

Two New Oligocene Desmostylians and a Discussion of Tethytherian Systematics

*Daryl P. Domning, Clayton E. Ray,
and Malcolm C. McKenna*



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ABSTRACT

Domning, Daryl P., Clayton E. Ray, and Malcolm C. McKenna. Two New Oligocene Desmostylians and a Discussion of Tethytherian Systematics. *Smithsonian Contributions to Paleobiology*, number 59, 56 pages, 23 figures, 1986.— A new genus, comprising two new species of desmostylians, is described from marine Oligocene deposits of the Pacific Northwest. *Behemotops proteus*, new genus, new species, is based on an immature mandibular ramus and apparently associated skeletal fragments from the middle or (more likely) upper Oligocene lower part of the Pysht Formation of Clallam County, Washington. A related new species, *Behemotops emlongi*, is founded on a mandibular ramus of an old individual and a mandibular fragment with canine tusk from the uppermost Oligocene (early Arikareean equivalent) Yaquina Formation of Lincoln County, Oregon. The two new species are the most primitive known desmostylians and compare favorably with the primitive Eocene proboscideans *Anthracobune* and *Moeritherium*, and to the still more primitive tethythere *Minchenella* from the Paleocene of China.

For many years the Desmostylia were widely regarded as members of the mammalian order Sirenia before being accepted as a taxon coordinate with the Sirenia and Proboscidea (Reinhart, 1953). On the basis of cladistic analysis we go a step further and regard the Desmostylia as more closely related to Proboscidea than to Sirenia because the Desmostylia and Proboscidea are interpreted herein to share a more recent common ancestor than either order does with the Sirenia. This analysis also suggests that the common ancestor of the Proboscidea and Desmostylia (but not the Sirenia) had suppressed P5 and the original last molar. These characters may be convergent with some other mammals. The Superorder Tokotheria McKenna, 1975, was originally thought to be characterized by loss of both P5 and M3. However, because early sirenians do not show these losses, they may have occurred independently in the common ancestor of proboscideans and desmostylians and in various other tokotheres.

The late Paleocene genus *Minchenella* Zhang, 1980, from China, is a suitable candidate to be the common ancestor of both the Desmostylia and the Proboscidea. It possesses a small entoconid II on M₃. The Eocene genus *Lammidhania* Gingerich, 1977, from Pakistan, and the late Paleocene and/or early Eocene Chinese and Mongolian phenacolophids had not acquired an entoconid II on M₃ but are otherwise similar to *Minchenella* and the anthracobunids. The Asiatic occurrence of phenacolophids, *Lammidhania*, *Minchenella*, and anthracobunids suggests an Asian origin for the Proboscidea and is in accord with the exclusively Pacific distribution of the Desmostylia.

We believe that desmostylians were amphibious herbivores that fed on marine algae and angiosperms, and that at least the earlier taxa depended to a large extent on plants exposed in the intertidal zone.

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Introduction

Douglas Emlong's Promethean prowess in discovery of unprecedented vertebrate fossils, alike in beds where many, few, or no collectors preceded him, is well known to specialists having personal knowledge of his activities (Ray, 1977). Only a handful of his specimens have thus far been described (Coombs, 1979; Emlong, 1966; Munthe and Coombs, 1979; S.L. Olson, 1980, 1981; Olson and Hasegawa, 1979), but many are under study. Tragically, the flow from the wellspring of these riches ended abruptly on 8 June 1980 with Emlong's death (Ray, 1980), but his already towering reputation as a fossil finder will be progressively and justifiably widened with every added publication of the results of studies in progress on the "Emlong Collection." The purpose of the present communication is to make known several of his more remarkable and provocative discoveries: putative desmostylians, much more primitive than any previously known and forging hitherto "missing links" (E.C. Olson, 1981) with primitive proboscideans. Brief men-

tion of these fossils was made by Barnes et al. (1985).

