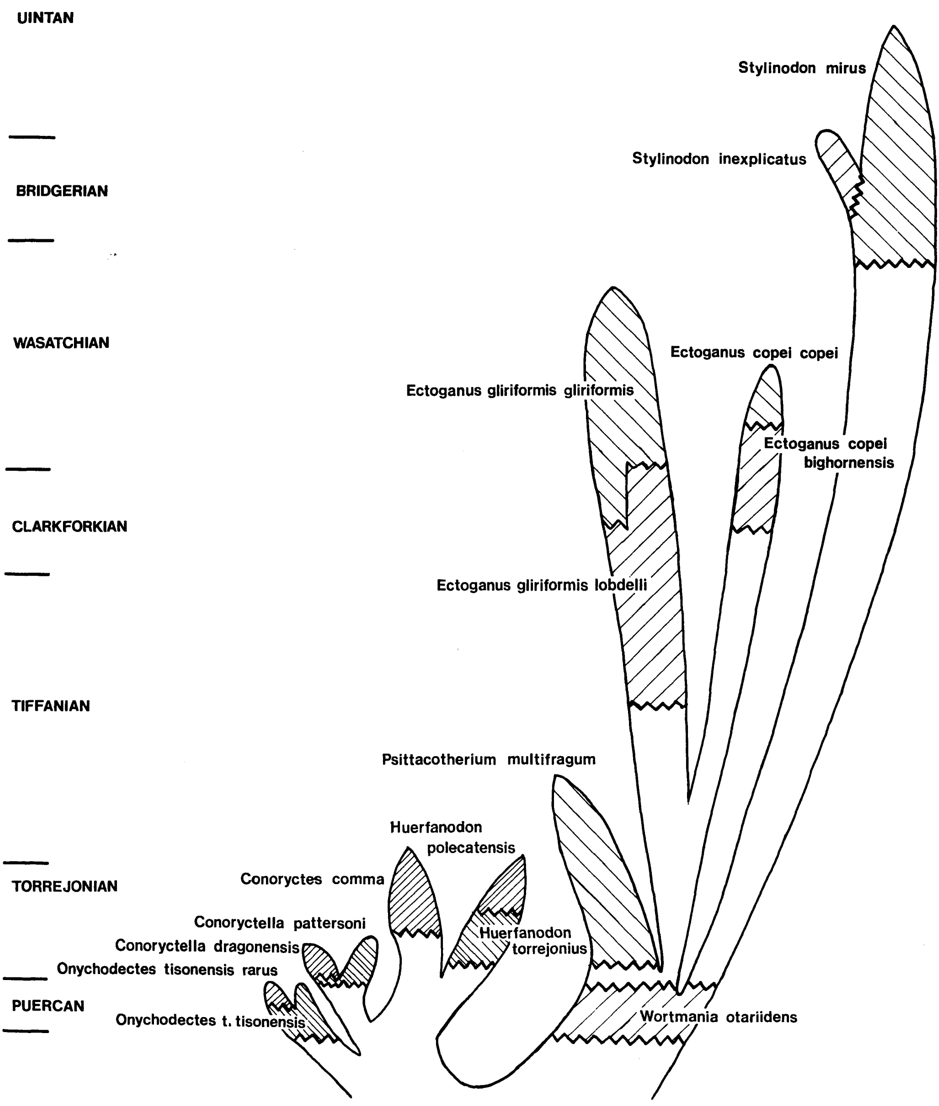


FIG. 58. A possible phylogenetic tree for the Taeniodonta.

stylinodontids. *Psittacotherium,* while more advanced and apparently closely related to *Ectoganus* and *Stylinodon,* bears a reduced P_1, the same tooth that is elaborated in *Ectoganus* and *Stylinodon,* and is therefore probably not directly ancestral to either, but is perhaps slightly off on a side branch. *Psittacotherium* and *Ectoganus* both appear to bear only one upper incisor on either side while *Stylinodon* bears two; this may further eliminate either as being directly ancestral to *Stylinodon.* However, the possibility exists that the I^2 of *Stylinodon* is a retained deciduous incisor often seen in *Ectoganus* (see previous discussion in Chapter 3). However, it is also interesting that *Stylinodon* replaces *Ectoganus* quite suddenly

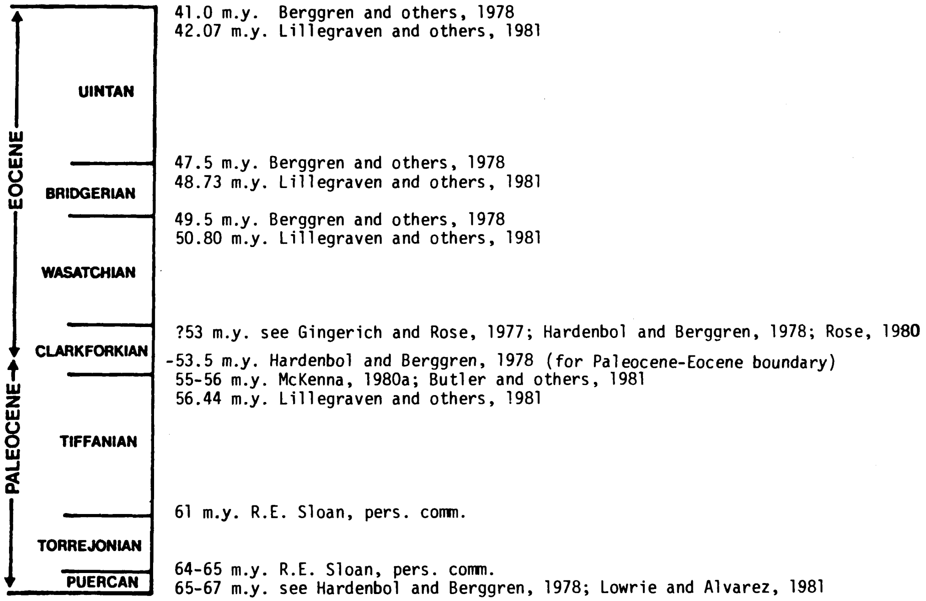


FIG. 59. Absolute dating of the North American land mammal "ages." References are cited in the figure, text and bibliography. For the corresponding summary of the biostratigraphic distribution of the Taeniodonta, see Figures 44 and 58. Dates presented by Lillegraven and others (1981) are recalibrated according to new IUGS standards (Dalrymple 1979). Older references (e.g., Berggren and others 1978; Hardenbol and Berggren 1978) are according to the older calibrations. Recalibration may place the Cretaceous–Paleocene boundary near 67 m.y. (cf. Lowrie and Alvarez 1981).

in the Lostcabinian; no intermediate forms are known and it may be that the first known occurrences of *Stylinodon* are due to migration rather than in situ evolution.

When the relative proportions of the teeth of *Wortmania, Psittacotherium, Ectoganus* and *Stylinodon* are plotted using *Onychodectes* as a baseline of 100% (Fig. 57; Table 8), the relative development of the teeth in the various genera can be examined. The curve for *Wortmania* shows that it is primarily the canines and P_1 that are better developed (larger) than in *Onychodectes.* In addition, the curve for *Wortmania* lies completely under (i.e., is primitive to) the curves for *Psittacotherium, Ectoganus* and *Stylinodon,* further suggesting that it could be ancestral to any or all of these forms. Likewise, the curve for *Psittacotherium* falls between those for *Wortmania* and *Ectoganus* (however, the value for P_1 of *Psittacotherium* in Figure 57 is not real; it is an average for the values of *Wortmania* and *Ectoganus*). However, while the points for C^1, P^1, C_1, and P_1 of *Stylinodon* lie well above those for the corresponding teeth of *Psittacotherium* and *Ectoganus,* the points for P^2, P^4–M^3, P_2 and M_{2-3} of *Stylinodon* fall below the curve for *Ectoganus* and those for P^3 and P_3–M_3 of *Stylinodon* fall below the curves for both *Psittacotherium* and *Ectoganus.* This suggests that if *Psittacotherium multifragum* or *Ectoganus gliriformis* were directly ancestral to *Stylinodon mirus,* a reversal in the trend toward increasing size in these teeth took place. In contrast, the hypothesis which I prefer, and which appears to be supported by other evidence presented above, is that neither *P. multifragum* nor *E. gliriformis* was directly ancestral to *Stylinodon mirus.*

Phylogram of the Taeniodonta

Based on the above cladogram (Fig. 56) and preceding discussion, the phylogram (or phylogenetic tree) which I personally favor after taking into account all of

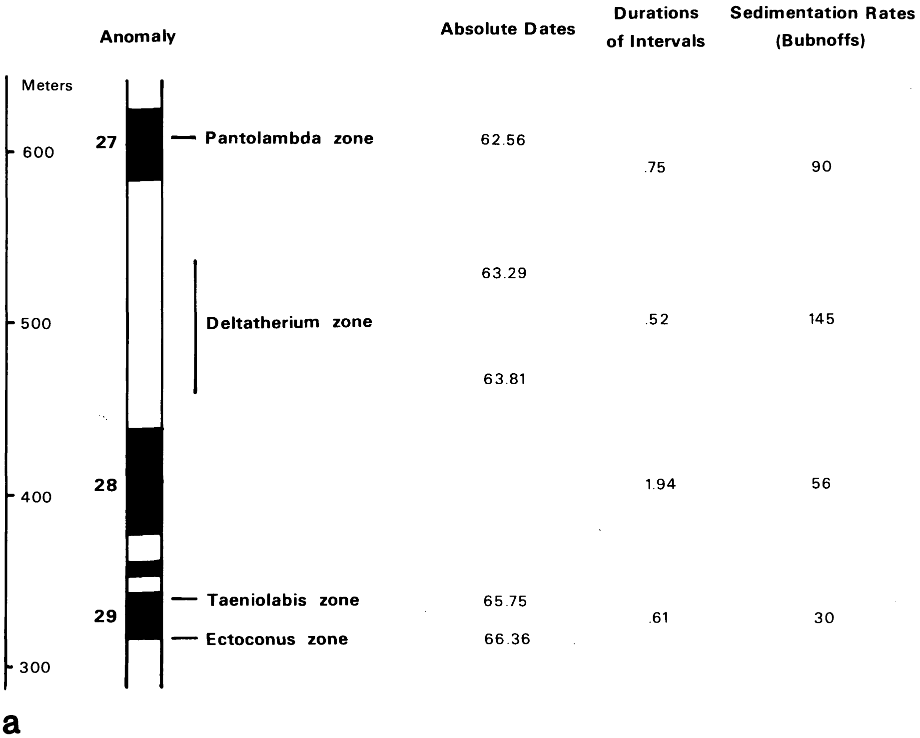


FIG. 60. Composite magnetic polarity sequence for *a*) the San Juan Basin (after Lindsay et al. 1978, as renumbered by Lucas and Schoch 1982) and *b*) the Bighorn Basin (after Butler et al. 1981). Absolute dates for the *Taeniolabis, Ectoconus, Deltatherium* and *Pantolambda* zones and the Tiffanian–Clarkforkian boundary were calculated using the dating of the standard magnetic polarity intervals presented by Lowrie and Alvarez (1981) and by assuming a constant sedimentation rate within any normal or revised polarity interval. See text for further explanation.

the considerations discussed above, is presented here (Fig. 58). The known taxa are arranged temporally (cf. Fig. 44) and linked in permissive ancestor–descendant relationships. Hypothetical ancestors would occur at the bases of the branches and if all taeniodonts were known, many more side branches and end points would probably also be shown in the figure.

ABSOLUTE CHRONOLOGY OF THE TAENIODONTA

The distribution of the taeniodont taxa relative to lithologic formations and the North American land mammal ages (H. E. Wood and others 1941) has been discussed above. Recently, more precise dating (i.e., ages in millions of years ago = m.y.) for the land mammal age boundaries (Fig. 59) has been carried out based primarily on radioisotopic dating, the magnetopolarity time scale and sedimentation rates (e.g., Berggren and others 1978; Hardenbol and Berggren 1978; McKenna and others 1973; McKenna 1980a; Robert E. Sloan, personal communication; Lindsay and others 1978; Lowrie and Alvarez 1981; Lindsay and others 1981). In Figure 59 I have summarized the best estimates for the absolute dating of the Puercan to Uintan land mammal age boundaries. The Cretaceous–Puercan, Paleocene–Eocene, Wasatchian–Bridgerian, Bridgerian–Uintan and Uintan–Duchesnean boundary ages are fairly securely based on radioisotopic dating (Berggren and others 1978; Hardenbol and Berggren 1978; McKenna

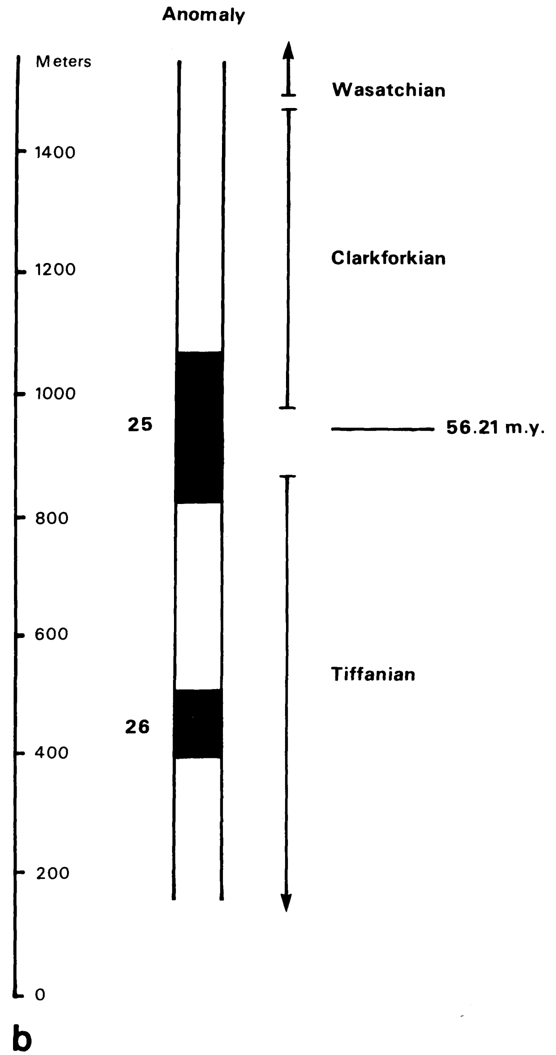


FIG. 60.—*Continued.* See legend on previous page.

and others 1973). Here the "Mantuan" (Van Valen 1978) is included within the Puercan, and the durations of the Puercan, Torrejonian and Tiffanian land mammal ages are based primarily on estimated sedimentation rates (R. E. Sloan, personal communication, 1981; see also Van Valen 1978) and paleomagnetic correlation (Lindsay and others 1981; Lucas and Schoch 1982) and the "absolute" dates tied to the magnetopolarity time scale (Lowrie and Alvarez 1981).

The Clarkforkian North American land mammal age (H. E. Wood and others 1941), whose distinctness and validity has been questioned (R. C. Wood 1967) in the past, has lately been resurrected and redefined (Gingerich and Rose 1977; Rose 1980, 1981) as a valid North American land mammal age which straddles the Paleocene–Eocene boundary. However, the temporal duration of the Clarkforkian is not known. Apparently it is rather short; R. E. Sloan (personal communication, 1981; see also Butler and others 1981) considers the Paleocene part of the Clarkforkian to have a duration of approximately one million years. Likewise, the Eocene duration of the Clarkforkian appears to be relatively short.

Using the composite magnetic polarity sequence of Lindsay and others (1978, fig. 3; see also Lindsay and others 1981) for the San Juan Basin, New Mexico, as renumbered by Lucas and Schoch (1982) and the durations of the normal polarity intervals in millions of years as given by Lowrie and Alvarez (1981), and by assuming a constant sedimentation rate within any normal or reversed polarity interval, absolute ages and approximate durations for the Puercan and Torrejonian land mammal ages and their included zones within the San Juan Basin can be calculated (Fig. 60). Thus, by this method, the *Ectoconus* zone is dated at 66.36 m.y., the *Taeniolabis* zone at 65.75 m.y., the *Deltatherium* zone from 63.81 to 63.29 m.y. and the *Pantolambda* zone at 62.56 m.y. Incorporating magnetic polarity and biostratigraphic data from the Bighorn Basin (Butler and others 1981) the composite section can be extended into the Wasatchian (Fig. 60). Assuming that the Tiffanian–Clarkforkian boundary falls in approximately the middle of normal polarity interval 25, it can be dated at 56.21 m.y. The Clarkforkian–Wasatchian boundary occurs before Anomaly 24, i.e., before 52.97 m.y. These dates are congruent with those calculated otherwise and shown in Figure 59. It must be kept in mind that the entire durations of the Puercan and Torrejonian are not represented in the San Juan Basin. Furthermore, I have presented the absolute dates in this paragraph as they are calculated to two decimal places. In reality, at best one decimal place (0.1 × 1 m.y. = 100,000 years) might be significant.

In the San Juan Basin, incorporating the above dates, sedimentation rates (calculated in Bubnoffs, one Bubnoff = $1 \frac{\text{m}}{\text{m.y.}}$) can be calculated for the Nacimiento Formation during the intervals between the dated points. These sedimentation rates range from 30 to 145 Bubnoffs, with an average of 80. Schindel (1980, fig. 1) has plotted observed rates of sedimentation against period of observation for various depositional environments. If his logarithmic plot for fluvial systems is linearly extrapolated to include a period of observation from ten to the sixth to ten to the seventh years, the sedimentation rate for fluvial systems is on the order of magnitude of one hundred Bubnoffs. This is consistent with the rate of sedimentation calculated above for the Nacimiento Formation and the interpretation that these sediments were deposited primarily in a fresh water, fluvial environment.

My taxonomic revision of the Taeniodonta, coupled with the more precise geochronology, reveals that Patterson (1949b) overstated the average organismal (taxonomic) rate (calculated by Patterson in genera per million years; see also Simpson 1953) for the stylinodontids. Using Simpson's (1947a) estimates as to the durations of the Tertiary epochs, Patterson (1949b) estimated that the Paleocene has a duration of 17 m.y. and the part of the Eocene up until the extinction of *Stylinodon* (middle Eocene) was 16 m.y. The more precise geochronology can be combined with the known stratigraphic ranges of the taeniodont taxa as documented above (Figs. 44, 59) and with the proposed phylogeny for the taeniodonts (Figs. 56, 58) to recalculate organismal rates for the group (Table 9).

Patterson (1949b) assumed there were six or seven genera of stylinodontid taeniodonts which formed a direct ancestor–descendant series from the early Paleocene to middle Eocene (Uintan) times. Patterson (1949b) believed this series consisted of *Wortmania, Psittacotherium, "Lampadophorus"* (= *Ectoganus*), *Ectoganus* and *Stylinodon.* Furthermore, Patterson (1949b) thought there was an unnamed genus intermediate between *Wortmania* and *Psittacotherium* and that those specimens labeled as *Stylinodon* might also consist of two distinct genera.

TABLE 9. Evolutionary rates of taeniodonts and other selected groups in genera/m.y. (and m.y./genus)

PHYLOGENY USED GEOCHRONOLOGY USED	PATTERSON 1949	PATTERSON 1983	SCHOCH 1949	SCHOCH 1983
Stylinodontids	0.18–0.21 (4.76–5.56)	0.30–0.35 (2.86–3.33)	0.12 (8.33)	0.20 (5.00)
Conoryctids	Not calculated			0.75 (1.33)
Stylinodontids (Puercan–Torrejonian)				0.50 (2.00)
Tillodontia (Schoch and Lucas MS)				0.20–0.25 (4.00–5.00)
Plesiadapidae (Gingerich 1976)				0.22–0.33 (3.00–4.50)
Average Puercan Ungulate (Sloan 1970)				0.66 (1.50)
Average Torrejonian Ungulate (Sloan 1970)				0.33–0.50 (2.00–3.00)
Average Wasatchian Ungulate (Sloan 1970)				0.20 (5.00)

Using 33 m.y. as an estimate for the duration of the stylinodontid lineage, Patterson (1949b) thus calculated a rate of 0.18 to 0.21 genera per million years for the stylinodontids. However, using Patterson's (1949b) phylogeny, but incorporating the more recent geochronology (which gives an estimate of approximately 20.0 m.y. for the duration of the stylinodontids) the organismal rate is approximately 0.30 to 0.35 genera per m.y.

In contrast, I recognize only four stylinodontid genera as valid: *Wortmania, Psittacotherium, Ectoganus* and *Stylinodon.* The unnamed genus of Patterson (1949b) was based on a single incisor (Gazin 1941) which may belong to *Psittacotherium.* Patterson's (1949b) "*Lampadophorus*" is here regarded as a junior subjective synonym of *Ectoganus gliriformis.* The characters which distinguish this morph, primarily less hypsodont and more bulbous cheek teeth than later forms, are regarded as of subspecific value and Patterson's "*Lampadophorus*" is here labeled *Ectoganus gliriformis lobdelli* and *Ectoganus* (sensu Patterson 1949b) is here labeled *Ectoganus gliriformis gliriformis* (see Systematic Paleontology above). A smaller species (composed of two subspecies), *Ectoganus copei,* is also recognized. The genus *Stylinodon* is relatively long-ranging, coherent, and invariable, and appears to be known from only two species: *Stylinodon mirus* is known from numerous specimens of late Wasatchian to early Uintan age and *Stylinodon inexplicatus* is known from a single specimen of Bridgerian age.

A phylogeny of the stylinodontids has been hypothesized above, incorporating a cladistic analysis of the taeniodonts and their known stratigraphic ranges (Fig. 58; however, one must be aware of the assumptions made, see above and Englemann and Wiley 1977; Szalay 1977). At a generic level *Wortmania* is primitive relative to *Psittacotherium* and an unknown species of *Psittacotherium* may have been primitive relative to *Ectoganus*; thus these three genera form an ancestor–descendant lineage. Both *Psittacotherium* and *Ectoganus* appear to be derived relative to *Stylinodon* in having one upper incisor on either side, whereas *Stylinodon* has two upper incisors. Thus, although *Stylinodon* is in many respects the most derived taeniodont (Patterson 1949b), it is probably not a direct descendant of *Psittacotherium* or *Ectoganus.* Using this hypothesized phylogeny and the more recent geochronologic dating (Figs. 59, 60), three stylinodontid genera may have occurred in an ancestor–descendant relationship between the beginning of the

Paleocene (65 m.y. ago) to the beginning of the late Wasatchian (approximately 50 m.y. ago). This gives an organismal rate of 0.2 genera per m.y. for the stylinodontids. This is only two-thirds or less of Patterson's revised rate (using Patterson's phylogeny and the revised geochronologic time scale) of 0.30 to 0.35 and indicates that stylinodontids were apparently not evolving at as fast an average rate as Patterson (1949b) believed.

Similarly, as for the stylinodontids, a phylogeny is here hypothesized for the conoryctids. This phylogeny is essentially the same as Patterson's (1949b) (at the generic level some species of *Onychodectes* may have been ancestral to *Conoryctella* which may have been ancestral to *Conoryctes* and *Huerfanodon*) except that the genus *Huerfanodon* (named since Patterson's work) can also be derived from *Conoryctella*. Thus, there are two sets of three genera (*Onychodectes, Conoryctella, Conoryctes*; and *Onychodectes, Conoryctella, Huerfanodon*) which may stand in an ancestor–descendant relationship over approximately four m.y. (Fig. 58). This gives an organismal rate 0.75 genera per m.y. that is comparable to the organismal rate seen in many lineages of condylarths, primates, and multituberculates that may contain three, four, or more successive genera over the same interval (R. E. Sloan, personal communication, 1981).

8. CONCLUSIONS—ADAPTATION AND EXTINCTION SCENARIOS FOR THE TAENIODONTA

The Taeniodonta were a bizarre, archaic order of Puercan to Uintan mammals that, as far as is known based on their fossil record, were neither particularly diverse nor abundant. Rather, they appear to be an early Paleocene "palaeoryctid" or "leptictimorph" offshoot which may have originally evolved under little predation pressure (as was apparently the case for Puercan mammals in general, cf. Van Valen 1978). They lasted in one form or another for approximately 20 million years (until Uintan times) before finally becoming extinct.

One clade of taeniodonts, the conoryctids, were relatively small, generalized animals which may have been primarily omnivorous (or perhaps more descriptively, semicarnivorous and semiherbivorous). The conoryctids rapidly diversified taxonomically during the Puercan–Torrejonian. At first, conoryctids were not terribly uncommon, and many may have lived to moderately or extremely old ages, as indicated by many specimens in which the teeth were completely worn down during the life of the individual. Possibly, such individuals were dying of old age rather than from other causes, such as predation. Alternatively, they may simply have worn their teeth extremely quickly due to the diet upon which they fed, thus dying young but with well-worn teeth. However, by the end of the Torrejonian this group was extinct. I suggest that conoryctids may have tended toward becoming carnivores, herbivores, and rooters and grubbers; not pursuing any of these strategies particularly well, they were outcompeted on these three major fronts by creodonts, condylarths and the contemporaneous stylinodontids, respectively. Perhaps also contributing to their extinction was the general climatic deterioration in western North America during late Torrejonian times from a subtropical to a warm temperate climate (Wolfe and Hopkins 1967; Wolfe 1978; Hickey 1980, 1981).

The stylinodontids evolved relatively quickly (by the Torrejonian) all of their major distinguishing characteristics (such as comparatively large size; hypsodont teeth, robust skull and postcranial proportions; and large, compressed claws) and moved into their specific niche. Later forms merely specialized further along the same lines. Based on my analysis (see Chapters 5 and 6), the stylinodontids appear to have been primarily open-country, upland, fossorial to subfossorial rooters and grubbers, feeding on vegetable matter, much of which took the form of underground roots and tubers. We can imagine them as relatively slow but powerful, bulky, small-brained, perhaps solitary, archaic mammals. As discussed above, their dental/masticatory apparatus may have been a rather crude and inefficient solution to the problem of processing coarse, gritty vegetable matter. The solution was highly wasteful of metabolic energy, but might have been successful (in the sense that the animals survived and reproduced) as long as no other more efficient animals moved into the same, or a similar, niche in the same geographic area.

The trogosine tillodonts of the Bridgerian (middle Eocene) developed a morphology superficially similar to that of the stylinodontids (see Gazin 1953), including such features as large size, hypsodont cheek teeth, a heavy mandible and gliriform tusks (incisors in tillodonts rather than canines as in taeniodonts). We can speculate that the trogosines and stylinodontids perhaps actively competed for the same or similar resources during Bridgerian times in western North America, and the stylinodontids won out, as indicated by the apparent extinction of the trogosines and persistence of the stylinodontids into the Uintan. However, by middle Eocene times many mammals of more "modern aspect" were evolving and invading the homeland and niche of stylinodontids. In particular, the latest taeniodont, *Stylinodon mirus,* may have been at a competitive disadvantage with newly appearing, larger-brained (and in some cases having absolutely larger heads and bodies) contemporaneous artiodactyls, such as achaenodonts (Black and Dawson 1966), which are superficially similar to taeniodonts and whose modern suid analogues dig, root and grub as taeniodonts probably did.

Thus, the taeniodonts may have been displaced ecologically by such forms (cf. Mellett 1977 and West 1981a, 1981b, for similar hypothesized scenarios to explain the extinctions of *Hyaenodon* and the large mesonychids, respectively). There may have also been a more diffuse competition between stylinodontids and other relative newcomers, such as rodents and some perissodactyls. Furthermore, the appearance of more advanced carnivores such as the sabertoothed *Machaeroides* of the Bridgerian (Gazin 1946) and *Apataelurus* of the middle Eocene (Emerson and Radinsky 1980) may also have placed considerable predation pressure on the latest stylinodontids. All of these factors conspiring together may have driven the last taeniodonts, which were perhaps "overspecialized" for too narrow a niche, to extinction (cf. Van Valen 1963, p. 371, on competitive exclusion in the Paleocene).

In the discussions above I have suggested that competition, both active and diffuse, may have at least in part contributed to the decline and extinction of the taeniodonts. The work of Mellett and West has already been mentioned in this context and in a similar vein Van Valen and Sloan (1977) have suggested that diffuse competition between a southward-moving temperate mammalian community and an original dinosaur-bearing subtropical community contributed to the dinosaur extinctions. Also, and perhaps forming a better analogy for taeniodont extinction, Van Valen and Sloan (1966) have suggested that multituberculates became extinct due to competition with placental mammals. More specifically, Van Valen and Sloan (1966) suggest that multituberculates were driven to extinction first by condylarths, then by primates and finally by rodents (cf. also Krause 1981). Van Valen and Sloan (1966) also suggest that throughout the early Tertiary, multituberculates became increasingly specialized and less diverse as they were driven into relatively smaller niches by diffuse competition; as an analogy, we can suggest that the stylinodontid taeniodonts were driven to a similar end. They became increasingly specialized (as seen in the progressively later forms) before they finally became extinct.

However, competition of any kind is extremely difficult or impossible to resolve within the fossil record. Active (for example, predation of one species on another) or diffuse competition is one of the lowest level biological/ecological phenomena we can hypothesize. It involves one animal having an effect (direct or indirect) on another: to gather strong evidence for interactions such as these we should like to be able to demonstrate that various fossil forms lived truly contemporaneously and sympatrically, and furthermore interacted in the manners hypothesized. Yet, it appears—to me, at least—that given the present state and extent of our knowledge of the vertebrate fossil record, such questions are unresolvable (cf. Schindel 1980; Schopf 1981). For example, one species may have lived in an area for a few years or centuries and may then have been replaced by a second species, yet the fossil record as preserved and recovered may associate the two species, which were actually never sympatric; these would thus be indistinguishable from a pair of species that were truly sympatric in an area and lived, died, and were fossilized together.

In order to try to demonstrate competitive exclusion in the fossil record between multituberculates and primates, and multituberculates and rodents, Van Valen and Sloan (1966) analyzed statistically the Four Mile Fauna of the early Eocene of Colorado (McKenna 1960) which "actually consists of samples from several sites that represent in part rather different communities and perhaps different ages" (Van Valen and Sloan 1966, p. 274). They found that among the sites there was a negative correlation between multituberculates and primates and between multituberculates and rodents, and thus argued that there was interference and competition between these taxa. Yet the absolute values for these correlations are only 0.38; there are only seven sites which make up the Four Mile Fauna and it is not really clear what the differences among the frequency distributions of taxa of these sites really mean. Do the sites represent different communities, different ages, or is what we are seeing just sampling error? Rarefaction curves, for example, were not calculated for the sites in order to try to determine if the frequency of taxa at any one site is really representative of the frequency of taxa which were originally present at that site. However, even given all these difficulties, the correlations are tantalizing.

Unfortunately, for the purposes of the present study, there are no taeniodonts from Four Mile. Furthermore, at present there are not sufficient data available to do a similar analysis for any taeniodont-bearing faunas. The best possibility for trying a similar correlation might be in the Torrejonian by comparing several sites in Kutz Canyon (Taylor 1981), a screen-washing site in Torreon Wash (C. Tsentas, personal communication, 1981), Silberling and Gidley Quarries in the Crazy Mountain Field (Simpson 1937), Rock Bench Quarry (Gingerich and others 1980) and Swain Quarry (Rigby 1980); these sites, however, are from geographically widespread areas. They are surely not of exactly comparable ages, and specimens were collected by very different means (quarrying, screening, surface collecting), all of which would undoubtedly bias the samples significantly. Furthermore, much of the data that would be needed to perform this type of analysis are presently unavailable, either unpublished or still in the initial stages of preparation.

Lastly, we must consider the possibility that the extinction of the taeniodonts was a purely random event. Assuming a model of relatively constant speciation and extinction events for taeniodonts, Raup (1981) gives the following equation for random (sampling accident) extinction:

$$P_{o(t)} = \left[\frac{\mu t}{1 + \mu t}\right]^{a}$$

where $P_{o(t)}$ = the probability of the group going extinct after t million years, μ is the extinction probability (= the reciprocal of the mean species duration in millions of years) and a is the number of coexisting species at $t = 0$. Thus for the taeniodonts if we use as values $\mu = 0.25$, $a = 2$ (*Wortmania* and *Onychodectes* as founders), $t = 20$ (m.y. = duration of the order Taeniodonta), then the chances that the taeniodonts would have gone extinct in 20 m.y. or less by chance is 0.7. If we change the parameters to $\mu = 0.75$ (inverse of the average duration of all species), $a = 15$ (all known species groups), $t = 20$, then $P_{o(t)} = 0.4$ which is still a fairly high probability. If $\mu = 0.20$, $a = 15$, $t = 20$, then $P_{o(t)} = 0.03$. From these manipulations it should be evident that at present we do not have a sufficiently complete knowledge of taeniodonts to speculate in such a way; by altering values assumed for μ and a, virtually any answer can be had. Therefore, although there is the distinct possibility that taeniodonts became extinct by chance, at present this cannot be demonstrated.

BIBLIOGRAPHY

Abel, O. 1912. Grundzuge der Palaeobiologie der Wirbeltiere. E. Schweizerbart, Stuttgart. 708 p.

——— 1913. Saugetiere (Palaontologie), Handwortbuch Naturwissenschaften. Gustav Fischer, Jena, Fol. 8, p. 695–759.

——— 1914. Die vorzeitlichen Saugetiere. G. Fischer, Jena. 309 p.

——— 1919. Die Stamme der Wirbeltiere. W. de Gruyter, Berlin and Leipzig. 914 p.

——— 1920. Lehrbuch der Paläozoologie. G. Fischer, Jena. 500 p.

Amaral, A. do. 1935. Contribuição ao conhecimento dos ophidios do Brazil. VII. Novos generos e especies de Colubrideos opisthoglyphos. Mem. Inst. Butantan, Sao Paulo 9: 203–6.

Ameghino, F. 1885. Nuevos restos de mamiferos fosiles oligocenos recogidos por el profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la Ciudad del Parana. Bol. Acad. Nac. Cienc. Cordoba, Argent. 8: 5–205.

——— 1889. Contribucion al conocimiento de las mamiferos fosiles. Actas Acad. Nac. Cienc. Cordoba, Argent. 6: 1–1027.

——— 1891. Caracteres diagnosticos de cincuenta especies nuevas de mamiferos fosiles argentinos. Rev. Argent. Hist. Nat. 1: 131–67.

——— 1897. Mammifères cretàces de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à Pyrotherium. Bol. Inst. Geogr. Argent., Buenos Aires 18: 1–117.

——— 1902. Première contribution à la connaissance de la faune mammalogique des couches a *Colpodon*. Bol. Acad. Nac. Cienc. Cordoba, Argent. 17: 71–141.

——— 1906a. Les édentés fossiles de France et d'Allemagne. An. Mus. Nac. Hist. Nat., Buenos Aires 6: 175–250.

——— 1906b. Les formations sédimentaires du crétacé supérieur et du tertiare de Patagonie. An. Mus. Nac. Hist. Nat., Buenos Aires 8: 1–568.

Anonymous. 1897. The origin of the edantate mammals. Nat. Sci. London 11: 150–53.

Archibald, J. D. 1977. Ectotympanic bone and internal carotid circulation of eutherians in reference to anthropoid origins. J. Hum. Evol. 6: 609–22.

Arldt, T. 1907a. Die älteste Saugetierfauna Südamerikas und ihre Beziehungen. Arch. für Naturgesch. Berlin 73: 233–44.

——— 1907b. Die Entwicklung der Kontinente und ihrer Lebenwelt: ein Beitrag zur vergleichenden Erdgeschichte. W. Engelmann. 730 p.

——— 1912. Die Fauna der alten Tierregionen des Festlandes, p. 633–783. *In* Neues Jahrb. Mineral. Geol. Palaeontol. Stuttgart, vol. 34.

Bakker, R. T. 1980. Dinosaur heresy—dinosaur renaissance, why we need endothermic archosaurs for a comprehensive theory of bioenergetic warm-blooded evolution, p. 351–462. *In* R. D. K. Thomas and E. C. Olson [eds.]. A cold look at the warm-blooded dinosaurs. Washington, Amer. Assoc. Adv. Sci. Sel. Symp. 28.

Baltz, E. H. 1967. Stratigraphy and regional tectonic implications of part of Upper Cretaceous and Tertiary rocks, east-central San Juan Basin, New Mexico. U.S. Geol. Surv. Prof. Pap. 552. 101 p.

Baltz, E. H., S. R. Ash, and R. Y. Anderson. 1966. History of nomenclature and stratigraphy of rocks adjacent to the Cretaceous-Tertiary boundary western, San Juan Basin, New Mexico. U.S. Geol. Surv. Prof. Pap. 524-D. 23 p.

Baltz, E. H., and S. W. West. 1967. Ground-water resources of the southern part of Jicarilla Apache Indian Reservation and adjacent areas. U.S. Geol. Surv. Water-Supply Paper 1576-H. 89 p.

Barclay, O. R. 1953. Some aspects of the mechanics of mammalian locomotion. J. Exp. Biol. 30: 116–200.

Barnes, H., E. H. Baltz, and P. T. Hayes. 1954. Geology and fuel resources of the Red Mesa area, La Plata and Montezuma Counties, Colorado. U.S. Geol. Surv. Oil Gas Invent. Map OM-149.

Becht, G. 1953. Comparative biologic-anatomical researches in some mammals. K. Ned. Akad. Wet. Ser. C. 56: 508–27.

Beddard, F. E. 1902. Mammalia: the Cambridge natural history. Macmillan & Co., London, vol. 10, p. 1–605.

Behlen, H. 1906. Über das Milchgebiss der Paarhurer. I. Teil: Literaturgeschichtes, p. 185–212. *In* Jahrb. Nassau. Ver. Natur. Wiesbaden, vol. 49.

Berggren, W. A., M. C. McKenna, J. Hardenbol, and J. D. Obradovich. 1978. Revised Paleogene polarity time scale. J. Geol. 86: 67–81.

Black, C. G. 1967. Middle and late Eocene mammals: a major discrepancy. Science 156: 62–64.

Black, C. G., and M. R. Dawson. 1966. A review of late Eocene mammalian faunas from North America. Am. J. Sci. 264: 321–49.

Borissiak, A. A. 1945. The chalicotheres as a biological type. Am. J. Sci. 243: 667–79.

Bown, T. M. 1979. Geology and mammalian paleontology of the Sand Creek facies, lower Willwood Formation (lower Eocene), Washakie County, Wyoming. Mem. Geol. Surv. Wyo. 2: 1–151.

——— 1980. The Willwood Formation (lower Eocene) of the southern Bighorn Basin, Wyoming,

p. 127–33. *In* P. D. Gingerich [ed.]. Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol. 24.

Bradley, R. M. 1971. Warthog (*Phacochoerus aethiopicus* Pallas) burrows in Nairobi National Park. East Afr. Wildl. J. 9: 149–52.

Bramble, D. M. 1978. Origin of the mammalian feeding complex: models and mechanisms. Paleobiology 4: 271–301.

Brown, R. W. 1962. Paleocene flora of the Rocky Mountains and Great Plains. U.S. Geol. Surv. Prof. Pap. 375. 119 p.

Butler, P. M. 1977. Evolutionary radiation of the cheek teeth of Cretaceous placentals. Acta Palaeontol. Pol. 22: 241–71.

Butler, R. F., P. D. Gingerich, and E. H. Lindsay. 1981. Magnetic polarity stratigraphy and biostratigraphy of Paleocene and lower Eocene continental deposits, Clark's Fork Basin, Wyoming. J. Geol. 89: 299–316.

Case, E. C. 1898. The development and geological radiation of the vertebrates. Part V: Mammalia. J. Geol. 6: 820–39.

Chow, M. 1963a. A xenarthran-like mammal from the Eocene of Honan. Sci. Sin. 12: 1889–93.

——— 1963b. Tillodont materials from the Eocene of Shantung and Honan: Vertebr. PalAsiatica 7: 97–104.

Chow, M., C. Li, and Y. Chang. 1973. Late Eocene mammalian faunas of Honan and Shansi with notes on some vertebrate fossils collected therefrom. Vertebr. PalAsiatica 11: 165–81.

Cifelli, R. L. 1982. The petrosal structure of *Hyposodus* with respect to that of some other ungulates, and its phylogenetic implications. J. Paleontol. 56: 795–805.

Clemens, W. A. Jr. 1968. Origin and early evolution of marsupials. Evolution 22: 1–18.

——— 1973. Fossil mammals of type Lance Formation, Wyoming. Part 3: Eutheria and summary. Univ. Calif. Publ. Geol. Sci. 94: 1–102.

——— 1980. *Gallolestes pachymandibularis* (Theria, incertae sedis; Mammalia) from late Cretaceous deposits in Baja California del Norte, Mexico. Paleobios 33. 10 p.

Colbert, E. H. 1941. A study of *Orcyteropus gaudryi* from the island of Samos. Bull. Am. Mus. Nat. Hist. 78: 305–51.

Cope, E. D. 1874. Notes on the Eocene and Pliocene lacustrine formations of New Mexico, including descriptions of new species of vertebrates. Ann. Rep. Chief Eng., Appendix FF_3 (43rd Congress, 2nd Session, House Executive Doc. 1, part 2, vol. 2, part 2), p. 561–606.

——— 1875a. Report on the geology of that part of northwestern New Mexico examined during the field season of 1874. Ann. Rep. Chief Eng. Appendix LL, p. 961–1067.

——— 1875b. Systematic catalogue of Vertebrata of the Eocene of New Mexico collected in 1874. Rep. Eng. Dep., U.S. Army, in charge of Lieut. Geo. M. Wheeler (Washington), p. 5–37.

——— 1875c. Note on the genus *Calamadon*. Am. J. Sci. (3) 9: 228.

——— 1876a. On the Taeniodonta, a new group of Eocene Mammalia. Proc. Acad. Nat. Sci. Philadelphia 28: 39.

——— 1876b. On the supposed Carnivora of the Eocene of the Rocky Mountains. Proc. Acad. Nat. Sci. Philadelphia 28: 444–48.

——— 1877. The extinct Vertebrata obtained in New Mexico by parties of the Expedition of 1874. Fossils of the Eocene period. Rep. U.S. Geogr. Surv. west of the one hundredth meridian (G. M. Wheeler, in charge), vol. 4 (Paleontology), part 2, chap. 12, p. 37–282.

——— 1880. Sur les relations des niveaux de vertebrés éteints dans l'Amérique du Nord et en Europe. C.R. Congrès Geol. Int. (1878), vol. #1, p. 144–63.

——— 1881a. Mammalia of the lowest Eocene. Am. Nat. 15: 829–31.

——— 1881b. On some Mammalia of the lowest Eocene beds of New Mexico. Proc. Am. Phil. Soc. 19. 484–95.

——— 1881c. On the Vertebrata of the Wind River Eocene beds of Wyoming. Bull. U.S. Geol. Geogr. Surv. Territories 6: 183–202.

——— 1882a. The characters of the Taenidonta. Am. Nat. 16: 72.

——— 1882b. A new genus of Tillodonta [sic]. Am. Nat. 16: 156–57.

——— 1882c. Contributions to the history of the Vertebrata of the lower Eocene of Wyoming and New Mexico made during 1881. Proc. Am. Philos. Soc. 20: 139–97.

——— 1882d. A new genus of Taenidonta. Am. Nat. 16: 604–5.

——— 1882e. A new form of Taenidonta. Am. Nat. 16: 831–32.

———. 1882f. Synopsis of the Vertebrata of the Puerco Eocene epoch. Proc. Am. Philos. Soc. 20: 461–71.

——— 1883a. The fauna of the Puerco Eocene. Proc. Am. Assoc. Adv. Sci. 31st meet. Montreal, 1882, p. 479–80.

——— 1883b. On some fossils of the Puerco formation. Proc. Acad. Nat. Sci. Philadelphia (1883): 168–70.

——— 1883c. Some new Mammalia of the Puerco formation. Am. Nat. 17: 968.

——— 1884a. The Condylarthra. Am. Nat. 18: 892–906.

——— 1884b. On the mutual relations of the bunotherian Mammalia. Proc. Acad. Nat. Sci. Philadelphia 1883, p. 77–83.

——— 1884c. The Vertebrata of the Tertiary formations of the West. Rep. U.S. Geol. Surv. Territories (F.V. Hayden, in charge), vol. 3, p. 1–1009.

——— 1885a. The mammalian genus *Hemiganus*. Am. Nat. 19: 492–93.

——— 1885b. The genealogy of the Vertebrata as learned from paleontology. Trans. Vassar Brothers Inst. (Poughkeepsie, N.Y.) 2: 60–80.

——— 1887a. The origin of the fittest. Essays on evolution. New York. 467 p.

——— 1887b. Some new Taenidonta of the Puerco. Am. Nat. 21: 469.

——— 1888a. The mechanical causes of the origin of the dentition of the Rodentia. Am. Nat. 22: 3–11.

——— 1888b. The vertebrate fauna of the Puerco epoch. Am. Nat. 22: 161–63.

——— 1888c. Rutimeyer on the classification of Mammalia, and on American types recently found in Switzerland. Am. Nat. 22: 831–35.

——— 1888d. Synopsis of the vertebrate fauna of the Puerco series. Trans. Am. Philos. Soc., n.s., 16: 298–361.

——— 1889. The mechanical causes of the development of the hard parts of the Mammalia. J. Morphol. 3: 137–277.

——— 1891. Syllabus of lectures on geology and paleontology. Univ. Pennsylvania, Philadelphia. 90 p.

——— 1894. Schlosser on American Eocene Vertebrata in Switzerland. Am. Nat. 28: 585–94.

——— 1897. Recent papers relating to vertebrate paleontology. Am. Nat. 31: 315–23.

——— 1898. Syllabus of lectures on the Vertebrata. Univ. Pennsylvania. 135 p.

Costa, R. L., and W. S. Greaves. 1981. Experimentally produced wear facets and the direction of jaw motion. J. Paleontol. 55: 635–38.

Coues, E. 1872. The osteology and myology of *Didelphys virginiana*. Mem. Boston Soc. Nat. Hist. 2: 41–149.

Crompton, A. W., and K. Hiimae. 1970. Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis* L. J. Linn. Soc. London, Zool. 49: 21–47.

Cuvier, G. 1821–24. Recherches sur les ossemens fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe on détruit les espèces. E. d'Ocagne, Paris, 5 vols.

Dalrymple, G. B. 1979. Critical tables for conversion of K-Ar ages from old to new constants. Geology 7: 558–60.

Davis, D. D. 1949. The shoulder architecture of bears and other carnivores. Fieldiana, Zool. 31: 285–305.

——— 1964. The giant panda. A morphological study of evolutionary mechanisms. Fieldiana, Zool. Mem. 3: 1–339.

Davison, A. 1917. Mammalian anatomy with special reference to the cat. P. Blakiston's Son and Co., Philadelphia. 243 p.

Dehm, R., and T. Oettingen-Speilberg. 1958. Paläontologische und geologische Untersuchen im Tertiär von Pakistan. 2. Die mittel eocänen Säugetiere von Ganda kas bei Basel in Nordwest Pakistan. Abh. Bayer. Akad. Wiss. Math. Naturwiss. Kl., neue folge 91: 1–54.

Delafontaine, M. 1875. Les vertèbres fossiles des mauvaises terres du Nebraska. Bibl. Univers. Geneve. Arch. Sci. Phys. Nat. 53: 169–79.

Depéret, C. 1905. L'évolution des mammifères tertiares, importance des migrations. C. R. Acad. Sci. 141: 702–5, 792.

Dorst, J. 1969. A field guide to the larger mammals of Africa. Houghton Mifflin Co., Boston. 287 p.

Douglass, E. 1908. Vertebrate fossils from the Ft. Union beds. Ann. Carnegie Mus. 5: 11–26.

