Life Sciences Contributions
Royal Ontario Museum

122

Tertiary Mammals
of Saskatchewan
Part V: The Oligocene
Entelodonts

Loris S. Russell

**ROYAL ONTARIO MUSEUM LIFE SCIENCES PUBLICATIONS
INSTRUCTIONS TO AUTHORS**

Authors are to prepare their manuscripts carefully according to the following instructions. Failure to do so will result in the manuscript's being returned to the author for revision. All manuscripts are considered on the understanding that if accepted they will not be offered for publication elsewhere.

1. **GENERAL** Papers for publication are accepted from ROM staff members, Research Associates, or from researchers reporting on work done with ROM collections. In exceptional cases, monographic works on the flora and/or fauna of Ontario will be considered for publication by authors not affiliated with the ROM. Authors are expected to write clearly and concisely, and to omit all material not essential for an understanding of the main theme of the paper.
2. **FORMAT** Manuscripts are to be typed double-spaced (including captions, synonymies, literature cited, and tables) on 11" × 8½" paper with a 1½" margin on all sides. Three xerox copies are to be submitted to the Chairman of the Editorial Board, and the original retained by the author(s). A separate sheet is to be submitted giving author(s) names, affiliation, title of publication, series in which it is to appear, number of typed pages, number of tables, and number of figures. Manuscripts should normally be organized in the following order: Table of Contents, Abstract, Introduction, Materials and Methods, Results, Discussion, Conclusions, Summary (if paper is long), Acknowledgements, Literature Cited, and Appendices. Authors are encouraged to include foreign language translations of the Summary where appropriate. Headings of sections are to be left-justified to the text margin. The first line of the first paragraph in each new section should not be indented. Text-figures are referred to as "Fig. 1". Literature cited in the text is in the form "Jones (1972)" or "(Jones, 1972)" or "(Smith, 1960:71-79, fig. 17)".
3. **STANDARD SOURCES** The primary source for decisions on format and style is **A Guide for Contributors and Editors of ROM Life Sciences Publications**, available from the Chairman of the Editorial Board. Otherwise, consult CBE (AIBS) Style Manual (3rd Edition). Other standard sources are as follows: for English spelling (Concise Oxford Dictionary), for Canadian place names and coordinates (Gazetteer of Canada), and for spelling of geographic names (Times [London] Atlas).
4. **ABSTRACT** All papers are preceded by a short and factual abstract, about 3 per cent as long as the text, but not longer than 400 words. The abstract is to be followed by four to six keywords enclosed in brackets.
5. **TAXONOMY** The name of a taxon is given in full in headings, where it appears for the first time, or when the name begins a paragraph. Use authority and date if appropriate, with first mention of each taxon and not thereafter. Taxonomic papers follow the layout in Life Sciences Contribution 99, particularly the synonymies.
6. **LITERATURE CITED** References in the text cite author and date and are enclosed in parentheses (Smith, 1978). Complete references are listed in alphabetical order by author at the end of the paper. When there are two or more citations for an author, the works are listed chronologically. Names of journals are not abbreviated. Consult Life Sciences Contributions beginning with 117 for correct bibliographic form.
7. **TABLES** All tables are numbered consecutively in arabic numerals in numerical order of their first mention in the text. Mark the appropriate text location of each table with a marginal notation. Each table is typed on a separate sheet. Avoid footnotes etc., to tables by building them into the title.
8. **FIGURES** All figures are numbered consecutively in arabic numerals. Component photographs or drawings are labelled sequentially in upper case letters. Mark the appropriate text location of each figure with a marginal notation. The intended reduction for figures is ideally one and a half to two times. All labelling on figures is in blue pencil and **not** inked or letaset. Halftones must be photographic prints of high contrast on glossy paper. Authors are to submit 10" × 8" copies with the MS and retain originals until they are requested. Figure captions are to appear grouped together on a separate page at the end of the MS.

LIFE SCIENCES CONTRIBUTIONS
ROYAL ONTARIO MUSEUM
NUMBER 122

LORIS S. RUSSELL Tertiary Mammals
 of Saskatchewan
 Part V: The Oligocene
 Entelodonts

ROM

ROYAL ONTARIO MUSEUM PUBLICATIONS IN LIFE SCIENCES

The Royal Ontario Museum publishes three series in the Life Sciences:

LIFE SCIENCE CONTRIBUTIONS, a numbered series of original scientific publications including monographic works.

LIFE SCIENCES OCCASIONAL PAPERS, a numbered series of original scientific publications, primarily short and usually of taxonomic significance.

LIFE SCIENCES MISCELLANEOUS PUBLICATIONS, an unnumbered series of publications of varied subject matter and format.

All manuscripts considered for publication are subject to the scrutiny and editorial policies of the Life Sciences Editorial Board, and to review by persons outside the Museum staff who are authorities in the particular field involved.

LIFE SCIENCES EDITORIAL BOARD

Senior Editor: J. H. McANDREWS

Editor: R. D. JAMES

Editor: C. McGOWAN

LORIS S. RUSSELL is Curator Emeritus in the Department of Vertebrate Palaeontology, Royal Ontario Museum, Toronto, Ontario.

Canadian Cataloguing in Publication Data

Russell, Loris S., 1904—

The oligocene entelodonts

(Tertiary mammals of Saskatchewan ; pt. 5)

(Life sciences contributions ; no. 122 ISSN 0384-8159)

Bibliography: p.

ISBN 0-88854-254-2

1. Artiodactyla, Fossil. 2. Paleontology — Oligocene.
3. Paleontology — Saskatchewan. I. Royal Ontario
Museum. II. Title. III. Series. IV. Series: Life
sciences contributions ; no. 122.

QE882.U3R88

569.73

C80-094134-9

Publication date: 7 March 1980

ISBN 0-088854-254-2

ISSN 0384-8159

© The Royal Ontario Museum, 1980

100 Queen's Park, Toronto, Canada M5S 2C6

PRINTED AND BOUND IN CANADA AT THE ALGER PRESS

Tertiary Mammals of Saskatchewan

Part V: The Oligocene Entelodonts

Abstract

Archaeotherium coarctatum (Cope) has been known since 1884 from fragmentary remains found in the Lower Oligocene Cypress Hills Formation of Saskatchewan. New material, consisting of three skulls and four mandibles in the Royal Ontario Museum, and a skull and mandible in the National Museum of Natural Sciences, Ottawa, permit a full description of the cranial and dental anatomy. This shows that the species has a number of distinctive characteristics, the most conspicuous being the double sagittal crest, and the absence of the posterior mental process on the mandible. Compared with White River entelodonts, *A. coarctatum* shows resemblances to *A. mortoni* Leidy, but is somewhat less advanced towards the distinctive entelodont characteristics. Apart from the aberrant sagittal crest, the structure of *A. coarctatum* is compatible with its status as one of the oldest known North American entelodonts.

Introduction

The Entelodontidae are medium- to large-sized bunodont artiodactyls known from the Lower and Middle Oligocene of Europe, the Lower Oligocene to Lower Miocene of North America, and Lower Eocene to Upper Oligocene of Asia. They are sometimes called giant pigs, but they show more resemblances to the Tayassuidae and the Hippopotamidae than to the Suidae. From all three of these extant families the entelodonts are clearly distinguished by the foot structure, there being only two digits, numbers 3 and 4, on both front and hind feet.

Entelodont remains were first found in the Oligocene of Ronzon, near Puy-en-Velay, Haute-Loire, France. There is still some uncertainty as to the priority of the names that have been applied to these fossils. Aymard named them *Entelodon magnum* in a publication that usually bears the date 1848. In 1847 Pomel described similar material as *Elotherium magnum*. However, Lucy Bush (1903) concluded that 1848 is only the date on separates of Aymard's paper, and that the whole volume XII of the Annals was printed in 1846. Against this interpretation, Peterson (1909) has noted that Aymard's paper includes a footnote reference to a publication of late 1847. Thus Pomel's 1847 description could have priority after all, but Aymard's account is much more adequate, and on this basis Peterson chose to use *Entelodon* rather than *Elotherium* as the valid generic name. This practice has been followed by subsequent authors, such as Troxell (1920), Sinclair (1921, 1922), and Scott (1940).