The three specimens to be described herein are from marine Oligocene deposits of the Pacific Northwest (Figures 1–3). The first to be found, from the Yaquina Formation of coastal Oregon, consists of a massive tusk with a bit of poorly preserved bone at the anterior end of the mandible (USNM 186889; Figures 16 and 18). At the time of its discovery in 1969 it was regarded by Emlong (field list and pers. comm. to Ray) as possibly representing a land mammal but more likely a "new and very aberrant desmostylian." The second specimen to be found, discovered in 1976 in the Pysht Formation on the Olympic Peninsula in Washington, is an immature half mandible with apparently associated postcranial fragments (USNM 244035; Figures 4–11, 12A–D, 14A,C, 15A,B,E,F). It was thought by Emlong to be a desmostylian or possibly a land mammal, although he also believed that the one molar exposed in the field resembled those of sirenians (field list; pers. comm. to Ray, 1976). The third specimen found by Emlong, a half mandible of an old animal with only M_3 preserved (USNM 244033; Figures 12F, 16, and 17), collected in 1977 from the Yaquina Formation of Oregon, was described in Emlong's field list as a desmostylian or a land mammal and as elephant-like. In

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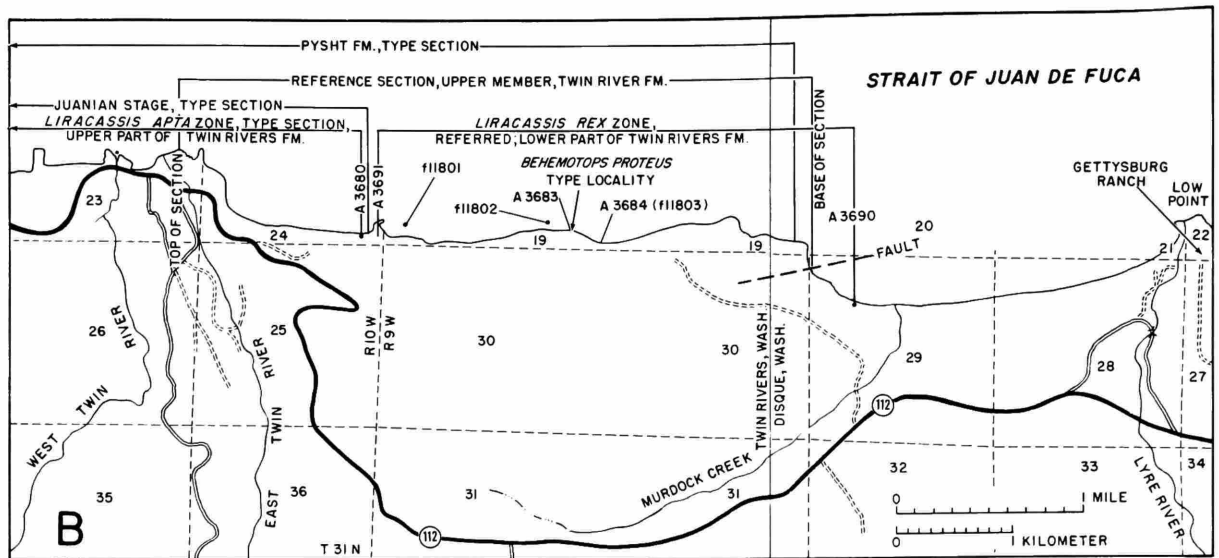


FIGURE 1.—Index maps of Pacific Northwest: A, sketch map of part of western Canada, Washington, and Oregon, showing some major place names, localities mentioned in text, and location of enlarged area shown in B; B, detail of part of Twin Rivers and Disque 7.5-minute quadrangles, USGS, along north shore of Olympic Peninsula, showing type-locality of *Behemotops proteus*, and other relevant localities and boundaries discussed in text; data primarily from Durham (1944:113, fig. 6), Brown and Gower (1958:2502, fig. 5), Rau (1964:G27, pl. 1), Addicott (1976a:98, fig. 3), Snavely et al. (1978:A118, fig. 8), and Moore (1984a:719). Spelling "Twin Rivers Formation" is that of Durham only.

to resemble those of the specimen from the Twin River [USNM 244035]. This Oligocene specimen is far larger and heavier and I am sure it is a great find, whether desmostylian or land mammal. It came from the Cornwallius horizon, but is not Cornwallius.

It may be related to that giant tusk [USNM 186889] from the Yaquina Formation, and is not far from that area. I am afraid to expose much of the specimen, so I am largely guessing.