Eaton, J. G. 1980. Preliminary report on paleontological exploration of the southeastern Absaroka Range, Wyoming, p. 139–42. *In* P. D. Gingerich [ed.]. Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol. 24.

Edinger, T. 1929. Das fossil Gehirne: Ergebnisse der Anatomie und Entwicklungsgeschichte (= Anatomische Hefte). J. Springer, München, vol. 23, p. 1–249.

Eldredge, N., and J. Cracraft. 1980. Phylogenetic patterns and the evolutionary process: Method and theory in comparative biology. Columbia Univ. Press, New York. 349 p.

Elftman, H. O. 1929. Functional adaptations of the pelvis in marsupials. Bull. Am. Mus. Nat. Hist. 58: 189–232.

Ellseworth, A. H. F. 1976. The North American opossum, an anatomical atlas. Robert E. Krieger Publ. Co., Huntington, N.Y. 209 p.

Emerson, S. B., and L. Radinsky. 1980. Functional analysis of sabertooth cranial morphology. Paleobiology 6: 296–312.

Englemann, G. F., and E. O. Wiley. 1977. The place of ancestor–descendant relationships in phylogeny reconstruction. Syst. Zool. 26: 1–11.

Ewer, R. F. 1958. Adaptive features in the skulls of African Suidae. Proc. Zool. Soc. London, 131: 135–55.

——— 1970. The head of the forest hog, *Hylochoerus meinertshageni*. East Afr. Wildl. J. 8: 43–52.

Fasset, J. E., and J. S. Hinds. 1971. Geology and fuel resources of the Fruitland and Kirtland Shale of the San Juan Basin, New Mexico and Colorado. U.S. Geol. Surv. Prof. Pap. 676. 73 p.

Field, C. R. 1970. Observations on the food habits of tame warthog and antelope in Uganda. East Afr. Wildl. J. 8: 1-17.

Fischer, E. 1903. Bau und Entwickelung des Carpus and Tarsus vom *Hyrax*. Zeitschrift fur Naturwiss. 37: 691-726.

Flower, W. H. 1876a. The extinct animals of North America. Not. Proc. R. Inst. G. B. 8: 103-25.

——— 1876b. An introduction to the osteology of the Mammalia. Macmillan and Co., London. 344 p.

Flower, W. H., and R. Lydekker. 1891. An introduction to the study of animals living and extinct. London. 763 p.

Gambaryan, P. P. 1974. How mammals run: anatomical adaptations. John Wiley and Sons. 367 p.

Gardner, J. H. 1910. The Puerco and Torrejon Formations of the Nacimiento Group. J. Geol. 28: 702-41.

Gaudry, A. 1906. Fossiles de Patagonie. Étude sur une portion du monde antarctique. Ann. Paleontol. (Paris) 1: 101-43.

Gazin, C. L. 1936. A taeniodont skull from the lower Eocene of Wyoming. Proc. Am. Philos. Soc. 76: 597-612.

——— 1939. A further contribution to the Dragon Paleocene fauna of central Utah. J. Wash. Acad. Sci. (Washington, D.C.) 29: 273-86.

——— 1941. The mammalian faunas of the Paleocene of central Utah, with notes on the geology. Proc. U.S. Nat. Mus. 91: 1-53.

——— 1946. *Machaeroides eothen* Matthew, the sabre-tooth creodant of the Bridger Eocene. Proc. U.S. Nat. Mus. 96: 335-47.

——— 1952. The lower Eocene Knight Formation and its mammalian faunas. Smithson. Misc. Collect. 117: 1-82.

——— 1953. The Tillodontia: an early Tertiary order of mammals. Smithson. Misc. Collect. 121: 1-110.

——— 1962. A further study of the lower Eocene mammalian faunas of southwestern Wyoming. Smithson. Misc. Collect. 144: 1-98.

Gidley, J. W. 1924. Report on the fossils in "Tiffany" zone, Colorado. U.S. Geol. Surv. Prof. Pap. 134. 47 p.

Gingerich, P. D. 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. J. Paleontol. 48: 895-903.

——— 1976. Cranial anatomy and evolution of the early Tertiary Plesiadapidae (Mammalia, Primates). Univ. Mich. Pap. Paleontol. 15: 1-141.

——— 1977. A small collection of fossil vertebrates from the middle Eocene Kuldana and Kohat Formations of Punjab (Pakistan). Contrib. Mus. Paleontol. Univ. Mich. 24: 190-203.

——— ed. 1980. Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol. 24, 146 p.

Gingerich, P. D., and G. F. Gunnell. 1979. Systematics and evolution of the genus *Esthonyx* (Mammalia, Tillodontia) in the early Eocene of North America. Contrib. Mus. Paleontol. Univ. Mich. 25: 125-53.

Gingerich, P. D., and K. D. Rose. 1977. Preliminary report on the American Clark Fork mammal fauna, and its correlation with similar faunas in Europe and Asia. Geobios, Mem. Spec. 1: 39-45.

Gingerich, P. D., K. D. Rose, and D. W. Krause. 1980. Early Cenozoic mammalian faunas of the Clark's Fork Basin-Polecat Bench area, p. 51-64. *In* P. D. Gingerich [ed.]. Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol. 24.

Gingerich, P. D., and M. J. Schoeninger. 1979. Patterns of tooth size variability in the dentition of primates. Am. J. Phys. Anthropol. 51: 457-566.

Gingerich, P. D., and D. A. Winkler. 1979. Patterns of variation and correlation in the dentition of the red fox, *Vulpes vulpes*. J. Mammal. 60: 691-704.

Goldstein, B. 1972. Allometric analysis of relative humerus width and olecranon length in some unspecialized burrowing mammals. J. Mammal. 53: 148-56.

Granger, W. 1910. Tertiary faunal horizons in the Wind River Basin, Wyoming, with descriptions of new Eocene mammals. Bull. Am. Mus. Nat. Hist. 28: 235-51.

——— 1914. On the names of lower Eocene faunal horizons of Wyoming and New Mexico. Bull. Am. Nat. Hist. 33: 201-7.

——— 1917. Notes on Paleocene and lower Eocene horizons of northern New Mexico and Colorado. Bull. Am. Mus. Nat. Hist. 37: 821-30.

Grant, P. G. 1973. Biomechanical significance of the instantaneous center of rotation: the human temporomandibular joint. J. Biomech. 6: 109-13.

Greaves, W. J. 1974. Functional implications of mammalian jaw joint position. Forma Functio 7: 363-76.

Greene, E. C. 1935. Anatomy of the rat. Trans. Am. Philos. Soc., n.s. 37: 1-370.

Gregory, W. K. 1910. The orders of mammals. Bull. Am. Mus. Nat. Hist. 28: 1-524.

——— 1912. Quadrupedal locomotion of hoofed mammals. Ann. N.Y. Acad. Sci. 22: 267-94.

——— 1920. Studies of comparative myology and osteology: Number 4, a review of the evolution of the lacrymal bone of vertebrates with special reference to that of mammals. Bull. Am. Mus. Nat. Hist. 42: 95–203.

——— 1922. The origin and evolution of the human dentition. Williams and Wilkins Co., Baltimore. 548 p.

——— 1951. Evolution emerging. Macmillan Co., New York, vol. 1, 736 p.; vol. 2. 1013 p.

Grzimek, B. 1975. Grzimek's animal life encyclopedia. Van Nostrand Reinhold Co., New York, 13 vols.

Guthrie, D. A. 1967. The mammalian fauna of the Lysite Member, Wind River Formation (early Eocene) of Wyoming. Mem. South. Calif. Acad. Sci. 5: 1–53.

——— 1971. The mammalian fauna of the Lost Cabin Member, Wind River Formation (early Eocene) of Wyoming. Ann. Carnegie Mus. 43: 47–113.

Hardenbol, J., and W. A. Berggren. 1978. A new Paleogene numerical time scale, p. 213–34. *In* G. V. Cohee, M. F. Glaessner, and H. D. Hedberg [eds.]. Contributions to the geologic time scale. Geöl., Tulsa, Oklahoma.

Hatley, T., and J. Kappelman. 1980. Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of belowground food resources. Hum. Ecol. 8: 371–87.

Haug, E. 1911. Traité de géologie, II: Les périodes géologique. A. Colin, Paris, p. 539–2024.

Hay, O. P. 1899. On the names of certain North American fossil vertebrates. Science 9: 593–94.

Hecht, M. K. 1976. Phylogenetic inferences and methodology as applied to the vertebrate record. Evol. Biol. 9: 335–63.

Hecht, M. K., and J. Edwards. 1976. The determination of parallel or monophyletic relationships: the proteid salamanders—a test case. Am. Nat. 110: 653–77.

Hennig, W. 1965. Phylogenetic systematics. Ann. Rev. Entomol. 10: 97–116.

——— 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana. 263 p.

Herring, S. W. 1975. Adaptations for gape in the hippopotamus and its relatives. Forma Functio 8: 85–100.

Herring, S. W., and S. E. Herring. 1974. The superficial masseter and gape in mammals. Am. Nat. 108: 561–76.

Hickey, L. J. 1980. Paleocene stratigraphy and flora of the Clark's Fork Basin, p. 33–49. *In* P. D. Gingerich [ed.]. Early Cenozoic paleontology and stratigraphy in the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol. 24.

——— 1981. Land plant evidence compatible with gradual, not catastrophic, change at the end of the Cretaceous. Nature 292: 529–31.

Hiiemae, K., and F. A. Jenkins, Jr. 1969. The anatomy and internal architecture of the muscles of mastication in *Didelphis marsupialis.* Postilla (Peabody Mus. Nat. Hist., Yale Univ.) 140. 49 p.

Hildebrand, M. 1974. Analysis of vertebrate structure. John Wiley and Sons, New York. 710 p.

Hilzheimer, M. 1913. Stammageschichte der Wirbeltiere. Naturwiss. Monatsh. Biol. Chem. Geol. Unterr., n.s. 6: 465–75, 512–23, 564–70.

Hoernes, R. 1886. Manuel de Paléontologie (translated from the German by L. Dollo). Paris. 741 p.

Howell, A. B. 1944. Speed in animals. Univ. Chicago Press, Chicago. 270 p.

Jenkins, F. A., Jr. 1971a. The postcranial skeleton of African cynodonts. Peabody Mus. Nat. Hist. Yale Univ. Bull. 36. 216 p.

——— 1971b. Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. J. Zool., London 165: 303–15.

Jerison, H. J. 1973. Evolution of brain and intelligence. Academic Press, New York. 482 p.

Kielan-Jaworowska, Z. 1980. Absence of ptilodontiodean multituberculates from Asia and its paleontological implications. Lethaia 13: 169–73.

Kielan-Jaworowska, Z., T. M. Bown, and J. A. Lillegraven. 1979. Eutheria, p. 221–58. *In* J. A. Lillegraven, Z. Kielan-Jaworowska, and W. A. Clemens, Jr. [eds.]. Mesozoic mammals: the first two-thirds of mammalian history. Univ. Calif. Press, Berkeley.

Kiltie, R. A. 1981. The function of interlocking canines in rain forest peccaries (Tayassuidae). J. Mammal. 62: 459–69.

King, C. 1878. Systematic geology. Rep. U.S. Geol. Explor. Fortieth Parallel, vol. 1, p. 1–803.

Koken, E. 1893. Die Vorwelt und ihre Entwicklungsgeschichte. T. O. Weigel, Leipzig. 626 p.

Krause, D. W. 1981. Extinction of multituberculates and plesiadapidiform primates: examples of competitive exclusion in the mammalian fossil record. Geol. Soc. Am. Abstr. Progr. 13: 491.

Kues, B. S., J. W. Froehlich, J. A. Schiebout, and S. G. Lucas. 1977. Paleontological survey, resource assessment, and mitigation plan for the Bisti-Star Lake area, northwestern New Mexico. Open File Rep. U.S. Bur. Land Manage. Albuquerque. 1525 p.

Kurtén, B. 1966. Holarctic land connexions in the early Tertiary. Commenta. Biol. Soc. Sci. Fenn. 29(5): 1-5.

Lane, H. H. 1909. A suggested classification of the edentates. Res. Bull. Univ. Okla. 2: 19–27.

——— 1910. A corrected classification of the edentates. Science 31: 913–14.

Lavocat, R. 1955. Ordre des Taeniodontes. Traité Zool. 17(2): 1173–79.

——— 1958. Taeniodonta. Traité Paleontol. 2(6): 508–21.

Leister, C. W. 1939. The wild pigs of the world. Bull. N.Y. Zoolog. Soc. 42: 130–39.

Lillegraven, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. Univ. Kans. Paleontol. Contrib., Art. 50 (Vertebrata 12): 1–122.

Lillegraven, J. A., M. C. McKenna, and L. Krishtalka. 1981. Evolutionary relationships of middle and younger species of *Centetodon* (Mammalia, Insectivora, Geolabididae) with a description of the dentition of *Anklodon* (Adapiscoricidae). Univ. Wyo. Publ. 45: 1–115.

Lindsay, E. H., R. F. Butler, and N. M. Johnson. 1981. Magnetic polarity zonation and biostratigraphy of late Cretaceous and Paleocene continental deposits, San Juan Basin, New Mexico. Am. J. Sci. 281: 390–435.

Lindsay, E. H., L. L. Jacobs, and R. F. Butler. 1978. Biostratigraphy and magnetostratigraphy of Paleocene terrestrial deposits, San Juan Basin, New Mexico. Geology 6: 425–29.

Loomis, F. B. 1921. Origin of South American faunas. Geol. Soc. Am. Bull. 32: 187–96.

——— 1922. Derivation of South American faunas. Pan-Am. Geol. 37: 61–63.

Lowrie, W., and W. Alvarez. 1981. On hundred million years of geomagnetic polarity history. Geology 9: 392–97.

Lucas, S. G. 1977. Vertebrate paleontology of the San Jose Formation, east-central San Juan Basin, New Mexico. N.M. Geol. Soc. Guide. 28: 221–25.

——— 1981. Dinosaur communities of the San Juan Basin: a case for lateral variations in the composition of Late Cretaceous dinosaur communities, p. 337–93. *In* S. G. Lucas, J. K. Rigby, and B. S. Kues [eds.]. Advances in San Juan Basin paleontology. Univ. N.M. Press, Albuquerque.

——— 1982. Vertebrate paleontology, stratigraphy and biostratigraphy of the Eocene Galisteo Formation, north-central New Mexico. N.M. Bur. Mines Min. Resour. Circ. 186: 1–34.

Lucas, S. G., and B. S. Kues. 1979. Vertebrate biostratigraphy of the Eocene Galisteo Formation, north-central New Mexico. N.M. Geol. Soc. Guide. 30: 225–29.

Lucas, S. G., and F. M. O'Neill. 1981. Occurrence of *Pantolambda* Mammalia; Pantodonta) in the Torrejonian *Deltatherium* "zone," San Juan Basin, New Mexico. Am. J. Sci. 281: 187–91.

Lucas, S. G., and R. M. Schoch. 1981a. *Basalina,* a tillodont from the Eocene of Pakistan. Bayer. Staatssam. Paleontol. Hist. Geol. Mitt. München 21: 89–95.

——— 1981b. Paleoenvironments in north-central New Mexico during the early and late Eocene. Geol. Soc. Am. Abstr. Progr. 13: 500.

——— 1982. Discussion: Magnetic polarity zonation and biostratigraphy of late Cretaceous and Paleocene deposits, San Juan Basin, New Mexico. Am. J. Sci. 282: 920–27.

Lucas, S. G., R. M. Schoch, E. Manning and C. Tsentas. 1981. The Eocene biostratigraphy of New Mexico. Geol. Soc. Am. Bull. 92, part 1: 951–67; 92, part 2: 2268–2307.

Lull, R. S. 1915. The mammals and horned dinosaurs of the Lance formation of Niobrara County, Wyoming. Am. J. Sci. 90: 319–348.

Lydekker, R. 1903. The paleontological case for evolution. Knowledge 26: 73–76, 100–2, 123–26.

MacIntyre, G. T. 1972. The trisulcate petrosal pattern of mammals. Evol. Biol. 6: 275–303.

MacPhee, R. D. E. 1981. Auditory regions of primates and eutherian insectivores: morphology, ontogeny, and character analysis. Contrib. Primatol. 18: 1–282.

Major, C. J. F. 1893. On some Miocene squirrels, with remarks on the dentition and classification of the Sciurinae. Proc. Zool. Soc. London (1893): 179–215.

Manter, J. T. 1938. The dynamics of quadrupedal walking. J. Exp. Biol. 15: 522–40.

Marsh, O. C. 1874. Notice of new Tertiary mammals, III. Am. J. Sci. 7: 531–34.

——— 1875a. [Untitled] Am. J. Sci. 9: 151.

——— 1875b. New order of Eocene mammals. Am. J. Sci. 9: 221.

——— 1876a. Recent discoveries of extinct animals. Am. J. Sci. 12: 59–61.

——— 1876b. Notice of new Tertiary mammals, V. Am. J. Sci. 12: 401–4.

——— 1877. Introduction and succession of vertebrate life in America. Am. J. Sci. 14: 337–78.

——— 1897. The Stylinodontia, a suborder of Eocene edentates. Am. J. Sci. 3: 137–46.

Marshall, L. G. 1980. Marsupial paleobiogeography, p. 345–86. *In* L. L. Jacobs [ed.]. Aspects of vertebrate history: essays in honor of Edwin Harris Colbert. Mus. North. Ariz. Press, Flagstaff.

Matthew, W. D. 1897. A revision of the Puerco fauna. Bull. Am. Mus. Nat. Hist. 9: 259–323.

——— 1899. A provisional classification of the fresh-water Tertiary of the West. Bull. Am. Mus. Nat. Hist. 12: 19–75.

——— 1906. Hypothetical outlines of the continents in Tertiary times. Bull. Am. Mus. Nat. Hist. 22: 353–83.

——— 1909a. Faunal lists of the Tertiary Mammalia of the West. U.S. Geol. Surv. Bull. 361: 91–138.

——— 1909b. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. Am. Mus. Nat. Hist. Mem. 9: 291–567.

——— 1914. Evidence of the Paleocene vertebrate fauna on the Cretaceous-Tertiary problem. Geol. Surv. Am. Bull. 25: 381–402.

——— 1915a. Climate and evolution. Ann. N.Y. Acad. Sci. 24: 171–318.

——— 1915b. The Tertiary sedimentary record and its problems: Dana Commemorative Lectures. Problems of American Geology, p. 377–478.

——— 1918. A revision of the Lower Eocene Wasatch and Wind River faunas. Insectivora (continued), Glires, Edentata. Bull. Am. Mus. Nat. Hist. 38: 565–657.

——— 1921. Fossil vertebrates and the Cretaceous-Tertiary problem. Am. J. Sci. 2: 209–27.

——— 1924. Correlation of the Tertiary formations of the Great Plains. Geol. Soc. Am. Bull. 35: 743–54.

——— 1928. The evolution of the mammals in the Eocene. Proc. Zool. Soc. London (1927): 947–85.

——— 1937. Paleocene faunas of the San Juan Basin, New Mexico. Trans. Am. Philos. Soc., n.s. 30: 1–510.

Matthew, W. D., and W. Granger. 1921. New genera of Paleocene mammals. Am. Mus. Novit. 13. 7 p.

——— 1925. Fauna and correlation of the Gashato formation of Mongolia. Am. Mus. Novit. 189. 12 p.

McDowell, S. J., Jr. 1958. The greater Antillean insectivores. Bull. Am. Mus. Nat. Hist. 115: 113–214.

McKenna, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene, of northwest Colorado. Univ. Calif. Publ. Geol. Sci. 37: 1–130.

——— 1969. The origin and early differentiation of the therian mammals. Ann. N.Y. Acad. Sci. 167: 217–40.

——— 1972. Vertebrate paleontology of the Togwotee Pass area, northwestern Wyoming, p. 80–101. *In* R. M. West, coordinator. Field conference on tertiary biostratigraphy of southern and western Wyoming. Aug. 5–10, 1972. Privately printed and distributed.

——— 1975. Toward a phylogenetic classification of the Mammalia, p. 21–46. *In* W. P. Luckett and F. S. Szalay [eds.]. Phylogeny of the primates. Plenum Press, New York.

——— 1980a. Late Cretaceous and early Tertiary vertebrate paleontological reconnaisance, Togwotee Pass area, northwestern Wyoming, p. 321–43. *In* L. L. Jacobs [ed.]. Aspects of vertebrate history, essays in honor of Edwin Harris Colbert. Mus. North. Ariz. Press, Flagstaff.

——— 1980b. Eocene paleolatitude, climate, and mammals of Ellesmere Island. Palaeogeogr. Palaeoclimat. Palaeoecol. 30: 349–62.

McKenna, M. C., G. F. Engelmann, and S. F. Barghoorn. 1977. Review: Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates) by Philip D. Gingerich. Syst. Zool. 26: 233–38.

McKenna, M. C., E. E. Russell, R. M. West, C. C. Black, W. D. Turnbull, M. R. Dawson, and J. A. Lillegraven. 1973. K/Ar recalibration of Eocene North American land mammal "ages" and European ages. Geol. Soc. Am. Abstr. Progr. 5: 733.

McManus, J. J. 1970. Behavior of captive opossums, *Didelphis marsupialis virginiana.* Am. Mid. Nat. 84: 144–69.

Mellett, J. S. 1977. Paleobiology of North American *Hyaenodon* (Mammalia, Creodonta). Contrib. Verteb. Evol. 1: 1–134.

Melton, D. A. 1976. The biology of aardvark (Tublidentata-Orycteropidae). Mammal Rev. 6: 75–88.

Merrill, G. P. 1907. Catalogue of the types, cotypes, and figured specimens of fossil vertebrates in the department of geology, U.S. National Museum. U.S. Nat. Mus. Bull. 53, part 2. 81 p.

Miller, M. E. 1952. Guide to the dissection of the dog, 3rd ed. Edwards Brothers, Inc., Ithaca, N.Y. 369 p.

Mills, J. R. E. 1966. The functional occlusion of the teeth of Insectivora. J. Linn. Soc. London, Zool. 47: 1–25.

Minkoff, E. C. 1983. Evolutionary biology. Addison-Wesley Publishing Co., Reading, Mass. 627 p.

Mivart, St. G. 1881. The cat: an introduction to the study of backboned animals, especially mammals. Charles Scribner's Sons, New York, 557 p.

Murie, J. 1872. On the Malayan tapir, *Rhinochoerus sumatranus* (Gray). J. Anat. Physiol. 6 (2nd ser., vol. 5): 131–69.

Nicholson, H. A., and R. Lydekker. 1889. A manual of palaeontology for the use of students, with a general introduction on the principles of palaeontology. W. Blackwood and Sons, London, vol. 2, p. 889–1624.

Novacek, M. J. 1977. Aspects of the problem of variation, origin and evolution of the eutherian auditory bulla. Mammal Rev. 7: 131–49.

——— 1980. Cranioskeletal features in tupaiids and selected Eutheria as phylogenetic evidence, p. 35–93. *In* W. P. Luckett [ed.]. Comparative biology and evolutionary relationships of tree shrews. Plenum Press, New York.

——— 1982. Information for molecular studies from anatomical and fossil evidence on higher eutherian phylogeny, p. 3–41. *In* M. Goodman [ed.]. Macromolecular sequences in systematic and evolutionary biology. Plenum Press, New York.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Ann. Rev. Ecol. Syst. 4: 125–52.

Olivier, G. A. 1789. Entomologie, ou histoire naturelle des insectes, avec leurs caractères gêneriques et spécifiques, 1(7): 1–4.

Osborn, H. F. 1897a. The Ganodonta, or primitive edentates with enameled teeth. Science 5: 611–12.

——— 1897b. Abstracts of papers read before the New York Academy of Sciences. Science 6: 107.

——— 1898a. Paleontological problems. Science 7: 145–47.

——— 1898b. Wasatch and Bridger beds in the Huerfano Lake basin. Proc. Am. Ass. Adv. Sci. 96: 205–6.

——— 1899. The origin of the mammals. Am. J. Sci. 7: 92–96.

——— 1902. The law of adaptive radiation. Am. Nat. 36: 353–63.

——— 1905. Ten years of progress in the mammalian palaeontology of North America. Verh. Int. Zool. Kongr. Bern, 1904, vol. 6, p. 86–113.

——— 1907. Evolution of mammalian molar teeth. Macmillan Co., New York. 250 p.

——— 1909. Cenozoic mammal horizons of western North America. U.S. Geol. Surv. Bull. 161: 1–90.

——— 1910. The age of mammals in Europe, Asia, and North America. Macmillan Co., New York. 635 p.

——— 1912. Symposium on ten years of progress in vertebrate paleontology. Correlation and paleogeography. Geol. Soc. Am. Bull. 23: 232–56.

——— 1925. Final conclusions on the evolution, phylogeny, and classification of the Proboscidea. Proc. Am. Philos. Soc. 64: 17–35.

——— 1929. The titanotheres of ancient Wyoming, Dakota and Nebraska. U.S. Geol. Surv. Monogr. 55, vol 1, p. 1–702, vol. 2, p. 703–953.

Osborn, H. D., and C. Earle. 1895. Fossil mammals of the Puerco beds, collection of 1892. Bull. Am. Mus. Nat. Hist. 7: 1–70.

Osborn, H. F., and J. L. Wortman. 1892. Fossil mammals of the Wahsatch and Wind River beds, collection of 1891. Bull. Am. Mus. Nat. Hist. 4: 80–147.

Ottoway, C. W. 1955. The mechanism of movement, p. 619–58. *In* J. Hammond [ed.]. Progress in the physiology of farm animals. Butterworths, London, vol. 2.

Palacký, J. 1902. Zur Verbreitung der Edentate. Sitzungsber. Böhmis. Ges. Wiss. 1901, Art. 13, p. 1–5.

Patterson, B. 1936. Mounted skeleton of *Titanoides,* with notes on the associated fauna. Proc. Geol. Soc. Am. 1935, p. 397–98.

——— 1949a. A new genus of taeniodonts from the late Paleocene. Fieldiana, Geol., 10: 41–42.

——— 1949b. Rates of evolution in taeniodonts, p. 243–78. *In* G. L. Jepsen, G. G. Simpson, and E. Mayr [eds.]. Genetics, paleontology, and evolution. Princeton Univ. Press, Princeton.

——— 1975. The fossil aardvarks (Mammalia: Tublidentata). Bull. Mus. Comp. Zool. 147: 185–237.

Pavlow, M. 1887. Études sur l'histoire paléontologique des ongulés en Amérique et en Europe. I. Groupe primitif de l'éocène inférieur. Bull. Soc. Impér. Nat. Moscou 1: 343–73.

Prins, N., and R. M. Schoch. 1983. New skeletal and life restorations of Paleocene and Eocene mammals. Geol. Soc. Am. Abstr. Progr. 15: 144.

Puttick, G. M., and J. U. M. Jarvis. 1977. The functional anatomy of the neck and forelimbs of the Cape Golden Mole, *Chrysochloris asiatica* (Lipotyphyla: Chrysochloridae). Zool. Afr. 12: 445–58.

Radinsky, L. 1968. A new approach to mammalian cranial analysis, illustrated by examples of prosimmian primates. J. Morphol. 124: 167–80.

——— 1976. The brain of *Mesonyx,* a middle Eocene mesonychid condylarth. Fieldiana, Geol., 33: 323–37.

——— 1978. Evolution of brain size in carnivores and ungulates. Am. Nat. 112: 815–31.

Raup, D. M. 1981. Extinction: bad genes or bad luck? Acta Geol. Hisp. 16: 25–33.

Reeside, J. B., Jr. 1924. Upper Cretaceous and Tertiary formations of the western part of the San Juan Basin, Colorado and New Mexico. U.S. Geol. Surv. Prof. Pap. 134. 70 p.

Rigby, J. K., Jr. 1980. Swain Quarry of the Fort Union Formation, middle Paleocene (Torrejonian), Carbon County, Wyoming: geological setting and mammalian fauna. Evol. Monogr. 3: 1–179.

Rigby, J. K., Jr., and S. G. Lucas. 1977. Fossil mammals from the Ojo Alamo Sandstone. Suppl. N.M. Geol. Soc. Guide. 28, p. 55–56.

Riggs, E. S. 1912. New or little known titanotheres from the lower Uintah Formation; with notes on the stratigraphy and distribution of fossils. Field Mus. Nat. Hist. Geol. Ser. 4: 17–41.

Roberts, A. 1923. The burrowing habits of some South African mammals. S. Afr. J. Nat. Hist. 4: 187–208.

Robinson, P. 1966. Fossil Mammalia of the Huerfano Formation, Eocene, of Colorado. Peabody Mus. Nat. Hist. Yale Univ. Bull. 21: 1–95.

Robison, S., and S. G. Lucas. 1980. The early Paleocene Wagonroad local fauna, North Horn Formation, Utah: a case for early Paleocene provinciality in the western interior. Geol. Soc. Am. Abstr. Progr. 12: 302.

Romer, A. S. 1966. Vertebrate paleontology, 3rd ed. Univ. Chicago Press, Chicago. 468 p.

——— 1968. Notes and comments on vertebrate paleontology. Univ. Chicago Press, Chicago. 304 p.

Root, A. 1972. Fringe-eared oryx digging for tubers in the Tsavo National Park (East). East Afr. Wildl. J. 10: 155–57.

Rose, K. D. 1977. Evolution of carpolestid primates and chronology of the North American middle and late Paleocene. J. Paleontol. 51: 536–42.

——— 1980. Clarkforkian land-mammal age: revised definition, zonation, and tentative intercontinental correlations. Science 208: 744–46.

——— 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. Univ. Mich. Pap. Paleontol. 26. 197 p.

Roth, V. L. 1982. Dwarf mammoths from the Santa Barbara, California Channel Islands: size, shape, development, and evolution. Yale Univ. New Haven, unpub. Ph.D. dissert. 277 p.

Russell, D. E. 1967. Le Paléocène continental d'Amérique du Nord. Mus. Nat. d'Hist. Nat. Paris, Mém., Ser. C, 16: 37–39.

——— 1968. Succession, en Europe, des faunes mammaliennes au début du Tertiare. Mém. Bur. Rech. Géol. Min. 58: 291–96.

Rütimeyer, L. 1890. Uebersich der eocänen Fauna von Egerkingen nebst einer Erwiederung an Prof. E. D. Cope. Verh. Naturforsch. Ges. Basel 91: 3–34.

——— 1891. Die Eocäne Säugethier-Welt von Egerkingen. Abh. Schweizer. Paläontol. Ges. 18: 1–153.

Saban, R. 1958. Insectivora. Traité Paléontol. 2(6): 822–909.

Sandidge, L. L. 1953. Food and dens of the opossum (*Didelphis virginiana*) in northeastern Kansas. Trans. Kans. Acad. Sci. 56: 97–106.

Savage, D. E. 1971. Taeniodonta. McGraw-Hill Encycl. Sci. Technol. Vol. 13, p. 408.

Savage, J. G. 1957. The anatomy of *Potamotherium,* an Oligocene lutrine. Proc. Zool. Soc. London 129: 151–244.

Scapino, R. P. 1976. Function of the digastric muscle in carnivores. J. Morph. 150: 843–60.

Schaeffer, B., M. K. Hecht, and N. Eldredge. 1972. Phylogeny and paleontology. Evol. Biol. 6: 31–46.

Schankler, D. M. 1980. Faunal zonation of the Willwood Formation, Wyoming: preliminary results, p. 99–110. *In* P. D. Gingerich [ed.]. Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol. 24.

——— 1981. Local extinction and ecological re-entry of early Eocene mammals. Nature 293: 135–38.

Schiebout, J. A. 1974. Vertebrate paleontology and paleoecology of Paleocene Black Peaks Formation, Big Bend National Park, Texas. Tex. Mem. Mus. Bull. 24: 1–88.

Schindel, D. E. 1980. Microstratigraphic sampling and the limits of paleontological resolution. Paleobiology 6: 408–26.

Schlosser, M. 1885. Zur Stämmesgeschichte dur Hufthiere. Zool. Anz. 8: 683–91.

——— 1886. Beitrage zur Kenntnis der Stämmesgeschichte der Hufthiere und Versuch einter Systematik der Paar- und Unpaarhufer. Morphol. Jahrb. 12: 1–136.

——— 1890. Die Differenzierung des Saugetiergebisses. Biol. Zentralbl. 10: 1–136.

——— 1892. Die Entwickelung der verschiedenen Säugetierzahnformen im Laufe der geologischen Perioden. Verh. Deutsch. Odontol. Ges. Berlin 3: 203–30.

——— 1894. Bemerkungen zu Rütimeyer's "eocäne Säugetheirwelt von Egerkingen." Zool. Anz. 17: 157–62.

——— 1911. Mammalia, p. 325–585. *In* F. Broili, E. Koken, and M. Schlosser [eds.]. Grundzuge der Paläontologie (Paläozoologie) von Karl A. von Zittel. Druck und Verlag von R. Oldenbourg, München and Berlin, vol. 2.

Schoch, R. M. 1981a. Revision of the middle Paleocene (Torrejonian) taeniodont (Mammalia) *Psittachotherium* Cope, 1882, p. 177–85. *In* S. G. Lucas, J. K. Rigby, Jr., and B. S. Kues [eds.]. Advances in San Juan Basin paleontology. Univ. N.M. Press, Albuquerque.

——— 1981b. Taxonomy and biostratigraphy of the early Tertiary Taeniodonta (Mammalia: Eutheria): summary. Geol. Soc. Am. Bull. 92: part 1, p. 933–41; part 2, p. 1982–2267.

——— 1982a. Phylogeny, classification and paleobiology of the Taeniodonta (Mammalia: Eutheria). Third North Am. Paleontol. Conv. Proc. 2: 465–70.

——— 1982b. The evolution of the Taeniodonta (Mammalia: Eutheria). J. Paleontol., Suppl., 56(2): 24 (abstract).

——— 1982c. Gaps in the fossil record; fossils and stratigraphy. Nature 299: 490.

——— 1983a. An endocranial cast of Ectoganus, an early Tertiary taeniodont. J. Mammal. 64: 180–83.

——— 1983b. Third North American Palaeontological Convention. Geoscience Canada 10: 204–7.

——— 1985. Preliminary description of a new Late Paleocene land-mammal fauna from South Carolina, U.S.A. Postilla (Peabody Mus. Nat. Hist., Yale Univ.) 196. 13 p.

Schoch, R. M., and S. G. Lucas. 1981a. The biostratigraphic and geographic distribution of the mammalian order Taeniodonta. Geol. Soc. Am. Abstr. Progr. 13: 225.

——— 1981b. New conoryctines (Mammalia; Taeniodonta) from the middle Paleocene (Torrejonian) of western North America. J. Mammal. 62: 683–91.

——— 1981c. A new species of *Conoryctella* (Mammalia: Taeniodonta) from the Paleocene of the San Juan Basin, New Mexico, and a revision of the genus. Postilla (Peabody Mus. Nat. Hist. Yale Univ.) 185. 23 p.

——— 1981d. The systematics of *Stylinodon,* a middle to late Eocene taeniodont (Mammalia) from western North America. J. Vertebr. Paleontol. 1: 175–83.

——— 1981e. Negative evidence and the fossil record: alternative explanations for the rarity of Taeniodonts (Mammalia, Eutheria). Geol Soc. Am. Abstr. Progr. 13: 548.

——— 1982. Apparent evolutionary stasis in the Eocene taeniodont (Mammalia) *Stylinodon mirus.* Geol. Soc. Am. Abstr. Progr. 14: 611.

Schopf, T. J. M. 1981. Puntuated equilibrium and evolutionary stasis. Paleobiology 7: 156–66.

Schumacher, G. H. 1961. Funktionelle morphologie der Kaumuskulatur. Gustav Fischer Verlag, Jena. 262 p.

Scott, W. B. 1892a. A revision of the North American Creodonta, with notes on some genera which have been referred to that group. Proc. Acad. Nat. Sci. Philadelphia (1892): 291–323.

——— 1892b. The genera of American Creodonta. Princeton Coll. Bull. 4: 76–81.

——— 1905. Mammalia of the Santa Cruz beds. Princeton Univ. Exped. Patagonia. 499 p.

——— 1937. A history of land mammals in the western hemisphere. Macmillan Co., New York. 786 p.

Sera, G. L. 1947. L'occultamento subacqueo e l'ancoramento nella paleobiologia di parte dei monodelfi e la distinzione di questi in due gruppi filetici. Paleontogra. Ital. 41: 63–120.

Shimer, H. W. 1903. Adaptations to aquatic, arboreal, fossorial, and cursorial habits in mammals. III. Fossorial adaptations. Am. Nat. 37: 819–26.

Simons, E. L. 1960. The Paleocene Pantodonta. Trans. Am. Philos. Soc., n.s. 50: 1–81.

Simpson, G. G. 1929a. A collection of Paleocene mammals from Bear Creek, Montana. Ann. Carnegie Mus. 19: 115–22.

——— 1929b. Third contribution to the Fort Union fauna at Bear Creek, Montana. Am. Mus. Novitates 345. 12 p.

——— 1931. *Metacheiromys* and the Edentata. Bull. Am. Mus. Nat. Hist. 59: 259–381.

——— 1933. Braincasts of *Phenacodus, Notostylops,* and *Rhyphodon.* Am. Mus. Novitates 622. 19 p.

——— 1935a. The Tiffany fauna, upper Paleocene. I. Multituberculata, Marsupialia, Insectivora, and ?Chiroptera. Am. Mus. Novitates 795. 19 p.

——— 1935b. The Tiffany fauna, upper Paleocene. II. Structure and relationships of *Plesiadipis.* Am. Mus. Novitates 816. 30 p.

——— 1935c. The Tiffany fauna, upper Paleocene. III. Primates, Carnivora, Condylarthra and Amblyopoda. Am. Mus. Novitates 817. 28 p.

——— 1937. The Fort Union of the Crazy Mountain Field, Montana and its mammalian faunas. U.S. Nat. Mus. Bull. 169: 1–287.

——— 1943. Criteria for genera, species, and subspecies in zoology and paleozoology. Ann. N.Y. Acad. Sci. 44: 145–77.

——— 1945. The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist. 85: 1–350.

——— 1947a. A continental Tertiary time chart. J. Paleontol. 21: 480–83.

——— 1947b. Holarctic mammalian faunas and continental relationships during the Cenozoic. Geol. Soc. Am. Bull. 58: 613–88.

——— 1948. The Eocene of the San Juan Basin, New Mexico. Am. J. Sci. 246: 257–82, 363–85.

——— 1953. The major features of evolution. Columbia Univ. Press, New York. 434 p.

——— 1959. Fossil mammals from the type area of the Puerco and Nacimiento strata, Paleocene of New Mexico. Am. Mus. Novitates 1957. 22 p.

——— 1961. Principles of animal taxonomy. Columbia Univ. Press, New York. 247 p.

——— 1971. Concluding remarks; Mesozoic mammals revisited, p. 181–98. *In* D. M. Kermack, and K. A. Kermack [eds.]. Early mammals. Suppl. I to J. Linn. Soc. London, Zool. 50.

——— 1981. History of vertebrate paleontology in the San Juan Basin, p. 3–25. *In* S. G. Lucas, J. K. Rigby, Jr., and B. S. Kues [eds.]. Advances in San Juan Basin paleontology. Univ. N.M. Press, Albuquerque.

Simpson, G. G., and H. O. Elftman. 1928. Hind limb musculature and habits of a Paleocene multituberculate. Am. Mus. Novitates 333, 19 p.

Simpson, G. G., A. Roe, and R. C. Lewontin. 1960. Quantitative zoology. Harcourt, Brace & Co., New York. 440 p.

Sinclair, W. J. 1905. Mammalia of the Santa Cruz beds: Edentata, Insectivora, Glires. Princeton Expeditions to Patagonia, 1896–1899. 499 p.

——— 1912. Notes on the Tertiary deposits of the Bighorn Basin. Bull. Am. Mus. Nat. Hist. 31: 57–67.

Sinclair, W. J., and W. Granger. 1911. Eocene and Oligocene of the Wind River and Bighorn Basins. Bull. Am. Mus. Nat. Hist. 30: 83–117.

——— 1914. Paleocene deposits of the San Juan Basin, New Mexico. Bull. Am. Mus. Nat. Hist. 33: 297–316.

Slijper, E. J. 1946. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. Verh. K. Akad. Wet. Amsterdam, Afd. Natuurk. (Tweede Sectie) 42: 1–128.

Sloan, R. E. 1970. Cretaceous and Paleocene terrestrial communities of Western North America. Proc. North Am. Paleontol. Conv. Chicago, 1969, p. 427–53.

Sloan, R. E., J. H. Hartman, L. J. Dempsey, M. E. Jordan, and E. B. Robertson. 1980. Paleontological resources evaluation: West Divide Project. U.S. Dep. Int. Water Power Resour. Serv. Bur. Reclama. Salt Lake City. 55 p.

Sloan, R. E., and L. Van Valen. 1965. Cretaceous mammals from Montana. Science 149: 220-27.

Smith, J. Maynard, and R. J. C. Savage. 1956. Some locomotory adaptations in mammals. J. Linn. Soc., Zool. 42: 603-22.

——— 1959. The mechanics of mammalian jaws. Sch. Sci. Rev. 40: 289-301.

Stegeman, L. C. 1938. The European wild boar in the Cherokee National Forest. J. Mammal. 19: 279-290.

Stehlin, H. G. 1916. Die Säugetiere des schweitzerischen Eocaens. Critischer Catalog der Materialien, 7ter. Th. 2te. Hälfte. Abh. Schweizer. Palaeontol. Ges. 41: 1297-1552.

Steinmann, G. 1907. Einführung in die Paläontologie. W. Engelmann, Leipzig. 542 p.

Steinmann, G., and L. Döderlein. 1890. Elemente der Paläontologie. W. Engelmann, Leipzig. 848 p.

Stoll, N. R., R. P. Dollfus, J. Forest, N. D. Riley, C. W. Sabrosky, C. W. Wright, and R. V. Melville. 1964. International Code of Zoological Nomenclature. Int. Trust for Zool. Nomencl., London. 176 p.

Stromer, E. 1912. Lehrbuch der Paläozoologie. II. Theil: Wirbeltiere. B. G. Teubner, Leipzig and Berlin. 325 p.

Szalay, F. S. 1966. The tarsus of the Paleocene leptictid *Prodiacodon* (Insectivora, Mammalia). Am. Mus. Novitates 2267. 13 p.

——— 1969. Mixodectidae, Microsyopidae, and the insectivore-primate transition. Bull. Am. Mus. Nat. Hist. 140: 193-330.

——— 1977. Phylogenetic relationships and a classification of the eutherian Mammalia, p. 315-74. *In* M. K. Hecht, P. C. Goody, and B. M. Hecht [eds.]. Major patterns in vertebrate evolution. Plenum Press, New York and London.

Taylor, B. F. 1978. The anatomy of the forelimb of the anteater (*Tamandua*) and its functional implications. J. Morphol. 157: 347-68.

Taylor, L. H. 1981. The Kutz Canyon local fauna, Torrejonian (middle Paleocene) of the San Juan Basin, New Mexico, p. 242-63. *In* S. G. Lucas, J. K. Rigby, Jr., and B. S. Kues [eds.]. Advances in San Juan Basin paleontology. Univ. N.M. Press, Albuquerque.

Taylor, L. H., and R. F. Butler. 1980. Magnetic-polarity stratigraphy of Torrejonian sediments, Nacimiento Formation, San Juan Basin, New Mexico. Am. J. Sci. 280: 97-115.

Terra, P. de. 1911. Vergleichende Anatomie des menschlichen Gebeisses und der Zähne der Vertebraten. Jena. 451 p.

Thacker, A. G. 1922. The geological history of the primates. Sci. Prog. (London) 16: 595-607.

Thompson, D'Arcy W. 1942. On growth and form. Cambridge Univ. Press, Cambridge. 1116 p.

Tidwell, W. D., S. R. Ash and L. R. Parker. 1981. Cretaceous and Tertiary floras of the San Juan Basin, p. 307-32. *In* S. G. Lucas, J. K. Rigby, Jr., and B. S. Kues [eds.]. Advances in San Juan Basin paleontology. Univ. N.M. Press, Albuquerque.

Tims, H. W. M. 1901. Tooth genesis in the Caviidae. J. Linn. Soc. London, Zool., 28: 261-90.

Tomida, Y. 1981. "Dragonian" fossils from the San Juan Basin and status of the "Dragonian" land mammal "age," p. 222-41. *In* S. G. Lucas, J. K. Rigby, Jr., and B. S. Kues [eds.]. Advances in San Juan Basin paleontology. Univ. N.M. Press, Albuquerque.

Tomida, Y., and R. F. Butler. 1980. Dragonian mammals and Paleogene magnetic polarity stratigraphy, North Horn Formation, central Utah. Am. J. Sci. 280: 787-811.

Trofimov, B. A. 1968. Taeniodonta, p. 145-46. *In* Yu A. Orlov [ed.]. Fundamentals of paleontology (translated from the 1962 Russian edition). Isr. Prog. Sci. Trans. vol. 13.

Tsentas, C. 1981. Mammalian biostratigraphy of the middle Paleocene (Torrejonian) strata of the San Juan Basin: notes on Torreon Wash and the status of the *Pantolambda* and *Deltatherium* faunal "zones," p. 246-92. *In* S. G. Lucas, J. K. Rigby, Jr., and B. S. Kues [eds.]. Advances in San Juan Basin paleontology. Univ. N.M. Press, Albuquerque.

Tsentas, C., and S. G. Lucas. 1980. Position of the Paleocene-Eocene boundary in the south-central San Juan Basin, New Mexico. Geol. Soc. Am. Abstr. Progr. 12: 538.

Tsentas, C., S. G. Lucas, and R. M. Schoch. 1981. Lithofacies of the upper part of the Nacimiento Formation, San Juan Basin, New Mexico. Geol. Soc. Am. Abstr. Progr. 13: 229.

Turnbull, W. D. 1970. Mammalian masticatory apparatus. Fieldiana Geol. 18: 149-356.

——— 1972. The Washakie Formation of Bridgerian-Uintan ages, and the related faunas, p. 20-31. *In* R. M. West, coordinator. Field conference on tertiary biostratigraphy of southern and western Wyoming, Aug. 5-10, 1972. Privately printed and distributed.

——— 1978. The mammalian faunas of the Washakie Formation, Eocene age, of southern Wyoming. Fieldiana, Geol. 33: 569-601.

Van Houten, F. B. 1945. Review of latest Paleocene and early Eocene mammalian faunas. J. Paleontol. 19: 421-61.

Van Valen, L. 1963. The origin and status of the mammalian order Tillodontia. J. Mammal. 44: 364-73.

——— 1964. A possible origin for rabbits. Evolution 18: 484-91.

——— 1966. Deltatheridia, a new order of mammals. Bull. Am. Mus. Nat. Hist. 132: 1-123.

——— 1969. The multiple origins of the placental carnivores. Evolution 23: 118–30.

——— 1978. The beginning of the age of mammals. Evol. Theory 4: 45–80.

Van Valen, L., and R. E. Sloan. 1966. The extinction of the multituberculates. Syst. Zool. 15: 261–78.

——— 1977. Ecology and extinction of the dinosaurs. Evol. Theory 2: 37–64.

Wake, M. H. 1979. Hyman's comparative vertebrate anatomy. 3rd ed. Univ. Chicago Press, Chicago. 1500 p.

Walker, E. P. 1975. Mammals of the world, 3rd ed. Johns Hopkins Univ. Press, Baltimore. 1500 p.

Wallace, A. R. 1876. The geographical distribution of animals. New York, vol. 1, 503 p.; vol. 2. 607 p.

Webb, S. D. 1977. A history of savanna vertebrates in the new world. Part I: North America. Annu. Rev. Ecol. Syst. 8: 355–80.