The first description of American entelodonts was published by Leidy in 1850 and more fully in 1853. Originally he named his material *Archaeotherium mortoni* but subsequently abandoned his generic name for Pomel's *Elotherium*. Leidy's specimens came from the Oligocene of the White River badlands in what is now South Dakota. Many fine specimens, including complete skeletons, came from this provenience in subsequent years and usually the describers followed Leidy's example and called them *Elotherium*. It was Peterson (1909) who pointed out important differences between these American specimens and the European *Entelodon* (*Elotherium*), and on these distinctions revived Leidy's genus *Archaeotherium*. This procedure was supported by Troxell (1920), who defined the genus as distinct from other American genera as well as from *Entelodon*. Scott's (1940) monograph stabilized the nomenclature of the family but still left in question the status of the Canadian material.

The first discovery of entelodont remains in Canada was made by T.C. Weston of the Geological Survey of Canada in 1884 in the Cypress Hills, District of Assiniboia, North-West Territory. In 1905, when part of the Territory was divided into provinces, this area of the Cypress Hills came within the province of Saskatchewan. Cope (1885) referred Weston's specimens, a right M¹ and a lower canine, to *Elotherium mortoni* (Leidy). In 1888 Weston collected an incomplete left mandibular ramus with P₁ to M₃. Cope (1889) made this the type of a new species, *Elotherium coarctatum*, but when in 1891 he published a description and illustrations, he used the name *Elotherium arctatum*. The locality is given as "near the head of the Swift Current Creek." This stream originates in a swampy area of a wide valley between Southfork station and the town of Eastend. The Cypress Hills escarpment forms the northwest side of this valley, and the most productive locality for fossils is the nearby promontory known as Anxiety Butte. Weston's specimen probably came from this vicinity. Lawrence Lambe collected in the Cypress Hills in 1904, and obtained additional entelodont jaw fragments and teeth, which he described in 1908. For many years the Cope and Lambe material was all that was known of "*Elotherium*" *coarctatum*, but various authors have commented on the species. Peterson (1909) assigned it to *Archaeotherium*, Troxell (1920) to *Entelodon*, and Scott (1940) to ?*Entelodon*.

Following Lambe's expedition of 1904, occasional finds of isolated entelodont teeth were made in the Cypress Hills. In 1936 Mr. and Mrs. Fenley Hunter, of Flushing, New York, assisted by Albert C. Silberling of Harlowton, Montana, opened a quarry in a rich deposit of brontothere and other remains on the north branch of Calf Creek, on the west side of section 8, township 8, range 22, west of the 3rd meridian. Hunter was working at his own expense but on behalf of the National Museum of Canada. He returned to what he called the Hazel Quarry in 1937 and obtained additional good specimens, but entelodonts were represented in his collections only by isolated teeth. Subsequently this locality became known as the Hunter Quarry, and under that designation important collections were made by field parties from the Royal Ontario Museum, the Provincial Museum of Saskatchewan, and the National Museum of Canada. However, it was not until 1949 that L. Sternberg of the Royal Ontario Museum found significant entelodont material, a nearly complete mandible that could be referred with confidence to *Archaeotherium coarcticum*. In 1952 G.E. Lindblad, collecting for the National Museum of Canada, obtained a nearly complete skull from the Hunter Quarry. Subsequently it was found

that the ROM mandible fitted the NMC skull, so an exchange for other material was arranged in order that the two specimens could be reunited at the National Museum of Canada, where some years later they were displayed together.

In 1967 Dr. A.G. Edmund, of the Royal Ontario Museum, reopened the Hunter Quarry using power machinery. Among the many fine specimens obtained by him were a complete entelodont skull with mandible, a second fine skull, and an incomplete mandible. In 1972 a Royal Ontario Museum field party under Roger Kildark collected an almost complete entelodont skull from the Hunter Quarry, the find being made by Michael Torszok.

Systematic Description

Order Artiodactyla

Family Entelodontidae

***Archaeotherium* Leidy 1850**

SYNONYMS. *Arctodon* Leidy 1851; *Entelodon* Leidy (nec. Aymard) 1853; *Elotherium* Leidy (nec. Pomel) 1857.

GENERIC DIAGNOSIS

Entelodonts of large but not largest size. Diastema present between first and second premolars and to a lesser extent between second and third premolars; premolars double-rooted except P^4 , which is triple-rooted, and P^1 , which may be single-rooted; P^4 trianguloid, due to anterad bulge of anterolabial portion; lower molars with trigonid higher than talonid. Lower margin of jugals produced as a long, flat process, projecting ventrolaterad and more or less posterad. Mandible with sloping symphysis; prominent mental process projecting ventrolaterad from ventral margin of ramus below canine root; most but not all species have a second, similar process below P_4 ; angular margin broadly rounded, projecting ventrad and somewhat laterad, not thickened.

***Archaeotherium coarctatum* (Cope)**

Elotherium mortoni Cope, 1886:84 C.

Elotherium coarctatum — Cope, 1889:629.

Elotherium arctatum — Cope, 1891:20, 21, pl. 14, figs. 3, 3a.

Elotherium coarctatum — Lambe, 1908:26–28, pl. 2, figs. 10–15, pl. 3, figs. 1–6.

Elotherium coarctatum — Peterson, 1909:55, 56, fig. 11.

?*Entelodon coarctatum* — Scott, 1940:427–429.

HOLOTYPE. National Museum of Natural Sciences (NMC) 6260: incomplete left

mandibular ramus with P₁ to M₃: collected by T.C. Weston, 1889, "near the head of Swift Current Creek" which would be at or in the vicinity of the locality now called Anxiety Butte.

REFERRED SPECIMENS. NMC 6255, right M¹, T.C. Weston, 1884, referred by Cope to "*Elotherium*" *mortoni*. NMC 6256, right M³, Lambe, 1904 (Lambe 1908, pl. 2, fig. 11). NMC 6257, right P⁴, Lambe, 1904. NMC 6258, right P³, Lambe, 1904. NMC 6253, fragment of left mandibular ramus with M₁–M₃, Lambe, 1904. NMC 8907, nearly complete skull, Hunter Quarry, G.E. Lindblad, 1952. NMC 8908, complete mandible, Hunter Quarry, L. Sternberg, 1949. Royal Ontario Museum, Department of Vertebrate Palaeontology (ROM) 11628, complete skull and associated mandible, Hunter Quarry, A.G. Edmund, 1967. ROM 22654, complete skull, Hunter Quarry, Edmund 1967. ROM 22655, nearly complete skull, Hunter Quarry, R. Kidlark, 1972. ROM 22656, incomplete mandible, Hunter Quarry, Edmund 1967. ROM 23028, small, nearly complete mandible, Hunter Quarry, 1968. ROM 23031, fragmentary mandible, Hunter Quarry, 1967?

SPECIFIC DIAGNOSIS

About the size of *A. mortoni* Leidy or smaller. Diastema between first and second premolars about equal in length to second premolar; slight diastema between second and third premolars. Upper molars with protocone higher than hypocone. Crenulated enamel largely confined to heel of P₃. Frontal bones have dorsal surface crenulated, with strong superciliary ridges, which are distinct from superior orbital rim; the supraorbital foramina close to midline, opening anterad into parallel sulci, which extend onto nasals. Parietals closely appressed dorsally, forming a double sagittal crest with narrow median sulcus; the two crests diverge posterad to form the flaring and overhanging lambdoidal crest. Jugals with ventral margin extended as suborbital processes, the margins of which taper rather regularly and do not expand distally, the termination being more or less rounded. Pterygoids with well-developed hamuli. Mandible with long symphysis, the ventral outline of which rises at a low angle to the anterior rim; prominent anterior mental processes but no trace of posterior mental processes.