Emlong's instant intuitions of affinities, although based on unprepared specimens, virtually no literature or comparative material, and almost no formal training, proved in this case as in many others to be uncannily perceptive and to foreshadow our own more belabored conclusions. However, it should be mentioned that his and our views have not been universally accepted by colleagues who have examined these specimens between 1969 and now.

a letter to Ray of 27 March 1977, two days after the discovery, Emlong commented as follows:

I stopped at Seal Rock . . . and found the most interesting thing of all—a giant desmostylian-like mandible, nearly complete, with teeth [only one as it turned out] that seem

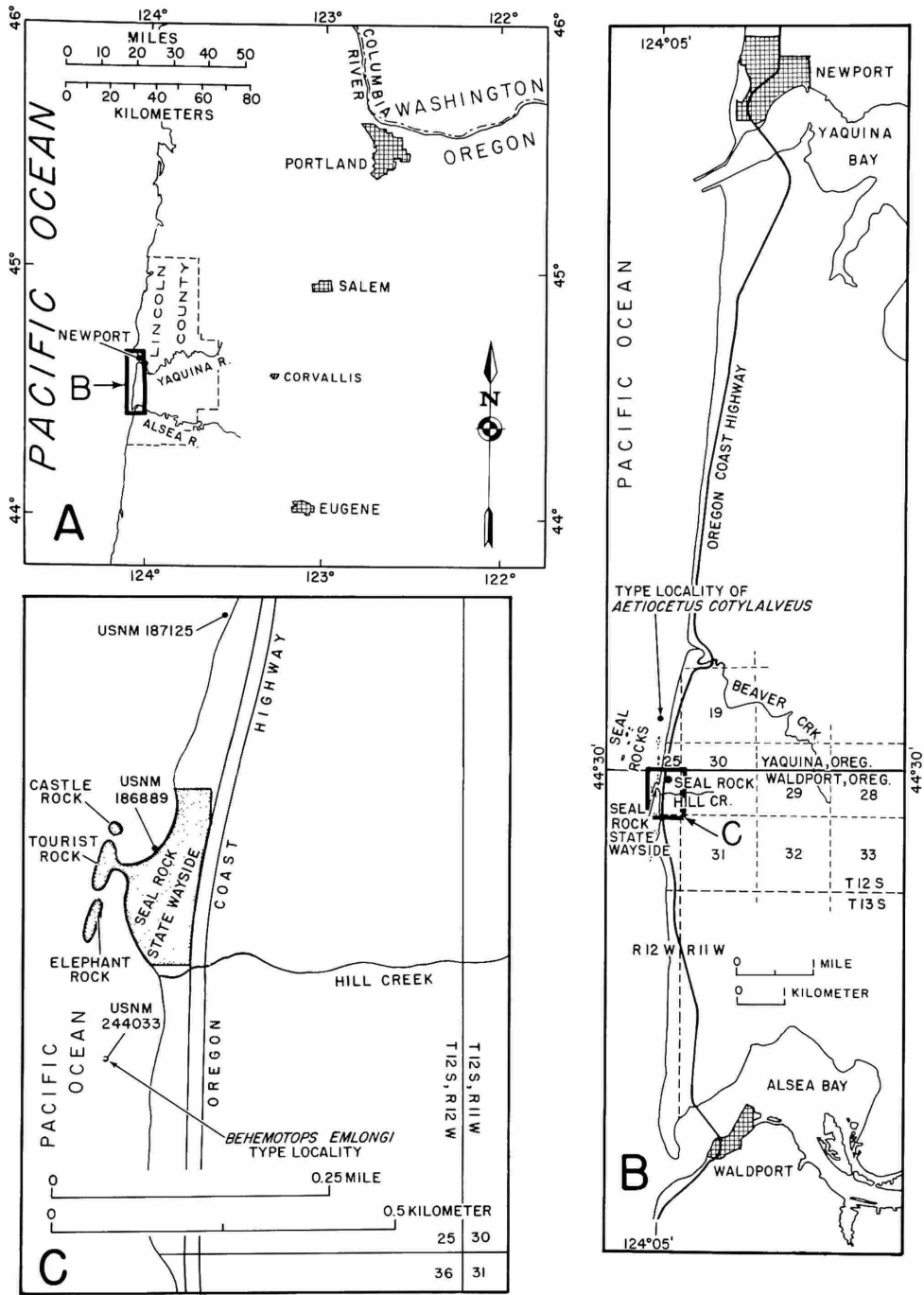


FIGURE 2.—Index maps of coastal Oregon: A, sketch map of part of northwestern Oregon, showing some major place names and location of enlarged area shown in B; B, detail of part of Yaquina and Waldport 15-minute quadrangles, USGS, along central west coast of Oregon, showing location of Seal Rock State Wayside and other localities discussed in text, including location of enlarged area shown in C; C, detail of area including Seal Rock State Wayside, showing localities for *Behemotops emlongi* and *Arretotherium*.