Weber, M. 1904. Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossien Mammalia. Jena. 866 p.

Weber, M., and O. Abel. 1928. Die Säugetiere. Zweite Auflage. Bd. II: Systematischer Teil. 898 p.

West, R. M. 1972a. Minimammals and their Bridger biostratigraphy, p. 40–50. *In* R. M. West, coordinator. Field conference of Tertiary biostratigraphy of southern and western Wyoming, Aug. 5–10, 1972. Privately printed and distributed.

——— coordinator. 1972b. Field conference on Tertiary biostratigraphy of southern and western Wyoming, Aug. 5–10, 1972. Privately printed and distributed.

——— 1973. Geology and mammalian paleontology of the New Fork-Big Sandy Area, Sublette County, Wyoming. Fieldiana, Geol. 29: 1–193.

——— 1978. Mammalia. McGraw-Hill Yearb. Sci. Technol. p. 248–51.

——— 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas region, Pakistan. J. Paleontol. 54: 508–33.

——— 1981a. Geology and paleontology of the Bridger Formation, southern Green River Basin, southwestern Wyoming. Part 5, *Harpagolestes macrocephalus* and comments on structure, function and diversity of middle Eocene to early Oligocene large mesonychids. Milwaukee Public Mus. Contrib. Biol. Geol. 43. 17 p.

——— 1981b. Ecologic replacement in Cenozoic fossil mammals-Eocene mesonychids and Oligocene entelodonts. Geol. Soc. Am. Abstr. Progr. 13: 230.

——— 1982. Fossil mammals from the lower Buck Hill group, Eocene of Trans-Pecos Texas: Marsupicarnivora, Primates, Taeniodonta, Condylarthra, Bunodont Artiodactyla, and Dinocerata. Tex. Mem. Mus. Pearce-Sellards series 35. 20 p.

West, R. M., M. R. Dawson, and J. H. Hutchison. 1977. Fossils from the Paleogene Eureka Sound Formation, N.W.T., Canada: occurrence, climatic and paleogeographic implications. Milwaukee Public Mus. Spec. Publ. Biol. Geol. 2: 77–93.

White, T. E. 1952. Preliminary analysis of the vertebrate fossil fauna of the Boysen Reservoir area. Proc. U.S. Nat. Mus. 102: 185–207.

——— 1959. The endocrine glands and evolution, no. 3: Os cementum, hypsodonty, and diet. Contrib. Mus. Paleontol. Univ. Mich. 13: 211–65.

Wilson, J. A. 1967. Early Tertiary mammals, p. 157–69. *In* R. A. Maxwell, J. T. Londsdale, R. T. Hazzard, and J. A. Wilson [eds.]. Geology of Big Bend National Park, Brewster County, Texas. Univ. Tex. Bur. Econ. Geol. Publ. 6711.

——— 1972. Vertebrate biostratigraphy of Trans-Pecos Texas and northern Mexico, p. 157–66. *In* K. Seewald and D. Sundeen [eds.]. The geologic framework of the Chihuahua tectonic belt. Midl. West Tex. Geol. Soc.

——— 1974. Early Tertiary vertebrate faunas, Vieja Group and Buck Hill Group, Trans-Pecos Texas: Protoceratidae, Camelidae, Hypertragulidae. Tex. Mem. Mus. Bull. 23: 1–34.

Wilson, R. W. 1951. Preliminary survey of a Paleocene faunule from the Angels Peak area, New Mexico. Univ. Kans. Publ. Mus. Nat. Hist. 5: 3–11.

——— 1956. A new multituberculate from the Paleocene Torrejon fauna of New Mexico. Trans. Kans. Acad. Sci. 59: 76–84.

Windle, B. C. A., and F. G. Parsons. 1901. On the muscles of the Ungulata. Part I. Muscles of the head, neck, and forelimb. Proc. Zool. Soc. London (1901): 656–704.

——— 1903. On the muscles of the Ungulata. Part II. On the muscles of the hind-limb and trunk. Proc. Zool. Soc. London (1903): 291–98.

Wing, S. L. 1980. Fossil floras and plant-bearing beds of the central Bighorn Basin, p. 119–25. *In* P. D. Gingerich. Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol. 24.

Winge, H. 1915. Jordfunde og nulevende Gumlere (Edentata) fra Lagoa Santa, Minas Gerais, Brasilien. E Mus. Lundii 3: 1–321.

——— 1917. Udsigt over Insektaedernes indbyrdes Slaeggtskab. Vidensk. Medd. Dan. Naturhist. Foren. Khobenhavn 68: 82–203.

——— 1923. Pattedyr-Slaegter, I. Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata. Copenhagen. 360 p.

Wolfe, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the northern hemisphere. Am. Sci. 66: 694–703.

Wolfe, J. A., and D. M. Hopkins. 1967. Climatic changes recorded by Tertiary land floras in northwestern America, p. 67–76. *In* K. Hatai [ed.]. Tertiary correlations and climatic changes in the Pacific. The 11th Pac. Sci. Congr., Tokyo, 1966, Symp., no. 25.

Wood, A. E. 1973. Eocene rodents, Pruett Formation, southwestern Texas; their pertinence to the origin of the South American Caviomorpha. Tex. Mem. Mus. Pearce-Sellards Series 20: 1–40.

Wood, H. E., R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, Jr., and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. Geol. Soc. Am. Bull. 52: 1–48.

Wood, R. C. 1967. A review of the Clark Fork vertebrate fauna. Breviora 257. 30 p.

Wood Jones, F. 1949. The study of a generalized marsupial (*Dasycercus cristicauda* Krefft). Trans. Zool. Soc. London 26: 409–501.

Woodburne, M. O., and W. J. Zinsmeister. 1982. Fossil land mammal from Antarctica. Science 218: 284–86.

Woodward, A. S. 1898. Outlines of vertebrate paleontology for students of zoology. Univ. Press, Cambridge, England. 470 p.

Wortman, J. L. 1885. Cope's Tertiary Vertebrata. Am. J. Sci. 30: 295–99.

——— 1896a. *Psittachotherium,* a member of a new and primitive suborder of Edentata. Bull. Am. Mus. Nat. Hist. 8: 259–62.

——— 1896b. The North American origin of the edentates. Science 4: 865–66.

——— 1897a. [Abstract of remarks on Ganodonta, made before the New York Academy of Sciences, Dec. 7, 1896] Science 5: 71.

——— 1897b. The Ganodonta and their relationship to the Edentata. Bull. Am. Mus. Nat. Hist. 9: 59–110.

Wright, S. 1949. Adaptation and selection, p. 365–389. *In* G. L. Jepsen, G. G. Simpson, and E. Mayr [eds.]. Genetics, paleontology, and evolution. Princeton Univ. Press, Princeton.

Yablokov, A. V. 1974. Variability of mammals. Translated from the Russian (Nauka Publishers, Moscow, 1966) and published for the Smithsonian Institution and the National Science Foundation, Washington, D.C., by Amerind Publishing Co. Put. Ltd., New Delhi. 350 p.

Yalden, D. W. 1966. The anatomy of mole locomotion. J. Zool. London 149: 55–64.

——— 1970. The functional morphology of the carpal bones in carnivores. Acta Anat. 77: 481–500.

——— 1971. The functional morphology of the carpus in ungulate mammals. Acta Anat. 78: 461–87.

Zittel, K. A. 1893. Handbuch der Palaeontologie. I. Abth. Palaeozool. IV. Band. Vertebrata (Mammalia). R. Oldenbourg, München und Leipzig. 799 p.

Zhou, M., Z. Qiu, and C. Li. 1975. On the terminology of molar structures in primitive eutherians and suggestions for modified Chinese translated terms. Vertebr. PalAsiatica 13: 257–66.

APPENDIX I

Tables of measurements of taeniodont specimens. In the following tables (10–33) cranial and postcranial measurements (in cm) and dental measurements (in mm) are given for taeniodont specimens described and discussed in the text. Asterisks (*) indicate approximate measurements.

TABLE 10. Skull measurements

Measurements taken: 1) maximum length; 2) maximum height—basioccipital to top of skull roof; 3) maximum width across occiput at mastoid process; 4) maximum width across zygomatic arches; 5) maximum length of tooth row; 6) maximum width across palate; 7) foramen magnum height; 8) foramen magnum transverse width.

	1	2	3	4	5	6	7	8
AMNH 785 *Onychodectes*	9.9+	2.7+	3.6+	—	5.3+	2.3	—	—
AMNH 16528 *Onychodectes*	11.0	2.7+	—	—	5.8	2.1	—	—
USNM 22484 *Conoryctes*	14.7	4.0	5.5	8.1±	7.3+	5.2	1.3±	1.6±
AMNH 3398 *Conoryctes*	14.9	—	—	—	7.8±	—	—	—
AMNH 15939 conoryctine	13.9+	4.2±	5.5±	8.3±	7.9±	4.6	—	—
MCZ 20181 *Huerfanodon*	13.7+	—	—	—	8.5±	4.5±	—	—
USNM 15412 *Huerfanodon*	9.5++	—	—	6.0++	5.6++	4.2	—	—
AMNH 3394 *Wortmania*	16.9+	—	—	8.3++	8.5++	5.0±	—	—
AMNH 36000 *Psittacotherium*	25.0±	8.9++	13.5±?	14–15±?	—	—	—	—
USNM 15411 *Psittacotherium*	—	—	—	11.6+	8.4++	5.8	—	—
AMNH 754 *Psittacotherium*	24.7	—	—	—	—	—	—	—
UK 8035 *Psittacotherium*	20.7+	9.7±	11.0±?	—	12.7±	7.5±	—	—
FMNH P 26083 *Ectoganus*	22.5+	—	—	—	12.0±	—	—	—
USNM 12714 *Ectoganus*	20.9	6.9	9.5	10.5±	10.1±	4.1+	1.5	1.8
PU 16102 *Stylinodon inexplicatus*	14.5	5.5	8.8	—	7.4	4.3	—	1.0
YPM 11096 *S. mirus*	—	13.5±	16.0+	—	—	—	2.0±	2.1±
AMNH 10795 *S. mirus*	—	—	—	—	13.4±	7.6±	—	—
FMNH P 12185 *S. mirus*	22.5+	—	18.0±	20.0±	12.8	8.2	—	—
DNHM V-25 *S. mirus*	28.0±	—	—	—	11.7±	—	—	—
UW 2270 *S. mirus*	26.0	10.3	16.3	18.6	12.5±	8.0	2.2	2.5±
FMNH PM 3895* *S. mirus*	30.1±	9.1++	19.3	21.9	12.5	8.6	1.8±	2.3±

* Note that FMNH PM 3895 has been dorsoventrally crushed (length from tip of snout to posterior edge of occipital condyles = 29.0 cm).

TABLE 11. Mandible measurements

Measurements taken: 1) maximum length (anteroposteriorly); 2) maximum height (angle to tip of coronoid process); 3) depth of mandible under posterior M_1; 4) maximum length of tooth row.

	1	2	3	4
AMNH 16528 *Onychodectes*	8.5	3.7	1.1	5.2+
UNM B-1258 *Conoryctella*	8.2++	—	2.0	6.1
AMNH 3396 *Conoryctes*	12.2	5.2++	2.5	7.8
AMNH 15939 conoryctine indet.	12.6	—	2.8	8.2
USNM 22484 *Conodyctes*	12.7	6.5	2.7	9.0±
AMNH 3394 *Wortmania*	15.6	8.3	3.7	8.6
USNM 15428 *Wortmania*	15.1	7.5+	3.4	8.4±
AMNH 16660 *Psittacotherium*	19.4±	10.4++	5.0±	11.0±
AMNH 754 *Psittacotherium*	18.1+	10.5++	4.6	10.9±
UK 8035 *Psittacotherium*	20.5	11.0++	5.8	12.5±
AMNH 3393 *Psittacotherium*	18.1	9.3±	—	—
AMNH 88383 *Psittacotherium*	19.4	9.7+	4.9	12.0
USNM 12714 *E. copei*	13.7+	8.0	3.7	9.3±
UM VP-6000 *E. gliriformis*	—	—	5.8±	12.4±
AMNH 4286 *E. gliriformis*	22.0	12.0	6.5±	14.8±
YPM 11100 *E. gliriformis*	—	—	6.2±	13.6±
USNM 16664 *Stylinodon*	—	—	6.6±	13.1
AMNH 107954 *Stylinodon*	—	—	7.4±	14.4
UW 2270 *Stylinodon*	22.3	11.0+	6.8±	14.1
FMNH PM 3895 *Stylinodon*	21.8	13.5±	7.1±	12.6

TABLE 12. Scapula measurements

Measurements taken: 1) maximum length (height); 2) maximum width; 3) length of glenoid surface.

	1	2	3
AMNH 3766a *Onychodectes*	—	—	1.5
FMNH P 26083 *Ectoganus*	15.5+	7.8+	—
YPM 11096 *Stylinodon*	23.5	12.1	5.7
FMNH PM 3895 *Stylinodon*	23.4	13.3	7.1

TABLE 13. Humerus measurements

Measurements taken: 1) maximum length; 2) maximum width proximally; 3) maximum width distally; 4) length deltopectoral crest; 5) maximum width deltopectoral crest.

	1	2	3	4	5
AMNH 16410 *Onychodectes*	10.6	2.1	3.0+	6.3	N.A.
AMNH 3396 *Conoryctes*	—	1.9	—	6.7±	N.A.
TMM 41364-1 *Psittacotherium*	—	—	9.7	—	—
FMNH P 26090 *Ectoganus*	21.0	6.9	10.7	11.3	5.4
YPM 27201 *Ectoganus*	22.6	7.6	10.0	12.8	5.8
FMNH P 26083 *Ectoganus*	—	—	8.6+	—	—
YPM 11096 *Stylinodon*	20.1	7.3	10.1+	12.1	5.5
FMNH PM 3895 *Stylinodon*	21.4	8.6±	11.0	11.4	4.8

N.A. = Not applicable.

TABLE 14. Ulna measurements

Measurements taken: 1) total length; 2) length of olecranon from the middle of the semilunar notch.

	1	2
AMNH 16410 *Onychodectes*	—	2.7
UNM B-1258 *Conoryctella*	—	3.3
AMNH 3394 *Wortmania*	—	4.2+
AMNH 16560 *Psittacotherium*	—	7.6
USGS 3838 *E. copei*	—	6.0+
UW 2270 *Stylinodon*	21.0	7.2
FMNH PM 3895 *Stylinodon*	23.0	8.8
YPM 11096 *Stylinodon*	23.2	8.2
USNM 18425 cf. *Stylinodon*	20.5+	7.7

TABLE 15. Radius measurements

Measurements taken: 1) total length; 2) maximum width proximally; 3) maximum width distally.

	1	2	3
AMNH 16410 *Onychodectes*	—	1.4	1.4
AMNH 3396 *Conoryctes*	—	—	1.6
AMNH 3394 *Wortmania*	10.1+	2.6	2.2+
AMNH 16560 *Psittacotherium*	—	2.6+	—
USNM 1001 *Ectoganus*	—	3.1	—
USGS 3838 *E. copei*	—	2.9	—
YPM 39805 *Ectoganus*	13.1	2.9	3.6
YPM 11096 *Stylinodon*	13.5	4.3	4.6
FMNH PM 3895 *Stylinodon*	14.0	4.0+	4.5

TABLE 16. Measurements of the manus

Measurements taken: 1) maximum length—metacarpal one; 2) maximum length—metacarpal two; 3) maximum length—metacarpal three; 4) maximum length—metacarpal four; 5) maximum length—metacarpal five; 6) maximum length—ungual II, III or IV; 7) anteroposterior length of carpal series across magnum and lunar; 8) width of carpal series across unciform—trapezium; 9) length of pisiform.

	1	2	3	4	5	6	7	8	9
AMNH 16528 *Onychodectes*	12.4	21.9	24.0*	19.2	11.5	8.0*	9.2	18.4*	12.0
USNM 22483 *Conoryctes*	19.2	32.0	—	26.6	15.7	—	12.0*	31.4*	—
AMNH 3394 *Wortmania*	—	24.2	—	—	—	31.5*	—	—	—
AMNH 2453 *Psittacotherium*	—	26.0*	40.0*	37.0*	—	38.0*	31.0*	53.0*	—
FMNH P 26083 *Ectoganus*	—	—	—	—	—	55.0*	—	—	—
YPM 11096 *Stylinodon*	—	—	44.7	36.9	—	—	44.5	?80.0*	—
FMNH PM 3895 *Stylinodon*	—	—	—	—	—	70.0*	—	—	—
USNM 18425 ?*Stylinodon*	—	—	—	34.9	24.1	—	—	—	39.0

Table 17. Femur measurements

Measurements taken: 1) maximum length; 2) maximum width proximally; 3) mid-shaft—narrowest width; 4) maximum width distally.

	1	2	3	4
AMNH 3405 *Onychodectes*	—	3.5±	1.8	—
AMNH 3394 *Wortmania*	—	5.7	3.1	—
AMNH 16560 *Psittacotherium*	22.6±	8.0+	4.8±	7.0±
TMM 41364-1 *Psittacotherium*	23.0	9.0	4.1	7.2
FMNH P 26083 *Ectoganus*[1]	14.3+	7.5+	4.4±	7.5+
USNM no number *Ectoganus*	27.3±	9.6±	4.3	7.5
USNM 18425 cf. *Stylinodon*	22.5+	—	—	—
USNM 16664 *Stylinodon*	21.0+	—	3.8	—
UW 2270 *Stylinodon*	24.5	8.8	3.6	7.4

[1] Young individual, badly damaged specimen.

Table 18. Tibia measurements

Measurements taken: 1) total length; 2) maximum proximal width; 3) maximum distal width.

	1	2	3
AMNH 3405 *Onychodectes*	—	2.4	2.1
AMNH 3394 *Wortmania*	15.6	—	3.6
AMNH 15938 *Psittacotherium*	—	—	4.9±
TMM 41364-1 *Psittacotherium*	—	6.4	4.8+
FMNH P 26083 *Ectoganus*	15.3+	6.5±	4.1±
USNM 18425 *Stylinodon*	18.5	—	—
UW 2270 *Stylinodon*	17.4	6.4	4.6

TABLE 19. Fibula measurements

Measurement taken: 1) maximum length.

	1
USNM 18425 cf. *Stylinodon*	15.5
UW 2270 *Stylinodon*	14.4

TABLE 20. Measurements of the pes

Measurements taken: 1) maximum length—metatarsal one; 2) maximum length—metatarsal two; 3) maximum length—metatarsal three; 4) maximum length—metatarsal four; 5) maximum length—metatarsal five; 6) maximum length—ungual II, III or IV; 7) length calcaneum; 8) length astragalus; 9) width across astragalar trochlea.

	1	2	3	4	5	6	7	8	9
AMNH 16528 *Onychodectes*	20.7	—	—	—	20.6	11.0*	33.4	20.8	12.0
AMNH 3576a *Onychodectes*	—	35.1	—	—	—	—	—	21.6	—
AMNH 16410 *Onychodectes*	—	—	—	41.7	—	—	—	—	—
AMNH 16560 *Psittacotherium*	33.2	48.5	—	—	—	29.0	—	—	—
TMM 41364-1 *Psittacotherium*	—	—	—	—	—	—	—	—	45.9
USNM 1001 *Ectoganus*	—	—	—	—	—	28.0*	—	—	—
USNM 18425 ?*Stylinodon*	29.6	39.0*	42.5	42.1	31.0*	30.0*	85.7	38.3	36.0

TABLE 21. Average skeletal measurements of taeniodont genera—maximum lengths

Taxa averaged: 1) *Onychodectes tisonensis*; 2) *Wortmania otariidens*; 3) *Psittachotherium multifragum*; 4) *Ectoganus gliriformis*; 5) *Stylinodon mirus*.

	1	2	3	4	5
Skull	10.5+	16.9+	22.7+	21.3+	28.0
Humerus	10.6	—	—	21.8	20.8
Ulna	—	—	—	—	21.9
Olecranon	2.7	4.2+	7.6	6.0+	8.0
Radius	—	10.1+	—	13.1	13.8
Femur	—	—	22.8	27.3[1]	22.7+
Tibia	—	15.6	—	15.3+	18.0
Fibula	—	—	—	—	15.0

[1] Based on a single, exceptionally large, individual.

TABLE 22. Maximum lengths (in cm) of various skeletal elements of *Stylinodon mirus*

	DNHM V-25	FMNH PM 3895	UW 2270	YPM 11096	USNM 18425
Skull	28.0	30.1	26.0	—	—
Scapula	—	23.6	—	23.5	—
Humerus	—	21.4	—	20.1	—
Ulna	—	23.0	21.0	23.2	20.5+
Radius	—	14.0	—	13.5	—
Carpals	—	—	—	4.6	—
Metacarpal III	—	—	—	4.5	—
Femur	—	—	24.5	—	22.5+
Tibia	—	—	17.4	—	18.5
Fibula	—	—	14.4	—	15.5
Tarsals	—	—	—	—	6.2
Metatarsal III	—	—	—	—	4.3
Estimated length of rib cage (thoracics)	—	36.0(?)	—	—	—
Length of neck (seven cervical vertebrae)	—	—	—	14.0*	—
Height of first dorsal vertebra spine	—	—	—	12.3	—

TABLE 23. Dental measurements of *Onychodectes*

	P^4		M^1		M^2		M^3		P_1		P_2	
	L	W	L	W	L	W	L	W	L	W	L	W
AMNH 785	4.8*	5.9*			5.3	7.0	4.7	5.4				
786												
812												
822a												
902a					5.3	6.6						
824[b]												
3040a					6.9	8.1						
3405[a]	5.2	5.1	6.5	6.8	6.0	6.9	4.3	6.4				
3405	4.5	5.0	6.0	6.6	5.6	6.5						
3406					5.6	7.4						
3407									2.7*	1.9*	4.2*	2.6*
3408											3.7	2.5*
3409												
3411	4.5*	5.2	5.7*	7.0	5.1*	6.7						
3576a												
16405	5.7	6.3	7.1	8.4	6.2	8.1					4.3	3.2
16406											4.4	2.6
16407												
16408												
16409												
16410											3.9	2.9
16411	5.0	5.5										
16528	5.0	6.0	6.0	6.9	5.3	6.7	4.1	5.1	2.4	2.1	4.1	2.8
23090	5.0	5.1	7.1	7.8	6.3	7.6						
27608					5.8	7.0						
27678												
27679			6.1*	7.1	6.2*	6.9						
36070					6.6	7.5						
36071	5.0	5.1										

Continued on next page

TABLE 23—*Continued*

	P^4		M^1		M^2		M^3		P_1		P_2	
	L	W	L	W	L	W	L	W	L	W	L	W
AMNH 58059a												
58172												
UCMP no number	5.1*	5.9*	7.1	8.0	5.9*	8.1*						
31293	5.6*	5.4*	6.1*	6.9*								
31817											4.1	3.0
31819												
36514	4.8*	5.6	6.3	6.6	5.5	6.7	4.5	5.6				
68668												
68687	5.2	5.3										
74792					5.2	7.2						
89695					5.9	7.0						
92156												
UK 8114					6.5	7.5						
8116	5.1	5.5										
9416												
9417												
12711												
13000												
USNM 15534												
15535												
15536	4.9	5.4	5.9*	6.8								
N	15	15	11	11	18	18	4	4			7	7
Mean	5.03	5.59	6.35	7.17	5.84	7.19	4.40	5.63			4.10	2.80
Standard Dev.	0.33	0.39	0.52	0.61	0.53	0.53	0.26	0.56			0.24	0.25
Coefficient of Variation	6.6	7.1	8.2	8.5	9.1	7.4	5.9	9.9			5.9	8.9

[a] Type specimen of *Onychodectes t. tisonensis.*

[b] Type specimen of *O. t. rarus.*

Continued on next page

TABLE 23—*Continued*

	P_3		P_4		M_1			M_2			M_3		
	L	W	L	W	L	W TRI	W TD	L	W TRI	W TD	L	W TRI	W TD
AMNH 785	5.1	3.4	5.5	4.0	6.7	5.4	5.0	7.4	5.5	4.6	6.0	4.7	3.8
786					6.4	5.1	4.9	6.4	4.9	4.9			
812			5.4	3.3	7.8*	5.1		6.4	5.2	4.7			
822a								6.5	4.7				
902a													
824[b]					7.8	4.6	4.7	6.9	5.0	5.0			
3040a													
3405[a]								6.5	4.7	4.4			
3405													
3406													
3407	4.9	3.3	5.4	3.9	6.1	4.6	4.6		4.9		6.0	4.5	3.7
3408				3.1	6.7	4.6		6.1	4.8		5.9	4.4	
3409			5.2*	3.3	6.1	4.8							
3411	4.4	2.9	5.1*		6.5	4.6	4.6	5.9	4.8	4.8	5.7	4.1	3.7
3576a			5.4	3.1				5.5	4.6	4.7	5.4	4.3	3.7
16405	5.1	3.8	6.0	4.9	7.2	5.5	5.9	6.7	5.5	5.5	5.9	4.6	4.1
16406	4.9	3.3	5.5*	3.9	7.8	5.0							
16407	5.5	3.3	5.8	3.7	6.4*	4.9*							
16408					6.6	4.6*	4.7	6.4	5.0	4.6			
16409			5.9*	4.3	6.5	4.8					5.8		3.7
16410	5.2	3.1	5.5	3.7	6.8	5.1	4.6						
16411	4.8	2.8						6.0	4.5	4.1	5.2		3.9
16528	4.7	3.1	5.2	3.2	5.9	4.6	4.3	5.4	4.3	4.1	5.4	3.5	3.2
23090													
27608													
27678			5.4	3.3	7.8*	5.1		6.4	5.2	4.7			
27679					6.6	4.6	4.7	6.3	4.8	4.7			
36070													
36071													

Continued on next page

TABLE 23—*Continued*

	P_3		P_4		M_1			M_2			M_3		
	L	W	L	W	L	W TRI	W TD	L	W TRI	W TD	L	W TRI	W TD
AMNH 58059a								6.7	4.9	4.3			
58172											5.7	4.4	3.9
UCMP no number			5.8*	4.2*	6.8	4.9	4.6	6.7	5.0	4.7	6.2	4.2	3.5*
31293													
31817	5.0	3.3	5.8										
31819			5.3	3.6	6.5	5.3		5.8	5.1				
36514													
68668			5.2	3.6									
68687													
74792													
89695													
92156								6.1	5.0	4.5	6.1	4.4	3.7
UK 8114													
8116													
9416					6.5	4.7	4.6	5.9	4.9	4.8			
9417					6.7	5.2	4.9						
12711					6.4	4.6*	4.5	6.0	4.8	4.4	6.1	4.0	3.4*
13000			6.1	4.1	7.9	5.2	5.2						
USNM 15534	4.9	3.3	5.4	3.8				6.3	5.1	4.6	5.7*	4.3*	
15535	5.0	3.1			6.7	5.2	4.6	6.3	5.2	4.4	5.9	4.6*	3.5*
15536													
N	12	12	19	18	24	24	16	23	24	20	15	13	13
Mean	4.96	3.23	5.52	3.72	6.80	4.92	4.78	6.29	4.93	4.63	5.80	4.31	3.68
Standard Dev.	0.27	0.26	0.29	0.48	0.59	0.29	0.37	0.45	0.28	0.32	0.29	0.31	0.24
Coefficient of Variation	5.4	8.0	5.3	12.9	8.7	5.9	7.7	7.2	5.7	6.9	5.0	7.2	6.5

[a] Type specimen of *Onychodectes t. tisonensis.*

[b] Type specimen of *O. t. rarus.*

TABLE 24. Dental measurements of *Conoryctella*

	USNM 15704[a]	AMNH 3412	UNM B-1258[b]	USNM 15722	USNM 16173	USNM 18358	UK 7807	UK 7888	UK 9562	UALP 11661
C^1 L		9.8*								
C^1 W		5.6*								
P^4 L	7.4	7.6*	5.8							
P^4 W	10.1	8.1*	7.9							
M^1 L	8.1	8.3*	7.2							7.4
M^1 W	11.1	9.8*	8.6							9.2
M^2 L	7.4		6.8						6.0	
M^2 W	8.9		8.0						7.7	
M^3 L			5.7							
M^3 W			6.4							
C_1 L			5.5*							
C_1 W			4.9							
P_3 L			5.2							
P_3 W			3.7							
P_4 L			6.9							
P_4 W			4.9							
M_1 L			8.7	8.0*					7.7	
M_1 W			5.8	5.6*	6.4				5.3	
M_2 L			8.0		7.8		7.2	7.4		
M_2 W			5.3		5.7		5.3	5.2		
M_3 L			6.9			6.2*				
M_3 W			4.5			4.8				

[a] Type specimen of *Conoryctella dragonensis*.
[b] Type specimen of *C. pattersoni*.

TABLE 25. Dental measurements of *Conoryctes comma*

		C^1		P^3		P^4		M^1		M^2		M^3	
		L	W	L	W	L	W	L	W	L	W	L	W
AMNH	3395[a]												
	3396[b]	8.8	7.5	6.3	6.8	7.5	11.5	7.9	12.1	7.2	11.1	5.5	8.2
	3397												
	3398	8.8	7.5	7.3	7.4	8.3	11.7	7.8	11.6	7.9	12.5	7.1*	8.9
	16029												
UK	8033												
UNM	B-890			7.6	7.5	8.2	12.0	9.1	13.0	7.6	11.7		
USNM	22484			7.1	8.3	8.4	13.9			7.9	16.9*	6.6	11.1
N				4	4	4	4	3	3	4	4	3	3
Mean				7.08	7.50	8.10	12.28	8.27	12.23	7.65	13.05	6.40	9.40
Standard Deviation				0.56	0.62	0.41	1.10	0.72	0.71	0.33	2.63	0.82	1.51
Coefficient of Variation				7.9	8.3	5.1	9.0	8.7	5.8	4.3	20.2	12.8	16.1

Continued on next page

TABLE 25—*Continued*

		C_1		P_3		P_4		M_1			M_2			M_3		
		L	W	L	W	L	W	L	W TRI	W TD	L	W TRI	W TD	L	W TRI	W TD
AMNH	3395[a]	10.1	7.9			10.7	7.6	9.4	8.1	8.0		7.7				
	3396[b]	9.5	7.5	7.2	6.4	9.9	7.1		8.3	7.9	8.7	7.0	6.6	7.8	5.4	5.0
	3397							10.1	8.4	8.1	9.2	7.9	7.3	7.9	6.3	5.5
	3398															
	16029							10.3	7.9	7.9	9.2	7.5	6.9			
UK	8033			9.0	6.6			9.8*	7.9	7.5						
UNM	B-890			8.8	6.5	10.8	7.4									
USNM	22484	7.7	8.3			10.8*	7.9	11.5	9.2		10.8	8.2				
N				3	3	4	4	5	6	5	4	5	3			
Mean				8.33	6.50	10.55	7.50	10.22	8.30	7.88	9.48	7.66	6.93			
Standard Deviation				0.99	0.10	0.44	0.34	0.79	0.49	0.23	0.91	0.45	0.35			
Coefficient of Variation				11.9	1.5	4.2	4.5	7.7	5.9	2.9	9.6	5.9	5.1			

[a] Type specimen of *Conoryctes comma.*

[b] Type specimen of "*Hexodon molestus.*"

TABLE 26. Dental measurements of *Huerfanodon*

	P^3		M^1		M^2		M^3		C_1	
	L	W	L	W	L	W	L	W	L	W
H. torrejonius										
USNM 15412	7.9	8.0	8.5	10.2	8.1	9.3	5.4	8.1	8.4	7.0
MCZ 20181			8.1	9.1	7.8	8.6				
H. polecatensis										
PU 14178										
?*H. "heilprinianus"*										
AMNH 3224										

	P_3		P_4		M_1			M_2			M_3		
	L	W	L	W	L	W TRI	W TD	L	W TRI	W TD	L	W TRI	W TD
H. torrejonius													
USNM 15412			11.3	8.2	10.1	8.5	8.5				8.7	6.9	6.7
MCZ 20181											8.5	6.0	5.3
H. polecatensis													
PU 14178	8.5	6.2	11.6	8.5	11.1	9.4	8.7	9.5	8.6	7.5			
?*H. "heilprinianus"*													
AMNH 3224								10.3		6.4			

TABLE 27. Dental measurements of *Wortmania otariidens*

	I^3		C^1		P^2		P^3	
	L	W	L	W	L	W	L	W
AMNH 755								
3394[a]	7.6*	6.4*	14.5*	11.7*	5.4*	6.6*	6.2*	8.3*
16342								
UK 12998								
USNM 15429								
15654								
15655							6.7*	9.7*
UCMP 31819								
89280								

	P^4		M^1		M^2		I_3		C_1		P_1	
	L	W	L	W	L	W	L	W	L	W	L	W
AMNH 755									13.7	10.0		
3394[a]	6.7*	9.4*	8.5*				8.1*	4.0*	14.0*	11.0*	5.5	8.8
16342					7.7*	12.5*					5.7	8.3
UK 12998											5.5	7.2
USNM 15429	7.8	10.6	7.7	11.1								
15654	8.3	11.7										
15655												
UCMP 31819							10.2*	5.7*	13.7*	13.6*	6.9	9.8
89280												

Continued on next page

TABLE 27—*Continued*

		P_2		P_3		P_4		M_1			M_2		
		L	W	L	W	L	W	L	W TRI	W TD	L	W TRI	W TD
AMNH	755												
	3394[a]	6.1	9.1	6.7	8.9	6.7*	8.5*	8.5*	8.1*	6.9*	8.1*	8.0	6.8*
	16342	6.2	8.9										
UK	**12998**	6.5	8.4								8.3	6.9*	5.5
USNM	15429												
	15654												
	15655												
UCMP	31819	6.7	9.9										
	89280			5.4	8.9								

[a] Type specimen of *Wortmania otariidens*.

TABLE 28. Dental measurements of *Psittacotherium multifragum*

		I^3		C^1		P^1		P^2		P^3		P^4	
		L	W	L	W	L	W	L	W	L	W	L	W
AMNH	754	17.0*	10.7			8.1	11.8						
	756												
	757												
	2453	18.6	9.7					9.4	15.7	10.9	15.9	10.5	18.0*
	3390[c]			25.2	16.4								
	3391							8.9	16.1			9.7	16.6
	3392												
	3393												
	3413[a]												
	3416[b]												
	3418[d]												
	15938							8.0	15.9			11.3*	16.5*
	16660												
	16661			21.5	15.1			9.3	13.9			8.6	
	16731	19.1	11.6					10.9	15.1			10.1	16.6
	88383												
	100563											9.8	15.0
CM	1674											9.3	14.7

Continued on next page

TABLE 28—*Continued*

	I^3		C^1		P^1		P^2		P^3		P^4	
	L	W	L	W	L	W	L	W	L	W	L	W
TMM 40147-3									10.2	14.7		
40148-2												
40535-86												
40536-119							9.5	13.4				
40537-26												
40537-33												
40537-61												
UK 8035							11.5*	17.0*	13.0*	18.4	10.0*	17.5*
UNM NP-220												
USNM 6162												
15410												
15411			18.8	13.0	9.3	10.7	9.3	13.2	8.4	13.7	8.7	12.9
N	3	3	3	3			7	7	3	3	9	8
Mean	18.23	10.66	21.83	14.83			9.61	15.27	10.77	16.0	9.78	15.98
Standard Deviation	1.09	0.95	3.21	1.72			1.20	1.32	2.30	2.35	0.85	1.67
Coefficient of Variation	6.0	8.9	14.7	11.6			12.5	8.6	21.4	14.9	8.7	10.5

[a] Type specimen of *Psittacotherium multifragum.*
[b] Type specimen of *P.* "*aspasiae.*"
[c] Type specimen of "*Hemiganus vultuosus.*"
[d] Type specimen of *P.* "*megalodus.*"

Continued on next page

TABLE 28—*Continued*

		M^1		M^2		M^3		I_3		C_1		P_2		P_3	
		L	W	L	W	L	W	L	W	L	W	L	W	L	W
AMNH	754														
	756														
	757									26.6	19.1				
	2453	12.0	17.5			10.5	13.1					9.4	13.9		
	3390[c]	10.2	15.9					13.5	6.9	28.9	18.2				
	3391														
	3392									28.7	17.0				
	3393									28.5	18.2				
	3413[a]											7.1	13.0		
	3416[b]														
	3418[d]									27.8	16.0	9.8	16.4		
	15938	11.5*	16.5*	10.0*	15.5*	11.4	13.1								
	16660									27.0	18.3				
	16661									25.4	15.9				
	16731					8.8	12.9								
	88383									31.2	19.5				
	100563														
CM	**1674**														

Continued on next page

TABLE 28—*Continued*

	M^1		M^2		M^3		I_3		C_1		P_2	
	L	W	L	W	L	W	L	W	L	W	L	W
TMM 40147-3												
40148-2	10.5	14.8										
40535-86							12.7	7.0				
40536-119												
40537-26	10.2	14.6										
40537-33	10.5	14.5										
40537-61	10.5	14.8										
UK 8035					8.9	15.1						
UNM NP-220												
USNM 6162									26.9	16.7		
15410									28.7	18.6		
15411	8.9	14.1	8.2	12.9	7.6*	12.0*						
N	4	4			5	5			10	10	3	3
Mean	10.65	16.0			9.44	13.24			27.97	17.75	8.77	14.43
Standard Deviation	1.39	1.43			1.51	1.13			1.61	1.27	1.46	1.76
Coefficient of Variation	13.1	8.9			16.0	8.5			5.6	7.2	16.6	12.2

[a] Type specimen of *Psittacotherium multifragum.*
[b] Type specimen of *P. "aspasiae."*
[c] Type specimen of *"Hemiganus vultuosus."*
[d] Type specimen of *P. "megalodus."*

Continued on next page

TABLE 28—*Continued*

		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W
AMNH	754	11.5*	14.5*						
	756	10.3	15.4						
	757								
	2453	13.5*	14.5	11.1	10.5*				
	3390[c]	11.4	10.8						
	3391								
	3392								
	3393			10.4	10.1	9.3	9.0		
	3413[a]					9.2	9.0	9.3	8.3
	3416[b]								
	3418[d]								
	15938	13.6	16.1						
	16660								
	16661	11.9	12.9	11.9	11.7			10.4	10.0
	16731			12.9					
	88383	12.5*	15.5*	14.0*	11.0*			15.5*	11.0*
	100563								
CM	1674								

Continued on next page

TABLE 28—*Continued*

	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
TMM 40147-3								
40148-2								
40535-86								
40536-119								
40537-26								
40537-33								
40537-61								
UK 8035								
UNM NP-220			10.6	10.8	9.1	9.5		
USNM 6162	12.0	11.9						
15410								
15411								
N	8	8	6	5	3	3	3	3
Mean	12.09	13.95	11.82	10.82	9.20	9.17	11.73	9.77
Standard Deviation	1.10	1.89	1.41	0.60	0.10	0.29	3.31	1.37
Coefficient of Variation	9.1	13.5	11.9	5.5	1.1	3.2	28.2	14.0

[a] Type specimen of *Psittacotherium multifragum.*
[b] Type specimen of *P.* "*aspasiae.*"
[c] Type specimen of "*Hemiganus vultuosus.*"
[d] Type specimen of *P.* "*megalodus.*"

TABLE 29. Dental measurements of *Ectoganus gliriformis*

		I^3		C^1		P^1		P^2		P^3		P^4	
		L	W	L	W	L	W	L	W	L	W	L	W
E. g. gliriformis													
AMNH	4286												
	4287												
	16244									12.0*	18.5*	13.0	17.9
	16245												
	16771	12.6	7.7	21.0	11.9	14.9	10.9	18.5*	17.5*	12.5*	16.5*	10.5*	16.0*
	48001												
	86859												
CM	11497	16.7	9.5	34.0*	17.4			16.5*	17.5*	13.5	17.8	13.9	19.6
PU	13173											14.9	18.9
UM	**VP-6000**												
UNM	**B-970/971**					12.0*	16.0*			11.3	15.7		
USNM	1012[b]											14.2	15.7
	1017[c]												
	1102[d]							11.5*	17.5*				
	1137[a] (unmeasurable)												
YPM	11100[e]												
N								3	3	4	4	5	5
Mean								15.50	17.5	12.23	17.13	13.3	17.62
Standard Deviation								3.61	0	0.93	1.26	1.71	1.73
Coefficient of Variation								23.3	0	7.5	7.4	12.9	9.8

Continued on next page

TABLE 29—*Continued*

	I^3		P^2		P^3		P^4	
	L	W	L	W	L	W	L	W
E. g. lobdelli								
AMNH 22234[f]								
22235	17.3	10.1						
CM 11560								
FMNH PM 241								
P 14906								
P 15569					13.7	17.5		
P 15575							14.1	17.9
P 26083[g]					12.0*	17.1		
PU 18345							12.6	15.5
18954								
18982					12.4	16.3		
18994							13.8	16.5
20864								
21499			11.5*	19.3*	13.1	18.2	13.7	18.9
N					4	4	4	4
Mean					12.8	17.28	13.55	17.20
Standard Deviation					0.75	0.79	0.66	1.50
Coefficient of Variation					5.9	4.6	4.9	8.7

[a] Type specimen of *Ectoganus gliriformis.*
[b] Type specimen of "*Calamodon simplex.*"
[c] Type specimen of "*Calamodon arcamaenus.*"
[d] Type specimen of "*Calamodon novomehicanus.*"
[e] Type specimen of "*Dryptodon crassus.*"
[f] Type specimen of "*?Psittacotherium*" *lobdelli.*
[g] Type specimen of "*Lampadophorus expectatus.*"

Continued on next page

TABLE 29—*Continued*

	M^1		M^2		M^3		I_3		C_1		P_1		P_2	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
E. g. gliriformis														
AMNH 4286							9.5*	7.6	29.2	16.1	17.6	12.9	19.1	16.7
4287													16.5*	22.0*
16244	12.8	15.4												
16245														
16771	14.8	16.3	15.2	14.5	11.1	11.9								
48001														
86859					12.2	16.5								
CM 11497														
PU 13173														
UM VP-6000							8.1	6.3	26.5	15.0	14.2	12.0	14.5	16.5
UNM B-970/971	13.3	14.7	12.9	15.9										
USNM 1012[b]														
1017[c]														
1102[d]														
1137[a] (unmeasurable)														
YPM 11100[e]								6.7*	6.0		17.3	16.5*	11.5*	
N	3	3								3	3	3	3	3
Mean	13.63	15.47								16.13	16.10	12.13	16.70	18.40
Standard Deviation	1.04	0.80								1.15	1.73	0.71	2.31	3.12
Coefficient of Variation	7.6	5.2								7.1	10.7	5.9	13.8	17.0

Continued on next page

TABLE 29—*Continued*

		M^1		M^2		M^3		I_3		C_1		P_1		P_2	
		L	W	L	W	L	W	L	W	L	W	L	W	L	W
E. g. lobdelli															
AMNH	22234[f]					13.8	14.5								
	22235														
CM	11560									27.0	16.3				
FMNH	PM 241							15.6	8.2						
	P 14906														
	P 15569														
	P 15575														
	P 26083[g]					12.5	14.3								
PU	18345					11.4	13.4								
	18954														
	18982													13.4	19.5
	18994													12.4	19.3
	20864			12.8	16.1	12.6	14.9								
	21499	13.2	17.4												
N						4	4								
Mean						12.58	14.28								
Standard Deviation						0.98	0.63								
Coefficient of Variation						7.8	4.4								

[a] Type specimen of *Ectoganus gliriformis.*
[b] Type specimen of "*Calamodon simplex.*"
[c] Type specimen of "*Calamodon arcamaenus.*"
[d] Type specimen of "*Calamodon novomehicanus.*"
[e] Type specimen of "*Dryptodon crassus.*"
[f] Type specimen of "*?Psittacotherium*" *lobdelli.*
[g] Type specimen of "*Lampadophorus expectatus.*"

Continued on next page

TABLE 29—*Continued*

		P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
E. g. gliriformis											
AMNH	4286	12.4	13.1	13.8	14.3	12.7	13.2	14.6	14.2	14.2	13.8
	4287			15.8	15.6	15.3	14.7				
	16244										
	16245	14.4	13.0*								
	16771										
	48001	14.7		15.7	13.7						
	86859			15.8	15.1	13.7	13.7				
CM	11497										
PU	13173			16.3	16.4						
UM	VP-6000	13.1	14.0	16.4	14.9	13.5*	15.8	14.0*	17.5*	13.4	14.7
UNM	B-970/971			14.6	14.2	14.2	14.1				
USNM	1012[b]										
	1017[c]							15.1	13.0		
	1102[d]										
	1137[a] (unmeasurable)										
YPM	11100[e]	16.0*	13.5*	16.0*	15.1	14.5*	13.5*	13.5*	14.5*	14.5*	15.0*
N		5	4	8	8	6	6	4	4	3	3
Mean		14.18	13.40	15.55	14.91	13.98	14.17	14.30	14.80	14.03	14.50
Standard Deviation		1.32	0.45	0.89	0.85	0.90	0.95	0.70	1.91	0.57	0.62
Coefficient of Variation		9.3	3.4	5.7	5.7	6.4	6.7	4.9	12.9	4.1	4.3

Continued on next page

TABLE 29—*Continued*

	P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W
E. g. lobdelli										
AMNH 22234[f]										
22235										
CM 11560										
FMNH PM 241										
P 14906	14.6	15.5	14.9	15.5						
P 15569										
P 15575										
P 26083[g]										
PU 18345										
18954					13.1	12.1				
18982			14.7	14.9						
18994			16.4	14.5	14.3	12.6				
20864			14.9	15.8	14.3	12.7	13.7	12.9	13.5	11.7
21499	16.3	15.6	16.4	16.0	14.4	14.7			14.6	13.8
N			5	5	4	4				
Mean			15.46	15.34	14.03	13.03				
Standard Deviation			0.86	0.63	0.62	1.15				
Coefficient of Variation			5.6	4.1	4.4	8.8				

[a] Type specimen of *Ectoganus gliriformis.*
[b] Type specimen of "*Calamodon simplex.*"
[c] Type specimen of "*Calamodon arcamaenus.*"
[d] Type specimen of "*Calamodon novomehicanus.*"
[e] Type specimen of "*Dryptodon crassus.*"
[f] Type specimen of "?*Psittacotherium*" *lobdelli.*
[g] Type specimen of "*Lampadophorus expectatus.*"

TABLE 30. Dental measurements of *Ectoganus copei*

	I^3		C^1		P^1		P^2		P^3		P^4	
	L	W	L	W	L	W	L	W	L	W	L	W
E. c. copei												
AMNH 15633												
PU 14689												
USGS 3838	14.3	6.7	24.0*	12.0*	13.5*	6.5			9.5	11.0*	11.5*	11.5*
USNM 12714[a]	10.9	6.7	19.0	10.6	10.7	7.7	10.7	13.7	9.9	12.3		
YPM 18618[c]									12.0	13.3		
N									3	3		
Mean									10.47	12.2		
Standard Deviation									1.34	1.15		
Coefficient of Variation									12.7	9.4		
E. c. bighornensis												
AMNH 86852												
PU 14678[b]									10.7	14.0		
PU 18052									10.7	13.3		

Continued on next page

TABLE 30—*Continued*

	M^1		M^2		M^3		I_3		C_1		P_1		P_2	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
E. c. copei														
AMNH 15633	11.8	13.2											11.0	18.7
PU 14689									25.4	14.1	16.4	11.5	11.8*	18.9
USGS 3838	11.0*	11.0*							22.9	15.0*	13.0*	14.5*	12.0*	17.0*
USNM 12714[a]	11.2	12.9	10.5	12.2									10.8	18.8
YPM 18618[c]														
N	3	3											4	4
Mean	11.33	12.36											11.40	18.35
Standard Deviation	0.42	1.19											0.59	0.90
Coefficient of Variation	3.7	9.6											5.2	4.9
E. c. bighornensis														
AMNH 86852														
PU 14678[b]	10.5	12.6	10.2	11.7	8.7	9.8								
PU 18052	9.9	12.2												

[a] Type specimen of *Ectoganus c. copei.*

[b] Type specimen of *E. c. bighornensis.*

[c] The identification of this tooth as a P^3 is uncertain; it may be a P^4 or M^1.