DESCRIPTION

The *dentition*, when complete, had the full complement of 44. The only upper incisor preserved is the right I³, on ROM 11628. The other incisors are represented by their alveoli, which indicate a progressive increase in size from I¹ to I³. The orientation of the incisors was radial, I¹ projecting anteroventrad, I² and I³ anteroventrolaterad. The upper canines are missing from all skulls except for the left C on NMC 8907, and even this lacks the tip. This tooth is not massive for an entelodont canine. It is directed ventrad, and only moderately anterad and laterad. The alveolus extends into the maxilla as far as the front of P². There is a distinct diastema between I³ and C, about the same on both sides except for ROM 11628, on which the left diastema is almost twice as long as the right.

P¹ is situated immediately posterior to the canine. It is a small tooth, with a low, conoid main cusp and a slight heel connected by a crest. It is directed anterad as well as ventrad, and the anteroposterior axis of the crown may be slightly oblique (ROM

22654), or in line (ROM 22655). All examples of P¹ are double-rooted except the left on ROM 22655, which was single-rooted.

P² is similar to P¹ but larger, and possibly more elongate anteroposteriorly. The main cusp is bluntly conoid, connected by a low crest to the shelflike heel. There is a posterior cingulum, and in the case of ROM 22654, anterior and lingual cingula also. The diastema between P² and P¹ may be as long as the P² itself.

P³ is much larger than P², but similar in form. The main cusp is more acute and the heel less distinct. P³ and P² are close together but not appressed.

P⁴ is a very different tooth, trianguloid in crown outline, with a main cusp that is smaller than that of P³, and a small, conjoined lingual cusp ("deuterocone"). The crown is in contact with that of P³. There is a distinct posterior cingulum, which may be striated, and rudiments of cingula elsewhere. Two labial roots and one lingual root are present.

The upper molars are low, massive, and rectanguloid in outline. Each has six low conoid cusps arranged in two transverse rows. With wear these are reduced to confluent facets. Each molar has one large lingual root and two smaller labial roots. M¹ is almost square in outline, and is slightly smaller in transverse diameter than P⁴. The protocone and paracone are about equally developed and are slightly larger than the metacone and hypocone. The paraconule and metaconule are smaller than the other cusps, and the former is slightly in advance of the protocone-paracone axis. The anterior cingulum is broad and straight, the posterior cingulum slightly bulging, with a cusplike posterior to the metaconule.

M² is the largest of the molars. It has a straight anterior margin, and slightly convex posterior, labial, and lingual margins. The latter two converge slightly posterad, so that the crown is wider in front than behind. The anterior cingulum is moderately developed. In other respects M² resembles M¹.

M³ is of about the same size as M¹, but the labial margin is oblique, so that the crown outline tapers posterad. The anterior cingulum is prominent, and may have a small protostyle. A posterior cingulum is present, especially toward the labial side.

The lower dentition is known from four more or less complete mandibles and two other mandibular fragments. The incisor series is in the form of a semicircle, with the teeth radiating outward and slightly upward; thus I₁ is directed mainly anterad and I₃, anterolabial. All of the incisors are peglike, slightly upcurved, with low vertical crests on either edge, and a slight prominence on each crest at the base of the crown. They increase in size progressively from I₁ to I₃, but none is tusklike.

The canines are large and tusklike, with swollen roots and more slender crowns. The roots are orientated forward, outward, and upward, but the crowns curve to a more nearly vertical direction. There are two low vertical crests along the posterior side of the crown, but the anterior side is rounded.

P₁ is known only from the alveolus, which indicates a single-rooted tooth, close to the canine, and orientated in much the same direction. P₂ is double-rooted; the crown is compressed-conoid, with slight anterior and posterior crests and a posterior cingulum. P₃ is like a greatly enlarged P₂, but with a straight lingual slope. It has a strong posterior cingulum but no heel; the enamel in this area may be strongly crenulated, although smooth elsewhere. P₄ is a little lower than P₃, and has a more distinct heel with a low, conoid cuspid. This tooth is more robust on ROM 22656 than on the other mandibles.

The lower molars are rectanguloid in crown view, except that M₃ has a rounded

hypoconulid spur. The cusps are low, rounded, and conoid; nearly all show some truncation by wear. On all the molars the trigonid is higher than the talonid. M_1 is the smallest of the three molars, and is usually the most worn. The paraconid and metaconid are worn confluent, and there is an area of wear extending from the protoconid around the anterior rim of the crown to the paraconid. The hypoconid and entoconid remain distinct on all specimens except ROM 22656 and 23028.

M_2 is similar to M_1 but more robust. The paraconid and metaconid may be merged, even without wear, producing a quadricuspid pattern. The posterior cingulum does not bulge, but has a prominence like a rudimentary hypoconulid. On M_3 the trigonid is similar to that of M_2 , except that the paraconid and metaconid are usually distinct. On ROM 23028 the M_3 is unusual in being more worn than the M_2 . In all specimens the talonid of M_3 is narrower than that of the other molars, and is extended posterad, although the hypoconulid is poorly developed. Unlike the other specimens, ROM 22656 has a distinct entoconid on M_3 . The enamel is somewhat crenulated, especially on the hypoconulid margin and (ROM 22656) the labial side.

The *skull*, in dorsal view, shows a striking contrast between the anterior and posterior halves. From the anterior ends of the zygomata the skull is snoutlike, slender, with lateral margins that contract to the area in front of the infraorbital foramen, then expand to the vicinity of the canine, and curve in again to the well-rounded anterior end. Posterior to the anterior rim of the orbit the cranium actually narrows, but the jugals are expanded laterad and ventrad as a broad but thin triangular plate, the suborbital process, which creates the appearance of a very broad skull posteriorly. The orbital margins are complete, and the orbits face anterolaterad. The temporal openings are large and subcircular; they are bounded in front by the postorbital bar, laterally by the zygomatic process of the squamosal, and internally by the parietal.

The dorsal outline of the skull is nearly straight from occiput to external nares, and slopes gently from rear to front. In posterior view the outline is that of a low triangle, due to the slope of the postorbital bars and zygomata, but the actual occiput is low and is extended laterally, curving upward to the high, flaring, and excavated occipital area.

The *nasals* are long, narrow bones, separated by a straight suture. They extend from the posterior margin of the external nares to a point on the dorsal surface of the skull about dorsal to the anterior rim of the orbit. The anterior margins form the posterior rim of the anterior nares. When this margin is preserved, the end of each nasal is distinctly notched, so that the two bones combine at the midline to form an anterad projection. The lateral margin of each bone, the suture with premaxilla and maxilla, is almost straight in ROM 11628 and ROM 22654, slightly sinuous in ROM 22655 and NMC 8907. At the point of juncture with the maxilla-frontal suture the lateral margins of the nasals converge inward to meet at the midline in an acute angle, within the notch formed by the anterior margin of the frontals. The posterior dorsal surface of the nasals is rugose, especially in ROM 22654. The sulcus from each supraorbital foramen of the frontal extends onto the surface of the adjacent nasal, becoming shallower and fading out about dorsal to the infraorbital foramen.

The *frontals* form the cranial roof in the orbital region. The dorsal surface is flat or slightly undulating transversely. Each bone has a supraorbital foramen which penetrates posterad and gently ventrad. Anteriorly the foramen is continued as a distinct sulcus, which extends onto the nasal. As noted, the anterior sutures of the

Fig. 1 *Archaeotherium coarctatum* (Cope), ROM 11628, skull, dorsal view; $\times 0.4$.

Fig. 2 *Archaeotherium coarctatum* (Cope), ROM 11628, skull, ventral view; $\times 0.4$.

Fig. 3 *Archaeotherium coarctatum* (Cope), ROM 11628, skull, right lateral view; $\times 0.4$.

Fig. 4 *Archaeotherium coarctatum* (Cope), ROM 11628, skull, anterior view; $\times 0.4$.

frontals form a notch to receive the posterior ends of the nasals. Each suture then turns acutely posteroventrad along the maxilla and continues along the lachrymal to the orbital rim, to enter the orbit well above the lachrymal notch. Within the orbit the suture extends posterad, then curves down along the posterior margin of the lachrymals to the internal orbital foramen, forming the upper margin of that opening and of the foramen lacerum anterius. From here it extends posterad within the groove from the f.lacerum anterius, becoming somewhat obscure posteriorly, but turning posterodorsad over the pterygoid across the brain case, then anterodorsad to the rim of the temporal opening, turning posterad along this rim, and then mediad to meet its fellow at the midline. The frontals form the upper rim of the orbits, but the superciliary ridge, if present, is separated from this rim by a sulcus. Posteriorly the frontals form with the jugals the postorbital bars, closing the rim of the orbits.