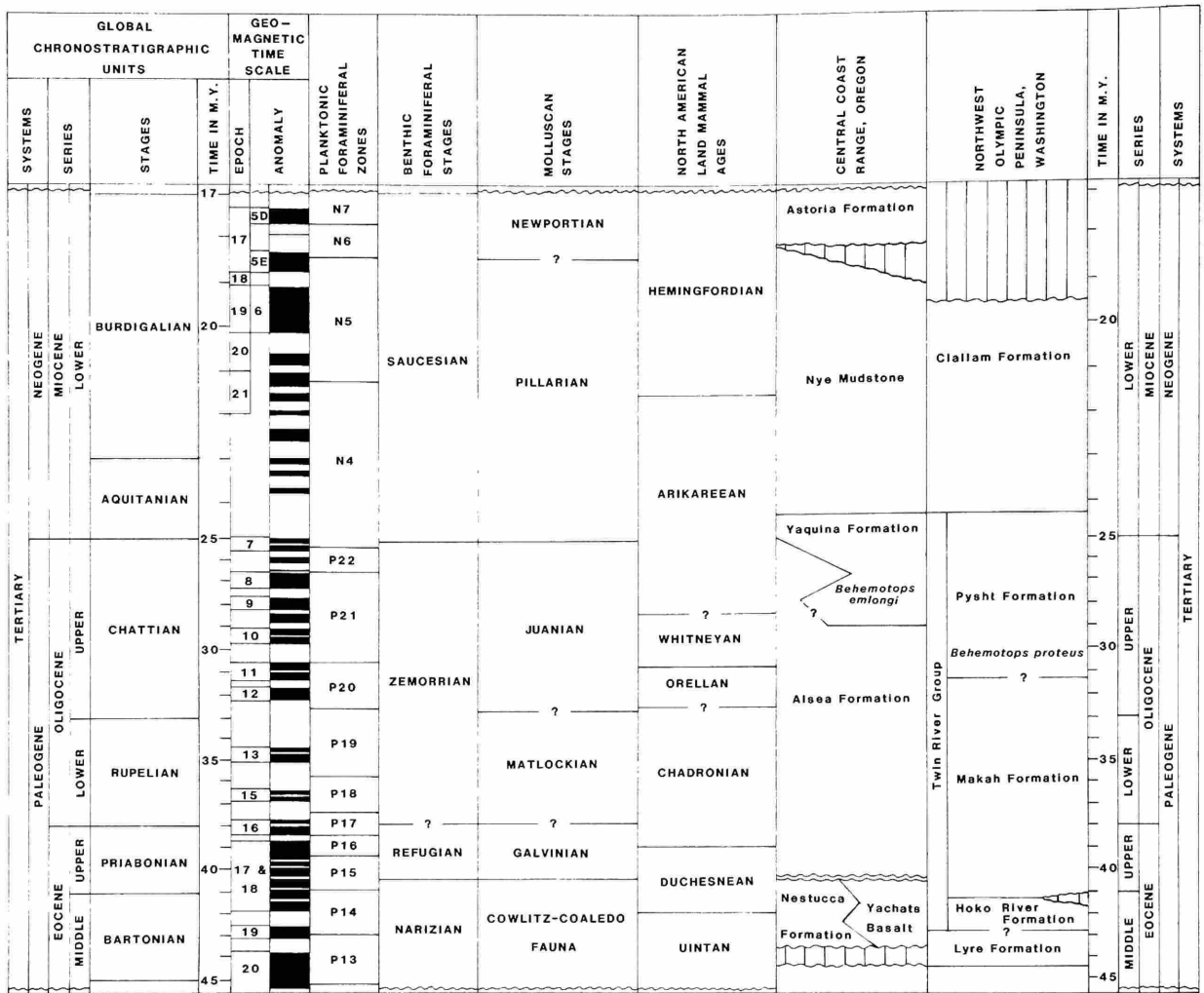


FIGURE 3.—Correlation of beds containing *Behemotops proteus* and *Behemotops emlongi* with some relevant systems of chronology; after Armentrout et al. (1983, chart). Wavy lines at top and bottom indicate continuation of unit beyond limits of chart.

ACKNOWLEDGMENTS.—Of course we are indebted above all to the late Douglas Emlong, whose perseverance in the field gave us the fascinating fossils considered herein.