Continued on next page

TABLE 30—*Continued*

	P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W
E. c. copei										
AMNH 15633	10.9	11.4								
PU 14689										
USGS 3838	11.0*	11.9								
USNM 12714[a]					12.9	11.9*	11.8	12.0		
YPM 18618[c]										
E. c. bighornensis										
AMNH 86852									11.8	11.0
PU 14678[b]					11.5	11.1				
PU 18052					11.5	11.3	11.7	11.3		

[a] Type specimen of *Ectoganus c. copei.*

[b] Type specimen of *E. c. bighornensis.*

[c] The identification of this tooth as a P^3 is uncertain; it may be a P^4 or M^1.

TABLE 31. Dental measurements of deciduous teeth of *Ectoganus*

	dP^3		dP^4		dP$_4$	
	L	W	L	W	L	W
AMNH 16771[a]	10.9	12.3	10.9	17.6		
USNM 1137[b]	10.3	14.1	9.8	17.4	12.7	9.6
USNM 12714[c]			9.8	16.1	12.1	10.4

[a] Specimen referred to *E. g. gliriformis.*
[b] Type specimen of *E. g. gliriformis.*
[c] Type specimen of *E. c. copei.*

TABLE 32. Statistics for pooled dental measurements of species of *Ectoganus*

	P^3		M^1		P$_2$		M$_1$	
	L	W	L	W	L	W	L	W
Ectoganus gliriformis								
N	8	8	4	4	5	5	10	10
Mean	12.56	17.20	13.53	15.95	15.18	18.80	14.00	13.71
Standard Deviation	0.82	0.98	0.88	1.17	2.67	2.27	0.76	1.14
Coefficient of Variation	6.5	5.7	6.5	7.3	17.6	12.1	5.4	8.3
E. copei								
N	5	5	5	5	4	4	3	3
Mean	10.56	12.78	10.88	12.38	11.40	18.35	11.97	11.43
Standard Deviation	0.95	1.16	0.72	0.86	0.59	0.90	0.81	0.42
Coefficient of Variation	9.0	9.1	6.6	6.9	5.2	4.9	6.8	3.7
All *Ectoganus*								
N	13	13	9	9	9	9	13	13
Mean	11.79	15.50	12.06	13.97	13.50	18.50	13.53	13.18
Standard Deviation	1.31	2.45	1.58	2.10	2.77	1.72	1.15	1.41
Coefficient of Variation	11.1	15.8	13.1	15.1	20.5	9.3	8.5	10.7

TABLE 33. Dental measurements of *Stylinodon*

SPECIMEN	AMNH 4810[b]	AMNH 107954	DNHM V-25	FMNH P-12185	PU 16102[c]	USNM 16664	YPM 11095[a]
I^2 L		10.0*			4.2		
I^2 W		6.0			3.6		
I^3 L		13.5*			4.7		
I^3 W		9.5*			4.5*		
C^1 L		38.0*	36.0*	40.1	15.0*		
C^1 W		17.5*	17.5*	19.5*	9.0*		
P^1 L		15.0*		18.0*			
P^1 W		14.5*		15.5*			
P^2 L		11.0*		10.5*			
P^2 W		12.5*		12.5*			
P^3 L		10.5*		10.5*	7.3		
P^3 W		11.0*		12.0*	7.4		
P^4 L		11.0*		9.5*	6.2		
P^4 W		11.0*		10.5*	7.0		
M^1 L		13.5*		12.0*	7.0		
M^1 W		12.5*		10.0*	7.5		
M^2 L		13.5*		10.3	6.5		
M^2 W		13.5*		10.2	7.0		
M^3 L	10.9	11.5*		9.7	5.2		
M^3 W	10.0	12.5*		9.2	5.7		
I_3 L		6.0	6.8*			7.7*	
I_3 W		6.1	6.2*			5.5*	
C_1 L		33.8	33.0*			33.2	
C_1 W		20.1	15.4*			18.2	
P_1 L		28.1	28.0*			25.3	22.2+
P_1 W		17.7	17.5*			17.0	
P_2 L		12.9	10.4*			10.5	
P_2 W		18.1	14.1*			17.0*	
P_3 L		11.0	11.1*			10.5*	
P_3 W		14.2	10.5*			12.0*	
P_4 L		10.5	11.7*				11.2
P_4 W		12.0	11.2*				12.3
M_1 L		12.5*	10.6*				11.5
M_1 W		12.5*	10.7*				12.0
M_2 L		12.0*	10.7				
M_2 W		12.0*	9.8				
M_3 L		13.7	11.8				
M_3 W		11.3	8.7				

[a] Type specimen of *Stylinodon mirus.*
[b] Type specimen of *S.* "*cylindrifer.*"
[c] Type specimen of *S. inexplicatus.*

APPENDIX II

Plates 1–65. The following plates illustrate the majority of specimens upon which this study is based.

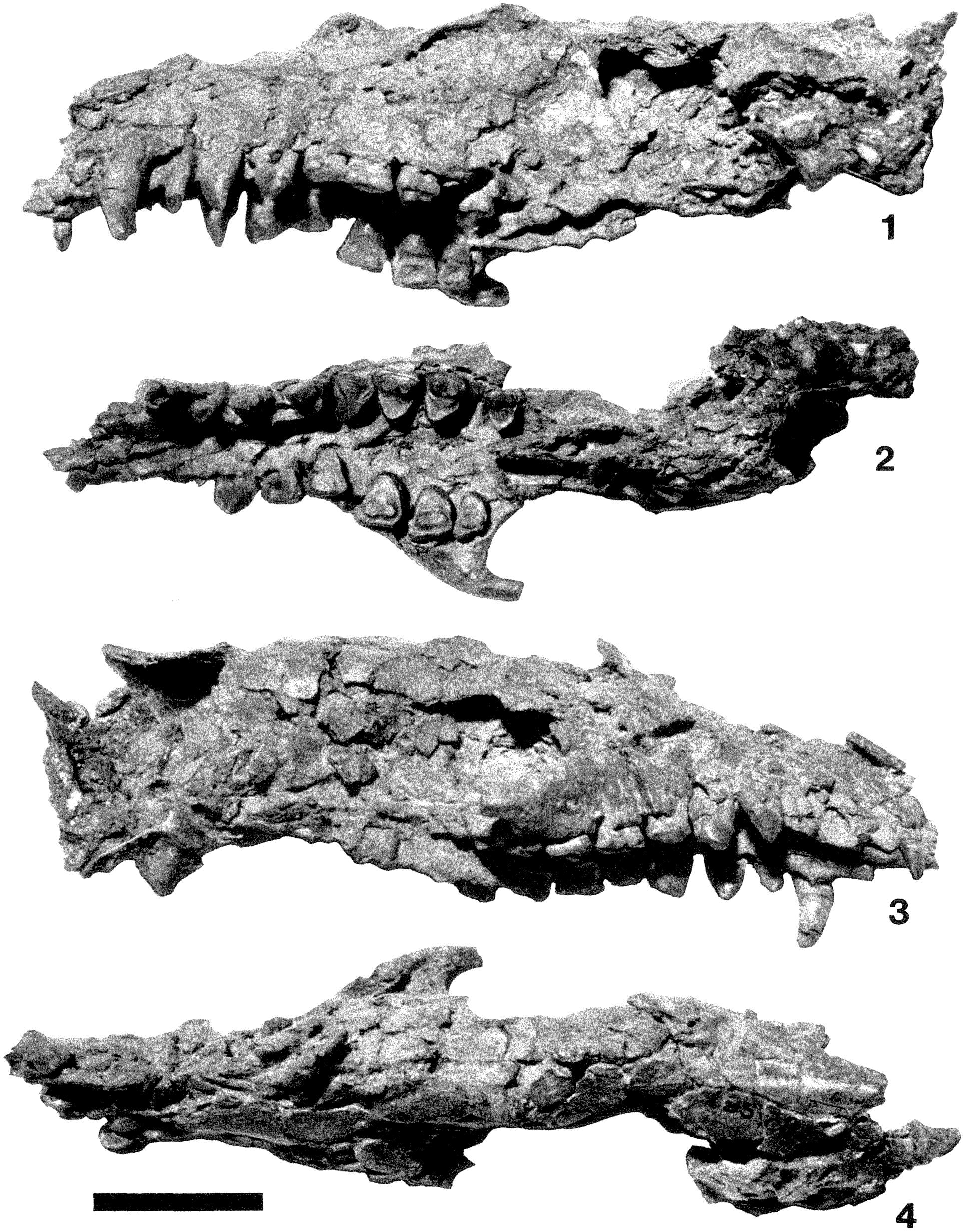


PLATE 1. A skull of *Onychodectes tisonensis tisonensis*.

1–4 AMNH 16528, skull with right $I^{2(?)}$, left C^1–P^1, right and left P^3–M^3: *1,* left lateral view; *2,* ventral view; *3,* right lateral view; *4,* dorsal view.

The bar is 2 cm long.

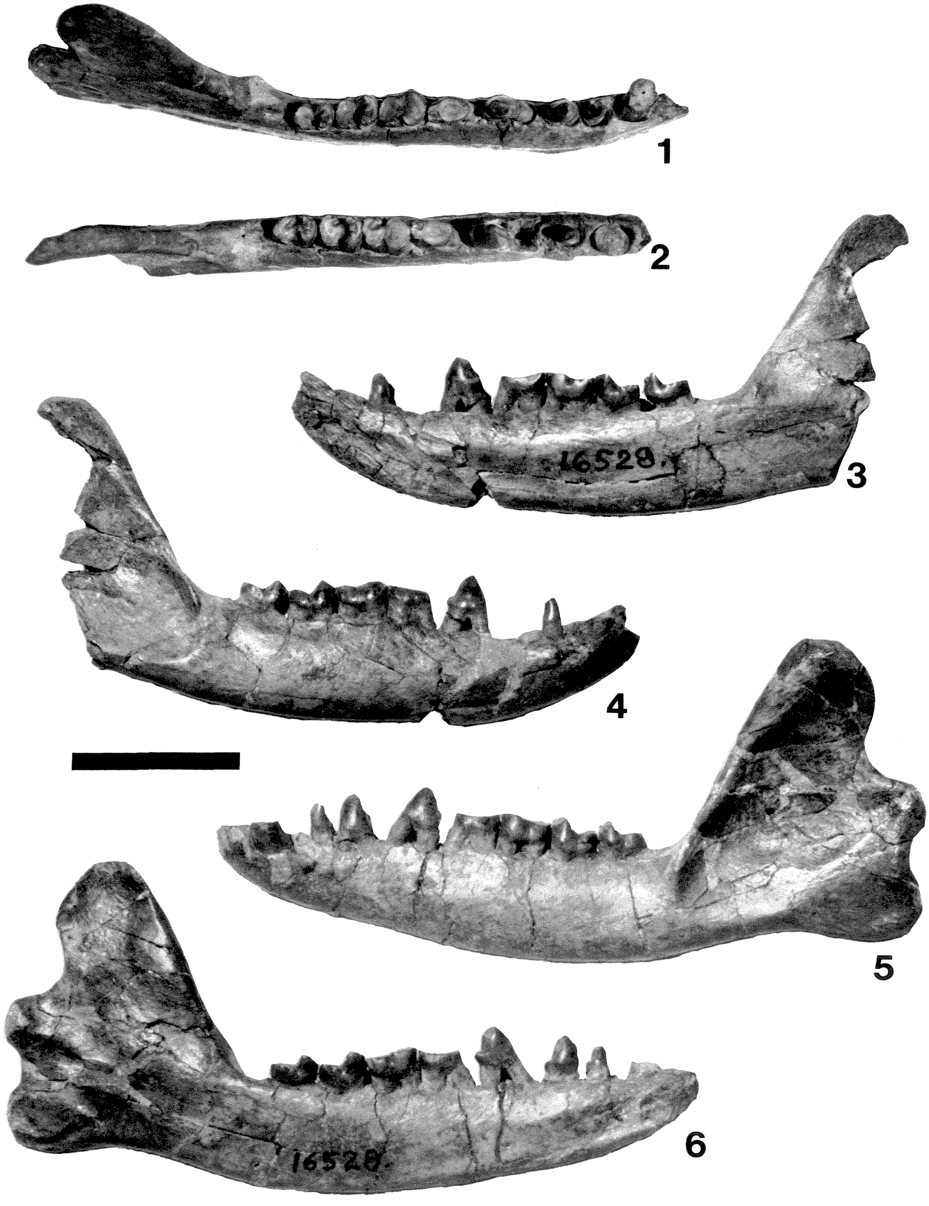


PLATE 2. The lower jaws of *Onychodectes tisonensis tisonensis*.

1–6 AMNH 16528, lower jaws with roots of right and left I$_2$ and C$_1$, complete right and left P$_1$, left P$_2$, right and left P$_3$–M$_3$, alveolus for right P$_2$: *1,* occlusal view of left dentary; *2,* occlusal view of right dentary; *3,* lingual view of right dentary; *4,* labial view of right dentary; *5,* labial view of left dentary; *6,* lingual view of left dentary.

The bar is 2 cm long.

1

2

3

4

PLATE 3. A skull of *Onychodectes t. tisonensis.*

1–4 AMNH 785, skull with left P^4, M^{2-3}, right M^{2-3} and alveoli for right and left I^3, C^1, P^{1-3}, right P^4, right and left M^1: *1,* left lateral view; *2,* ventral view; *3,* right lateral view; *4,* dorsal view.

The bar is 2 cm long.

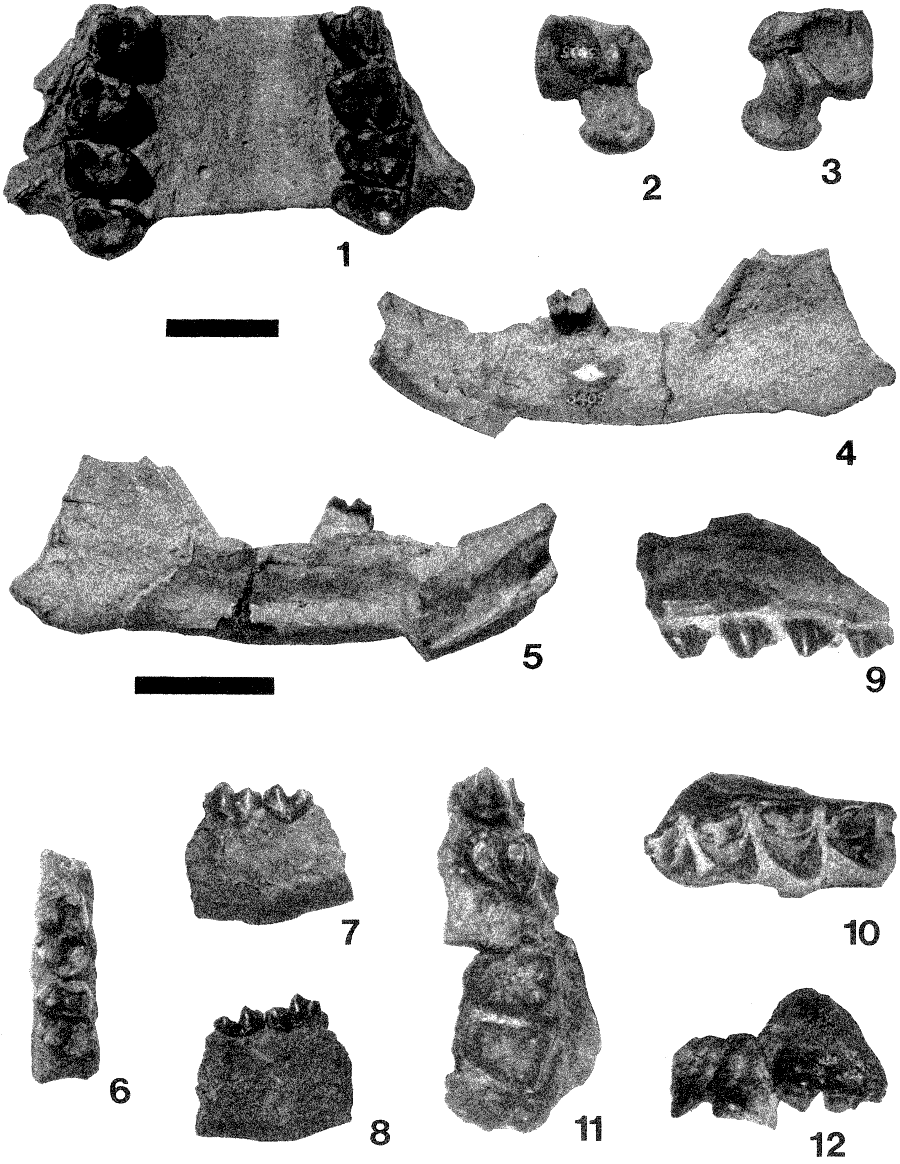


PLATE 4. The type specimens of *Onychodectes t. tisonensis* (*1–5*), *O. t. rarus* (*6–8*) and specimens referred to *Onychodectes t. tisonensis* (*9, 10*) and *O. t. rarus* (*11, 12*).

1–5 AMNH 3405: *1,* occlusal view of palate with right and left P^4–M^3; *2,* dorsal view of right astragalus; *3,* ventral view of right astragalus; *4,* labial view of left dentary with M$_2$, alveoli for C$_1$–M$_1$, M$_3$; *5,* lingual view of left dentary.

6–8 AMNH 824, left dentary fragment with M$_{1-2}$: *6,* occlusal view; *7,* labial view; *8,* lingual view.

9, 10 UCMP 36514, right maxilla fragment with P^4–M^3; *9,* lingual view; *10,* occlusal view.

11, 12 AMNH 16405, left maxilla with P^3–M^2 and roots of M^3: *11,* occlusal view; *12,* labial view.

The bar below *1* is 1 cm long and is for *1, 6, 9–11.*
The bar below *5* is 2 cm long and is for *2–5, 7, 8, 12.*

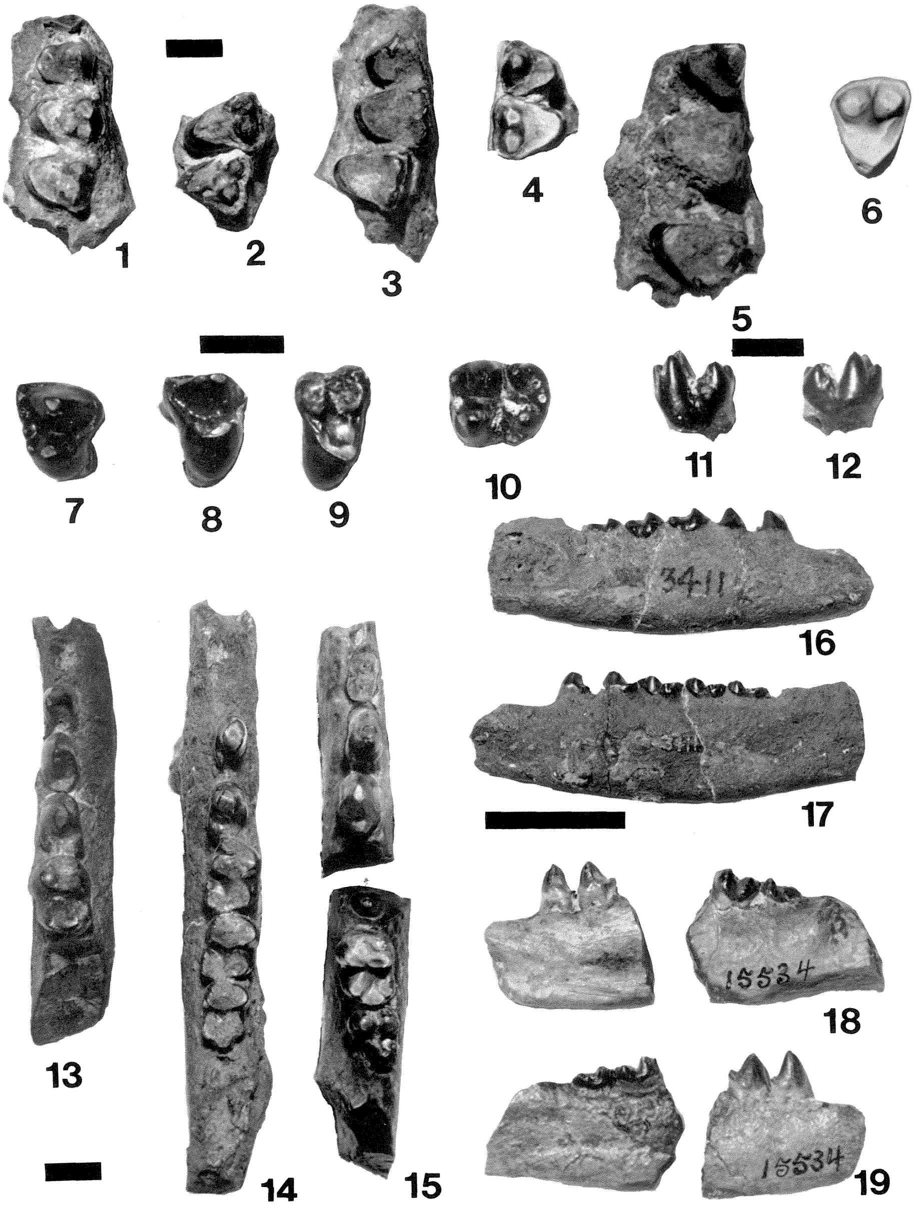


PLATE 5. The dentition of *Onychodectes t. tisonensis* (*1–4, 6–9, 13–19*) and *O. t. rarus* (*5, 10–12*).

1	AMNH 3411, left maxilla with partial P^3, P^4–M^2.
2	AMNH 3406, left maxilla with M^{1-2}.
3	AMNH 3405 (not the type specimen), left maxilla with P^4–M^2.
4	USNM 15536, right maxilla with P^4–M^1.
5	AMNH 23090, left maxilla with P^4–M^2.
6	AMNH 36070, left M^2.
7	UK 8116, right P^4.
8	AMNH 16411, right P^4.
9	AMNH 16411, right (?)dP^4.
10–12	UK 9416, left M_2: *10,* occlusal view; *11,* labial view; *12,* lingual view.
13	AMNH 16410, left dentary with P_2–M_1, alveoli for C_1–P_1.
14, 16, 17	AMNH 3411, right dentary with P_3–M_3: *14,* occlusal view; *16,* labial view; *17,* lingual view.
15, 18, 19	USNM 15534, left dentary with P_{3-4}, M_{2-3}, roots of P_{1-2}: *15,* occlusal view; *18,* labial view; *19,* lingual view.

The bar above *2* is 5 mm long and is for *1–6.*
The bar above *8* is 5 mm long and is for *7–10.*
The bar above *11, 12* is 5 mm long and is for *11, 12.*
The bar above *13* is 5 mm long and is for *13–15.*
The bar above *17* is 2 cm long and is for *16–19.*

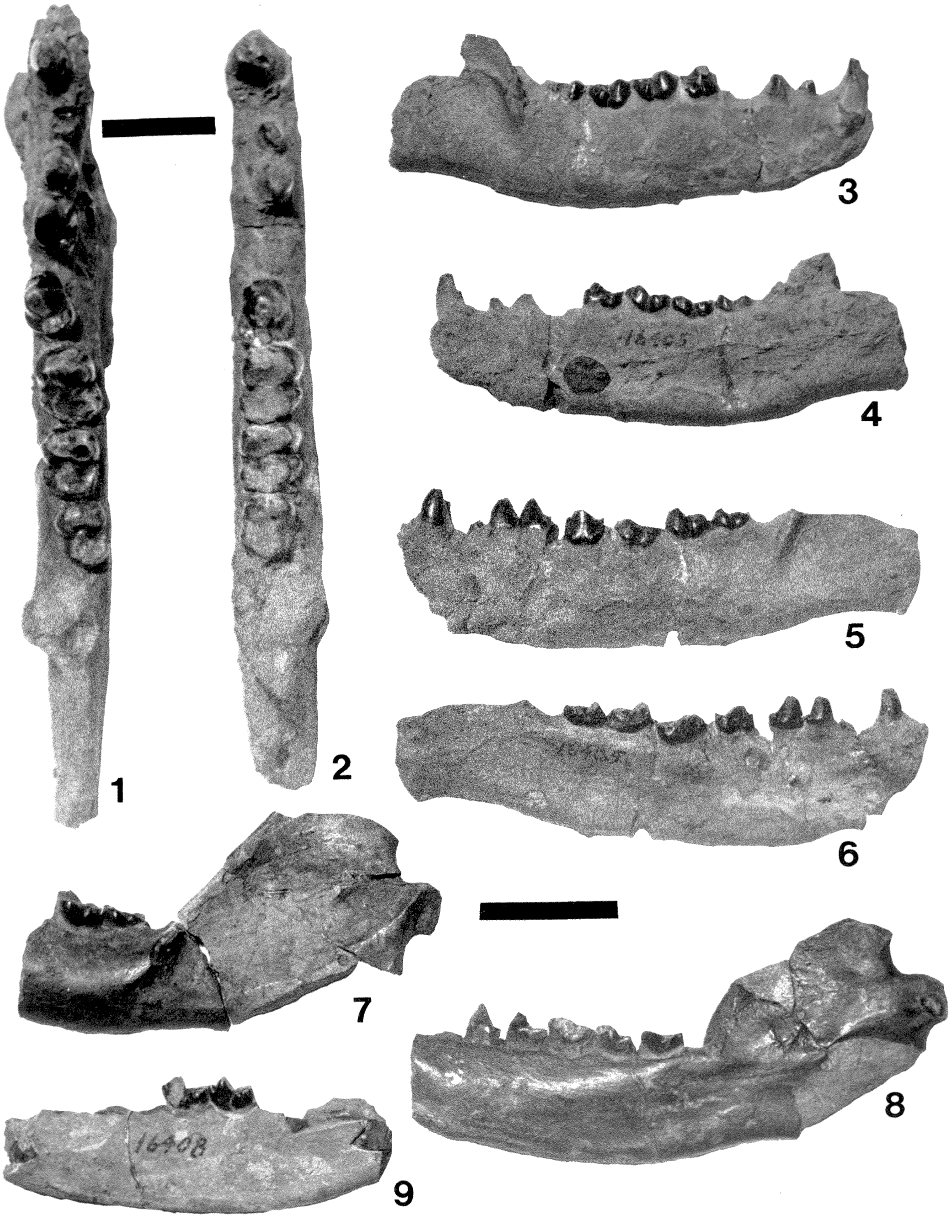


PLATE 6. Specimens referred to *Onychodectes tisonensis rarus* (*1–6*) and *O. t. tisonensis* (*7–9*).

1–6 AMNH 16405, right dentary with canine stub, parts of P_{1-2} and complete P_4–M_3: *1,* occlusal view of left dentary with canine; *2,* occlusal view of right dentary with canine; *3,* labial view of right dentary; *4,* lingual view of right dentary; *5,* labial view of left dentary; *6,* lingual view of left dentary.

7, 8 AMNH 785, left dentary fragment with M_{2-3} and right dentary fragment with roots of P_2 and complete P_3–M_3: *7,* labial view of left dentary; *8,* lingual view of right dentary.

9 AMNH 16408, lingual view of right dentary fragment with M_{1-2} and alveoli for C_1–P_4 and M_3.

The bar between *1* and *2* is 1 cm long and is for *1, 2.*
The bar below *6* is 2 cm long and is for *3–9.*

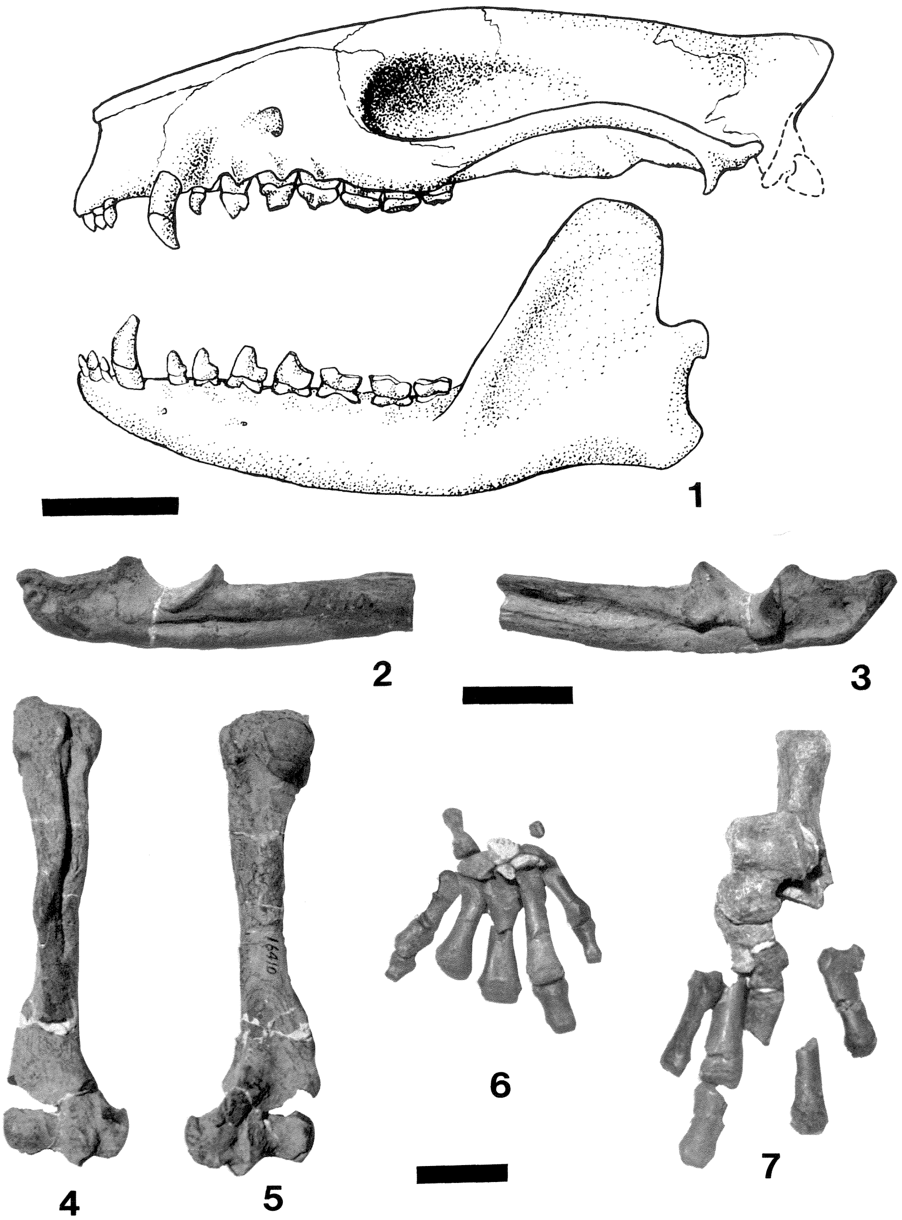


PLATE 7. The skull and skeleton of *Onychodectes t. tisonensis.*

1 Reconstruction of the skull based on AMNH 785 and AMNH 16528.
2, 3 AMNH 16410, left ulna: *2,* internal view; *3,* external view.
4, 5 AMNH 16410, right humerus: *4,* anterior view; *5,* posterior view.
6 AMNH 16528, partial right manus.
7 AMNH 16528, partial left pes.

The bar below *1* is 2 cm long and is for *1.*
The bar below *3* is 2 cm long and is for *2, 3, 6, 7.*
The bar below *6* is 2 cm long and is for *4, 5.*

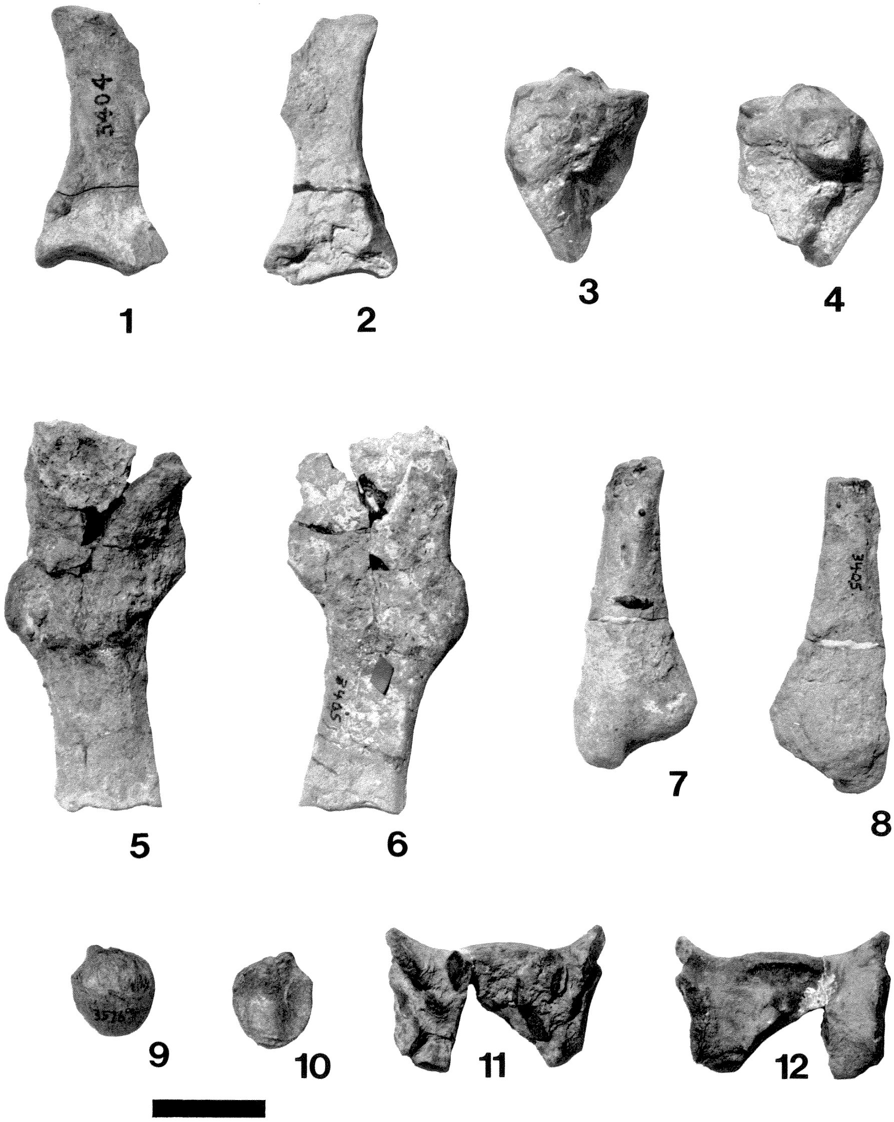


PLATE 8. Skeletal elements of specimens referred to ?*Onychodectes* sp. (*1, 2*), *Onychodectes t. tisonensis* (*3–8, 11, 12*) and *O. t. rarus* (*9, 10*).

1, 2	AMNH 3404, (?)right ilium: *1,* lateral view; *2,* medial view.
3, 4	AMNH 3405, proximal part of right tibia: *3,* anterior view; *4,* posterolateral view.
5, 6	AMNH 3405, proximal part of right femur: *5,* anterior view; *6,* posterior view.
7, 8	AMNH 3405, distal part of left tibia: *7,* anterior view; *8,* posterior view.
9, 10	AMNH 3576a, patella: *9,* anterior view; *10,* posterior view.
11, 12	AMNH 16410, sacrum: *11,* dorsal view; *12,* ventral view.

The bar is 2 cm long.

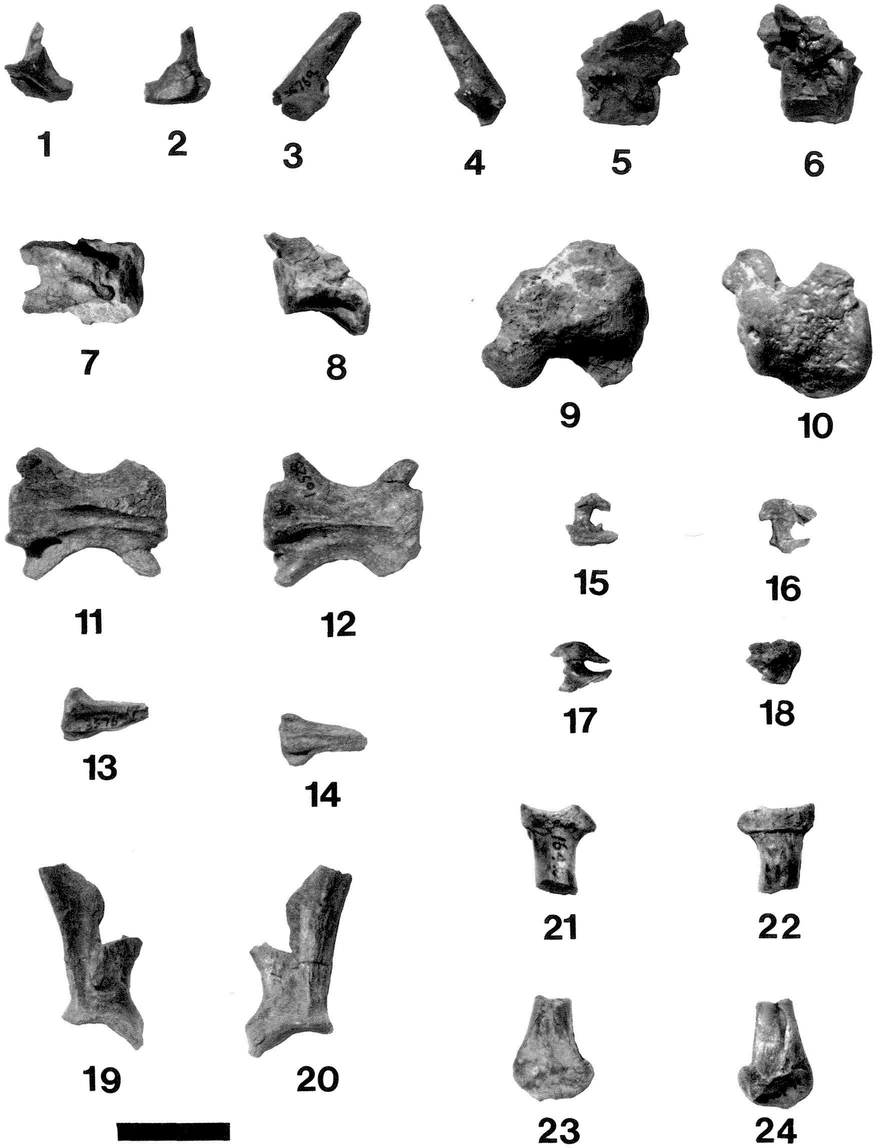


PLATE 9. Skeletal elements of specimens referred to *Onychodectes t. tisonensis* (*11, 12, 15–18, 21–24*), *O. t. rarus* (*1–8, 13, 14, 19, 20*) and ?*Onychodectes* sp. (*9, 10*).

1, 2 AMNH 3576a, right side of atlas: *1,* anterior view; *2,* posterior view.
3, 4 AMNH 3576a, neural spine of anterior thoracic vertebra: *3,* left lateral view; *4,* right lateral view.
5, 6 AMNH 3576a, posterior thoracic vertebra: *5,* left lateral view; *6,* right lateral view.
7, 8 AMNH 3576a, (?)anterior lumbar vertebra: *7,* dorsal view; *8,* left lateral view. Anterior is to the left.
9, 10 AMNH 3404, posterior lumbar vertebra: *9,* dorsal view; *10,* ventral view. Anterior is to the right.
11, 12 AMNH 16528, anterior caudal vertebra: *11,* dorsal view; *12,* ventral view. Anterior is to the left.
13, 14 AMNH 3576a, posterior caudal vertebra: *13,* dorsal view; *14,* ventral view. Anterior is to the left.
15, 16 AMNH 16528, chevron bone: *15,* dorsal view; *16,* ventral view. Anterior is to the left.
17, 18 AMNH 16528, chevron bone: *17,* ventral view; *18,* right lateral view.
19, 20 AMNH 3576a, right scapula: *19,* lateral view; *20,* medial view.
21, 22 AMNH 16410, proximal part of right radius: *21,* anterior view; *22,* posterior view.
23, 24 AMNH 16410, distal part of right radius: *23,* anterior view; *24,* posterior view.

The bar is 2 cm long.

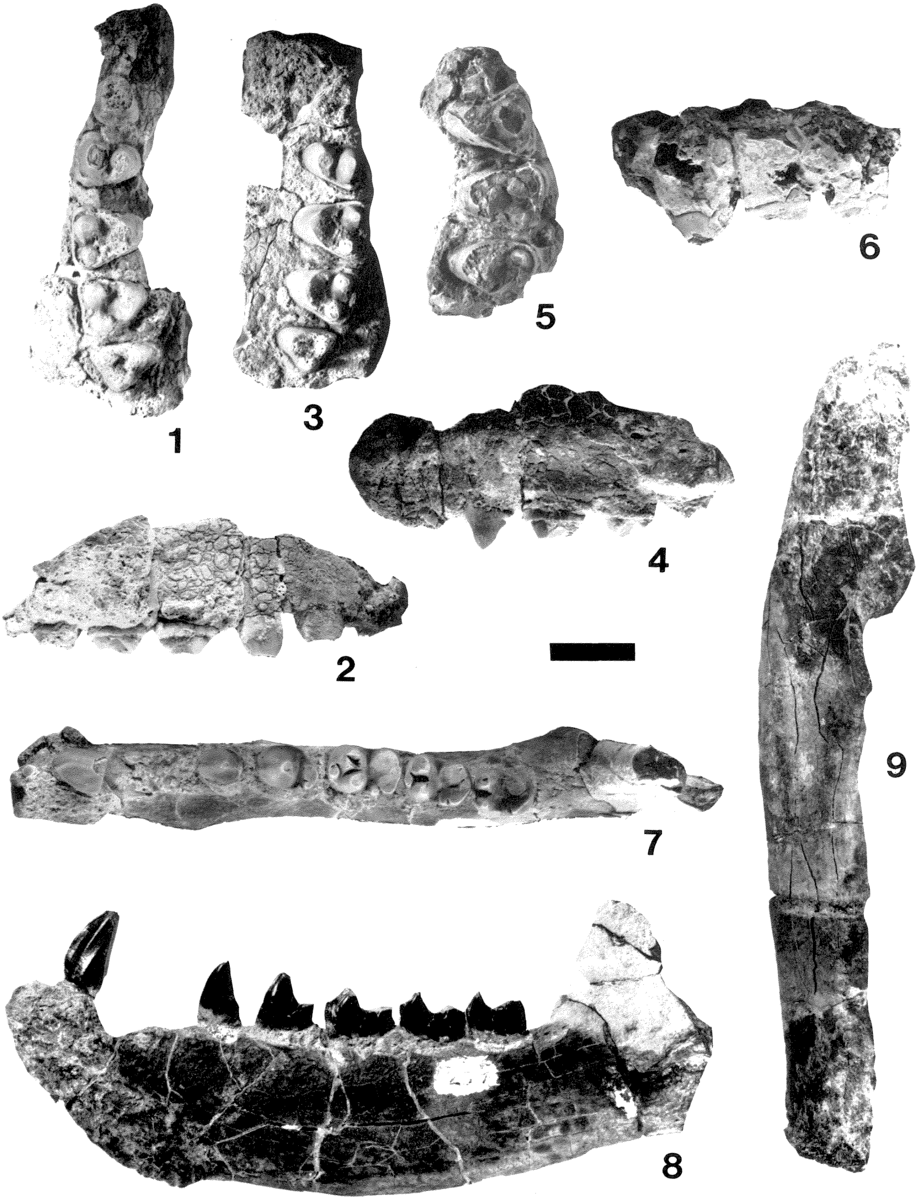
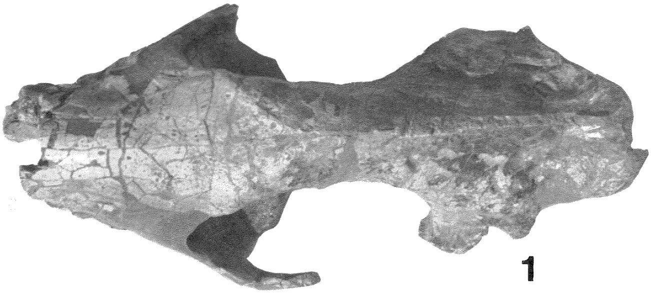
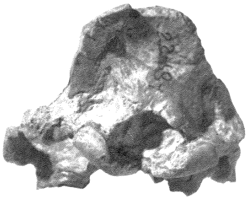


PLATE 10. The type specimens of *Conoryctella dragonensis* (*5, 6*) and *Conoryctella pattersoni* (*1–4, 7–9*).

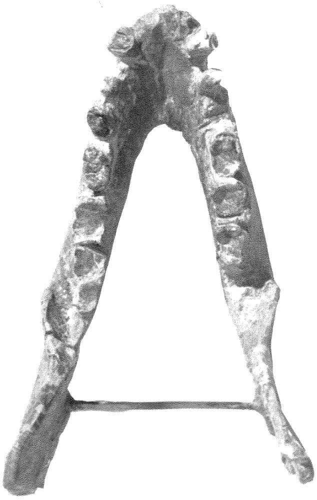
1, 2 UNM B-1258, right maxilla with P^4–M^3 and roots of P^{2-3}: *1,* occlusal view; *2,* labial view.
3, 4 UNM B-1258, left maxilla with P^4–M^3 and roots of P^{2-3}: *3,* occlusal view; *4,* labial view.
5, 6 USNM 15704, left maxilla with damaged P^4–M^2 and part of P^3 alveolus: *5,* occlusal view; *6,* labial view.
7, 8 UNM B-1528, right dentary with C_1, P_3–M_3 and roots of I_{1-3}: *7,* occlusal view; *8,* lingual view.
9 UNM B-1258, internal view of left ulna.

The bar is 1 cm long.


1


4


2


6


3

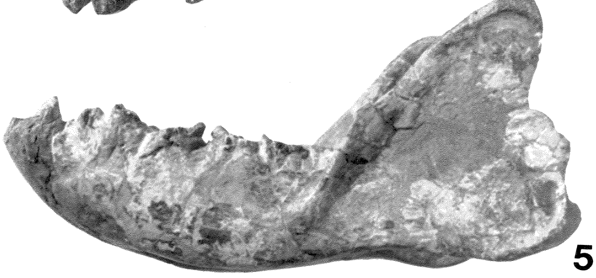

5

PLATE 11. USNM 22484, a skull and mandible of *Conoryctes comma*.

1 Dorsal view of skull.
2 Ventral view of skull.
3 Left lateral view of skull.
4 Left lateral view of mandible.
5 Occipital view of skull.
6 Occlusal view of mandible.

The bar is 4 cm long.