The *parietals* are greatly compressed dorsally, seemingly forming a single wall of bone in the upper temporal area. They flare out at the dorsal rim, forming two more or less vertical crests instead of a sagittal crest. In ROM 11628 these two crests project laterodorsad, and the sulcus between is a relatively wide V-shape in cross section. In ROM 22654 and ROM 22655 the crests are more nearly vertical and the sulcus between is narrow. This portion is not preserved in NMC 8907. Anteriorly the crests curve apart to continue as the superciliary ridges of the frontals. Posteriorly the crests become the dorsal rims of the parietals and diverge to form the lambdoidal crests of the occiput. There may be a small median boss at the occipital rim. Within the depression between the two lambdoidal crests the suture with the supraoccipital is not recognizable, but it must be below the occipital rim, as it can be picked up again externally well below the posterior extremity of the two parietals. Within the temporal fossae the parietals form a deep basin in the dorsal part evidently to seat a large temporal muscle. Below this the bones flare out to form the upper part of the cranial wall. Within the temporal fossae the lower margin of the parietals extend anteroventrad, meeting the squamosals laterally and the frontals anteriorly. The anterior margin is nearly vertical to the cranial rim.

Fig. 5 *Archaeotherium coarctatum* (Cope), ROM 11628, skull, posterior view; $\times 0.4$.

The facial portion of the *premaxillae* is a long, slender, gently convex wedge, which forms the outer rim of the external nares and extends posterad with an almost straight suture with the nasal. This meets the slightly oblique suture with the maxilla dorsal to the P^2 – P^3 gap, terminating the premaxilla as a slender point. Anteriorly the suture with the maxilla curves down the lateral surface of the snout to the anterior rim of the canine alveolus. On ROM 11628 the left premaxilla has a lateral depression with rough surface in this area, possibly the result of an injury. From the alveolus the suture with the maxilla runs diagonally across the palate to the anterior palatine foramen. It reappears near the posterior margin of each of these foramina and curves posterad and mediad to the midline, forming with its fellow a re-entrant between the two maxillae. The premaxillae thus form all of the bar between the anterior palatine foramina, as shown by ROM 22654. On this specimen the suture with the maxilla can be seen extending along the floor of the nasal passage, but its posterior path is concealed by matrix which could not be removed without disturbing the remnants of the ethmoturbinals.

The *maxillae* are similar in shape and position to these bones in *Tayassu*. The facial portion is convex transversely, gently concave anteroposteriorly. On ROM 22654 the lower rim of the zygoma continues as a low ridge, as in *Tayassu*, to the area over the infraorbital foramen. This ridge is absent on the other skulls. The rather large infraorbital foramen is situated dorsal to the P^3 – P^4 contact: it extends posterad into the bone, and is continued anterad as a short, shallow sulcus. The suture with the premaxillae curves gently to the end of these bones, then runs posterad along the nasals to the point where the nasals begin to narrow. Here the suture turns posterolaterad to the lachrymals, then anteroventrad along the anterior margin of these bones to the junction with the jugals, and posteroventrolaterad along those bones to the lower rim of the zygomata. On the ventral surface of the zygoma the suture with the jugals runs posterad to near the anterior rim of the temporal fossa, then

Fig. 6 *Archaeotherium coarctatum* (Cope), NMC 8907, skull, dorsal view; sagittal crest incorrectly restored; $\times 0.4$.

Fig. 7 *Archaeotherium coarctatum* (Cope), NMC 8907, skull, ventral view; $\times 0.4$.

Fig. 8 *Archaeotherium coarctatum* (Cope), NMC 8907, skull, right lateral view; $\times 0.4$.

Fig. 9 *Archaeotherium coarctatum* (Cope), ROM 22654, skull, dorsal view; $\times 0.4$.

turns mediad along that rim and passes under the jugal and the lachrymal. Within the orbit the maxillae form the floor of the internal orbital foramen. The ventral zygomatic portion of the maxillae is concave, curving steeply to the alveolar margin and extending anterad into the facial portion. Posterior to M^3 the maxillae extend as a more or less pointed and keeled process. From the base of this process the suture with the palatines runs anterad parallel with the alveolar rims of M^3 and M^2 , then obliquely mediad to the lateral rim of the posterior palatine foramen. On the surface between the two foramina the suture with the palatines zigzags to the midline. The palatal surface of the maxillae is broadly arched transversely, almost straight anteroposteriorly.

Externally the *lachrymals* are rhomboid in outline. The dorsal margin, with the frontals, and the ventral margin, with the maxillae, are straight, and orientated anteroposteriorly; the anterior margin, with the maxillae, may be rounded and oblique. At the orbital rim there is a distinct notch, and within the rim a lachrymal foramen running mediad. In ROM 22655 there is a small, hooklike process above the notch on the orbital rim. Within the orbit the dorsal suture of the lachrymals runs posterad along the orbital wall, then ventrad to the internal orbital foramen, and from here back to the orbital rim.

The *orbitosphenoids* and *alisphenoids* are poorly defined in all four skulls. A finely convoluted suture in front of the foramen lacerum anterius may be the posterior boundary of the orbitosphenoid. The dorsal margin of the alisphenoids extends posterad from the foramen lacerum anterius within the sphenoidal sulcus to the suture with the squamosals. On ROM 22628 the large foramen ovale may be seen near the juncture. The suture continues ventrad to meet the palatines, but the ventral border with those bones is obscure.

The *palatines* form the anterior and anterolateral rims of the internal nares. Just in front of the anterior rim the palatal surface bears a conspicuous ridge, which may bear two prominences. The lateral margin, with the maxillae, extends anterad along the alveolar margin to the vicinity of M^2 , then mediad to the posterior palatine foramen. It emerges on the palatal surface between the two foramina about opposite M^1 and continues anteromedial to meet its fellow at the midline. The dorsal portion of the palatines forms the roof of the posterior narial aperture and the fossa that continues posterad from it. The suture with the pterygoids lies within this fossa.

The *pterygoids* are best preserved on ROM 22654. They form the lateral walls of the deep, V-shaped fossa that extends posterad from the internal nares and they form part of the cranial floor. The ventral edge of the pterygoids projects ventrad as a prominent hamulus (cf. Scott, 1940:386), the anterior and ventral margins of which form a continuous convex curve, whereas the posterior margin is concave. The ventral edge of the hamulus is somewhat thickened. The suture with the palatines (ROM 22654) runs within a sulcus between the ventral rims of the two bones. This sulcus dies out anteriorly, and the suture curves over the anterior rim of the hamulus and ascends to the internal wall of the fossa, then turns abruptly posteromedial to the midline. The posterior rim of the pterygoids forms the lower part of a low aperture, noted by Scott, which extends anterad above these bones and presumably the palatines, and is roofed by the basisphenoid.