The specimens were skillfully prepared by Arnold D. Lewis, and the photographs made by Victor E. Krantz. Figures 1, 2, 5–11, and 14–19 were made by Lawrence B. Isham, including the exquisite drawings for Figures 5–7. Figures 22 and 23 were made by Lisa Lomauro. The remaining figures were made by Mary Parrish.

For the loan of comparative specimens or pro-

vision of casts from their respective institutions, we thank Lawrence G. Barnes, the Natural History Museum of Los Angeles County; Philip D. Gingerich, the Museum of Paleontology, University of Michigan; J. Howard Hutchison, the Museum of Paleontology, University of California; Charles R. Schaff, the Museum of Comparative Zoology, Harvard University; Richard H. Tedford, the American Museum of Natural History; Mary Ann Turner, Peabody Museum of Natural History, Yale University; and Robert M. West, then of the Milwaukee Public Museum.

Warren O. Addicott and Parke D. Snavelly, Jr., both of the United States Geological Survey, Menlo Park, California, have shared generously their special knowledge of the source beds of the fossils and of biostratigraphy and correlation in the Pacific Northwest in general. Kristin McDougall, also of the USGS at Menlo Park, provided foraminiferal analysis of rock samples, as did William A. Berggren of the Woods Hole Oceanographic Institution. For the privilege of examining Japanese desmostylian material, including many unpublished specimens, as well as for valuable discussions and superb hospitality, Domning is particularly grateful to Yoshikazu Hasegawa, Yokohama National University; Norihisa Inuzuka, University of Tokyo; Masaichi Kimura, Hokkaido University of Education; Osamu Sakamoto, Saitama Prefectural Museum of Natural History; and Yukimitsu Tomida, National Science Museum, Tokyo. James M. Clark generously gave access to his manuscript on a new species of *Paleoparadoxia* from Point Arena, California. Jeheskel Shoshani generously shared with us his data and ideas on paenungulate characters and relationships. We have also profited greatly through discussion of sirenians, proboscideans, and desmostylians in general and of our particular specimens with Lawrence G. Barnes, Kishor Kumar, Earl Manning, Adele Panofsky, Roy H. Reinhart, Charles A. Repenning, R.J.G. Savage, and Andrew Wyss. Further, Barnes, Repenning, and Savage have read the manuscript critically and have supplied us with important unpublished information. Although the end product has benefitted greatly from the assistance of all of the above-mentioned colleagues, its remaining deficiencies are of course our responsibility.

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The sequence of authorship was determined by lot.

ABBREVIATIONS.—The following abbreviations are used to identify the institutions listed:

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History, New York, N.Y.
AMNH CA	Department of Mammalogy, Comparative Anatomy Collection, American Museum of Natural History, New York, N.Y.
LACM	Natural History Museum of Los Angeles County, Los Angeles, Cal.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NSM	National Science Museum, Tokyo, Japan
UCMP	Museum of Paleontology, University of California, Berkeley, Cal.
USGS	United States Geological Survey
USNM	former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D. C.
YPM	Peabody Museum of Natural History, Yale University, New Haven, Conn.

Class MAMMALIA Linnaeus, 1758

Order DESMOSTYLIA Reinhart, 1953

Family Uncertain

DISCUSSION.—The family-level taxonomy of desmostylians is at present unsatisfactory. The original Family Desmostylidae Osborn, 1905, was supplemented by the Cornwalliidae Shikama, 1957 (emended from the original spelling "Cornwalliusidae" by Shikama, 1966:153), which was created to accommodate *Cornwallius* Hay, 1923. When Reinhart (1959:94) generically separated "*Cornwallius*" *tabatai* from the type-species *C. sookensis* and assigned the former to a new genus, *Paleoparadoxia*, he also erected a third family, Paleoparadoxidae (emended from "Family Paleoparadoxia" Reinhart, 1953); however, he retained *Cornwallius*, sensu stricto, in the Desmostylidae. Shikama (1966) instead placed both *Cornwallius* and *Paleoparadoxia* in his Cornwalliidae. Apart from these inconsistencies already in the literature, the few and dissimilar genera mak-

ing up the order could arguably be arranged in almost any arbitrary number of groups, from a single, all-embracing Desmostylidae to monotypic families for each genus. However, until desmostylian diversity and phylogeny are better understood, we prefer to reserve judgment on the familial assignment of the taxa described herein, and we suggest a temporary moratorium on new family-level arrangements within the order.