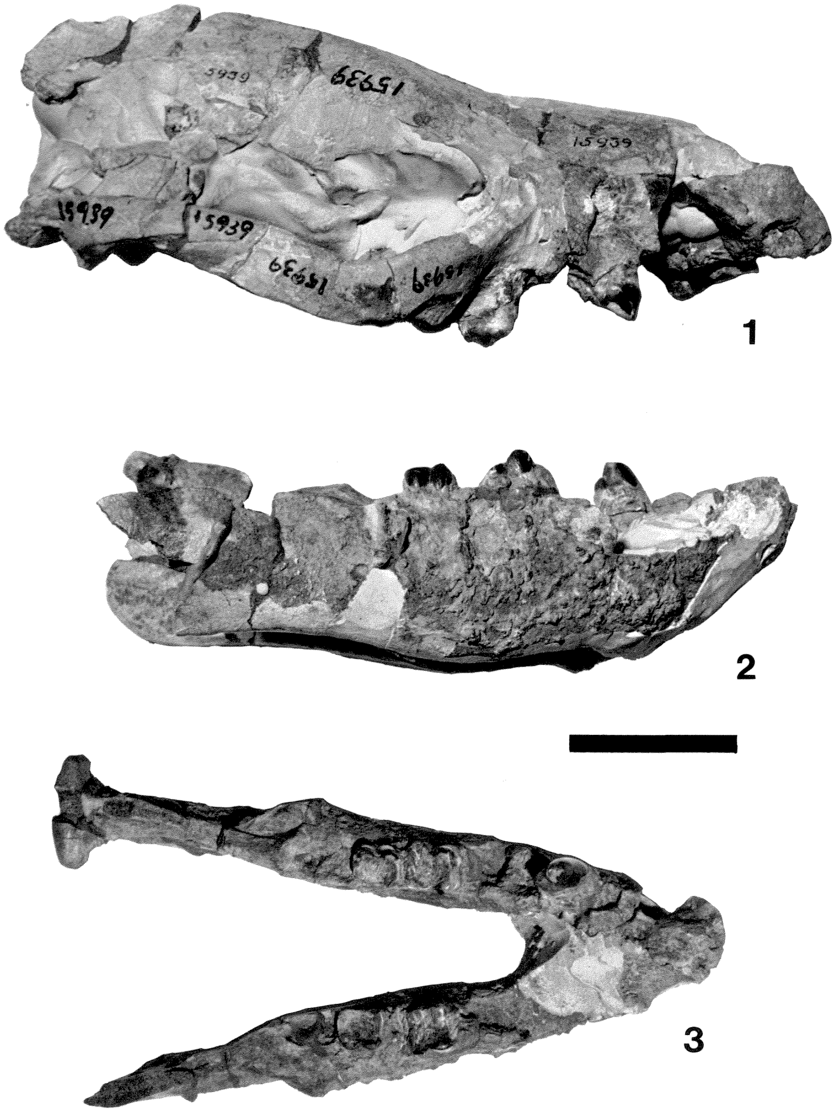


PLATE 12. AMNH 15939, skull and mandible of undetermined conoryctid.

1 Right lateral view of skull.
2 Right lateral view of mandible.
3 Occlusal view of mandible.

The bar is 3 cm long.

1

2

PLATE 13. AMNH 15939, skull of undetermined conoryctid.

1 Dorsal view of skull.

2 Ventral view of skull.

The bar is 3 cm long.

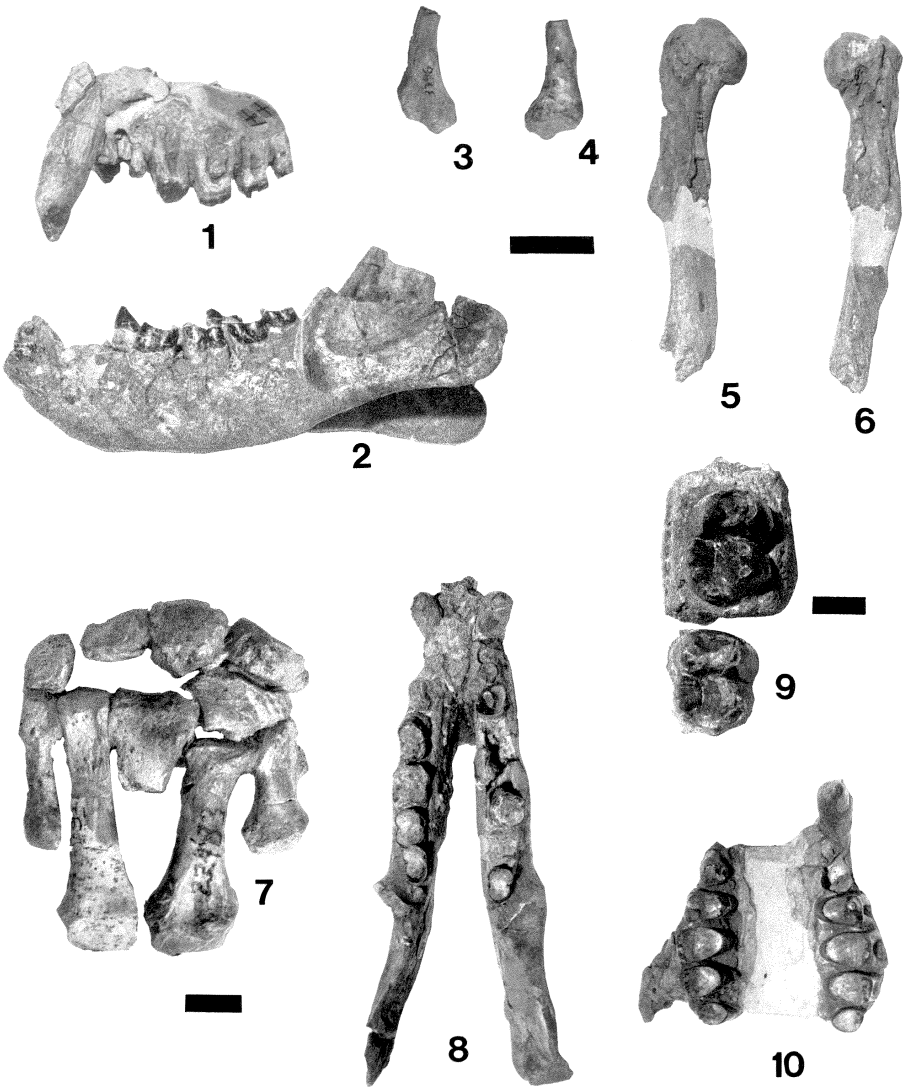


Plate 14. Specimens referred to *Conoryctes comma.*

1–6, 8, 10 AMNH 3396, the type specimen of *Hexodon molestus,* palate with left C^1, right P^3, right and left P^4–M^3; mandible with left C_1, P_4–M_3, right C_1, P_3, M_2 and M_3, and roots of left I_{1-3}, P_3 and right I_2, P_{1-2}; right proximal three-quarters of the humerus and right distal end of the radius: *1,* left lateral view of the palate; *2,* left lateral view of mandible; *3,* anterior view of the radius; *4,* posterior view of the radius; *5,* anterior view of the humerus; *6,* posterior view of the humerus; *8,* occlusal view of the mandible; *10,* occlusal view of the palate.

7 USNM 22483, partial left manus.

9 AMNH 16029, right M_{1-2} and dentary fragment.

The bar below *4* is 2 cm long and is for *1–6, 8, 10.*
The bar below *7* is 1.5 cm long and is for *7.*
The bar below *9* is 5 mm long and is for *9.*

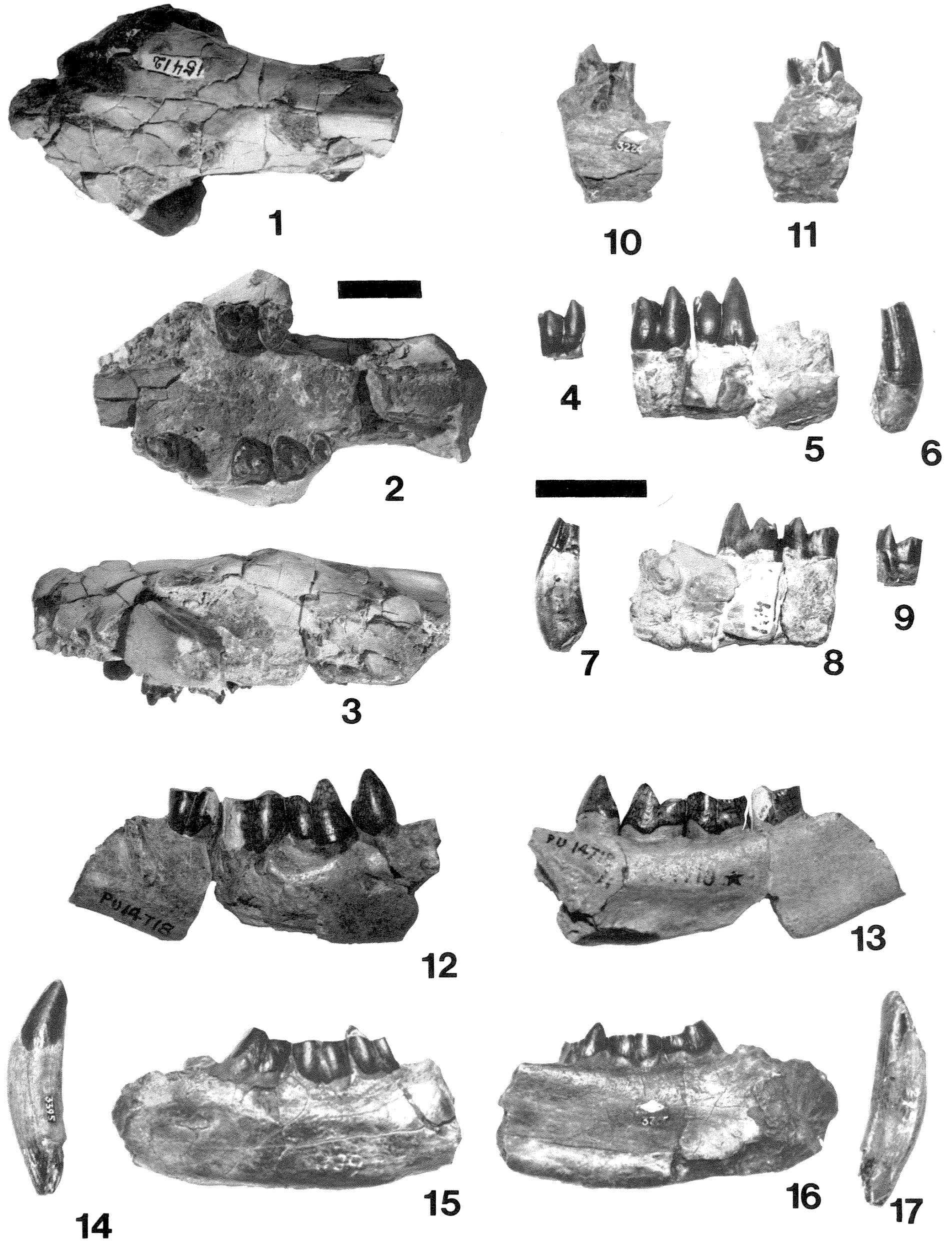


PLATE 15. The type specimens of *Huerfanodon torrejonius* (*1–9*), ?*H. heilprinianus* (*10, 11*), *H. polecatensis* (*12, 13*) and *Conoryctes comma* (*14–17*).

1–9	USNM 15412, partial skull with right P^3, right M^{1-3}, left M^{1-2}, partial root of P^2, alveoli for right P^4 and left P^{2-4}, and right dentary fragments bearing C_1, P_4, M_1, M_3 and the alveolus for P_3: *1,* dorsal view of skull; *2,* ventral view of skull; *3,* left lateral view of skull; *4,* labial view of right M_3; *5,* labial view of right P_4, M_1; *6,* labial view of right C_1; *7,* lingual view of right C_1; *8,* lingual view of right P_4, M_1; *9,* lingual view of right M_3.
10, 11	AMNH 3224, left dentary fragment with M_2: *10,* labial view; *11,* lingual view.
12, 13	PU 14718, right dentary with P_3–M_2, root of P_2, alveoli for C_1, P_1 and M_3: *12,* labial view; *13,* lingual view.
14–17	AMNH 3395, left C_1 and left dentary with P_4–M_2, alveolus for P_2 and roots of P_3 and M_3: *14,* labial view of left C_1; *15,* labial view of left P_4–M_2; *16,* lingual view of left P_4–M_2; *17,* lingual view of left C_1.

The bar above *2* is 2 cm long and is for *1–3*.
The bar above *7* is 2 cm long and is for *4–17*.

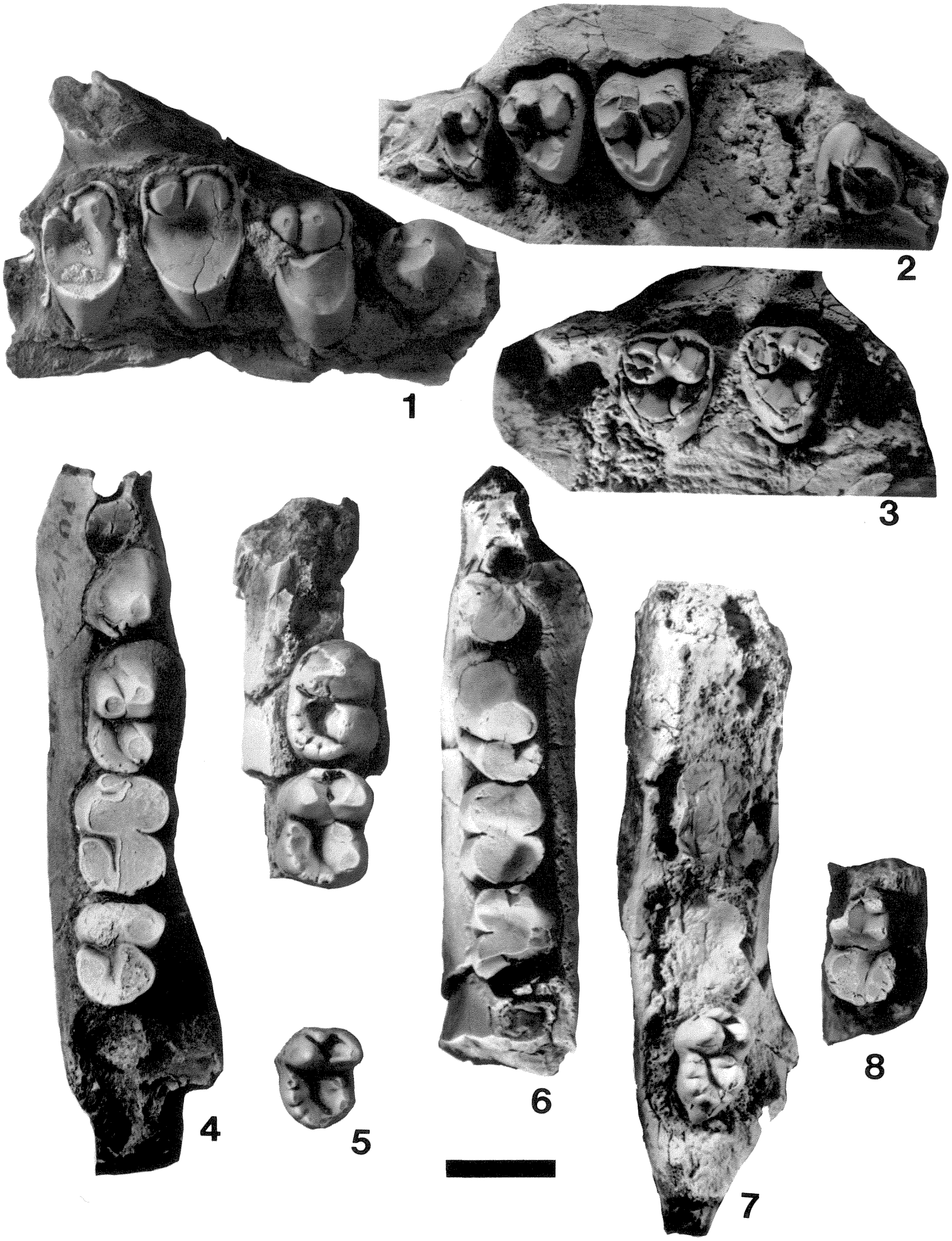


PLATE 16. The dentition of *Conoryctes comma* (*1*; *6*, type specimen), *Huerfanodon torrejonius* (*2, 5*, type specimen; *3, 7*), *H. polecatensis* (*4*, type specimen) and *?H. heilprinianus* (*8*, type specimen).

1 UNM B-890, right maxilla with P^3–M^2 and M^3 alveolus.
2 USNM 15412, right maxilla with P^3, M^{1-3} and P^4 alveolus.
3 MCZ 20181, left maxilla with M^{1-2} and P^4, M^3 alveoli.
4 PU 14718, right dentary fragment with P_3–M_2, root of P_2, and C_1, P_1, M_3 alveoli.
5 USNM 15412, right dentary fragments with P_4–M_1, M_3 and P_3 alveolus.
6 AMNH 3395, left dentary with P_4–M_2, roots of P_3, M_3 and P_2 alveolus.
7 MCZ 20181, right dentary with M_3, roots of M_{1-2} and P_4 alveolus.
8 AMNH 3224, left dentary with M_2.

The bar is 1 cm long.

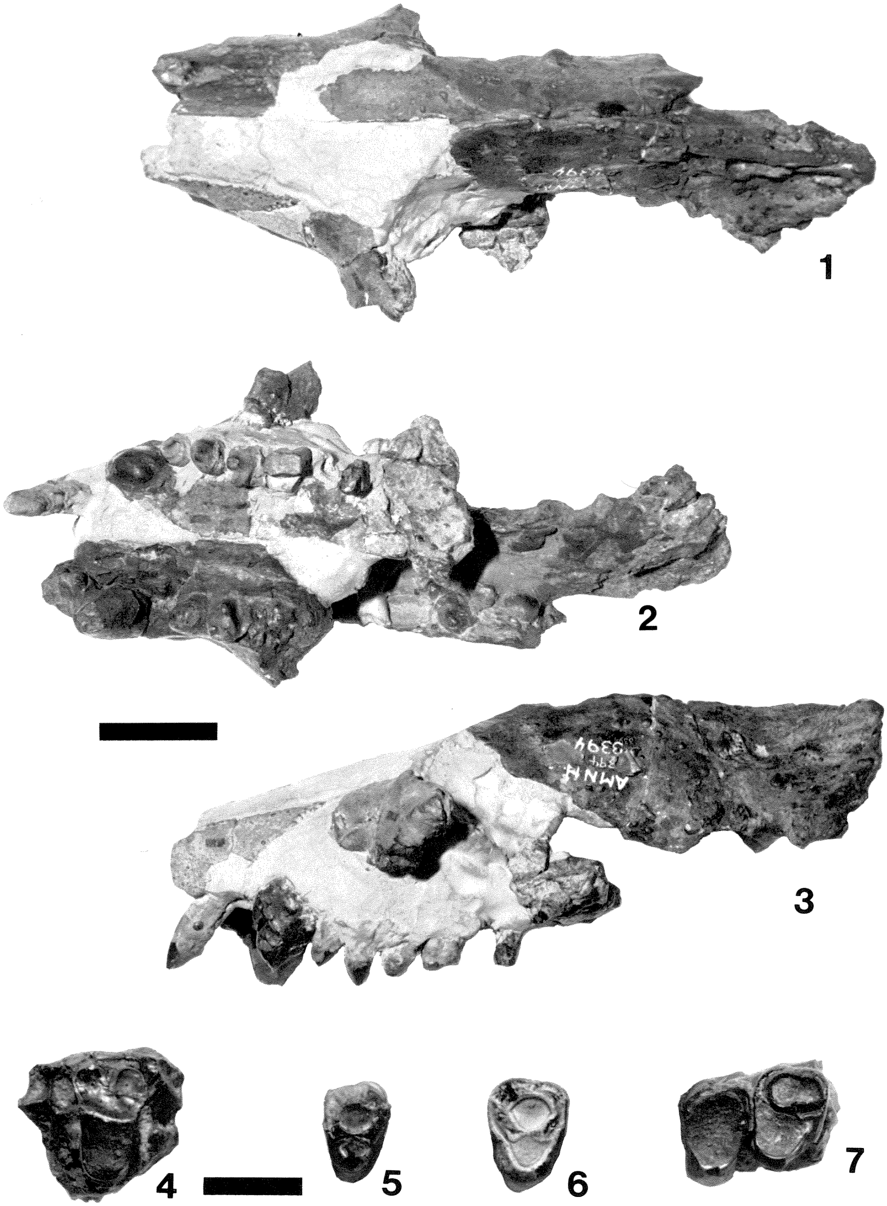


PLATE 17. The skull and upper dentition of *Wortmania otariidens.*

1–3 AMNH 3394, type specimen, partial skull with damaged and fragmentary right C^1, P$^{3-4(?)}$ and left I$^{3(?)}$, C^1, P^2–M$^{1(?)}$: *1,* dorsal view; *2,* ventral view; *3,* left lateral view.
4 AMNH 16342, maxilla fragment with M^2 and M^1, M^3 alveoli.
5 USNM 17655, left P$^{3(?)}$.
6 USNM 17654, right P$^{4(?)}$.
7 USNM 15429, left P^4–M$^{1(?)}$.

The bar below *2* is 3 cm long and is for *1–3.*
The bar next to *4* is 1 cm long and is for *4–7.*

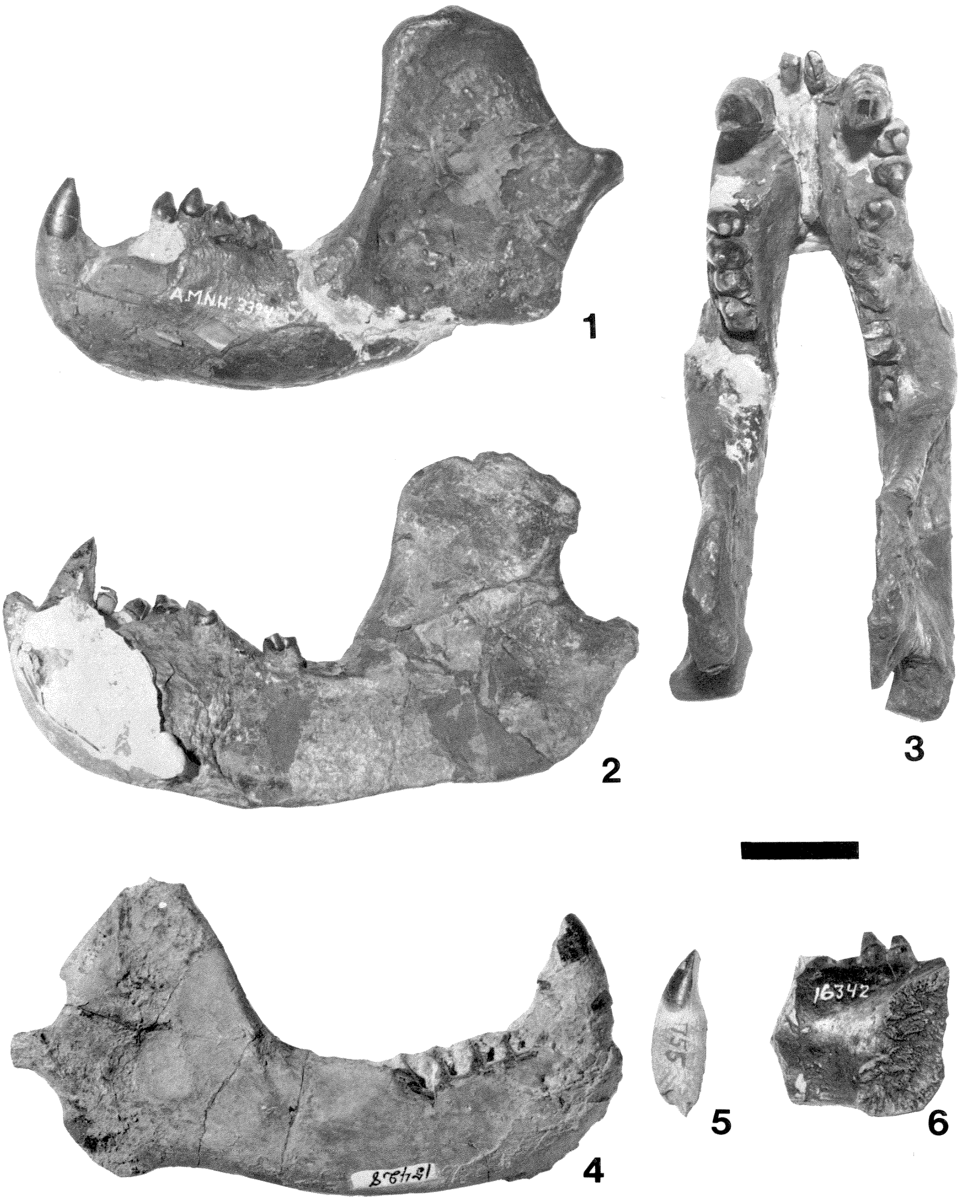


PLATE 18. The mandible and lower dentition of *Wortmania otariidens*.

1–3 AMNH 3394, type specimen, mandible with right and left I_3, C_1, P_{3-4}, right P_{1-2}, M_2, left M_1, roots of right M_1 and alveoli for left M_2 and right M_3: *1,* labial view of left dentary; *2,* lingual view of left dentary; *3,* occlusal view of mandible.

4 USNM 15428, labial view of right dentary with C_1.

5 AMNH 755, labial view of left C_1.

6 AMNH 16342, lingual view of left dentary fragment with P_{1-2} and roots of C_1, P_{3-4}.

The bar is 3 cm long.

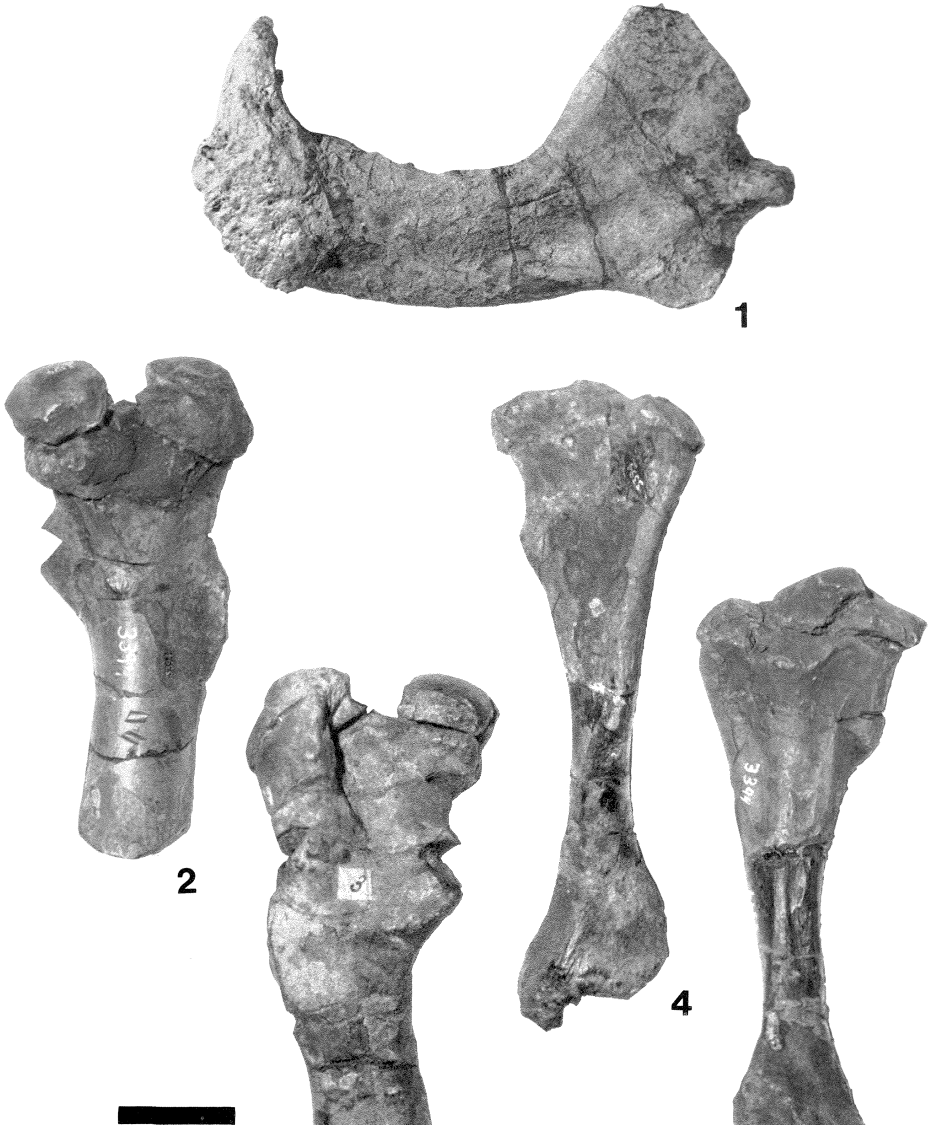


PLATE 19. The mandible and postcrania of *Wortmania otariidens.*

1 USNM 15428, lingual view of right dentary with C_1.
2 AMNH 3394, type specimen, anterior view of left femur.
3 AMNH 3394, posterior view of left femur.
4 AMNH 3394, anterior view of left tibia.
5 AMNH 3394, posterior view of left tibia.

The bar is 3 cm long.

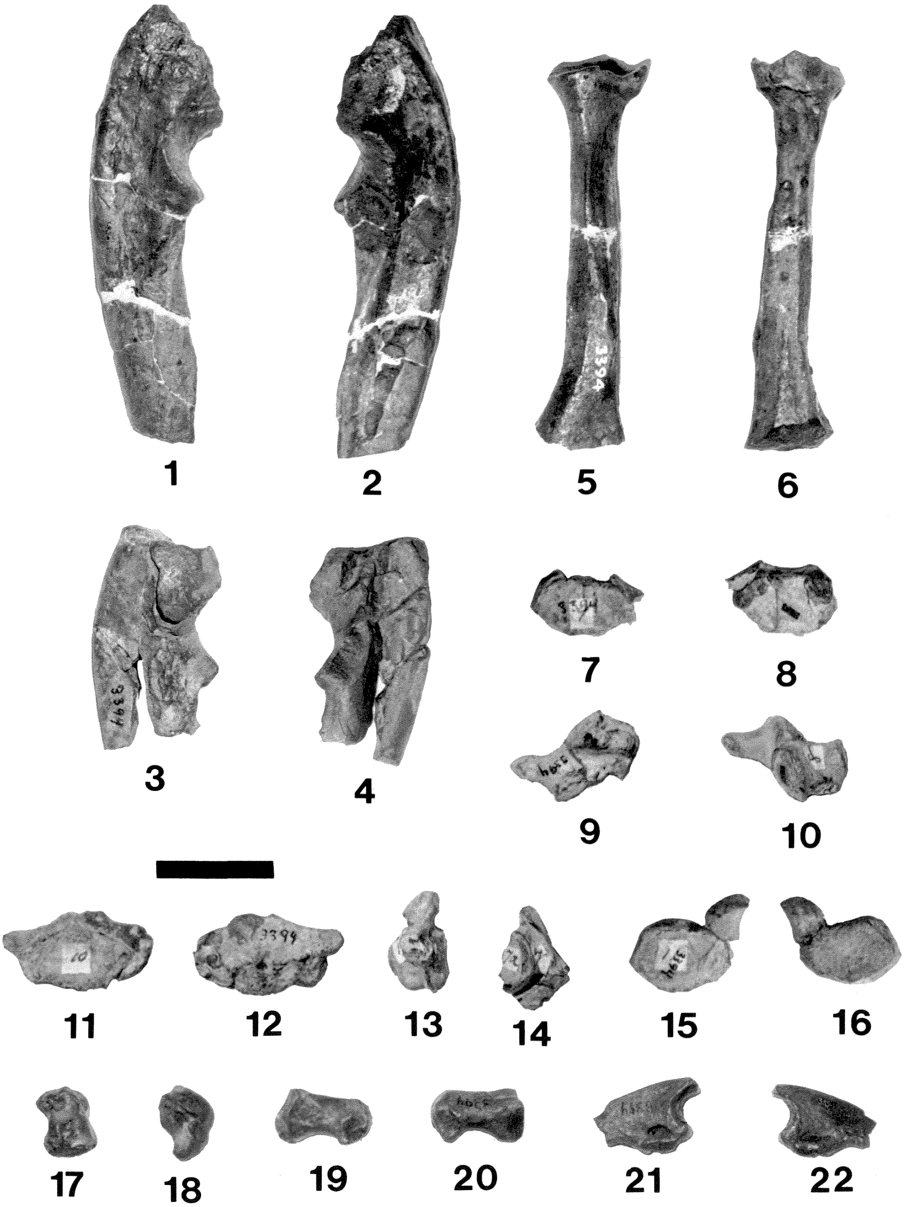


PLATE 20. The postcrania of *Wortmania otariidens,* AMNH 3394, type specimen.

1	Left ulna, internal view.
2	Left ulna, external view.
3	Right ulna, external view.
4	Right ulna, internal view.
5	Left radius, anterior view.
6	Left radius, posterior view.
7, 8	Cervical vertebra.
9	Dorsal view of axis.
10	Ventral view of axis.
11, 12	Cervical vertebra.
13	Left lateral view of partial atlas.
14	Anterior view of partial atlas.
15, 16	Cervical vertebra.
17, 18	(?)Left lunar: *17,* distal view; *18,* side view.
19, 20	(?)Second metacarpal.
21, 22	Ungual phalanx of the manus.

The bar is 3 cm long.

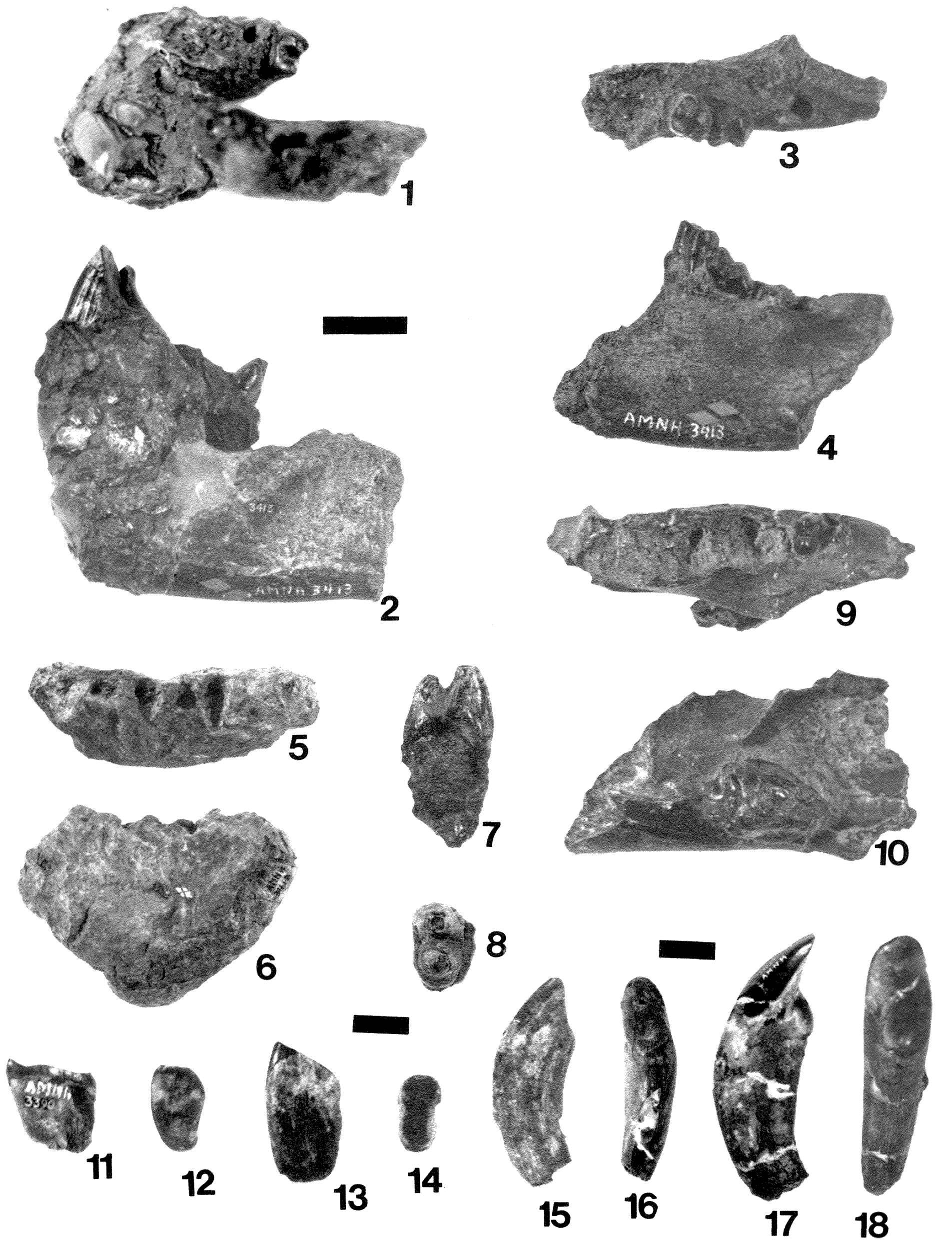


PLATE 21. The type specimens of *Psittacotherium multifragum* (*1–4*), *P. megalodus* (*5–8*), *P. aspasiae*, (*9–10*) and *Hemiganus vultuosus* (*11–18*).

1, 2 AMNH 3413, mandible with left I_3–C_1, right P_2, roots of right I_3–C_1 and alveoli for right P_1, left $M_{2\text{-}3}$: *1,* occlusal view; *2,* left lateral view.

3, 4 AMNH 3413, right dentary with $M_{1\text{-}2}$ and alveolus for M_3: *3,* occlusal view; *4,* lingual view.

5, 6 AMNH 3418, right dentary with C_1 root and alveoli for P_1–M_2: *5,* occlusal view; *6,* labial view.

7, 8 AMNH 3418, right P_2: *7,* posterior view; *8,* occlusal view.

9, 10 AMNH 3416, left dentary with partially erupted M_3, alveoli for $M_{1\text{-}2}$ and crushed M_2 cemented to the outside of the jaw: *9,* occlusal view; *10,* labial view.

11–18 AMNH 3390: *11,* lateral view of upper molar; *12,* occlusal view of upper molar; *13,* lateral view of (?)right I_3; *14,* occlusal view of (?)right I_3; *15,* labial view of right C^1; *16,* occlusal view of right C^1; *17,* labial view of left C_1; *18,* occlusal view of left C_1.

The bar above *2* is 2 cm long and is for *1–4*.
The bar above *13, 14* is 1 cm long and is for *7–14*.
The bar above *16, 17* is 2 cm long and is for *5, 6, 15–18*.

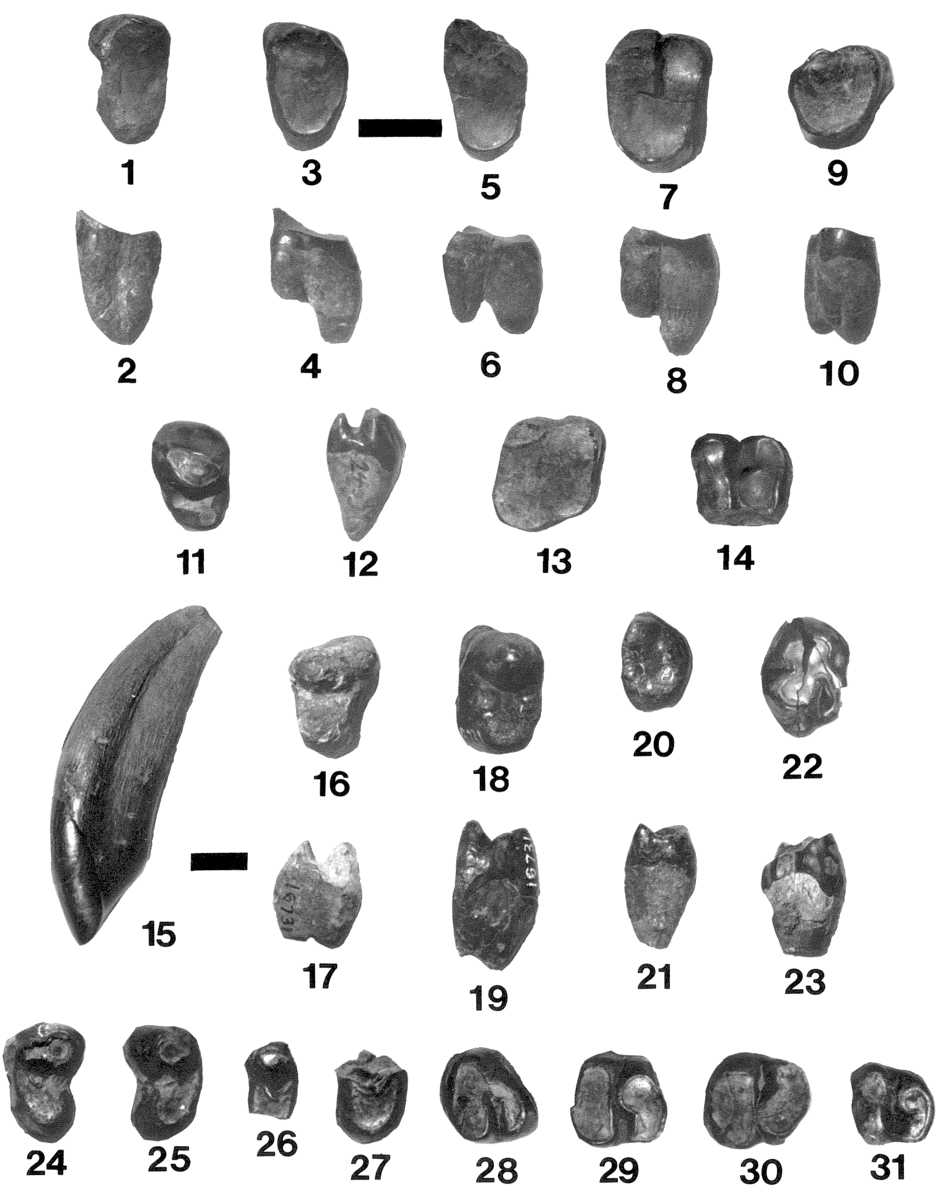


PLATE 22. The dentition of *Psittacotherium multifragum*.

1–14 AMNH 2453: *1,* occlusal view of left P^2; *2,* anterior view of left P^2; *3,* occlusal view of left P^3; *4,* anterior view of left P^3; *5,* occlusal view of left P^4; *6,* anterior view of left P^4; *7,* occlusal view of left M^1; *8,* anterior view of left M^1; *9,* occlusal view of (?)left M^3; *10,* anterior view of (?)left M^3; *11,* occlusal view of right P_2; *12,* posterior view of right P_2; *13,* occlusal view of left P_4; *14,* occlusal view of right M_1.

15–21 AMNH 16731: *15,* labial view of left I^3; *16,* occlusal view of right P^2; *17,* anterior view of right P^2; *18,* occlusal view of left P^4; *19,* anterior view of left P^4; *20,* occlusal view of left M^3; *21,* anterior view of left M^3.

22, 23 AMNH 756: *22,* occlusal view of right $P_{4(?)}$; *23,* posterior view of right $P_{4(?)}$.

24–31 AMNH 16661: *24,* occlusal view of right P^2; *25,* occlusal view of left P^2; *26,* occlusal view of undetermined upper cheek tooth fragment; *27,* occlusal view of partial $P^{4(?)}$; *28,* occlusal view of right P_4; *29,* occlusal view of right M_1; *30,* occlusal view of left M_1; *31,* occlusal view of right M_3.

The bar between *3* and *5* is 1 cm long and is for all occlusal views.
The bar between *15* and *17* is 1 cm long and is for all anterior, posterior and lateral views.

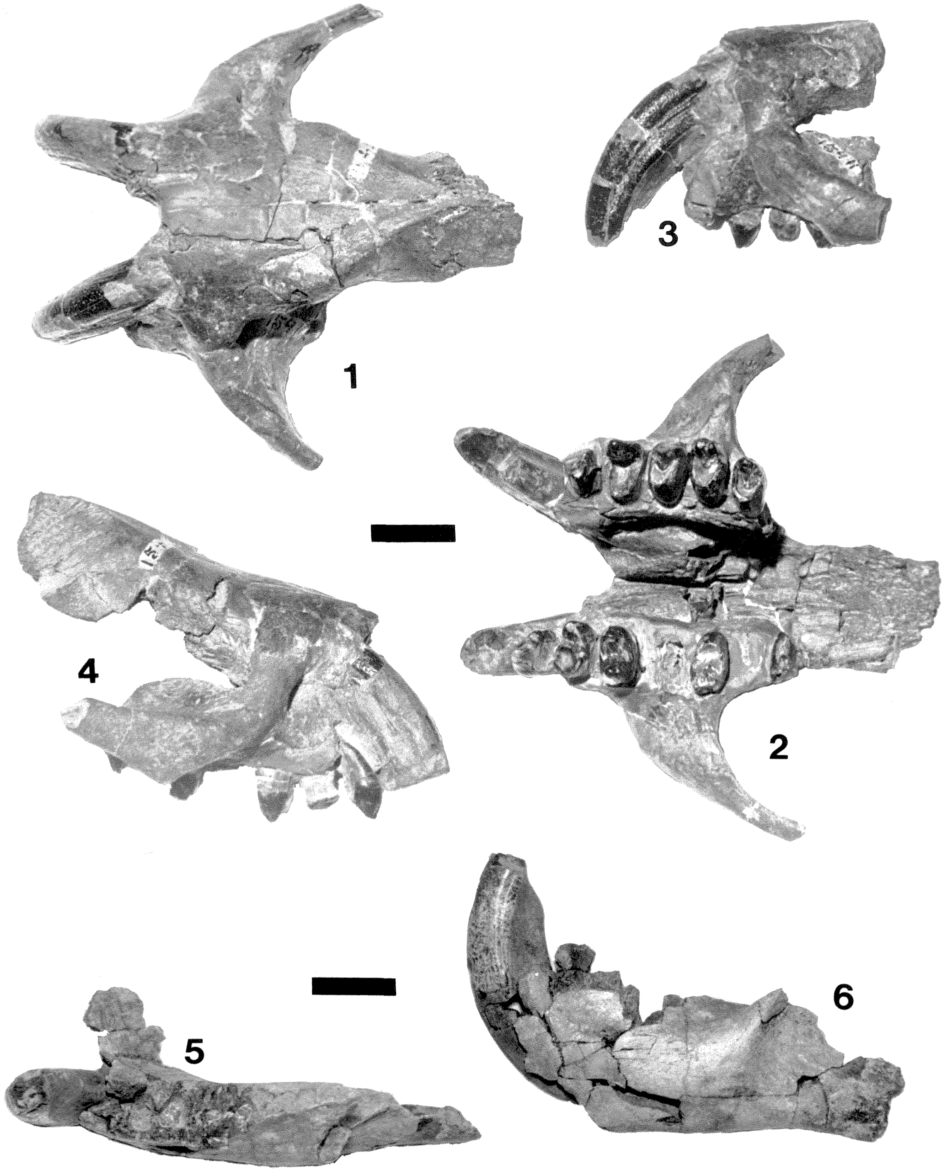


PLATE 23. A skull and mandible of *Psittacotherium multifragum*.

1–4 USNM 15411, partial skull with right and left C^1, right P^1, right and left P$^{2-3}$, left P^4, right and left M^1, left M^2 and right M^3: *1,* dorsal view; *2,* ventral view; *3,* left lateral view; *4,* right lateral view.

5, 6 USNM 15410, left dentary with C$_1$: *5,* occlusal view; *6,* labial view.

The bar above *4* is 2 cm long and is for *1–4*.
The bar above *5* is 3 cm long and is for *5, 6*.