The *squamosals* are complex bones, which differ somewhat in form and boundaries among the four skulls examined. The following account is based mainly on ROM 22654. Medially these bones form the posteroventral portion of the cranial

wall and the posterior margin of the temporal opening, meeting the parietals dorsally and the frontals anteriorly. The anterior suture, with the parietals, extends obliquely from the alisphenoids to the occipital rim. After crossing the extension of the lambdoidal crest it turns ventrad, then lateroventrad down the broad fossa on the posterior face of the paroccipital process. It crosses the pitted extremity of that process, turns anteromedial along the exoccipitals, then doubles back to cross the ventral rim of the zygomatic base. Here it re-enters the temporal fossa to run anterad to the alisphenoid. The zygomatic portion of the squamosals is large and complex. The dorsal margin is rounded into the temporal fossa as a saddleshaped area, which then rises to the incurved prominence which forms the posterolateral angle of the zygomal rim. From the base of this process a ridge descends toward the glenoid cavity, forming the anterior rim of the deep triangular fossa that houses the external auditory meatus. The external face of the squamosals anterior to the posterolateral angle is somewhat excavated, forming a vertical ridge at the margin, but this fades away ventrad before reaching the edge of the glenoid cavity. In front of this ridge the outer surface of the arch is flat, the inner somewhat thickened ventrally. The squamosal portion of the arch curves forward, then upward, terminating in a transverse, almost straight suture with the jugal, which, however, turns back parallel to the dorsal margin of the arch to lap against the jugal almost to the glenoid cavity. The latter is ovoid in shape, moderately concave anteroposteriorly, and very shallow mediolaterally. The postglenoid process is more prominent than the preglenoid. From the inner angle of the cavity the ventral edge of the squamosals curves medial and anterad to meet the pterygoids. Above this edge, on the posterior face of the temporal fossa, there is a large preglenoid foramen on each squamosal. On ROM 11628 there are two such openings on the right squamosal, confluent internally. On NMC 8907 the two openings are on the left squamosal. ROM 22655 has a single preglenoid foramen on each side, as in ROM 11628.

The *jugals* are flat, quadriradiate bones, forming the lower half of the orbital rim and the anterior part of the zygomatic arch. Anteriorly they form a portion of the facial surface, below the lachrymals. The suture with the lachrymals extends posterad to the orbital rim. Entering the orbit it continues to the internal orbital foramen, turns laterad along the zygomatic branch of the maxillae, then crosses this obliquely and reappears on the facial surface as a nearly vertical suture with the maxillae to the anterior end of the lachrymals. From the lower rim of the orbit the jugals extend nearly halfway up the postorbital bar, ending in a transverse suture with the frontals. From this suture the dorsal edge of the jugals curves ventrad and posterad to the suture with the squamosals, at which point there may be a slight prominence on the rim. The peculiar suture with the squamosals has been described: vertical in its upper part, at a very low angle with the horizontal in its lower and posterior part. The wedgelike extension so formed extends almost to the glenoid cavity. In the area below the orbit the lower part of the jugals is extended ventrolaterally as the peculiar suborbital process characteristic of entelodonts. The shape of this process is somewhat different in the four skulls examined, although trianguloid in all. In ROM 11628 the process projects somewhat forward as well as outward and downward. The termination is bluntly pointed. In ROM 22654 the extremity is well rounded and somewhat thickened and porous. The anterior portion of the process is thinner than the posterior. ROM 22655 has a somewhat asymmetrical process, the anterior margin being curved, the posterior margin nearly straight, and shorter. The extremity is

Fig. 10 *Archaeotherium coarctatum* (Cope), ROM 22654, skull, ventral view, $\times 0.4$.

Fig. 11 *Archaeotherium coarctatum* (Cope), ROM 22654, skull, right lateral view; $\times 0.4$.

Fig. 12 *Archaeotherium coarctatum* (Cope), ROM 22655, skull, dorsal view; $\times 0.4$.

Fig. 13 *Archaeotherium coarctatum* (Cope), ROM 22655, skull, ventral view; $\times 0.4$.

swollen, with a porous surface. In NMC 8907 there is some discrepancy between the right and left processes, that on the right being almost symmetrical, with moderate terminal swelling, that on the left a little oblique, with thicker terminal margin and a prominence about one-third way up the posterior margin.

The *suproccipital* forms the median dorsal portion of the occipital face. The suture with the parietals is obscure, but is evidently below the occipital rim, as in *Tayassu*, and not extending onto the skull roof, as described by Scott (1940:383). Dorsally it flares outward, parallel to the lambdoidal crest. Below this it narrows, and is deeply excavated, much more than in *Tayassu* and *Sus*. There may be a slight median keel extending from the median prominence of the occipital rim to the deepest part of the concavity. Below this the surface of the bone is striated or pitted, and there may be a discontinuous median groove. The suture with the exoccipitals is well above the foramen magnum, so that the supraoccipital is excluded from the margin of that opening.

The *exoccipitals* form the lateral portions of the occipital face, including the occipital condyles and the rim of the foramen magnum. The median portions, above the foramen rim, may be slightly swollen, and may have two small prominences, one for each bone, projecting posteroventrad over the opening. Laterally the exoccipitals are excavated above each condyle. The condyles are truncated medially at the foramen, and curve gracefully from here to a pointed lateral end. The ventral notch in the foramen rim between the condyles is formed by the exoccipitals; the suture with the basioccipital lies anterior to this, on the ventral surface of the basicranium. There is a large condylar foramen anterodorsal to the middle of each condyle. The exoccipitals form the lower and somewhat smaller part of the paroccipital process, the suture with the squamosals running along the middle of the posterior surface. The proximal portion of the paroccipital process, formed of squamosal and exoccipital, is broadly hollowed, and may be crenulated. The suture with the squamosals terminates abruptly against the tympanics.

The *tympanics* are best preserved on ROM 22654, but even here the boundaries of the bones are obscure in places. They form an irregular wedge between the exoccipitals and the squamosals, and make up the distal end of the paroccipital processes, which is pitted. The anterior side apparently forms the posterior wall of the external auditory meatus. On the left side of ROM 22654 there is a short, blunt process projecting laterad from the crevice between squamosal and tympanic; it points into a large, smooth, oval depression on the posterior face of the zygomatic branch of the squamosal, which may have housed a loose auditory bulla. Medially the ventral surface of the tympanics appears to form the posterior margin of the foramen lacerum posterius.

The *basioccipital* is the posterior segment of the basicranial series. The ventral surface is convex from side to side, and there may be a slight median keel. The suture with the exoccipitals is not clearly defined but lies in advance of the foramen magnum. Laterally the basioccipital appears to form part of the rim of the condylar foramen. The anterior suture, with the basisphenoid, is oblique on either side of the midline.

The *basisphenoid* continues the basicranial surface anterad from the basioccipital, and is embraced anteriorly by the posterior extensions of the pterygoids. There are two diverging prominences near the suture with the basioccipital. Anteriorly the basisphenoid extends into, and forms the roof of, the anterad-directed aperture that is

Fig. 14 *Archaeotherium coarctatum* (Cope), ROM 22655, skull, right lateral view; $\times 0.4$.

floored by the pterygoids.

The following is a resumé of the cranial foramina. The *infraorbital foramen* is in the middle of the facial portion of the maxilla. It is large, and opens anterad. The *lachrymal foramen* is located just inside the orbital rim, adjacent to a notch in the rim. It is wide at the aperture but narrows internally, and is directed mediad. The *internal orbital foramen* is located in the orbital portion of the maxilla, under the anterior end of the zygoma; it is large, and anterad-directed. The *foramen opticum* is poorly preserved on all specimens except ROM 22654, on the left side of which may be seen a large foramen apparently bordered by the frontal and orbitosphenoid. The *foramen lacerum anterius* is also poorly preserved except on ROM 22654. Here it appears as a distinct foramen opening posterad on the anteromedial wall of the temporal fossa, presumably between the alisphenoid and the frontal. The *foramen ovale* is located on the temporal-fossa side of the posterolateral extremity of the alisphenoid, and opens anterolaterad. The *foramen lacerum medium* is not well preserved. On ROM 22654 there is a large vacuity between the basioccipital, basisphenoid and squamosal, partly the result of damage, but probably occupying the site of this foramen. The *foramen lacerum posterius* is a large, irregular opening ventrolaterad between the exoccipital, basioccipital, and squamosal. The *condylar (hypoglossal) foramen* opens anteroventrad on the anteroventral surface of the exoccipital, close to or along the suture with the basioccipital. The *preglenoid foramen* is on the anterior face of the zygomatic branch of the squamosal, about halfway between the cranial wall and the distal end of the glenoid cavity. On ROM 11625 there are two such openings on the right side, the more proximal directed posterad and emerging as a small foramen ventral to the external auditory meatus, the more distal entering the squamosal at a mediad slant and joining the canal of the proximal foramen. The second foramen is represented in the left squamosal by a shallow depression. The *anterior palatine* is a slitlike opening, bounded laterally by the premaxilla and maxilla, and separated from its fellow medially by a narrow bar formed by the premaxillae. The *posterior palatine foramen* penetrates the palate opposite M². It is bordered posteriorly by the palatine and anteriorly by the maxilla, and is continued forward as a shallow, gradually disappearing sulcus. In addition to these more or less standard foramina, there is the flattened-ovoid aperture directed anterad between the pterygoids and the basisphenoid. This was noted by Scott (1940:386). Nothing comparable to this appears on the basicranium of *Tayassu*, but in *Hippopotamus* there is a similar aperture, roofed by the basisphenoid and floored by the presphenoid and laterally by the pterygoids. In *Archaeotherium* the pterygoids have expanded mediad to meet at the midline, and exclude the presphenoid from the ventral surface of the basicranium and the margin of the aperture. In *Sus* there is a slitlike aperture between the basisphenoid and the presphenoid, like an incipient development of the condition seen in *Hippopotamus*.