Behemotops, new genus

TYPE-SPECIES.—*Behemotops proteus*, new species.

INCLUDED SPECIES.—*Behemotops proteus* and *B. emlongi*, new species.

DIAGNOSIS.—Desmostylian differing from other members of the order in having seven lower postcanine cheek-teeth, without marked diastemata; P₁ (or DP₁) large, caniniform, procumbent, single-rooted; P₂ large, procumbent, with root partially or completely divided; molars brachydont, bunodont, with four principal cusps neither cylindrical nor appressed, and forming a square; metaconids of lower molars not twinned; all permanent teeth in use together at maturity; and lingual surface of mandible lacking swelling at rear of tooth row.

ETYMOLOGY.—From the biblical (Job 40:15–24) Hebraic (and Greek, Latin, and English by adoption) *b'hemoth*, plural, “great beast,” thought by many etymologists and zoologists (including Linnaeus, 1758:74, whose latinized *Behemot* is used herein) to refer to the Nilotic hippopotamus (and, by others, including Maglio, 1973:2, to the elephant, mammoth, etc.); or *b'hemah*, singular, “beast,” conjectured by some to be derived from a (possibly artificial) Coptic term *p-eh-mau* “water-ox”; plus *-ops*, Greek, suffix, masculine, like or similar aspect; in allusion to the Egyptian source of many specimens of tethytheres and to the hippopotamian habitus and proboscidean affinities of the fossil animal. In any case, we agree with Lydgate (1412–1420, volume 2: page xvii) that the animal’s name “doth in latin playne expresse A beast rude full of cursednesse.”

Behemotops proteus, new species

FIGURES 4–11, 12A–D, 14A,C, 15A,B,E,F

HOLOTYPE.—USNM 244035, right mandibular ramus of immature individual with DP₄, P₁ (or DP₁), and P₃–M₃; and, probably from the same individual, the distal half of the right femur, a proximal fragment of the right tibia, and two phalanges. Field number E76-14, collected 11 March 1976 by Douglas Emlong.

DIAGNOSIS.—Lower canine probably smaller than in *B. emlongi* (described below); premolars large, high, not molariform; P₃ with one dominant cusp (protoconid), P₄ with two (metaconid and protoconid); metaconid of P₄ not twinned; P₃ and P₄ double-rooted, unlike *B. emlongi*; DP₄ trilobate.

ETYMOLOGY.—From the Greek sea-god Proteus, son of the sea-goddess Tethys and sea-god Oceanus; old man of the sea and herdsman of the sea-calves (seals) of Poseidon; also able to assume different forms; Latin, masculine, noun in apposition. In allusion to (among other things) its tethytherian affinities and marine habitat, and the pronounced ontogenetic changes in its dental morphology.

TYPE-LOCALITY.—South side of Strait of Juan de Fuca, on north shore of Olympic Peninsula, Clallam County, Washington; some 34 km (21 miles) west of Port Angeles and approximately 3.6 km (2.2 miles) east of mouth of East Twin River; 1.6 km (1.0 miles) east and 290 meters (950 feet) north of SW corner, Sec. 19, T. 31 N, R. 9 W, Twin Rivers Quadrangle, 7.5-minute series, USGS; 48°09'38"N, 123°53'55"W; wave-cut bench 15 meters (50 feet) north of cliff face (Figure 1).

The postcranial elements came from the same bedding plane as the mandible but were separated from it horizontally by approximately 6 meters (20 feet).

HORIZON.—In place in northwesterly dipping, concretionary, silty, gray mudstone, within the lower part of the type section of the Pysht Formation (Snively et al., 1978:A118, A119).