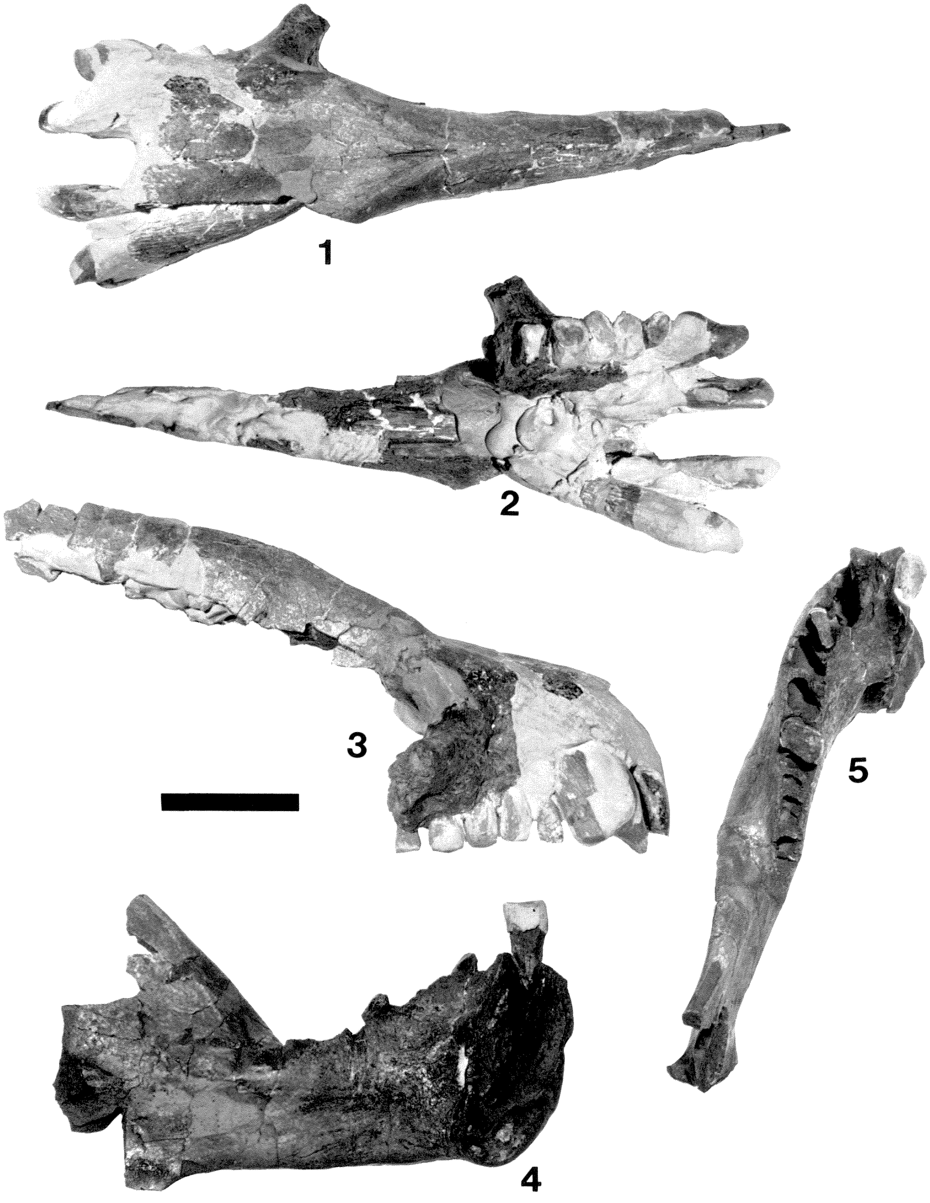


PLATE 24. A skull and mandible of *Psittacotherium multifragum.*

1–5 AMNH 754, partial skull and mandible with right and left I^3–C^1, fragmentary right P^1–M^1, partial right I_3, left P_1, left P_4, and alveoli for left C_1, P_{2-3}, M_{2-3}: *1,* dorsal view of skull; *2,* ventral view of skull; *3,* right lateral view of skull; *4,* lingual view of left dentary; *5,* occlusal view of left dentary.

The bar is 5 cm long.

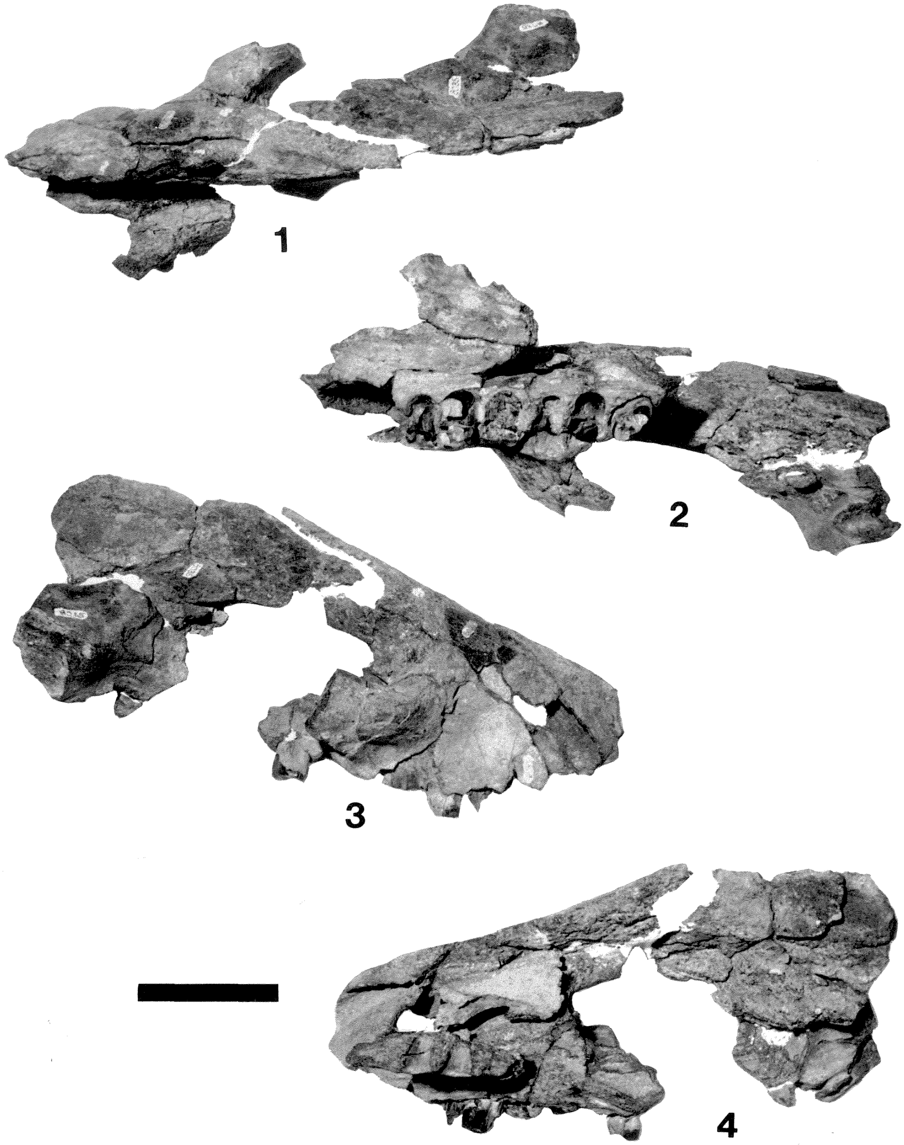


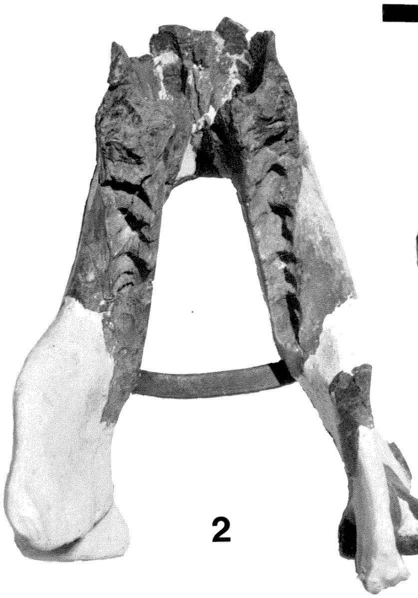
PLATE 25. A skull of *Psittacotherium multifragum*.

1–4 UK 8035, right side of skull with P^3, M^3, roots of P^2, P^4, alveoli for I^3, C^1, M$^{1-2}$: *1,* dorsal view; *2,* ventral view; *3,* right lateral (external view); *4,* left lateral (internal) view.

The bar is 5 cm long.

1

3



2

4

Plate 26. Two mandibles of *Psittacotherium multifragum.*

1, 2 UK 8035, mandible with alveoli for right and left C_1–M_3: *1,* right lateral view; *2,* occlusal view.

3, 4 AMNH 88383, mandible with right and left C_1, left P_4, M_3, roots of left M_1, alveoli for right and left I_3, P_{1-3}, right P_4–M_3: *3,* occlusal view; *4,* left lateral view.

The bar is 5 cm long.

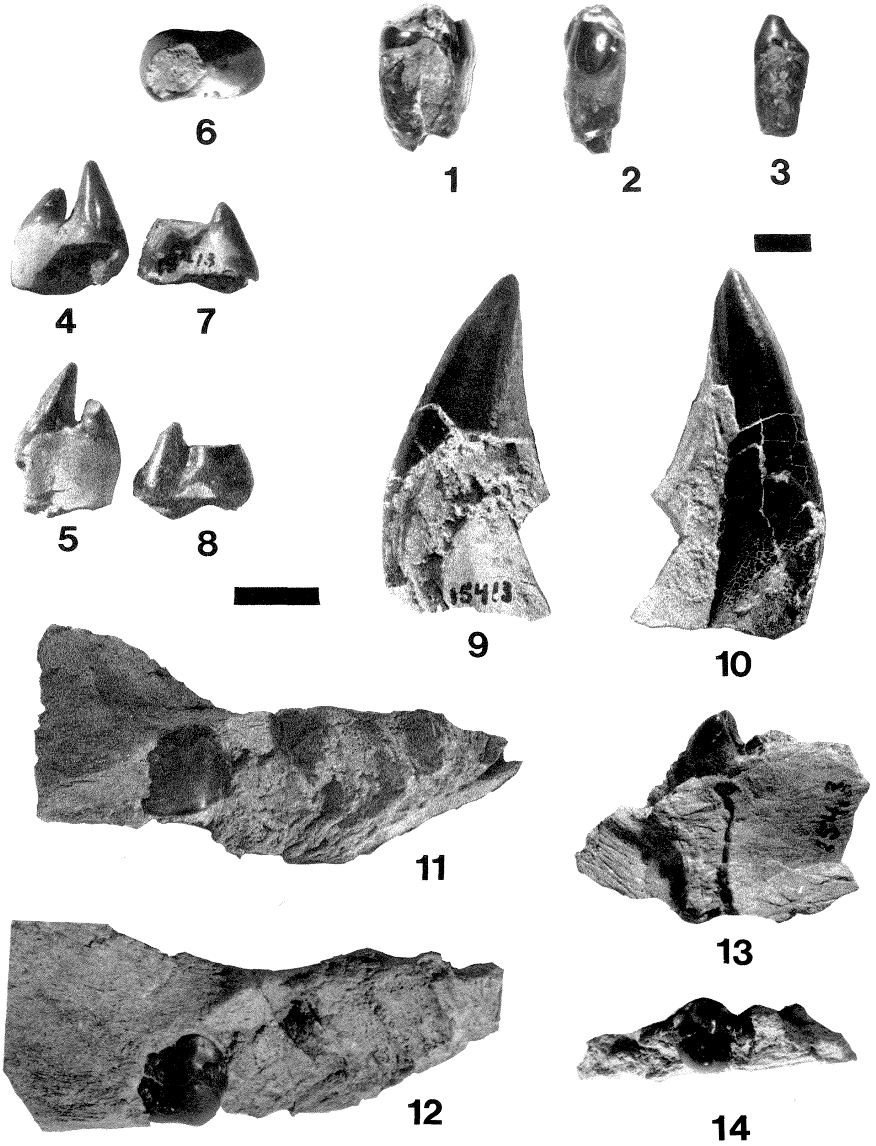


PLATE 27. Specimens referred to stylinodontid genus indeterminate (*1, 2*), ?*Psittacotherium* sp. or ?*Wortmania* sp. (*3*) and *Psittacotherium multifragum* (*4–14*).

1, 2	AMNH no number, cheek tooth: *1,* lateral view; *2,* lingual view.
3	USNM 16204, right I$_3$: internal view.
4, 5	USNM 15413, dP$_{2(?)}$: *4,* posterior view; *5,* anterior view.
6–8	USNM 15413, dP$_{1(?)}$: *6,* occlusal view; *7,* anterior view; *8,* posterior view.
9, 10	USNM 15413, dC$_{1(?)}$: lateral views.
11, 12	USNM 15413, left dentary fragment with unerupted M$_3$: *11,* lingual view; *12,* occlusal view.
13, 14	USNM 15413, right dentary fragment with unerupted M$_3$: *13,* lingual view; *14,* occlusal view.

The bar below *3* is 1 cm long and is for *3.*
The bar above *11* is 1 cm long and is for *1, 2, 4–14.*

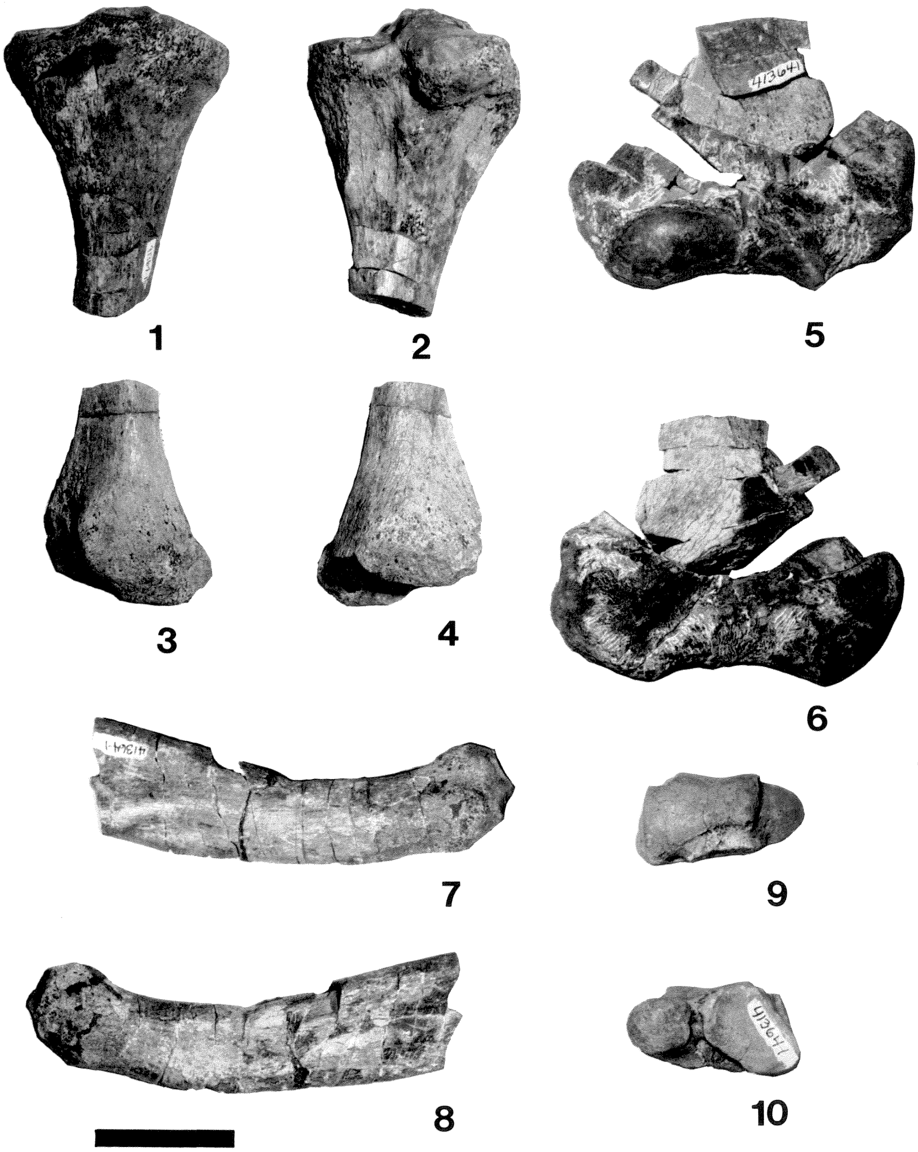


PLATE 28. Skeletal elements referred to *Psittacotherium multifragum.*

1, 2 TMM 41364-1, proximal part of right tibia: *1,* anterior view; *2,* posterior view.
3, 4 TMM 41364-1, distal part of left tibia: *3,* posterior view; *4,* anterior view.
5, 6 TMM 41364-1, distal part of right humerus: *5,* anterior view; *6,* posterior view.
7, 8 TMM 41364-1, (?)clavicle.
9, 10 TMM 41364-1, right astragalus fragment: *9,* dorsal view; *10,* ventral view.
The bar is 4 cm long.

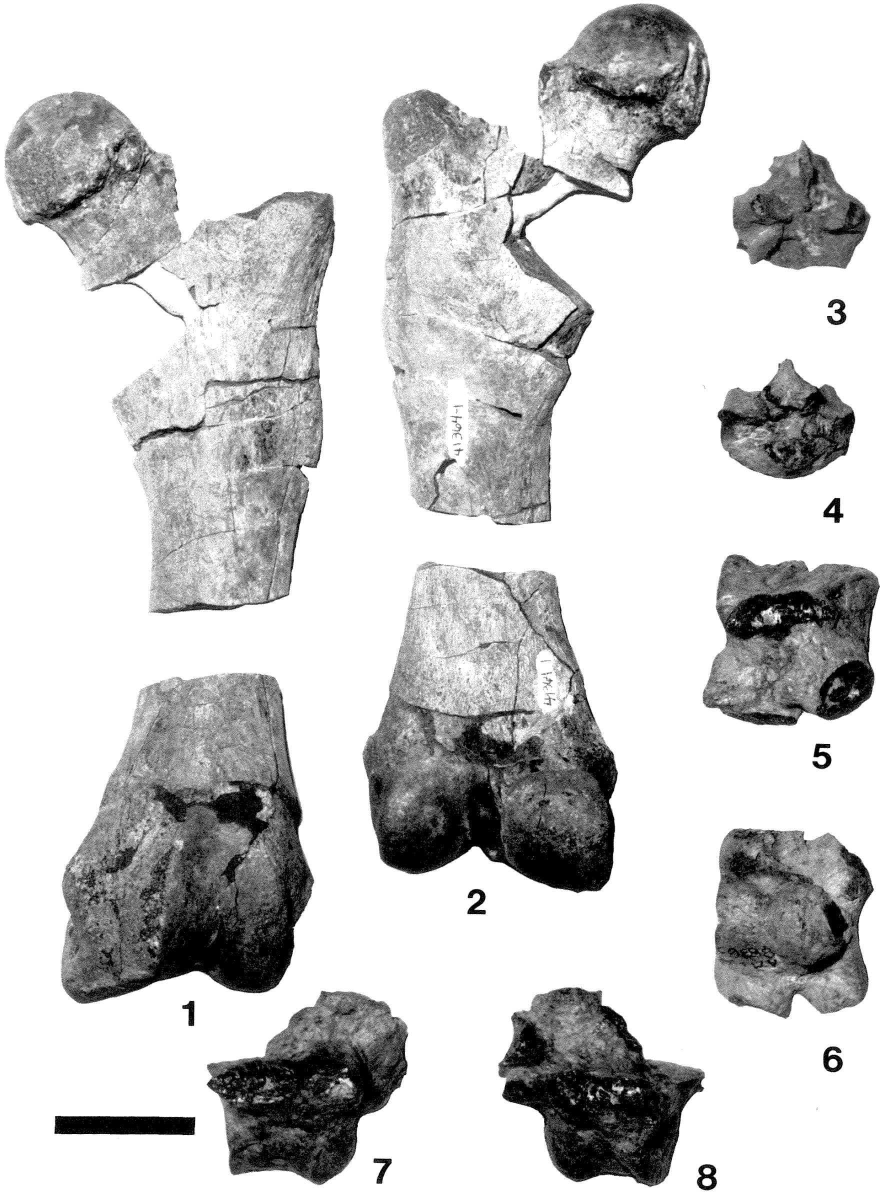


PLATE 29. Skeletal elements referred to *Psittacotherium multifragum*.

1, 2 TMM 41364-1, left femur: *1,* anterior view; *2,* posterior view.
3, 4 AMNH 3391, (?)anterior thoracic vertebra: *3,* anterior view; *4,* posterior view.
5, 6 AMNH 88383, (?)lumbar vertebra: *5,* dorsal view; *6,* ventral view. Anterior is to the right.
7, 8 AMNH 88383, (?)lumbar vertebra: *7,* right lateral view; *8,* left lateral view.
The bar is 4 cm long.

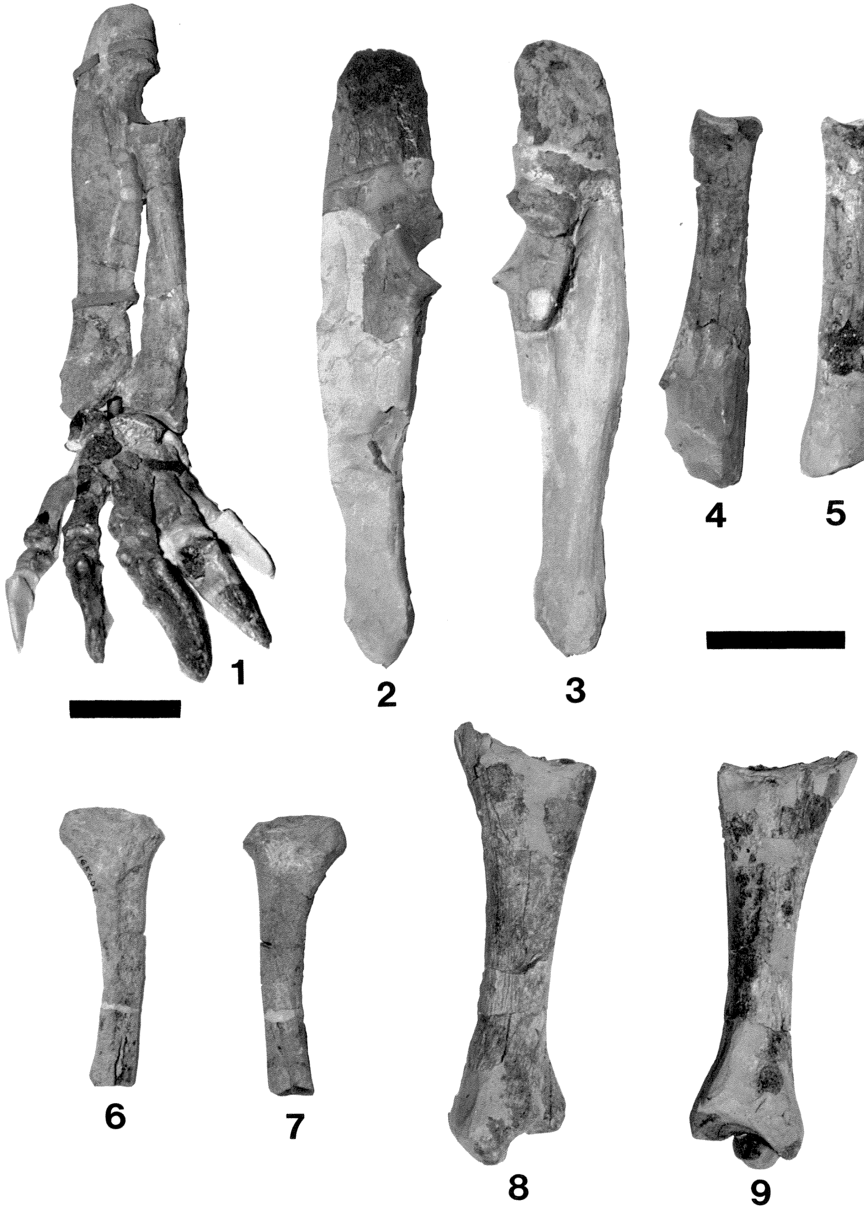


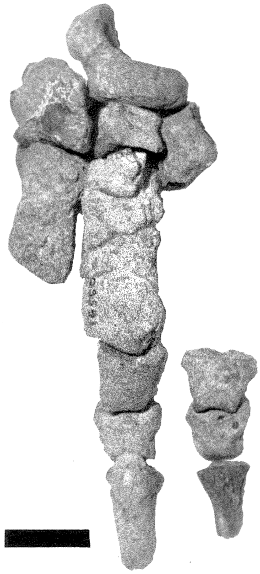
PLATE 30. Specimens referred to *Psittacotherium multifragum*.

1 AMNH 2453, right ulna, radius and manus: anterior view.
2, 3 AMNH 16560, left ulna: *2,* internal view; *3,* external view.
4, 5 AMNH 16560, left radius: *4,* internal view; *5,* external view.
6, 7 AMNH 16560, left (?)fibula: *6,* external view; *7,* internal view.
8, 9 AMNH 15938, left tibia: *8,* anterior view; *9,* posterior view.

The bar below *1* is 6 cm long and is for *1*.
The bar below *4, 5* is 5 cm long and is for *2–9*.

1

2



3

4

5

PLATE 31. Specimens referred to *Psittacotherium multifragum*.

1 USNM 15411, occlusal view of left maxilla with P^2–M^2.

2 USNM 15411, occlusal view of right maxilla with C^1, P^{1-3}, M^1 and M^3.

3 AMNH 16560, partial left pes.

4, 5 AMNH 16560, left femur: *4,* anterior view; *5,* posterior view.

The bar next to *1* is 1 cm long and is for *1, 2*.
The bar below *3* is 2 cm long and is for *3*.
The bar between *4* and *5* is 3 cm long and is for *4, 5*.

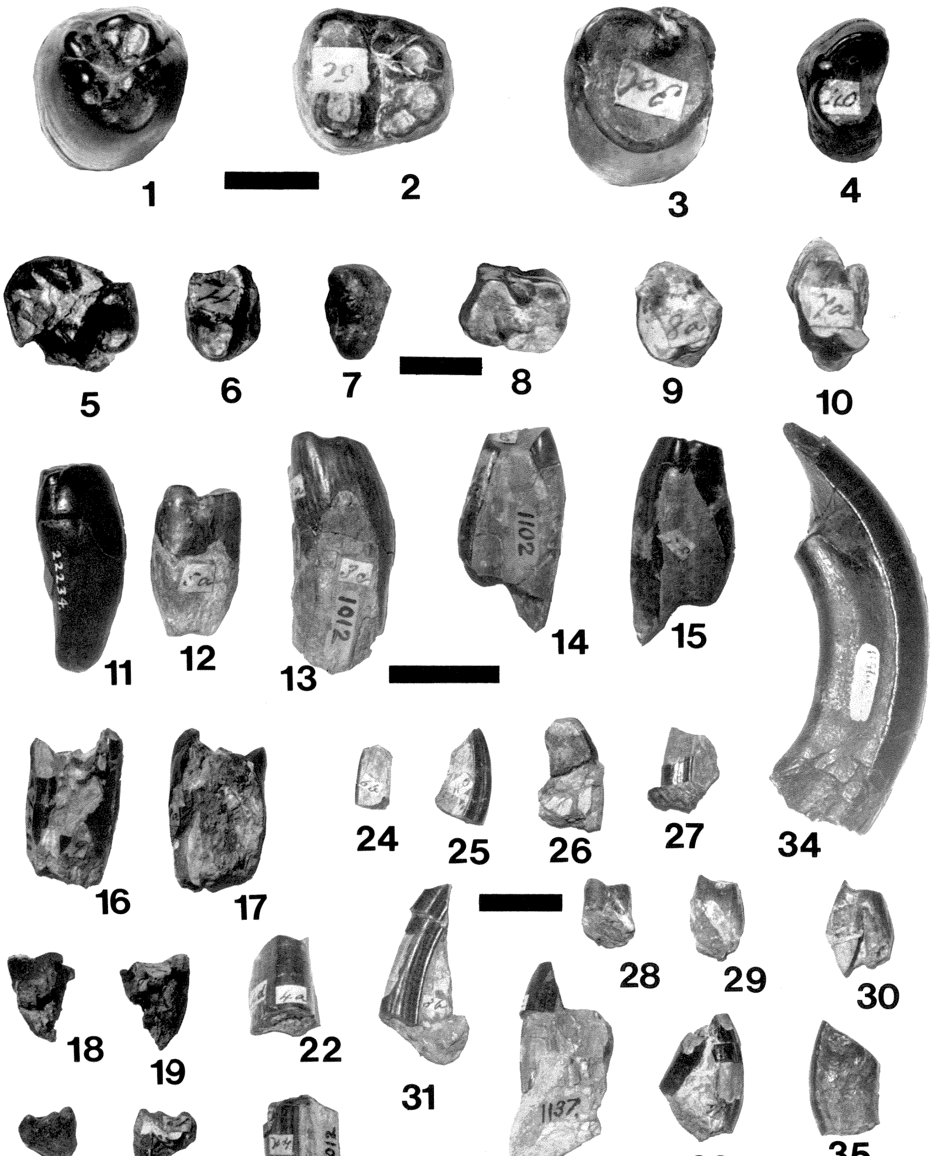


PLATE 32. The type specimens of *Ectoganus gliriformis* (*5–10, 16–21, 24–33*), *Calamodon simplex* (*3, 13, 22, 23*), *Calamodon arcamaenus* (*2, 12*), *Calamodon novomehicanus* (*4, 14, 15*), ?*Psittacotherium lobdelli* (*1, 11*) and paratype of ?*Psittacotherium lobdelli* (*34, 35*).

1, 11	AMNH 22234, right M^3: *1,* occlusal view; *11,* posterior view.
2, 12	USNM 1017, right M$_2$: *2,* occlusal view; *12,* lingual view.
3, 13, 22, 23	USNM 1012: *3,* occlusal view of left P^4; *13,* anterior view of left P^4; *22, 23,* canine fragments.
4, 14, 15	USNM 1102, right P^2: *4,* occlusal view; *14,* anterior view; *15,* posterior view.
5–10, 16–21, 24–33	USNM 1137: *5,* occlusal view of fragmentary upper molar; *6,* occlusal view of partial lower molar trigonid; *7,* occlusal view of partial lower molar talonid; *8,* occlusal view of left dP$_4$; *9,* occlusal view of (?)right dP^3; *10,* occlusal view of (?)right dP^4; *16,* (?)labial view of fragmentary upper molar; *17,* (?)lingual view of fragmentary upper molar; *18,* posterior view of partial lower molar trigonid; *19,* anterior view of partial lower molar trigonid; *20,* posterior view of partial lower molar talonid; *21,* anterior view of partial lower molar talonid; *24,* upper (?)deciduous incisor; *25,* left I^3, external view; *26,* right I^3, internal view; *27,* canine fragment; *28,* labial view of left dP^4; *29,* posterior view of right dP^3; *30,* posterior view of right dP^4; *31,* right C^1, external view; *32,* left C^1, internal view; *33,* right P$_2$, posterior view.

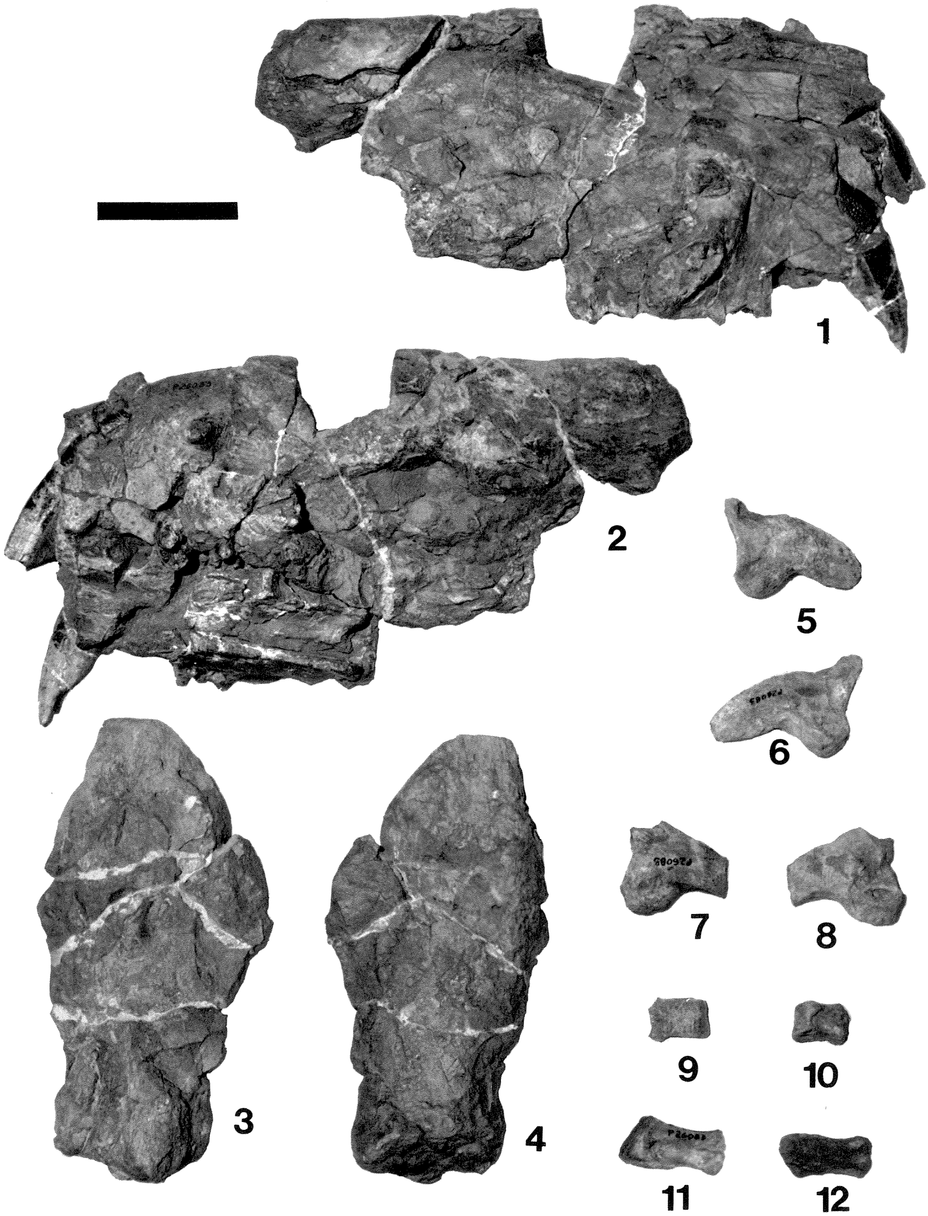


PLATE 33. The type specimen of *Lampadophorus expectatus,* FMNH P 26083.

1, 2	Crushed skull with right and left C^1, P^{3-4} and alveoli for right and left P^{1-2}, M^{1-2}: *1,* dorsal/right lateral view; *2,* ventral/left lateral view.
3	External view of left scapula.
4	Internal view of left scapula.
5, 6 and *7, 8*	Unguals of the manus.
9, 10	Phalanx.
11, 12	(?)Metacarpal.

The bar is 5 cm long.

←

34	CM 11560, external view of right C_1.
35	AMNH 22235, internal view of left I^3.

The bar below *1* and *2* is 1 cm long and is for *1–3.*
The bar between *7* and *8* is 1 cm long and is for *4–10.*
The bar between *13* and *14* is 2 cm long and is for *11–21.*
The bar between *31* and *28* is 2 cm long and is for *22–35.*

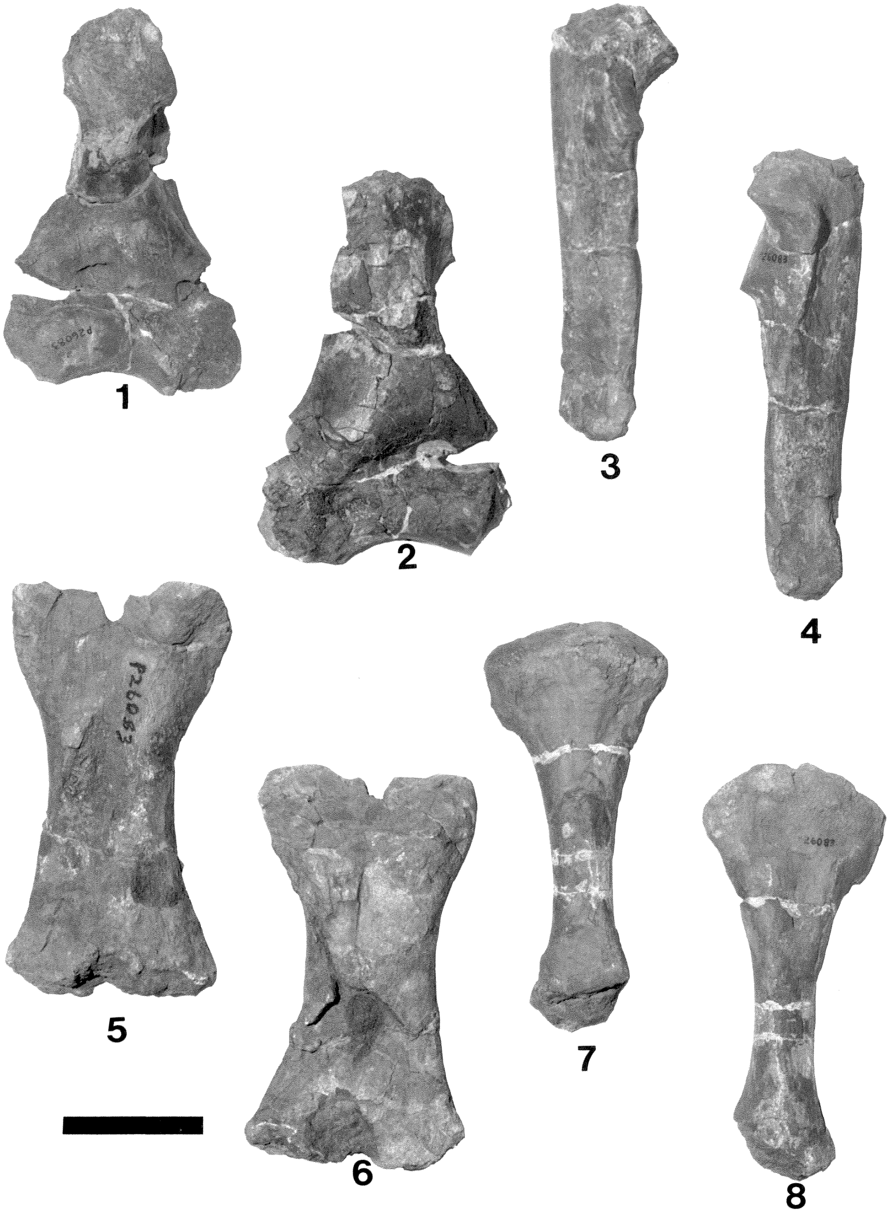


PLATE 34. The type specimen of *Lampadophorus expectatus,* FMNH P 26083.
1 Anterior view of right humerus.
2 Posterior view of right humerus.
3 Internal view of left ulna.
4 External view of left ulna.
5 Anterior view of (?)right femur.
6 Posterior view of (?)right femur.
7 Posterior view of right tibia.
8 Anterior view of right tibia.
The bar is 5 cm long.

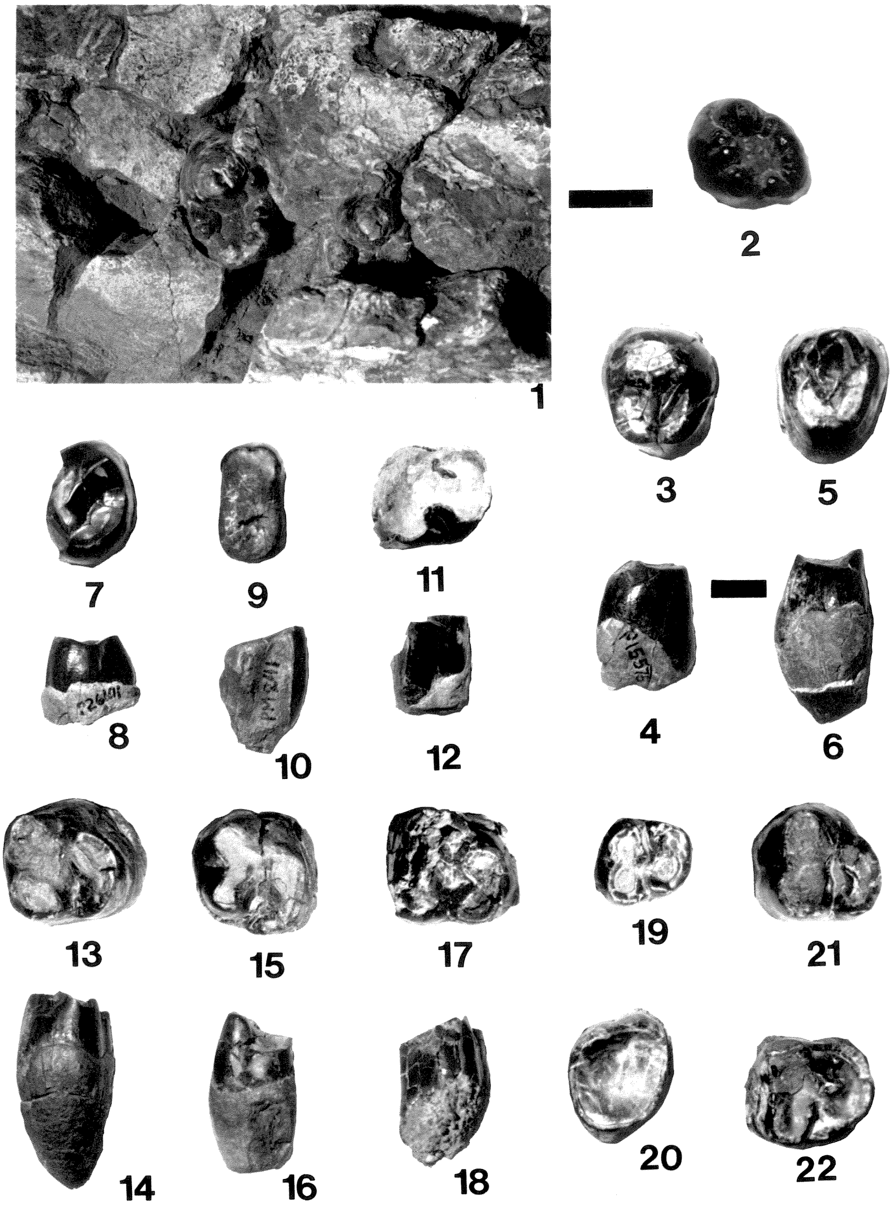


PLATE 35. The dentition of the type specimen (*1, 2*) and original hypodigm (*3–18*) of *Lampadophorus expectatus,* and *Ectoganus* from the Togwotee Pass area, Wyoming (*19–22*).

1 FMNH P 26083, occlusal view of left P^{3-4}, alveoli for P^2, M^1.
2 FMNH P 26083, occlusal view of left M^3.
3, 4 FMNH P 15575, left P^4: *3,* occlusal view; *4,* anterior view.
5, 6 FMNH P 15569, right P^3: *5,* occlusal view; *6,* anterior view.
7, 8 FMNH P 26101, lower molar talonid: *7,* occlusal view; *8,* posterior view.
9, 10 FMNH PM 241, left I_3: *9,* occlusal view; *10,* internal view.
11, 12 FMNH P 14954, fragmentary lower left molar: *11,* occlusal view; *12,* labial view.
13, 14 FMNH P 14906, right, $P_{3(?)}$: *13,* occlusal view; *14,* anterior view.
15, 16 FMNH P 14906, right $P_{4(?)}$: *15,* occlusal view; *16,* lingual view.
17, 18 FMNH P 26106, right $M_{1(?)}$: *17,* occlusal view; *18,* anterior view.
19 AMNH 86852, occlusal view of left M_3.
20 AMNH 86859, occlusal view of $M_{3(?)}$
21 AMNH 86859, occlusal view of right P_4.
22 AMNH 86859, occlusal view of left M_1.

The bar between *1* and *2* is 1 cm long and is for all occlusal views.
The bar between *4* and *5* is 1 cm long and is for all anterior, posterior, labial and lingual views.

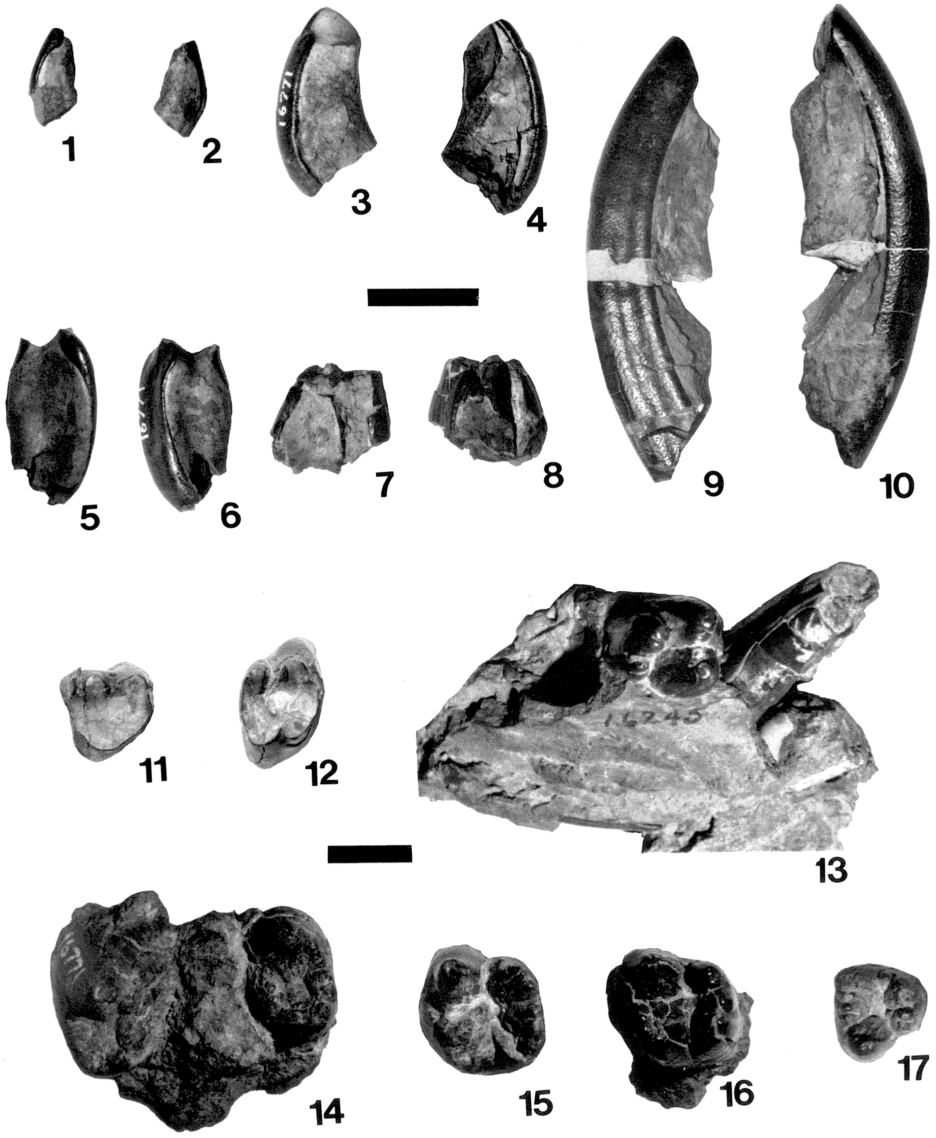


PLATE 36. The dentition of *Ectoganus gliriformis gliriformis*.