The *mandible*, seen from above, is narrowly V-shaped, the horizontal rami being only moderately divergent. The anterior (incisor) rim is semicircular. The symphysis is long, extending back to P₂ and the dorsal surface is shallowly sulcate. On ROM 22656 the lateral outline of the mandible is somewhat concave between P₁ and P₂, giving the symphysis a spoonlike shape in dorsal view. At the posterior end of the symphysis the outer and inner surfaces of the rami are nearly vertical, but posterad they become progressively twisted, so that the ventral margins are wider apart than the dorsal. Posterior to M₃ the upper rim of the rami curves gracefully posterodorsad to the coronoid process. This is nearly symmetrical in side view, the anterior and

Fig. 15 *Archaeotherium coarctatum* (Cope), ROM 11258, mandible, dorsal view; $\times 0.4$.

Fig. 16 *Archaeotherium coarctatum* (Cope), ROM 11258, mandible, right lateral view; $\times 0.4$.

Fig. 17 *Archaeotherium coarctatum*, (Cope), NMC 8908, mandible, dorsal view; $\times 0.4$.

Fig. 18 *Archaeotherium coarctatum*, (Cope), NMC 8908, mandible, right lateral view; $\times 0.4$.

Fig. 19 *Archaeotherium coarctatum* (Cope), ROM 23028, mandible, right lateral view; $\times 0.4$.

posterior slopes having about the same concavity, except for a slight posterad curvature near the summit. Behind the coronoid there is a relatively long portion of the ramus, rounded and somewhat thickened, and terminating at the condyle. The latter is large and ovoid, but is little elevated above the dorsal margin of the ramus immediately in front. The masseteric fossa is on the lateral face of the ramus between the coronoid process and the condyle, and just below the dorsal rim. It is a well-defined, elongate-ovoid impression, the ventral margin of which may be distinct or a little vague. On NMC 8908 there is a short but distinct ridge within the fossa near the posterior end. The ventral margin of the ramus is more or less everted, and this passes into the flaring angular portion, which extends laterad and ventrad, beyond the margin of the main part of the ramus.

Anteriorly, in the symphyseal region, the ventral margin of the mandible bears the curious flanges (mental processes of Scott) that characterize the entelodonts. There is some variation in the form of these processes in the various specimens from the Hunter Quarry. They are most prominent on ROM 11628, projecting from the ventral margin at the posterior half of the symphysis, and curving ventrad and laterad to a broadly rounded lateral margin. The outline of the process is not symmetrical, the anterior margin being oblique and slightly convex, the posterior margin short and concave. On NMC 8908 the processes project more laterad than ventrad, and the margin is broadly curved, thickened, and rough. ROM 22656 has only a blunt angulation below left P_1 and P_2 , flaring slightly but strongly striated. On ROM 23028, the smallest mandible, the processes are delicate, flaring laterad but projecting little below the ventral margin of the ramus. They have a low-angle, straight outline for most of their length, but are curved abruptly at the rear, creating a blunt angulation. The edges are slightly thickened. The small size and more delicate proportions of ROM 23028 presumably indicate a female rather than a juvenile, as the dentition is fully erupted and the molars are deeply worn.

All of the specimens in which the mandibular symphysis is preserved show the anterior mental foramen on the side of the ramus between the mental process and the alveolar margin. There may also be one or more small posterior foramina at about the same level, ventral to P_3 . The posterior mental processes, found in most entelodonts below P_4 , are completely absent on the present specimens, not even represented by rugosities.

Relationships

The entelodonts show a number of very distinctive characters that clearly separate them from other bunodont artiodactyls. Most of these characters are fully developed in *Archaeotherium coarctatum*. In contrast to differences, resemblances to other families should be more indicative of relationships, but these are subtle, and likely to be obscured by the obvious distinctive characters. It is generally agreed that the nearest living relatives of the entelodonts are the Tayassuidae, the Suidae, and the Hippopotamidae, the member of which constitute the suborder Suina in which some authors also include the Entelodontidae.

In Table 2 a number of entelodont skull characters are listed that are also developed or at least incipient in one or more of the suine families. In addition to these skull characters, it should also be noted that the ventrolaterad flaring of the mandibular angle is present in both the Entelodontidae and the Hippopotamidae. Counting the entelodont characters that also occur, or are approached, in the other three families, one finds seven in the Tayassuidae, five in the Suidae, and six in the Hippopotamidae. A straight count, therefore, suggests that the Entelodontidae are most closely related to the Tayassuidae and least related to the Suidae. Some of these characters could be more significant phylogenetically than others, but any attempt to weight them would be largely subjective. However, the similarities in the parietal and occipital regions in the Tayassuidae, and the resemblance of the tympanics in the Suidae and Hippopotamidae, are of phylogenetic significance. The evidence from any approach is indecisive, and the mélange of differences and resemblances suggests only that the entelodonts had a common ancestry with the suines in Eocene time.

Of the various other species that have been assigned to *Archaeotherium*, *A. mortoni* Leidy shows the most resemblance to *A. coarctatum*. This is seen in the relatively small size, and in the simple form of the suborbital processes. The long, gently sloping mandibular symphysis is like that described by Scott (1940:419) for *A. scotti* Sinclair, and by Wilson (1971:12) in a specimen from the Vieja Group, referred to *A. cf. mortoni*. Other described species of *Archaeotherium* are larger than *A. coarctatum* and most have more complex suborbital processes. The complete absence of posterior mental processes on the mandibles of *A. coarctatum* is almost unique, and this, as well as other features, would suggest an early stage in entelodont evolution, in keeping with the stratigraphic position. However, the crenulated frontals and the double sagittal crest, whether primitive or advanced characters, seem to exclude *A. coarctatum* as a possible ancestor of the other North American species of *Archaeotherium*.

The Living Entelodont

Figure 20 is an outline drawing of the skull and mandible of *Archaeotherium coarctatum*, based on ROM 11628, to which has been added a restoration of the temporal, masseter, and digastric muscles to show their probable position and size. On this and other bases the life-restoration sketch of Figure 21 has been prepared. This contrasts considerably with the interpretation of *Archaeotherium ingens*

published by Scott (1913:260; 1937:389) and drawn by R. Bruce Horsfall. In the Scott restoration the conspicuousness of the suborbital and mental processes has, I think, been exaggerated by not allowing for the obscuring effect of the masseter and digastric muscles.

Scott (1913:367–68) discussed the probable feeding habits of entelodonts, and noted the occurrence on one specimen of *Archaeotherium* of abrasion grooves at the base of the crowns of I³ and lower C. He deduced from this that entelodonts obtained some of their food by pulling up roots. No evidence of this kind of wear was observed on the Cypress Hills specimens of *Archaeotherium*, and in fact, in his 1937 edition Scott did not discuss this interpretation.

Postulation of entelodont feeding habits must take into consideration the following characteristics of the dentition: (1) relatively small, pointed, and anteriorly projecting incisors; (2) moderately large but robust canines; (3) compressed-conoid premolars, the more anterior of which are well spaced; (4) robust, rectanguloid molars with low, conoid cusps, which tend to be conjoined by wear transverse to the long axis of the tooth row. In addition to these dental characters the apparent nature of the jaw muscles appears significant. The temporal muscle evidently was large, and had a mainly vertical pull from temporal fossa to the inner side of the mandible. The masseter muscle, in contrast, arose from the laterally divergent zygoma and suborbital process, so that the main pull would have been oblique from this origin to the masseteric fossa.

The glenoid cavities and mandibular condyles are elongate and almost flat lateromedially, and short and shallowly arched anteroposteriorly. This suggests a loose articulation of the mandible, especially in the transverse axis.

These various features would have been compatible with a diet of foliage from herbacious plants and low shrubs, which was stripped off by the projecting incisors, comminuted by the bluntly pointed premolars, and ground by the molars. The first two operations would involve mainly a vertical (orthal) jaw movement, motivated by the temporal and digastric muscles. In the molar area great pressure could be applied vertically by the masseter muscles; also, by contracting alternately, they could impart a lateral motion to the mandible, made possible by the nature of the jaw articulation and the strong lateral component in the orientation of these muscles. The articulation is very similar to that of ruminants, especially the Bovidae, where the transverse motion of the cheek teeth is an essential part of cud-chewing. Ruminants, however, have a weak, almost absent dentition anterior to the second premolar, which offers little impediment to extal or ental movement. Entelodonts, in contrast, have interlocking canines and premolars, and in the fully occluded position this restricts the transverse motion of the mandible almost to zero. However, if the jaws are opened to provide as little as 5 mm clearance between molar triturating surfaces, the anterior teeth are sufficiently disengaged that the mandible can be moved transversely to such an extent as to pass the lower molar surfaces completely across the upper. It is probable that the powerful digastric muscles served to keep the mandible in the most effective angle of opening, as well as to help the masseters in the lateral movement.

Although the entelodonts evidently fed on relatively soft vegetation, they were not likely to have included swamp plants in their diet. The narrow, didactyl feet, even if they had a spreading pad, would have been suitable only for locomotion on firm ground.

The use of the canines and premolars as weapons, and the probable combativeness

Fig. 20 *Archaeotherium coarctatum* (Cope), outline drawing of the skull with the temporal and masseter muscles, and a portion of the digastric muscle, restored; $\times 0.4$.

Fig. 21 *Archaeotherium coarctatum* (Cope), life restoration of the head; $\times 0.4$.

of the entelodonts, have been discussed by Scott (1913:368; 1937:388). He also commented on the relatively small size of the braincase, and concluded that the entelodonts must have been "profoundly stupid." However, their survival from the Late Eocene (Mongolia; Chow, 1958) to the Early Miocene (Nebraska; Peterson, 1909), a time interval of about 20 million years, and their dispersal on three continents, indicates some success of adaptation, both physical and mental.

Table 1 Measurements (in millimetres)

	ROM 11628	ROM 22654	ROM 22655	NMC 8907	NMC 8908	ROM 22656	ROM 23028
I ³ right, anteroposterior at base of crown	13.0	—	—	—	—	—	—
I ¹ right, anteroposterior of alveolus	—	13.0	9.5	—	—	—	—
I ¹ left, anteroposterior of alveolus	—	—	—	11.0	—	—	—
I ² right, anteroposterior of alveolus	—	17.0	12.5	—	—	—	—
I ² left, anteroposterior of alveolus	—	—	—	14.0	—	—	—
I ³ right, anteroposterior of alveolus	—	21.0	16.0	—	—	—	—
I ³ left, anteroposterior of alveolus	—	—	—	18.0	—	—	—
C upper left, anteroposterior of alveolus	28.0	—	—	—	—	—	—
C upper right, anteroposterior of alveolus	—	26.0	26.0	—	—	—	—
C upper left, anteroposterior at base of crown	22.0	—	—	—	—	—	—
P ¹ right, anteroposterior at base of crown	13.4	15.1	—	—	—	—	—
P ¹ right, transverse at base of crown	8.0	8.6	—	—	—	—	—
P ¹ left, anteroposterior at base of crown	—	—	—	14.4	—	—	—
P ¹ left, transverse at base of crown	—	—	—	8.6	—	—	—
P ² right, anteroposterior at base of crown	16.8	19.4	—	—	—	—	—
P ² right, transverse, at base of crown	9.5	9.8	—	—	—	—	—
P ² left, anteroposterior at base of crown	—	—	16.5	20.4	—	—	—
P ² left, transverse at base of crown	—	—	8.9	11.5	—	—	—
P ³ right, anteroposterior at base of crown	23.4	25.5	23.2	—	—	—	—
P ³ right, transverse at base of crown	14.9	14.6	14.6	—	—	—	—
P ³ left, anteroposterior at base of crown	—	—	—	30.9	—	—	—
P ³ left, transverse at base of crown	—	—	—	18.9	—	—	—
P ⁴ right, anteroposterior at base of crown	20.9	22.7	21.2	—	—	—	—
P ⁴ right, transverse at base of crown	21.4	22.4	22.5	—	—	—	—
P ⁴ left, anteroposterior at base of crown	—	—	—	23.8	—	—	—
P ⁴ left, transverse at base of crown	—	—	—	24.4	—	—	—
M ¹ right, anteroposterior at base of crown	18.8	19.6	17.5	—	—	—	—
M ¹ right, transverse at base of crown	19.1	22.7	20.6	—	—	—	—
M ¹ left, anteroposterior at base of crown	—	—	—	19.6	—	—	—
M ¹ left, transverse at base of crown	—	—	—	23.0	—	—	—

Table 1 Measurements (in millimetres) (Cont'd.)

M ² right, anteroposterior at base of crown	20.1	22.8	22.2	—	—	—	—
M ² right, transverse at base of crown	22.4	24.0	24.7	—	—	—	—
M ² left, anteroposterior at base of crown	—	—	—	23.6	—	—	—
M ² left, transverse at base of crown	—	—	—	25.4	—	—	—
M ³ right, anteroposterior at base of crown	19.5	20.9	21.0	—	—	—	—
M ³ right, transverse at base of crown	20.2	20.9	21.8	—	—	—	—
M ³ left, anteroposterior at base of crown	—	—	—	22.0	—	—	—
M ³ left, transverse at base of crown	—	—	—	24.1	—	—	—
I ₁ right, anteroposterior at base of crown	7.8	—	—	—	—	—	—
I ₁ right, transverse at base of crown	11.0	—	—	—	—	—	—
I ₂ right, anteroposterior at base of crown	8.5	—	—	—	—	—	—
I ₂ right, transverse at base of crown	12.1	—	—	—	—	—	—
I ₃ right, anteroposterior at base of crown	10.1	—	—	—	—	—	—
I ₃ right, transverse at base of crown	13.2	—	—	—	—	—	—
C lower right, anteroposterior at base of crown	17.5	—	—	—	—	—	15.5
C lower right, transverse at base of crown	16.0	—	—	—	—	—	13.2
C lower right, from alveolar rim to worn tip of crown, measured along anterior face, approximately	59.0	—	—	—	—	—	33.0
P ₁ right, anteroposterior of alveolus	15.0	—	—	—	—	—	17.0
P ₁ right, transverse of alveolus	10.0	—	—	—	—	—	12.0
P ₂ right, anteroposterior at base of crown	15.0	—	—	—	18.6	16.7	—
P ₂ right, transverse at base of crown	8.0	—	—	—	9.5	8.5	—
P ₂ left, anteroposterior at base of crown	—	—	—	—	—	—	15.5
P ₂ left, transverse at base of crown	—	—	—	—	—	—	8.4
P ₃ right, anteroposterior at base of crown	24.3	—	—	—	30.9	—	26.5
P ₃ right, transverse at base of crown	11.7	—	—	—	13.0	—	11.9
P ₄ right, anteroposterior at base of crown	27.9	—	—	—	30.5	28.5	25.2
P ₄ right, transverse at base of crown	13.1	—	—	—	14.5	13.7	12.8