1, 2 AMNH 16771, right upper (?)deciduous incisor: *1,* external view; *2,* internal view.
3, 4 AMNH 16771, right I^3: *3,* external view; *4,* internal view.
5, 6 AMNH 16771, right P^1: *5,* anterior view; *6,* posterior view.
7, 8 AMNH 16771, right P^2: *7,* anterior view; *8,* posterior view.
9, 10 AMNH 16771, right C^1: *9,* external view; *10,* internal view.
11 AMNH 16771, occlusal view of right dP^3.
12 AMNH 16771, occlusal view of right dP^4.
13 AMNH 16245, occlusal view of left dentary fragment with broken and crushed C_1, P_2, complete P_3 and P_4 alveolus.
14 AMNH 16771, occlusal view of left P^{3-4} in matrix.
15 AMNH 16771, occlusal view of left M^1.
16 AMNH 16771, occlusal view of left M^2.
17 AMNH 16771, occlusal view of left M^3.

The bar above *7* is 2 cm long and is for all anterior, posterior, external and internal views.
The bar above *14* is 1 cm long and is for all occlusal views.

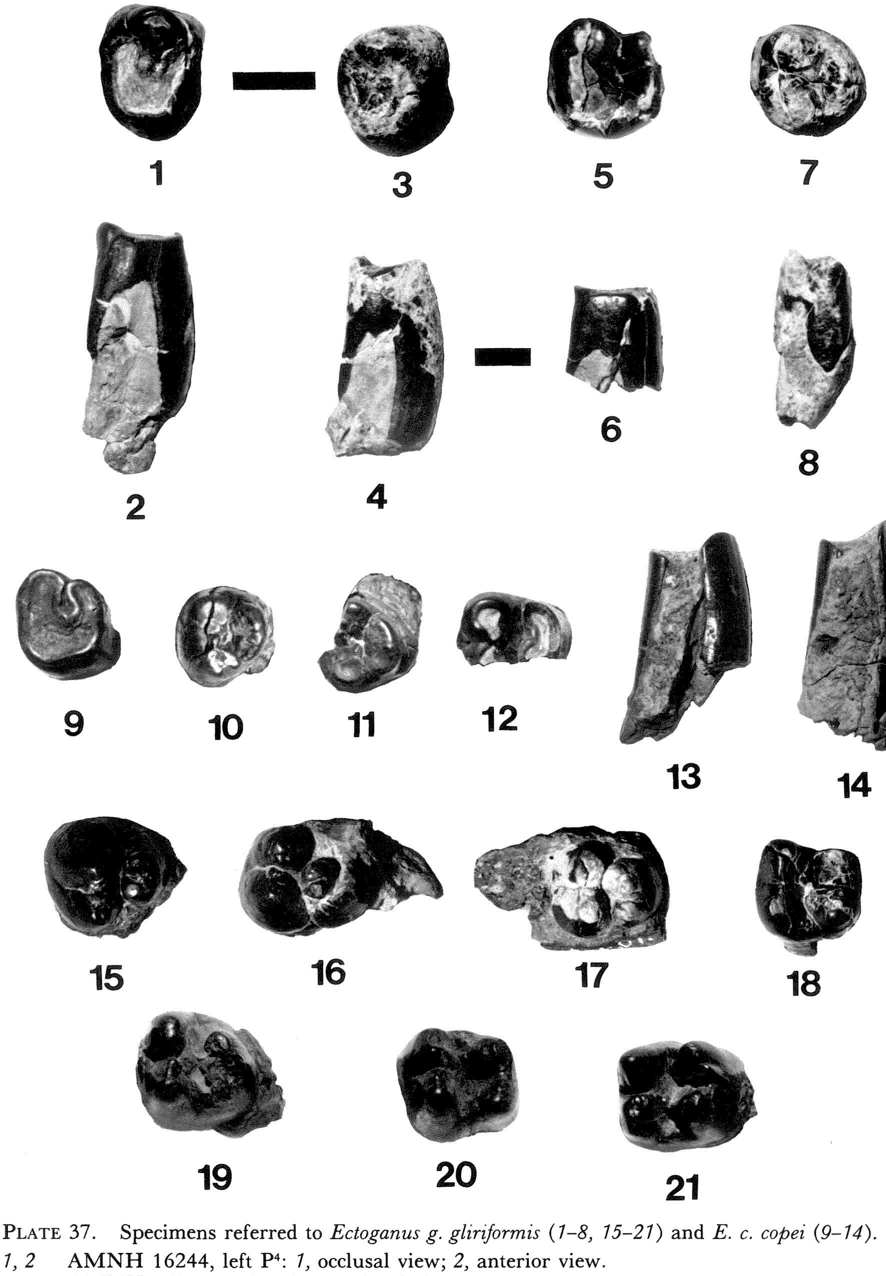


PLATE 37. Specimens referred to *Ectoganus g. gliriformis* (*1–8, 15–21*) and *E. c. copei* (*9–14*).

1, 2 AMNH 16244, left P^4: *1,* occlusal view; *2,* anterior view.
3, 4 AMNH 16244, right P^4: *3,* occlusal view; *4,* posterior view.
5, 6 AMNH 16244, left M^1: *5,* occlusal view; *6,* anterior view.
7, 8 AMNH 16244, right P_3: *7,* occlusal view; *8,* labial view.
9 AMNH 15633, occlusal view of left $M^{2(?)}$.
10 AMNH 15633, occlusal view of (?)right P_3.
11 AMNH 15633, occlusal view of (?)left P_3.
12 AMNH 15633, occlusal view of broken lower molar.
13 AMNH 15633, posterior view of right $P_{2(?)}$.
14 AMNH 15633, posterior view of right $P_{2(?)}$.
15 AMNH 48001, occlusal view of left P_3.
16 AMNH 48001, occlusal view of (?)right P_4.
17 AMNH 48001, occlusal view of (?)left P_4.
18 AMNH 48001, occlusal view of left M_3.
19 AMNH 4287, occlusal view of right P_4.
20 AMNH 4287, occlusal view of right M_1.
21 AMNH 4287, occlusal view of left M_1.

The bar between *1* and *3* is 1 cm long and is for all occlusal views.
The bar between *4* and *6* is 1 cm long and is for all anterior, posterior and labial views.

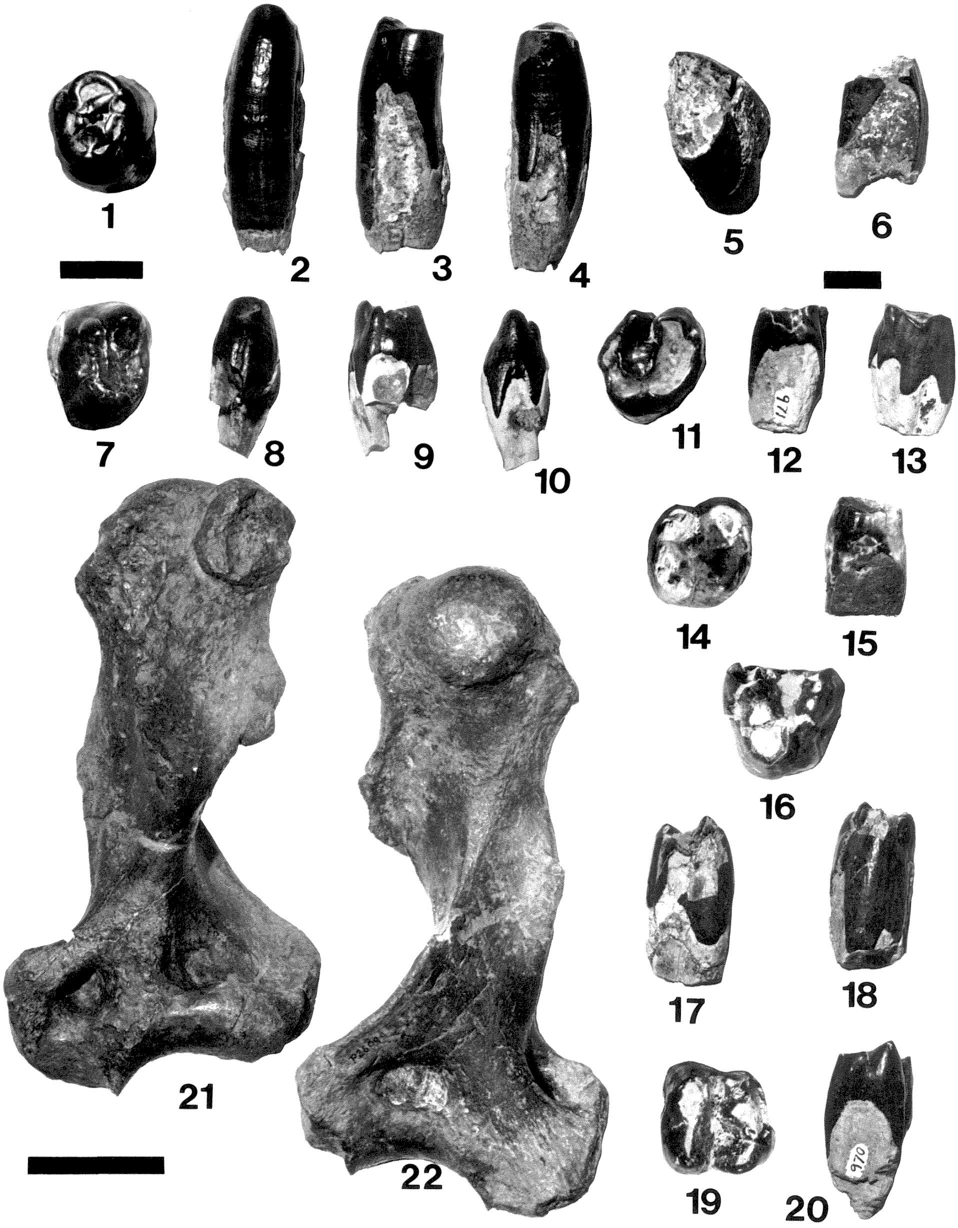


PLATE 38. Specimens referred to *Ectoganus c. copei* (*1–4*) and *E. g. gliriformis* (*5–22*).

1–4 YPM 18618, right $P^{3(?)}$: *1,* occlusal view; *2,* lingual view; *3,* anterior view; *4,* labial view.
5, 6 UNM B-970, left $P^{1(?)}$ fragment: *5,* occlusal view; *6,* posterior view.
7–10 UNM B-970, right $P^{3(?)}$: *7,* occlusal view; *8,* lingual view; *9,* posterior view; *10,* labial view.
11–13 UNM B-971, right $M^{1(?)}$: *11,* occlusal view; *12,* anterior view; *13,* posterior view.
14, 15 UNM B-970, right $M^{2(?)}$: *14,* occlusal view; *15,* anterior view.
16–18 UNM B-970, fragmentary left P_4: *16,* occlusal view; *17,* labial view; *18,* lingual view.
19, 20 UNM B-970, right M_1: *19,* occlusal view; *20,* anterior view.
21, 22 FMNH P 26090, left humerus: *21,* anterior view; *22,* posterior view.

The bar above *7* is 1 cm long and is for all occlusal views.
The bar above *12, 13* is 1 cm long and is for all anterior, posterior, labial and lingual views of teeth.
The bar below *21* is 5 cm long and is for the humerus.

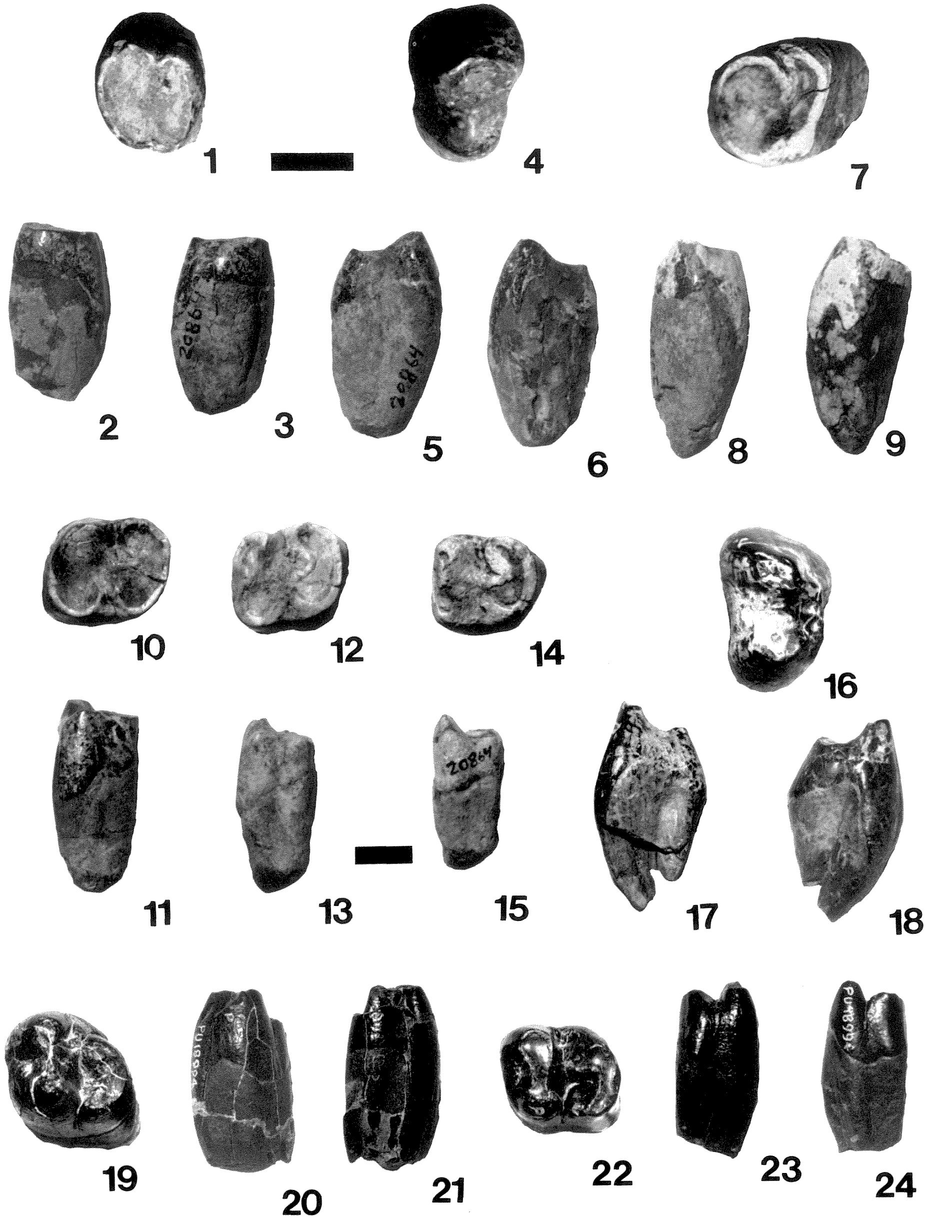


PLATE 39. The dentition of *Ectoganus gliriformis lobdelli.*

1, 3	PU 20864, left M$^{2(?)}$: *1,* occlusal view; *2,* anterior view; *3,* posterior view.
4–6	PU 20864, left P$_{2(?)}$: *4,* occlusal view; *5,* anterior view; *6,* posterior view.
7–9	PU 20864, left P$_4$: *7,* occlusal view; *8,* anterior view; *9,* labial view.
10, 11	PU 20864, left M$_1$: *10,* occlusal view; *11,* labial view.
12, 13	PU 20864, left M$_2$: *12,* occlusal view; *13,* labial view.
14, 15	PU 20864, left M$_3$: *14,* occlusal view; *15,* labial view.
16–18	PU 18994, right P$_{2(?)}$: *16,* occlusal view; *17,* anterior view; *18,* posterior view.
19–21	PU 18994, right P$_4$: *19,* occlusal view; *20,* anterior view; *21,* posterior view.
22–24	PU 18994, right M$_1$: *22,* occlusal view; *23,* labial view; *24,* lingual view.

The bar between *1* and *4* is 1 cm long and is for all occlusal views.
The bar between *13* and *15* is 1 cm long and is for all anterior, posterior, labial and lingual views.

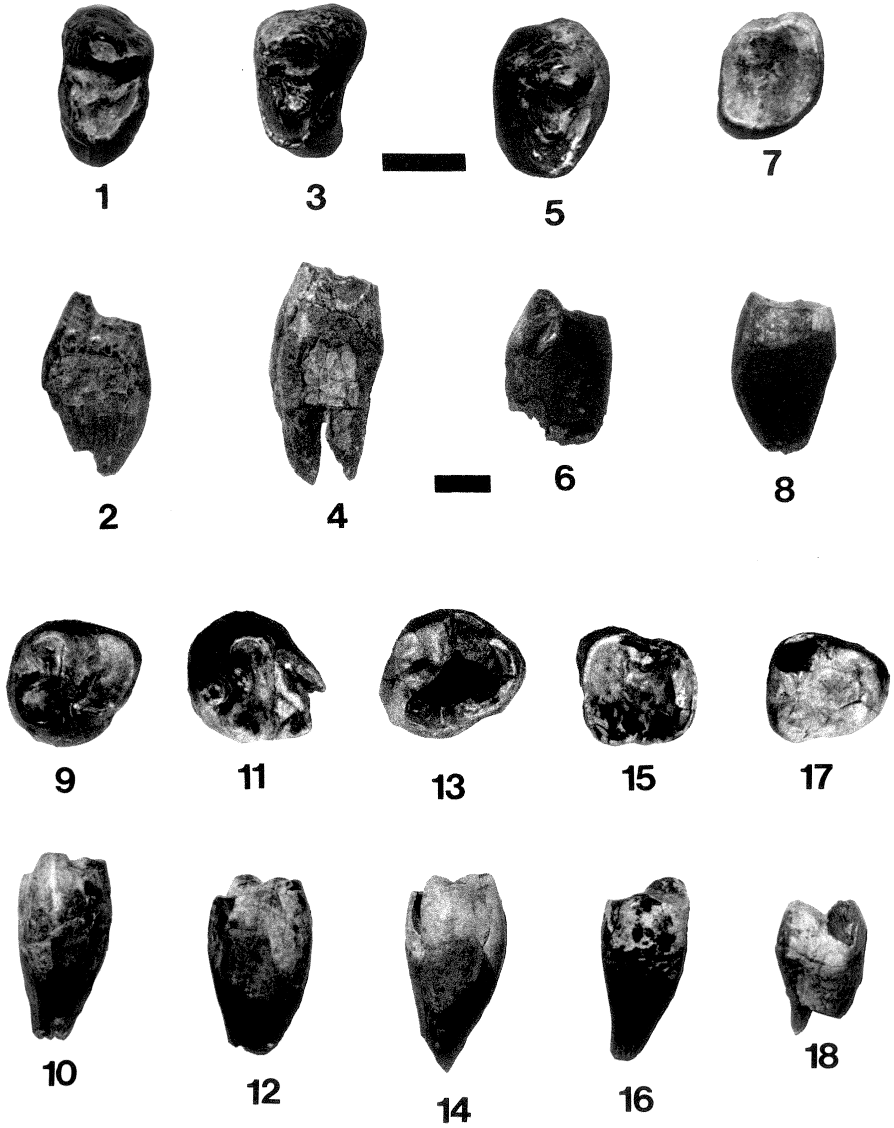


PLATE 40. The dentition of *Ectoganus gliriformis lobdelli.*

1, 2 PU 21499, left P$^{2(?)}$: *1,* occlusal view; *2,* anterior view.
3, 4 PU 21499, right P^{3}: *3,* occlusal view; *4,* posterior view.
5, 6 PU 21499, right P^{4}: *5,* occlusal view; *6,* posterior view.
7, 8 PU 21499, right M^{1}: *7,* occlusal view; *8,* anterior view.
9, 10 PU 21499, left P$_{3}$: *9,* occlusal view; *10,* anterior view.
11, 12 PU 21499, right P$_{4}$: *11,* occlusal view; *12,* labial view.
13, 14 PU 21499, left P$_{4}$: *13,* occlusal view; *14,* anterior view.
15, 16 PU 21499, right M$_{1}$: *15,* occlusal view; *16,* labial view.
17, 18 PU 21499, left M$_{3}$: *17,* occlusal view; *18,* lingual view.

The bar between *3* and *5* is 1 cm long and is for all occlusal views.
The bar between *4* and *6* is 1 cm long and is for all anterior, posterior, labial and lingual views.

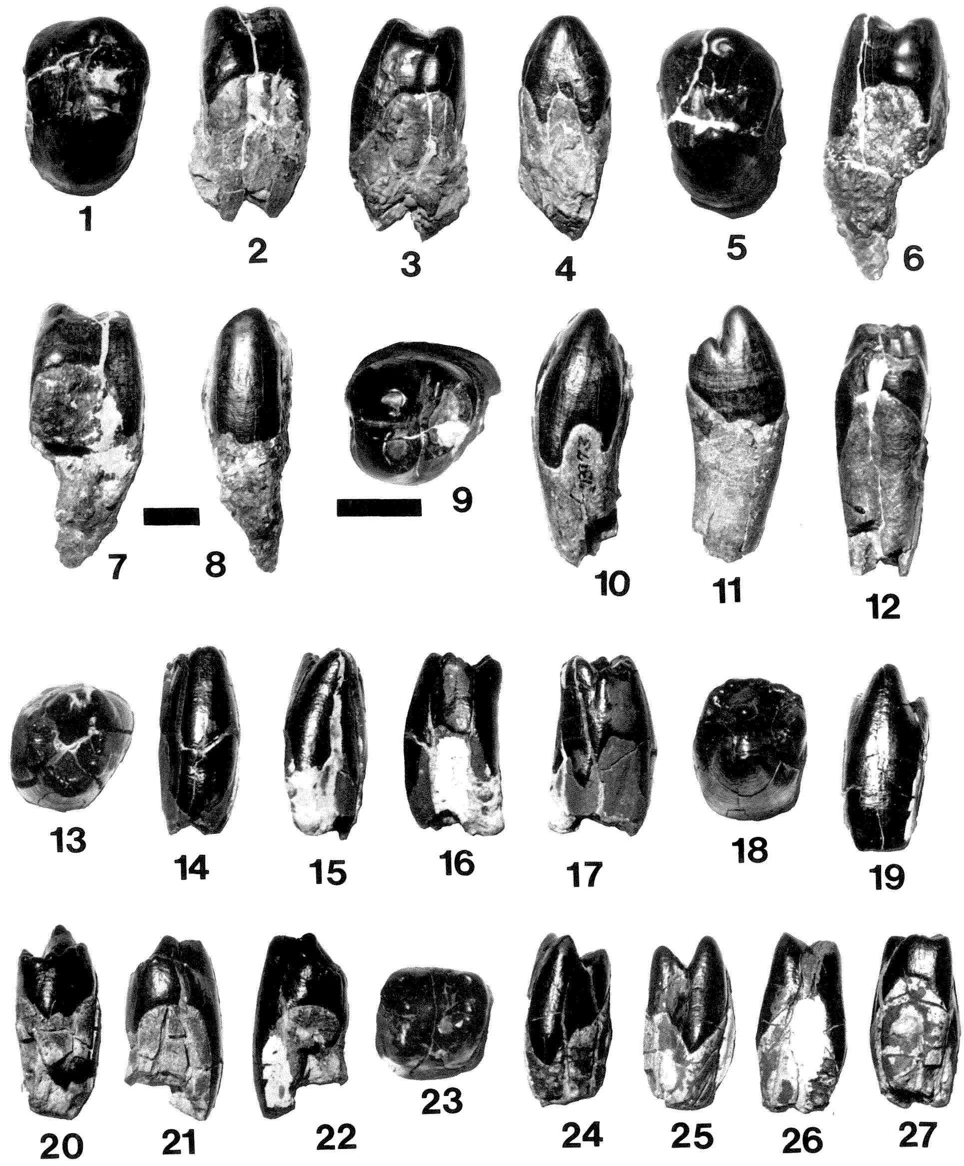
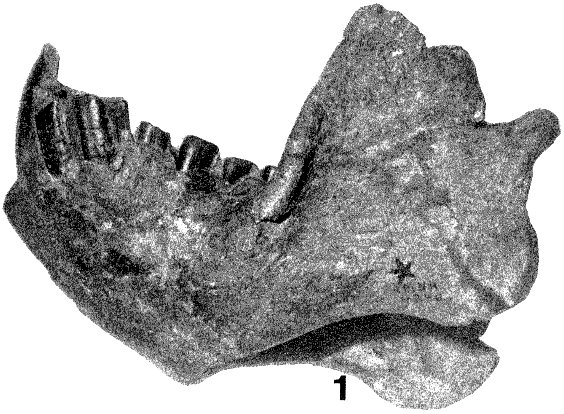


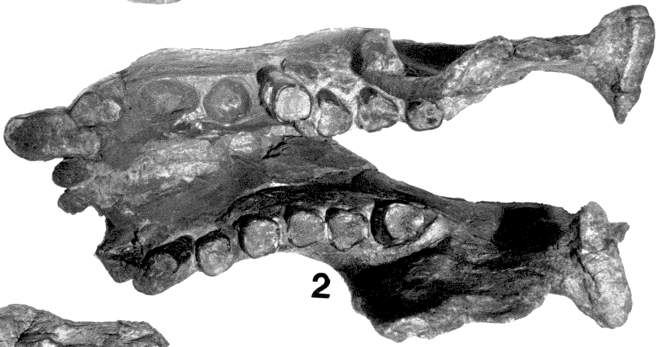
PLATE 41. Specimens referred to *Ectoganus g. gliriformis* (*1–12*) and *Ectoganus* sp. cf. *E. gliriformis* (*13–27*).

1–4	PU 13173, right $P^{3(?)}$: *1,* occlusal view; *2,* posterior view; *3,* anterior view; *4,* labial view.
5–8	PU 13173, right $P^{4(?)}$: *5,* occlusal view; *6,* anterior view; *7,* posterior view; *8,* lingual view.
9–12	PU 13173, left P_4: *9,* occlusal view; *10,* labial view; *11,* lingual view; *12,* posterior view.
13–17	UW 1823, right $P^{4(?)}$: *13,* occlusal view; *14,* lingual view; *15,* labial view; *16,* anterior view; *17,* posterior view.
18–22	UW 1823, left $P_{4(?)}$: *18,* occlusal view; *19,* labial view; *20,* lingual view; *21,* anterior view; *22,* posterior view.
23–27	UW 1823, left $M_{1(?)}$: *23,* occlusal view; *24,* labial view; *25,* lingual view; *26,* anterior view; *27,* posterior view.

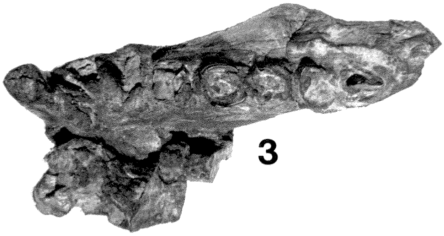
The bar between *7* and *8* is 1 cm long and is for all anterior, posterior, labial and lingual views. The bar below *9* is 1 cm long and is for all occlusal views.



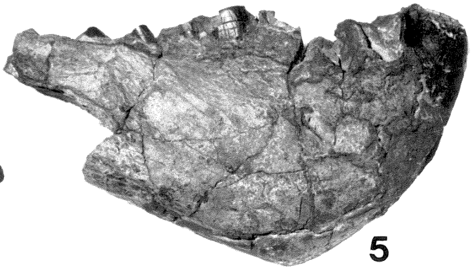
1



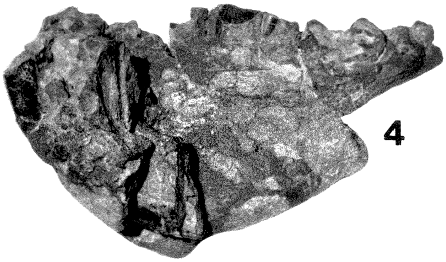
2



3



5



4

PLATE 42. Specimens referred to *Ectoganus g. gliriformis.*

1, 2 AMNH 4286, mandible with right and left I_3, right C_1, right and left P_1, left P_{2-3}, and right and left P_4–M_3: *1,* left lateral view; *2,* occlusal view.

3–5 YPM 11100, type specimen of *Dryptodon crassus,* mandible with fragmentary right and left C_1, right P_3–M_3, root of left I_3, and alveoli for right and left P_{1-2}: *3,* occlusal view; *4,* left lateral view; *5,* right lateral view.

The bar is 5 cm long.

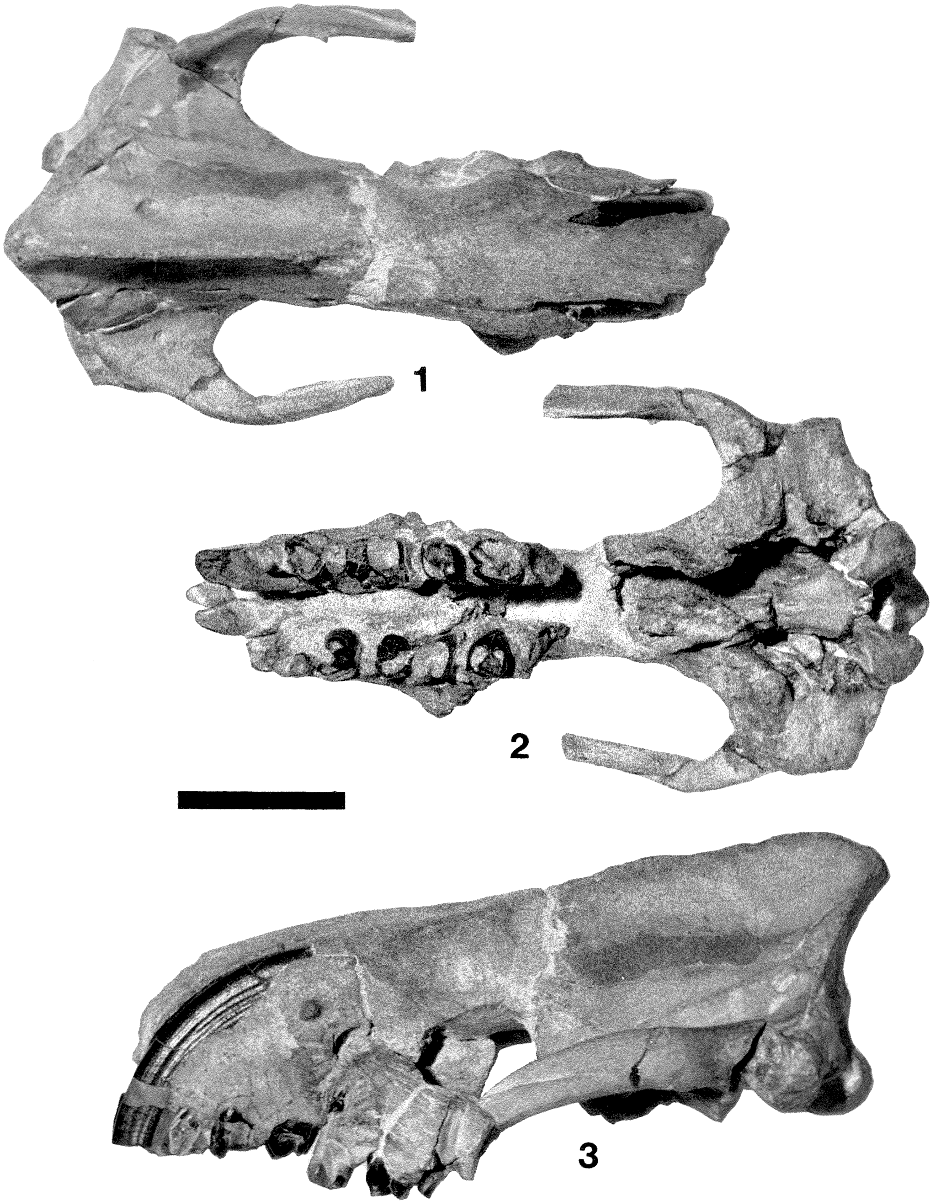


PLATE 43. The type specimen of *Ectoganus copei copei.*

1–3 USNM 12714, skull with right and left I^3–M^1 (P^{4}s unerupted), left M^2, alveoli for right M^2 and left M^3; right and left dP^4: *1,* dorsal view; *2,* ventral view; *3,* left lateral view.

The bar is 4 cm long.

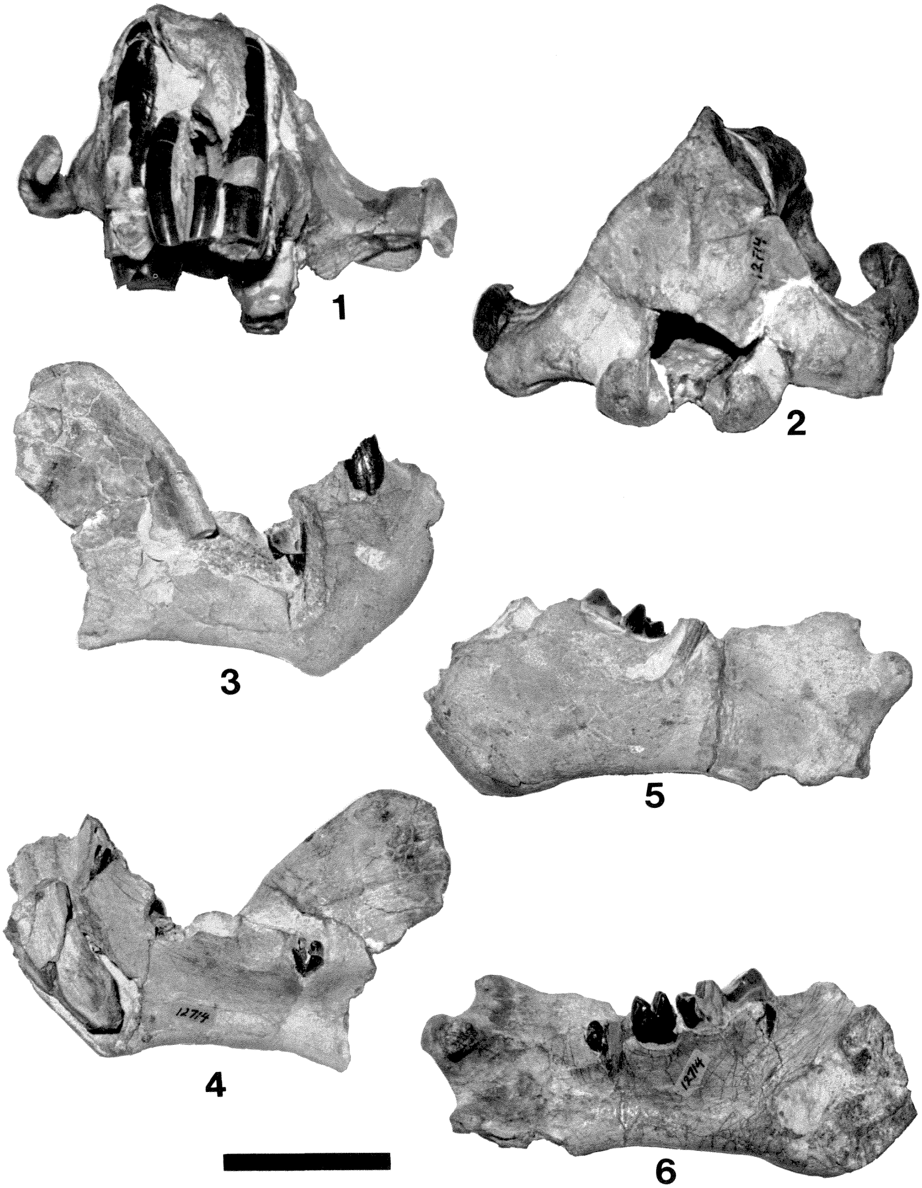


PLATE 44. The type specimen of *Ectoganus copei copei.*

1 USNM 12714, frontal view of skull.

2 USNM 12714, occipital view of skull.

3–6 USNM 12714, mandible with right P_2, left P_4 (unerupted), left dP_4, left M_{1-2}, right and left M_3, roots of right and left C_1, right P_4, alveoli for right M_{1-2}: *3,* labial view of right dentary; *4,* lingual view of right dentary; *5,* labial view of left dentary; *6,* lingual view of left dentary.

The bar is 4 cm long.

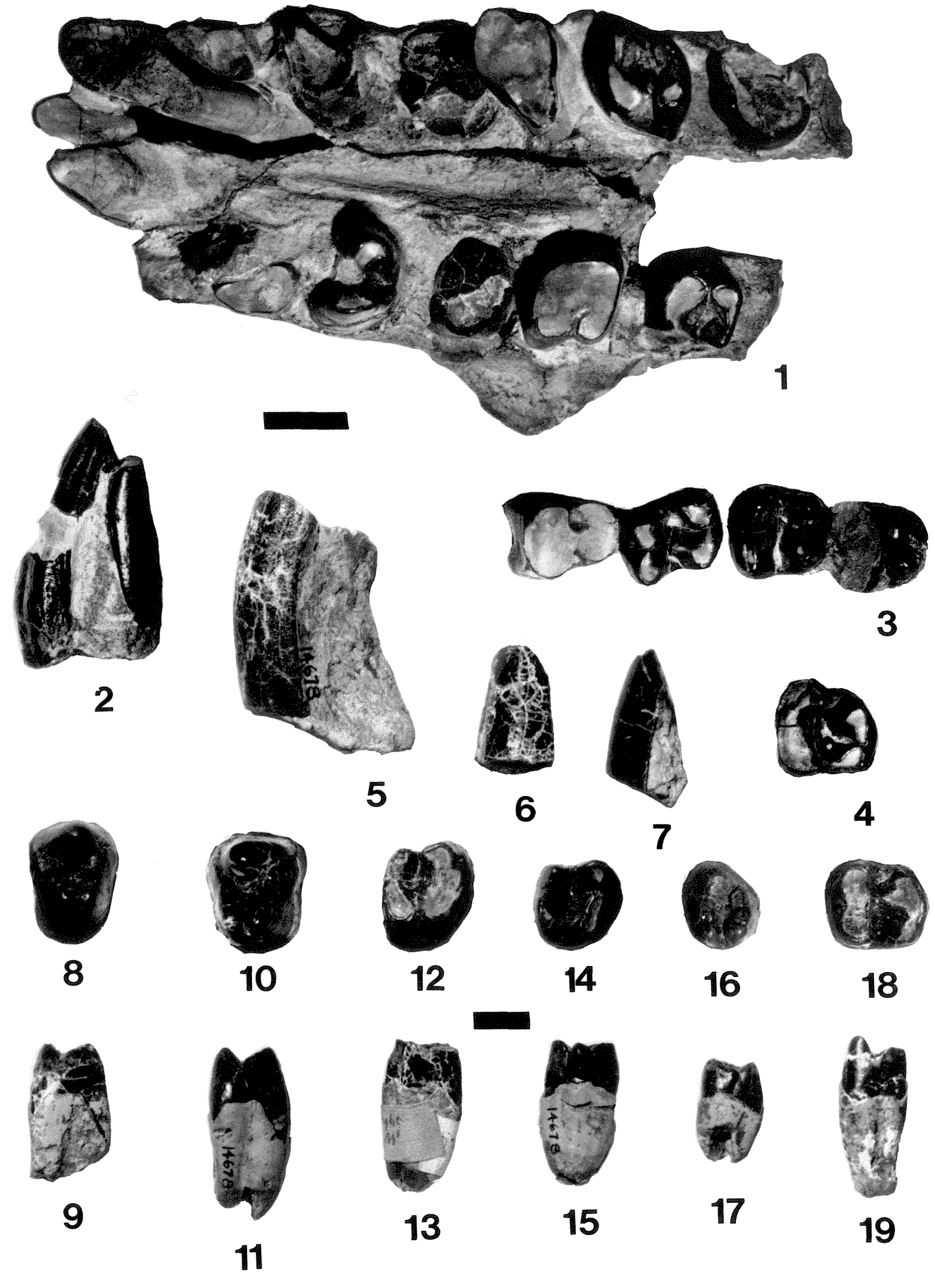


PLATE 45. The type specimens of *Ectoganus copei copei* (*1–4*) and *Ectoganus copei bighornensis* (*5–19*).

1 USNM 12714, palate with right and left I^3–M^1 (P^4s unerupted), right and left dP^4, left M^2 and alveoli for right M^2 and left M^3: occlusal view.
2 USNM 12714, left P_2: posterior view.
3 USNM 12714, left dP_4, partial M_1, M_2 and M_3 talonid: occlusal view.
4 USNM 12714, right M_1: occlusal view.
5–7 PU 14678, canine fragments.
8, 9 PU 14678, right P^3: *8,* occlusal view; *9,* posterior view.
10, 11 PU 14678, left P^3: *10,* occlusal view; *11,* anterior view.
12, 13 PU 14678, right M^1: *12,* occlusal view; *13,* posterior view.
14, 15 PU 14678, right M^2: *14,* occlusal view; *15,* posterior view.
16, 17 PU 14678, left M^3: *16,* occlusal view; *17,* posterior view.
18, 19 PU 14678, right M_1: *18,* occlusal view; *19,* lingual view.

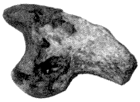
The bar below *1* is 1 cm long and is for *1–4, 8, 10, 12, 14, 16, 18.*
The bar above *13* and *15* is 1 cm long and is for *5–7, 9, 11, 13, 15, 17, 19.*

1

2

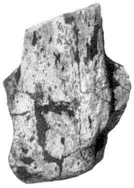
3

4



7

5



6

8

9

PLATE 46. Skeletal elements of specimens referred to *Ectoganus g. gliriformis* (*1–4*) and *Ectoganus c. copei* (*5–9*).

1, 2 USNM no number, left femur: *1,* anterior view; *2,* posterior view.
3, 4 YPM 39805, left radius: *3,* anterior view; *4,* posterior view.
5, 6 USGS 3838, left calcaneum fragment: *5,* dorsal view; *6,* ventral view.
7 USGS 3838, ungual of manus.
8 USGS 3838, ungual of manus.
9 USGS 3838, lateral view of left ulna.

The bar below *1* is 5 cm long and is for *1, 2.*
The bar below *8* is 4 cm long and is for *3–9.*

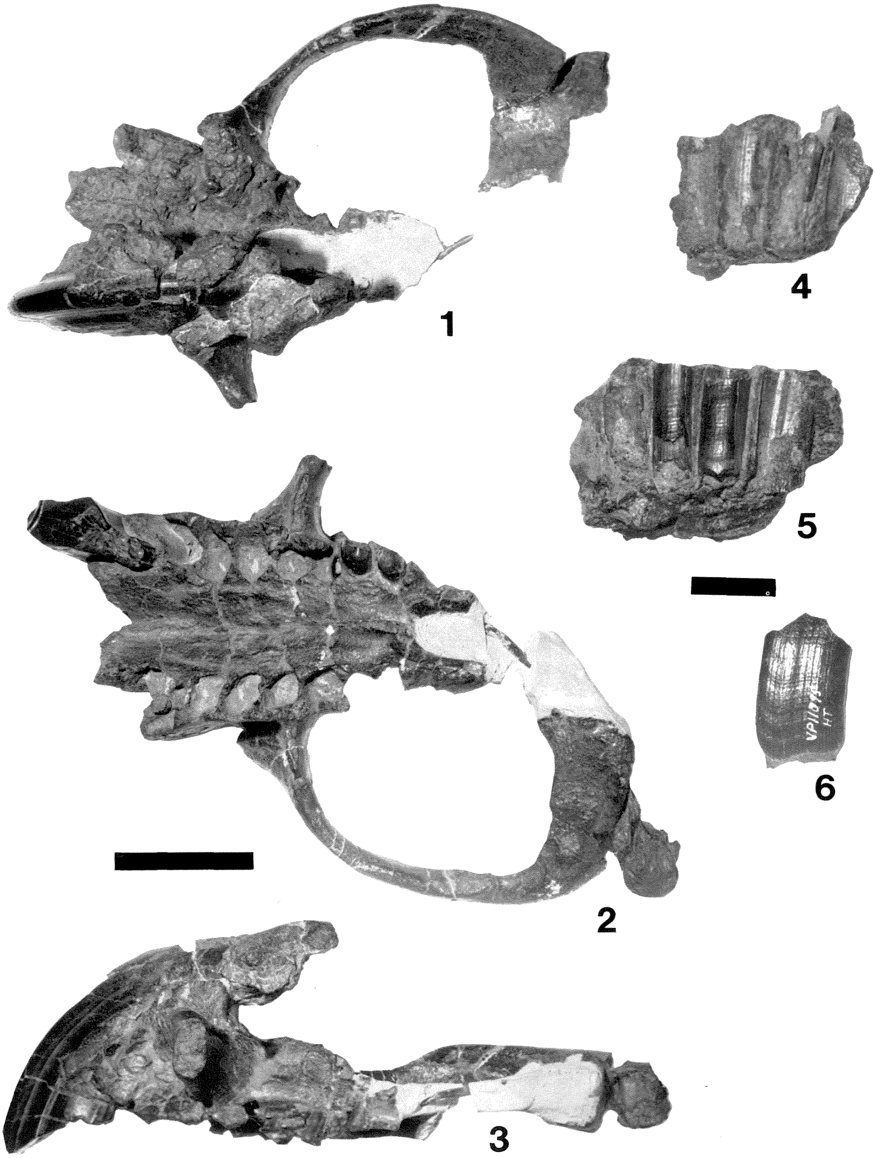
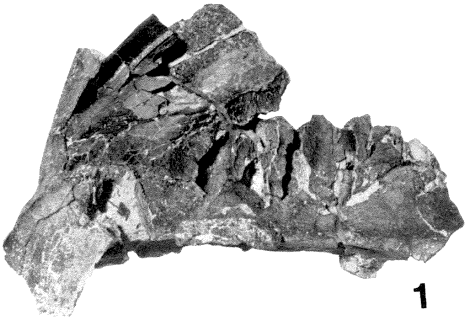


PLATE 47. The type specimen (*4–6*) and a referred specimen (*1–3*) of *Stylinodon mirus*.

1–3 FMNH P 12185, palate and skull with left C^1, M^{2-3}, and alveoli for right C^1, right and left P^1–M^1, right M^{2-3}: *1,* dorsal (internal) view; *2,* ventral view; *3,* left lateral view.

4–6 YPM 11095, right and left dentary fragments with partial right P_3–M_1, left P_3 and alveoli for right P_2, M_{2-3} and left P_2, P_4–M_1, and labial enamel fragment of left P_1: *4,* lingual view of left dentary fragment; *5,* lingual view of right dentary fragment; *6,* enamel fragment of left P_1.

The bar below *2* is 5 cm long and is for *1–3.*
The bar below *5* is 2 cm long and is for *4–6.*



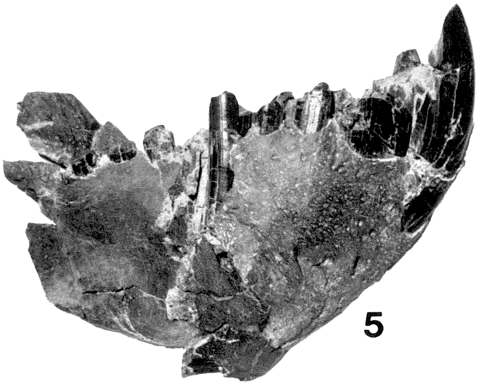
1

2

3

4

6



5

PLATE 48. Partial skull and mandible referred to *Stylinodon mirus.*

1–3 AMNH 107954, partial palate and right maxilla with roots of right C^1, M^{1-3} and alveoli for right and left I^{2-3}, right P^{1-4}: *1,* left lateral (internal) view; *2,* right lateral view; *3,* ventral view.

4 AMNH 107954, internal view of fragmentary left C^1.

5, 6 AMNH 107954, mandible with right and left I_3–P_4 and left M_{1-3}: *5,* right lateral view; *6,* occlusal view.

The bar is 5 cm long.

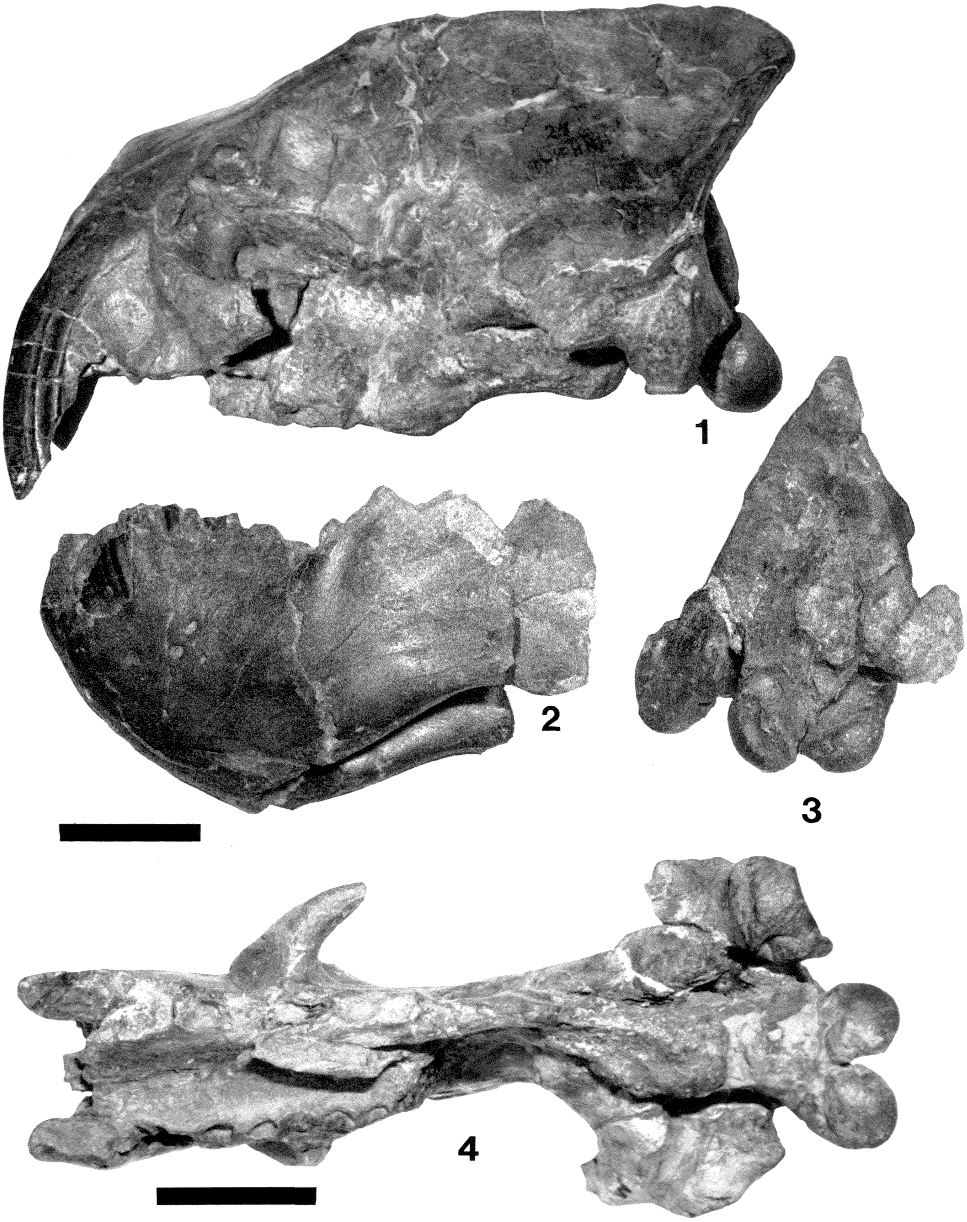


PLATE 49. DNHM V-25, a skull and mandible of *Stylinodon mirus*.

1 Left lateral view of skull.
2 Left lateral view of mandible.
3 Posterior view of skull.
4 Ventral view of skull.

The bar below *2* is 5 cm long and is for *1–3*.
The bar below *4* is 5 cm long and is for *4*.

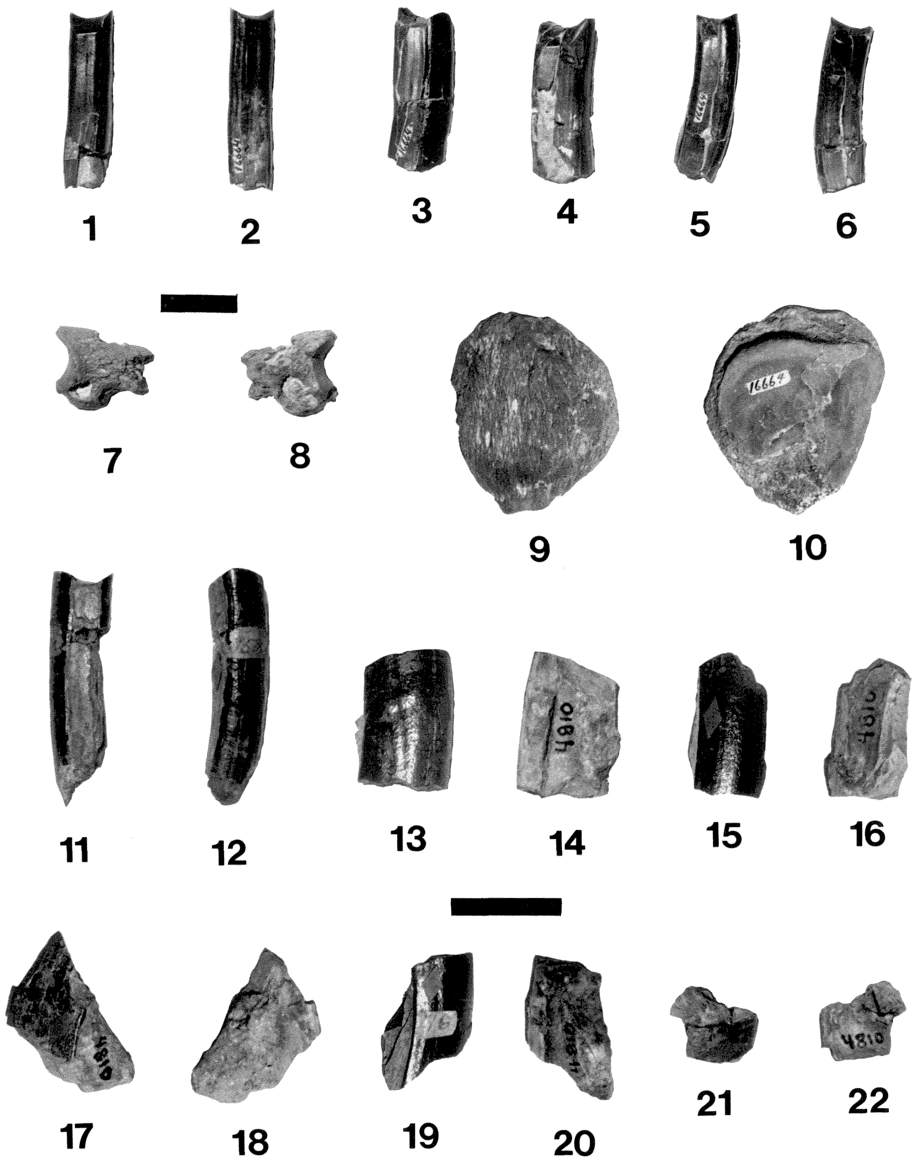
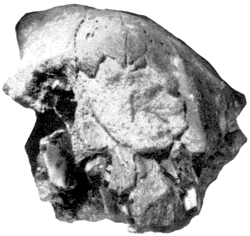


PLATE 50. Specimens referred to *Stylinodon mirus*.

1–6 USNM 16664, indeterminate cheek teeth (two views of each).
7, 8 USNM 16664, ungual of the pes: two side views.
9, 10 USNM 16664, patella: *9,* anterior view; *10,* posterior view.
11–22 AMNH 4810, the type specimen of *Calamodon cylindrifer*: *11, 12,* two views of molariform tooth, $M^{3(?)}$; *13–22,* two views each of (?)canine fragments.

The bar above *7, 8* is 2 cm long and is for *1–10.*
The bar above *19, 20* is 2 cm long and is for *11–22.*



1

2

3

4

5

PLATE 51. The type specimen of *Stylinodon inexplicatus*.

1–5 PU 16102, skull with complete and unerupted right and left M^3, and roots of right and left I^2–C^1, left P$^{1-3}$, right and left P^4–M^2: *1,* anterior view; *2,* dorsal view; *3,* ventral view; *4,* left lateral view; *5,* occipital view.

The bar is 5 cm long.

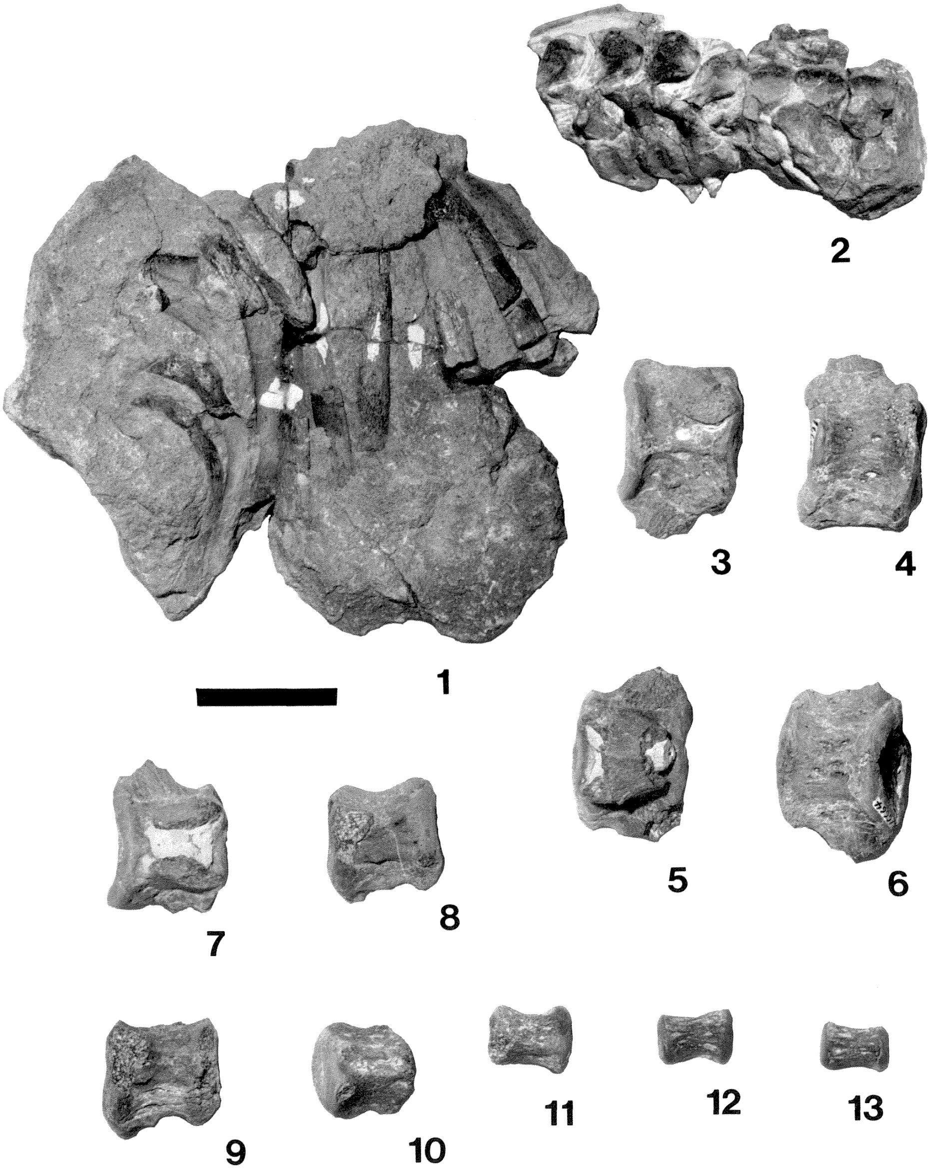


Plate 52. Skeletal elements of the type specimen of *Stylinodon inexplicatus* (*1, 2*) and those of a referred specimen of *S. mirus*.

1 PU 16102, lateral view of ribs in matrix.
2 PU 16102, left lateral view of (?)thoracic vertebrae.
3–13 USNM 16664, isolated caudal vertebrae.

The bar is 4 cm long.

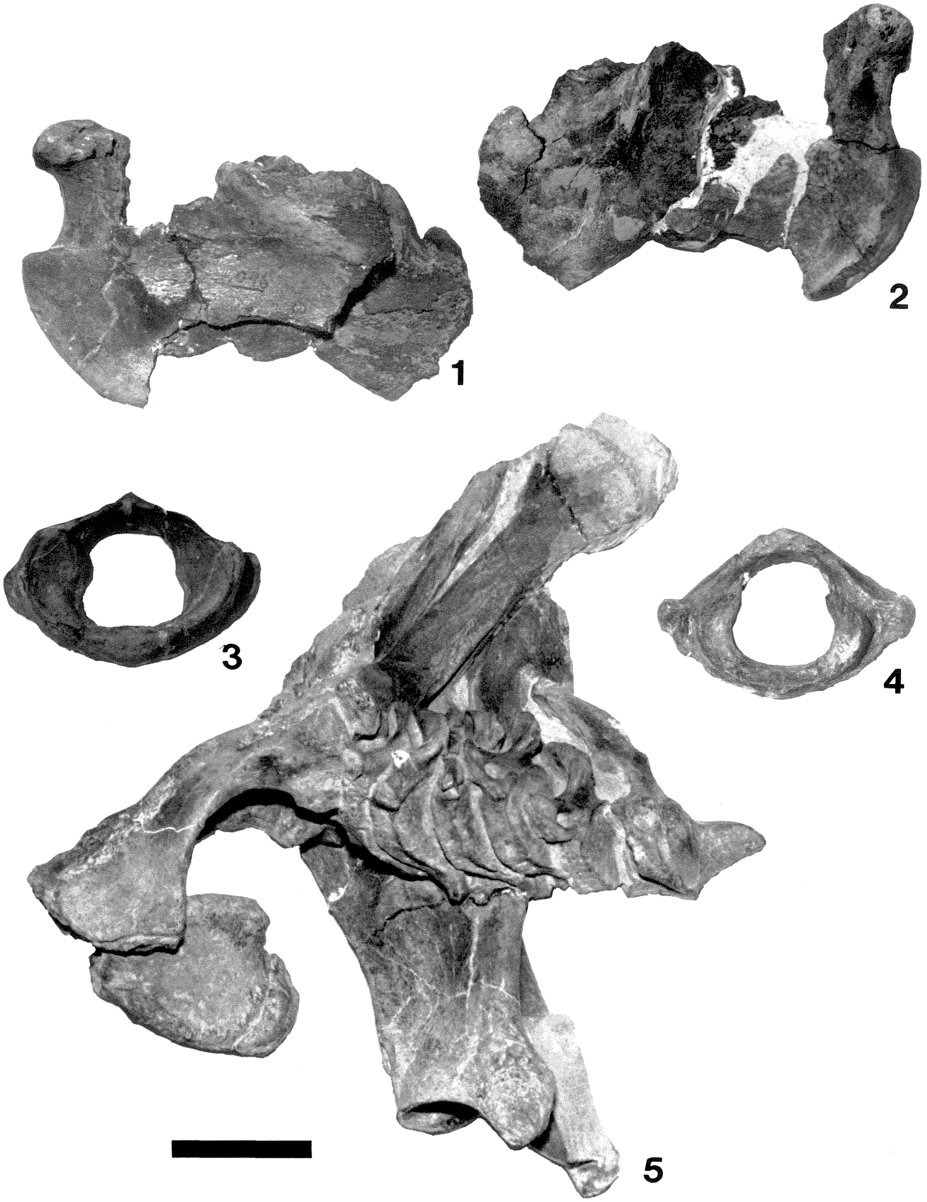


PLATE 53. YPM 11096, partial skeleton of *Stylinodon mirus*.

1, 2 Left dentary with alveoli for C_1, P_3–M_3: *1,* lingual view; *2,* labial view.
3 Anterior view of atlas.
4 Posterior view of atlas.
5 Right lateral view of axis, next five cervical vertebrae, first dorsal vertebra, left scapula, first ribs and manubrium of the sternum.

The bar is 5 cm long.

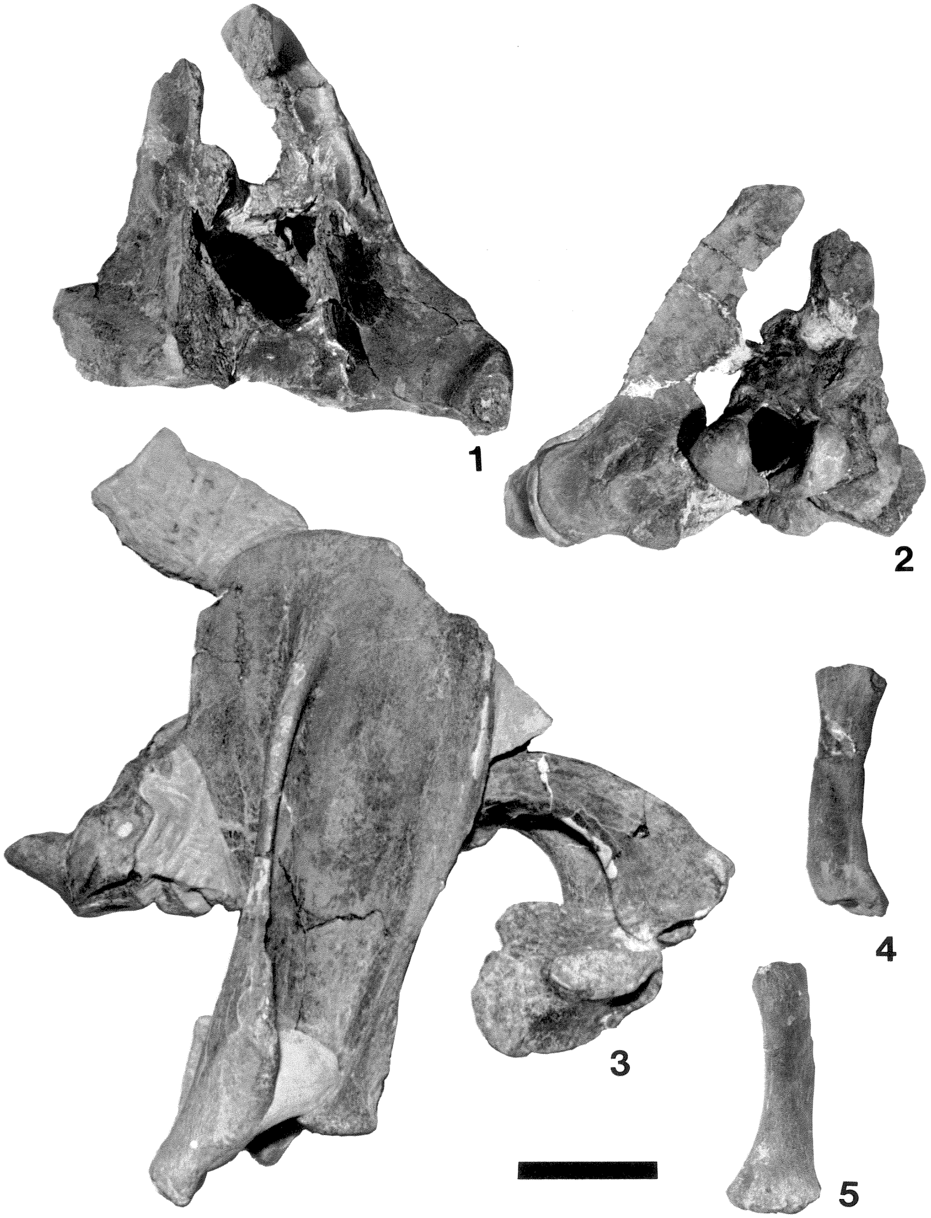


PLATE 54. YPM 11096, partial skeleton of *Stylinodon mirus*.

1, 2 Occiput of skull: *1,* anterior (internal) view; *2,* posterior view.

3 Left lateral view of axis, left scapula, first ribs and manubrium of the sternum.

4, 5 Unidentified bone fragment.

The bar is 5 cm long.

PLATE 55. YPM 11096, partial skeleton of *Stylinodon mirus*.

1, 2 Left humerus: *1,* anterior view; *2,* posterior view.

3, 4 Left radius: *3,* anterior view; *4,* posterior view.

5, 6 Left ulna: *5,* internal view; *6,* external view.

The bar is 5 cm long.

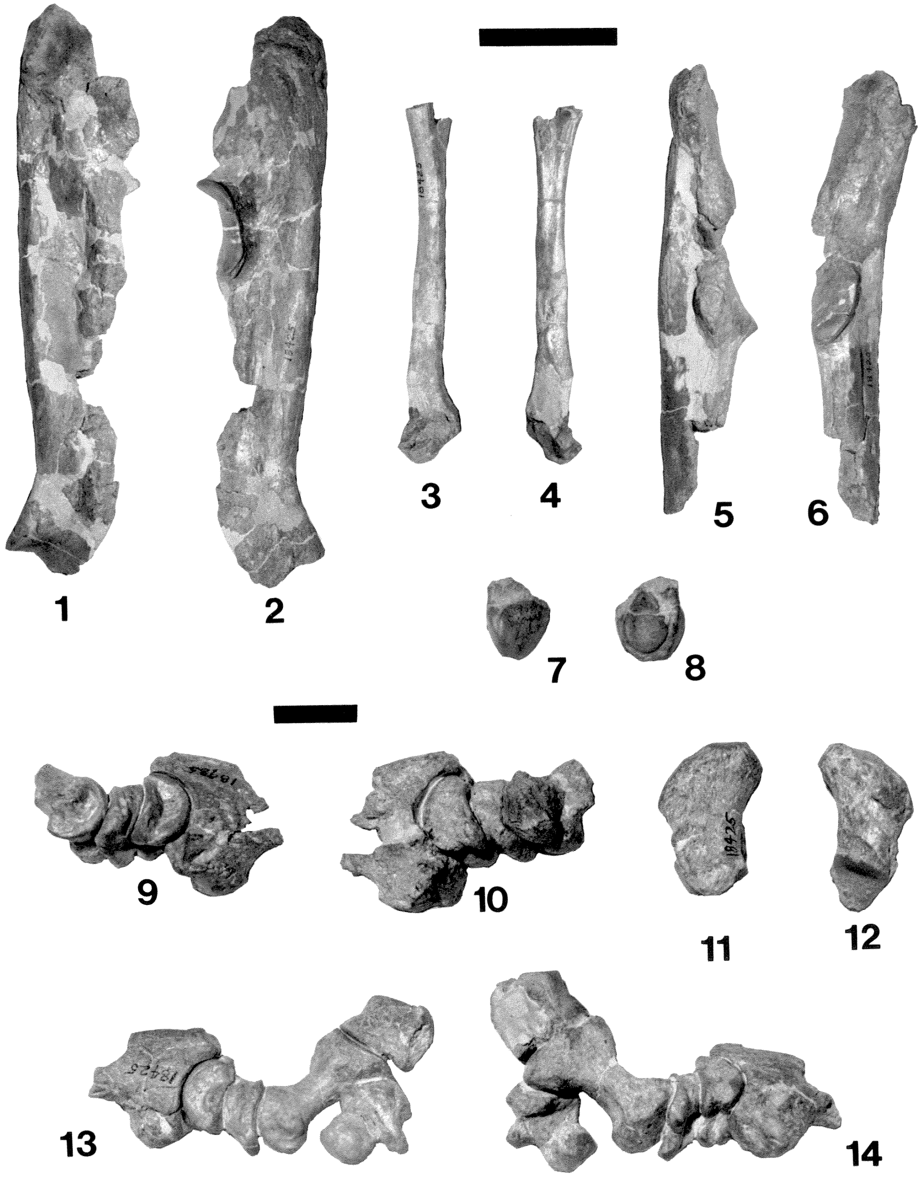


PLATE 56. USNM 18425, partial skeleton of undetermined stylinodont, cf. *Stylinodon mirus.*

1, 2 Left ulna: *1,* internal view; *2,* external view.
3, 4 Left fibula: *3,* external view; *4,* internal view.
5, 6 Right ulna: *5,* external view; *6,* internal view.
7, 8 Right scaphoid.
9, 10 (?)Third digit: *9,* external view; *10,* internal view.
11, 12 Left pisiform.
13, 14 Left digit with unciform and fifth metacarpal: *13,* external view; *14,* internal view.

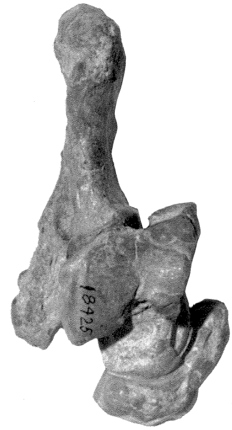
The bar above *4* is 5 cm long and is for *1–6.*
The bar above *9, 10* is 2 cm long and is for *7–14.*

PLATE 57. USNM 18425, partial skeleton of undetermined stylinodont, cf. *Stylinodon mirus*.

1, 2 Left femur: *1,* anterior view; *2,* posterior view.
3, 4 Right tibia: *3,* internal view; *4,* external view.
5, 6 Right fibula: *5,* external view; *6,* internal view.

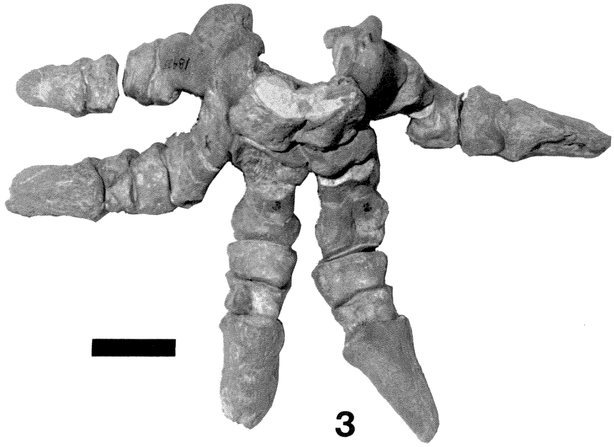
The bar is 5 cm long.

2



1

4



3

5

PLATE 58. USNM 18425, partial skeleton of undetermined sylinodont, cf. *Stylinodon mirus*.

1–3 Right hind foot: *1,* anterior view of calcaneum, astragalus and navicular; *2,* external view of calcaneum, astragalus and navicular; *3,* anterior view of tarsals and digits.

4, 5 Crushed left tibia, calcaneum and tarsals: *4,* internal view; *5,* external view.

The bar below *3* is 2 cm long and is for *1–3.*
The bar below *5* is 5 cm long and is for *4, 5.*

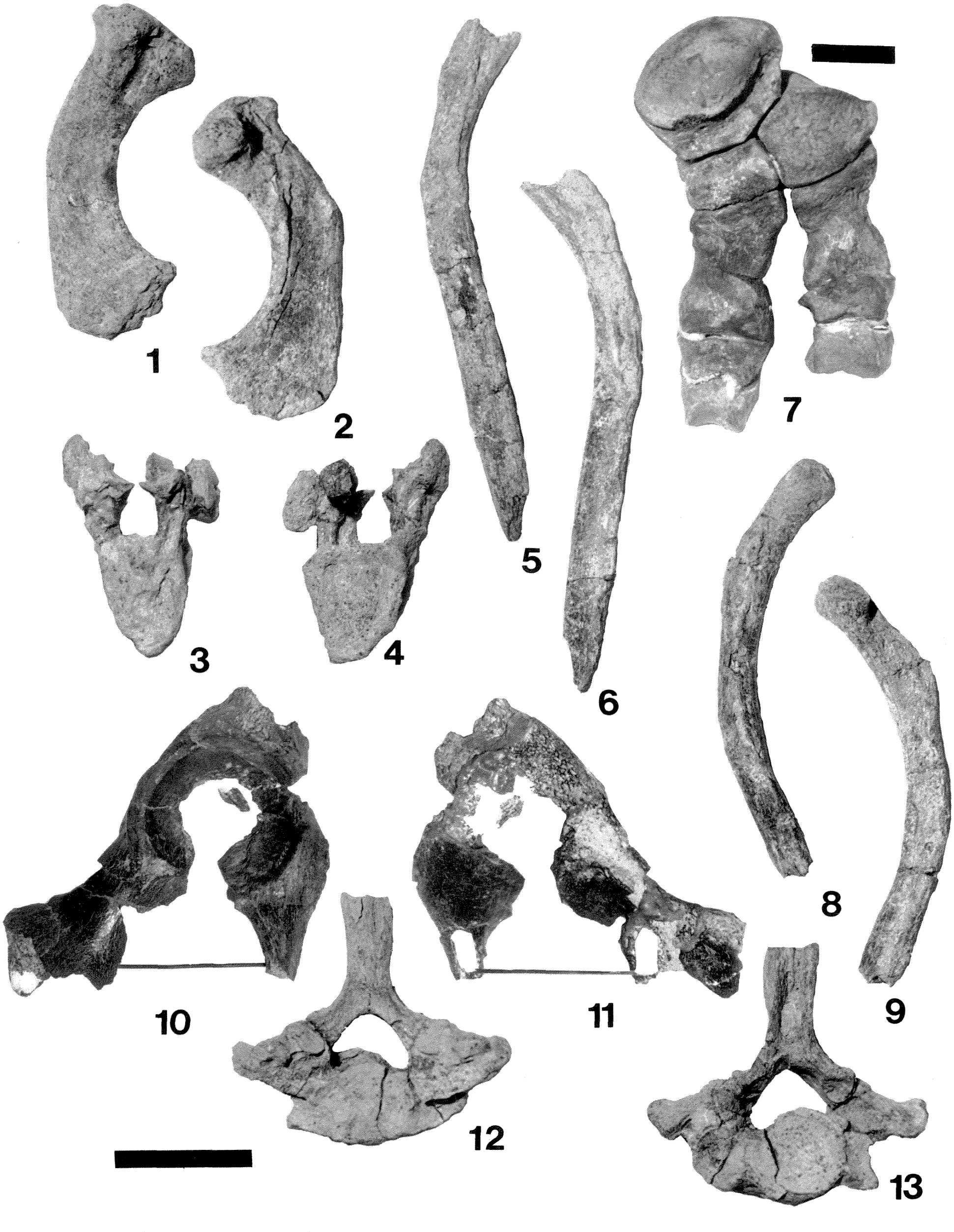


PLATE 59. Skeletal elements of specimens referred to *Stylinodon mirus*.

1, 2	AMNH 107954, right first rib: *1,* anterior view; *2,* posterior view.
3, 4	AMNH 107954, posterior thoracic vertebra: *3,* anterior view; *4,* posterior view.
5, 6	AMNH 107954, rib fragment.
7	YPM 11096, partial left manus, anterior view.
8, 9	AMNH 107954, rib fragment.
10, 11	USNM 16664, (?)right acetabular part of pelvis: *10,* external view; *11,* internal view.
12, 13	AMNH 107954, anterior thoracic vertebra: *12,* anterior view; *13,* posterior view.

The bar above *7* is 2 cm long and is for *7.*
The bar below *12* is 5 cm long and is for *1–6, 8–13.*

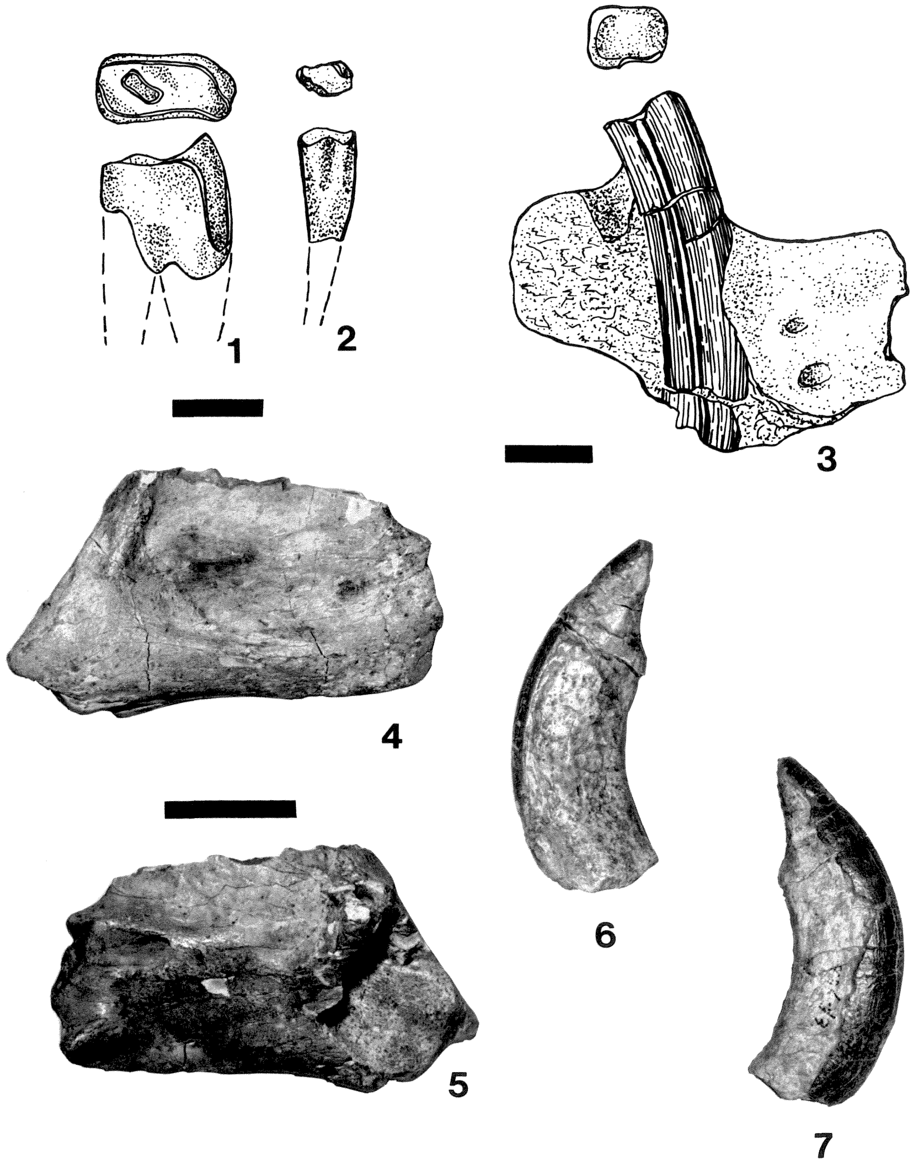


PLATE 60. The type specimens of *Entocasmus heterogenidens* (*1, 2*), *Chungchienia sichuanica* (*3*), *Calamodon europaeus* (*4, 5*) and a referred specimen of *Calamodon europaeus* (*6, 7*).

1, 2 The type specimen of *Entocasmus heterogenidens*: *1,* occlusal and lateral views of premolar; *2,* occlusal and lateral views of incisor (after Ameghino 1891, p. 139, fig. 37).

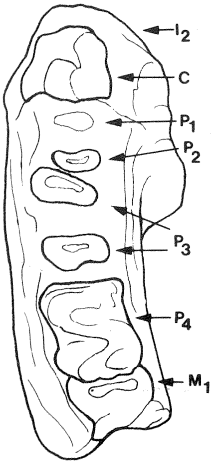
3 IVPP V. 2767, the type specimen of *Chungchienia sichuanica*: occlusal and external views of molariform tooth and right (?)dentary fragment (drawn from a cast of the specimen, AMNH 107906).

4, 5 BNM Ef. 983, the type specimen of *Calamodon europaeus,* left dentary fragment: *4,* external view; *5,* internal view.

6, 7 BNM Ef. 982, right lower incisor: *6,* external view; *7,* internal view.

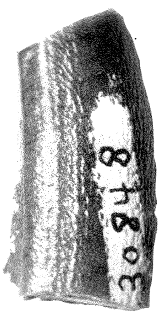
The bar below *1* is 1 cm long and is for *1, 2.*
The bar below *3* is 2 cm long and is for *3.*
The bar below *4* is 2 cm long and is for *4–7.*

1

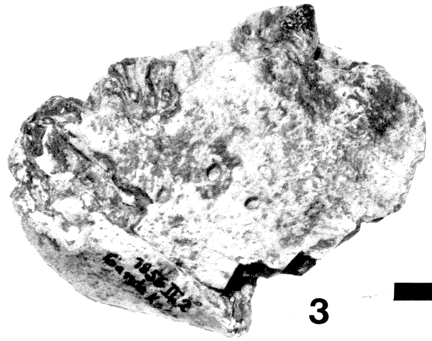


2

5

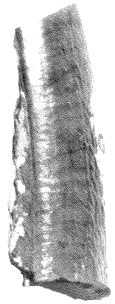


6

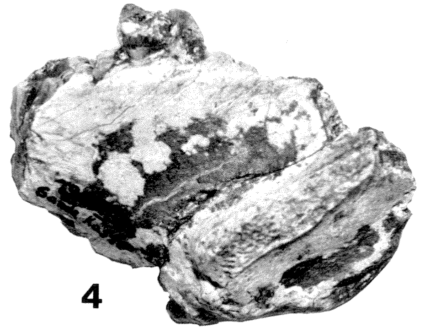


3

7

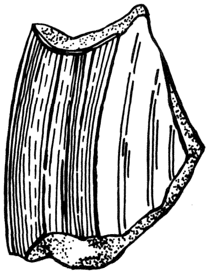


8



4

9



10

Plate 61. Specimens which probably are tillodonts but have been referred to the Taeniodonta.

1–4 BAWSM 1956 II 2, the type specimen of *Basalina basalensis*, left dentary fragment with I_2 alveolus, C_1 root, P_1 alveolus, P_{2-3} roots, partial P_4 and partial M_1 root: *1,* occlusal view; *2,* interpretation of the tooth formula; *3,* labial view; *4,* lingual view.

5 YPM no number, enamel fragment of *Trogosus* I_2: lateral view.

6–8 MPM 30848, enamel fragment of a tillodont incisor or a taeniodont canine from Ellesmere Island: *6,* lateral view; *7,* internal view of enamel fragment showing the internal dentine; *8,* oblique edge-on view.

9, 10 IVPP V. 2766, probable tillodont I_2 from China: *9,* cross-sectional view; *10,* lateral view (after Chow 1963b, p. 100, fig. 2, and photographs taken by P. D. Gingerich).

The bar below *5* is 1 cm long and is for *5.*
The bar between *3* and *7* is 2 cm long and is for *1–4, 6–8.*
The bar below *9* is 2 cm long and is for *9, 10.*

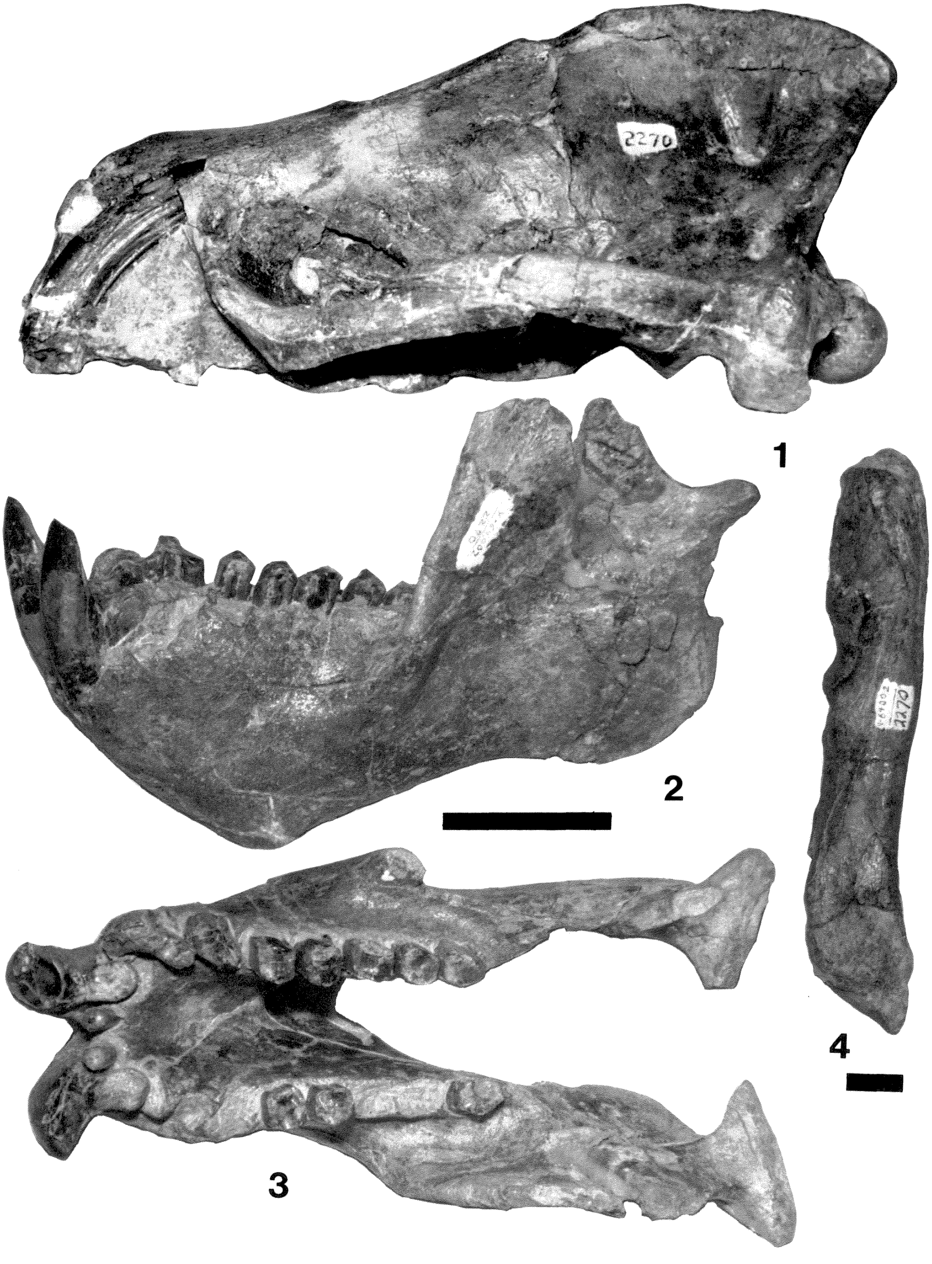


PLATE 62. UW 2270, a skull, mandible and ulna of *Stylinodon mirus*.

1 Left lateral view of skull.
2 Left lateral view of mandible.
3 Occlusal view of mandible.
4 Medial view of right ulna.

The bar below *2* is 5 cm long and is for *1–3*.
The bar below *4* is 2 cm long and is for *4*.

PLATE 63. UW 2270, a skull of *Stylinodon mirus*.

1 Dorsal view of skull.

2 Ventral view of skull.

The bar is 5 cm long.

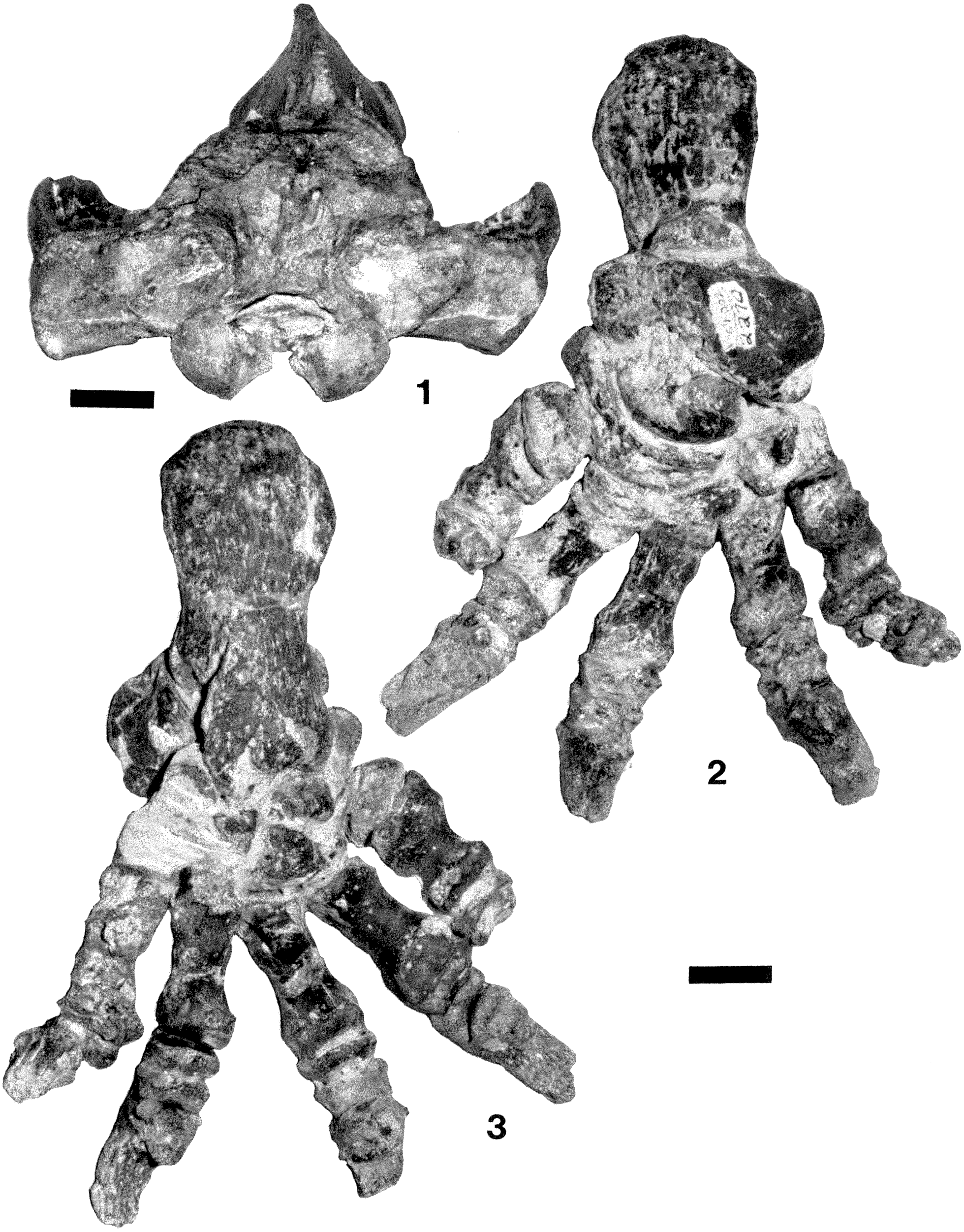


PLATE 64. UW 2270, a skull and left pes of *Stylinodon mirus.*

1 Posterior view of skull.
2 Dorsal view of left pes.
3 Ventral view of left pes.

The bar below *1* is 2.5 cm long and is for *1.*
The bar below *2* is 3 cm long and is for *2* and *3.*

Plate 65. UW 2270, skeletal elements of *Stylinodon mirus*.

1 Anterior view of right femur.
2 Anterior view of left femur.
3 Posterior view of right femur.
4 Posterior view of left femur.
5 Anterior view of left tibia and fibula.
6 Posterior view of left fibula and tibia.

The bar is 5 cm long.