M ₁ right, anteroposterior at base of crown	19.5	—	—	—	20.5	20.4	19.7
M ₁ right, transverse at base of crown	12.9	—	—	—	14.0	14.1	13.1
M ₂ right, anteroposterior at base of crown	20.9	—	—	—	22.8	22.5	23.0
M ₂ right, transverse at base of crown	14.7	—	—	—	16.5	16.3	16.9
M ₃ right, anteroposterior at base of crown	23.8	—	—	—	25.3	23.7	22.3
M ₃ right, transverse at base of crown	15.0	—	—	—	16.5	15.8	15.6
Length of skull from alveolar margin of premaxillae, as preserved, to posterior wings of parietals	430.0	470.0	447.0	—	—	—	—
Length of skull from alveolar margin of premaxillae to occipital condyles	408.0	435.0	413.0	420.0	—	—	—
Width between suborbital processes of the zygomata, as preserved	317.0	343.0	+332.0	343.0	—	—	—
Width of maxillae between outer walls of canine alveoli	94.0	97.0	88.7	±90.0	—	—	—
Width of maxillae at P ²	62.0	64.5	64.0	65.0	—	—	—
Width of maxillae at sutures with jugals	±95.0	106.0	106.0	±78.0	—	—	—
Maximum width of frontals	±170.0	178.0	173.0	±164.0	—	—	—
Minimum width of parietal roof between temporal fossae	±18.0	9.5	11.7	—	—	—	—
Maximum width between occipital wings of parietals	±77.0	+37.0	±86.0	—	—	—	—
Width between extremities of paroccipital processes	138.0	169.0	150.0	—	—	—	—
Width between distal ends of glenoid cavities	252.0	265.0	242.0	—	—	—	—
Width between lateral extremities of occipital condyles	70.0	70.0	71.6	—	—	—	—
Horizontal diameter of orbit, approx.	48.0	48.0	55.0	—	—	—	—
Horizontal diameter of foramen magnum	36.0	32.0	33.0	—	—	—	—
Length of mandible excluding incisors	385.0	—	—	—	390.0	410.0	+280.0
Maximum width of mandible between condyles	233.0	—	—	—	220.0	—	—
Maximum width between mandibular angles	±230.0	—	—	—	240.0	—	+160.0
Maximum width between extremities of anterior mental processes	±107.0	—	—	—	95.0	—	56.0

Table 2 Comparison of cranial structures in the Entelodontidae and the Suina

	Entelodontidae	Tayassuidae	Suidae	Hippopotamidae
Dental formula	3.1.4.3 3.1.4.3	2.1.3.3 3.1.3.3	3.1.4.3 3.1.4.3	2-3.1.4.3 1-3.1.4.3
Upper canines	Simple, robust tusks	Simple, slender tusks	Continuously growing; upcurved	Continuously growing; downcurved
Molars	Simple bunodont	Somewhat complex bunodont	Complex bunodont	Complex; high bunodont
Supraorbital foramina and sulci	Well-developed	Present	Moderately developed	Vestigial
Parietals	Strongly compressed from side to side	Expanded in front, compressed behind	Expanded	Expanded
Sagittal crest	High, long, incipiently to fully double	Moderately high, short, incipiently double	Absent	Low and short, incipiently double
Lambdoidal crest	Formed by parietals; overhangs and embraces supraoccipital	Formed by parietals; overhangs and embraces supraoccipital	Formed by supraoccipital; moderate overhang	Formed by supraoccipital; no overhang
Orbit	Rim completely closed	Rim open posteriorly	Rim open posteriorly	Rim almost closed
Lachrymals	Visible externally	Concealed by maxillae	Visible externally	Visible externally
Pterygoids	Meet at ventral midline; hamulus present	Separate at midline; no hamulus	Separate at midline; hamulus present	Separate at midline; moderate hamulus
Paroccipital processes	Short, stout	Short, pointed	Very long, slender	Short, stout
Tympanics	Wedgelike	Platelike	Wedgelike	Wedgelike
Basisphenoid	Sphenoidal aperture formed with pterygoids	No sphenoidal aperture	Incipient sphenoidal aperture formed with presphenoid	Distinct sphenoidal aperture formed with presphenoid

Literature Cited

AYMARD, A.

- 1846 Essai monographique sur un nouveau genre de mammifère fossile trouvé dans la Haute-Loire, et nommé Entelodon. *Annales de la Société d'agriculture, sciences, arts et commerce du Puy* 12 (1842-46):227-267, 1 pl.

BUSH, L.P.

- 1903 Notes on the dates of publication of certain genera of fossil vertebrates. *American Journal of Science*, ser. 4, 16(10):96-98.

CHOW, M.

- 1958 *Eoentelodon* — a new primitive entelodont from the Eocene of Lunan, Yunnan. *Vertebrata Palasiatica* 2:30-37, fig. 1, pl. 1.

COPE, E.D.

- 1885 The White River beds of Swift Current River, Northwest Territory. *American Naturalist* 19:163.
1886 The Vertebrata of the Swift Current Creek region of the Cypress Hills. *Annual Report of the Geological and Natural History Survey of Canada*, new. ser., 1(C), app.1:79-85.
1889 Vertebrata of the Swift Current River. No. III. *American Naturalist* 23:628, 629.
1891 On Vertebrata from the Tertiary and Cretaceous rocks of the Northwest Territory. I. The species from the Oligocene or Lower Miocene beds of the Cypress Hills. *Geological Survey of Canada, Contributions to Canadian Palaeontology* 3(1):1-25, pls. 1-14.

LAMBE, L.M.

- 1908 The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan. *Geological Survey of Canada, Contributions to Canadian Palaeontology* 3(4):1-65, figs. 1-13, pls. 1-8.

LEIDY, J.

- 1850 Observations on two new genera of fossil Mammalia, *Eucrophorus jacksoni*, and *Archaeotherium mortoni*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 5:90-93.
1851 [Description of the genus *Arctodon*.] *Proceedings of the Academy of Natural Sciences of Philadelphia* 5:278.
1853 The ancient fauna of Nebraska or, A description of remains of extinct Mammalia and Chelonians, from the Mauvaises Terres of Nebraska. *Smithsonian Contributions to Knowledge* 6:1-126, figs. 1-2, pls. 1-24, map.
1857 Rectification of the references of certain of the extinct mammalian genera of Nebraska. *Proceedings of the Academy of Natural Sciences of Philadelphia* 9:175, 176.

PETERSON, O.A.

- 1909 A revision of the Entelodontidae. *Memoirs of the Carnegie Museum* 4(3):41-158, figs. 1-80, pls. 54-62.

POMEL, A.

- 1847 Note sur un nouveau pachyderme du bassin de la Gironde (*Elotherium magnum*). *Bulletin de la Société géologique de France*, sér. 2, 4:1083-1085.

SCOTT, W.B.

- 1913 A history of land mammals in the western hemisphere. New York, Macmillan. 693 pp., frontisp., figs. 1-304.
1937 A history of land mammals in the western hemisphere. Rev. ed. New York, Macmillan. 786 pp., frontisp., figs. 1-420.
1940 Artiodactyla. In Scott, W.B. and G.L. Jepsen, The mammalian fauna of the White River Oligocene, part IV. *Transactions of the American Philosophical Society* 28:363-746, figs. 118-136, pls. 36-78.

SINCLAIR, W.J.

- 1921 Entelodonts from the Big Badlands of South Dakota in the Geological Museum of Princeton University. *Proceedings of the American Philosophical Society* 60:467-495, figs. 1-22.
- 1922 The small entelodonts of the White River Oligocene. *Proceedings of the American Philosophical Society* 61:53-64, figs. 1-5.

TROXELL, E.L.

- 1920 Entelodonts in the Marsh collection. *American Journal of Science* 50:243-255, 361-386, 431-445, figs. 1-20.

WILSON, J.A.

- 1971 Early Tertiary vertebrate faunas, Vieja Group, Trans-Pecos Texas: Entelodontidae. *Texas Memorial Museum, the Pearce-Sellards Series* 17:3-17, figs. 1-6.

ISBN 0-88854-254-2
ISSN 0384-8159