AGE AND CORRELATION (Figures 1B, 3).—The

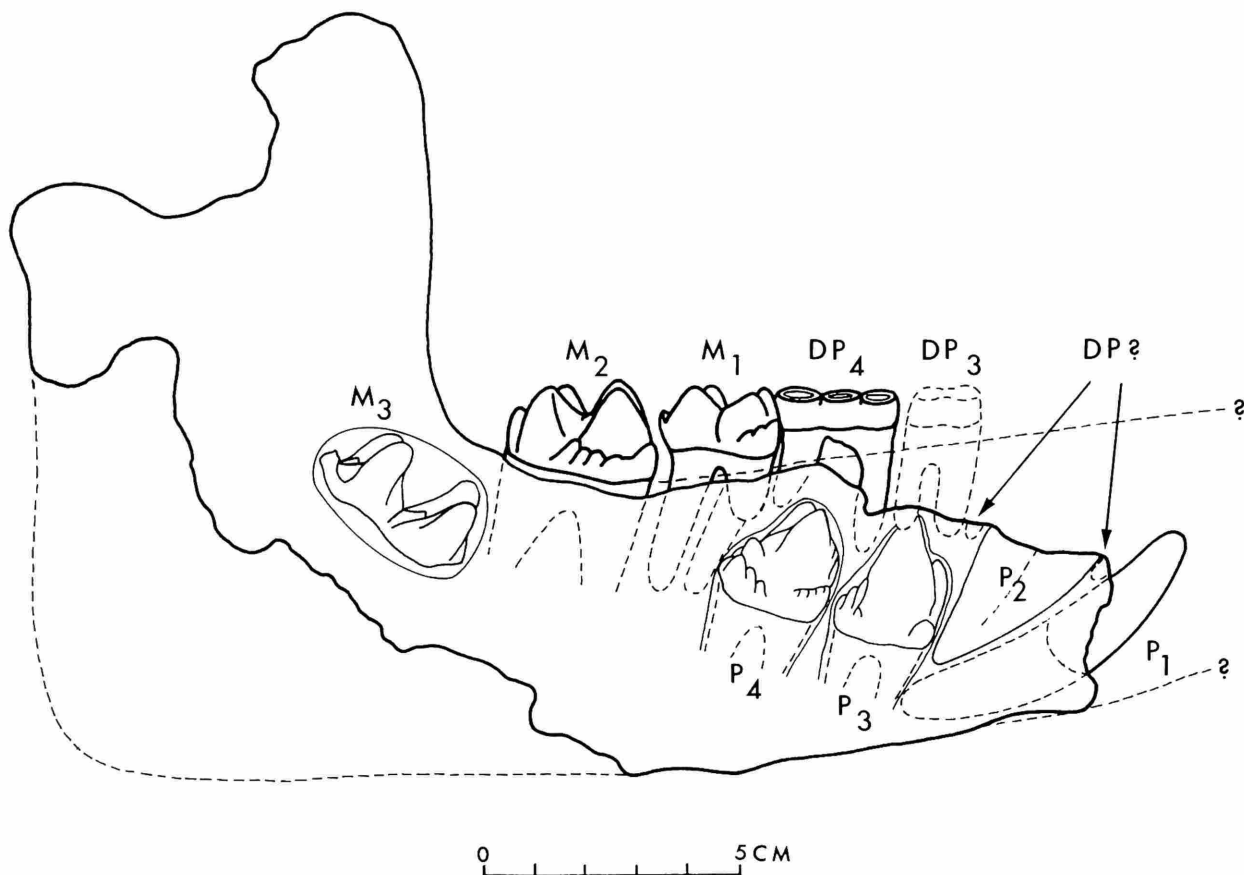


FIGURE 4.—*Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington, diagrammatic representation of right mandibular ramus in labial aspect, showing interpretation of dental loci.

rocks from which the holotype of *Behemotops proteus* was collected are by definition within the type section of the Pysht Formation (lower part), explicitly assigned to the *Echinophoria rex* Zone (now *Liracassis rex* Zone). The latter is coeval with the Matlockian and “lower” Zemorrian stages. We regard the lower part of the Pysht Formation as middle or (more likely) late (but not latest) Oligocene in age. In terms of North American Land Mammal Ages, this would imply that *B. proteus* is Orellan or Whitneyan in age.

Although the formational assignment and general age of the holotype are certain, the nature of deposition, internal conflicts in the biostratigraphic literature, limited exposures, complexity of the geology (including folding and faulting), and continuously evolving concepts of the rele-

vant biostratigraphy and correlation all recommend a more extended discussion of the subject than would otherwise be warranted. An introduction to the broad regional biostratigraphic framework can be obtained from the recent publications by Addicott (1981), Armentrout et al. (1983), Marincovich (1984), and Moore (1984a, 1984b). For a discussion of the position of the boundary between the Oligocene and the Miocene in both marine and continental deposits, see Berggren, Kent, and Flynn (in press).

The Twin River Formation (now Twin River Group) was named by Arnold and Hannibal (1913:584, 585) for rocks exposed on the coast from “about three miles east of Twin River west nearly to Pysht Bay,” thus including the type-locality of *Behemotops proteus*. The locality lies

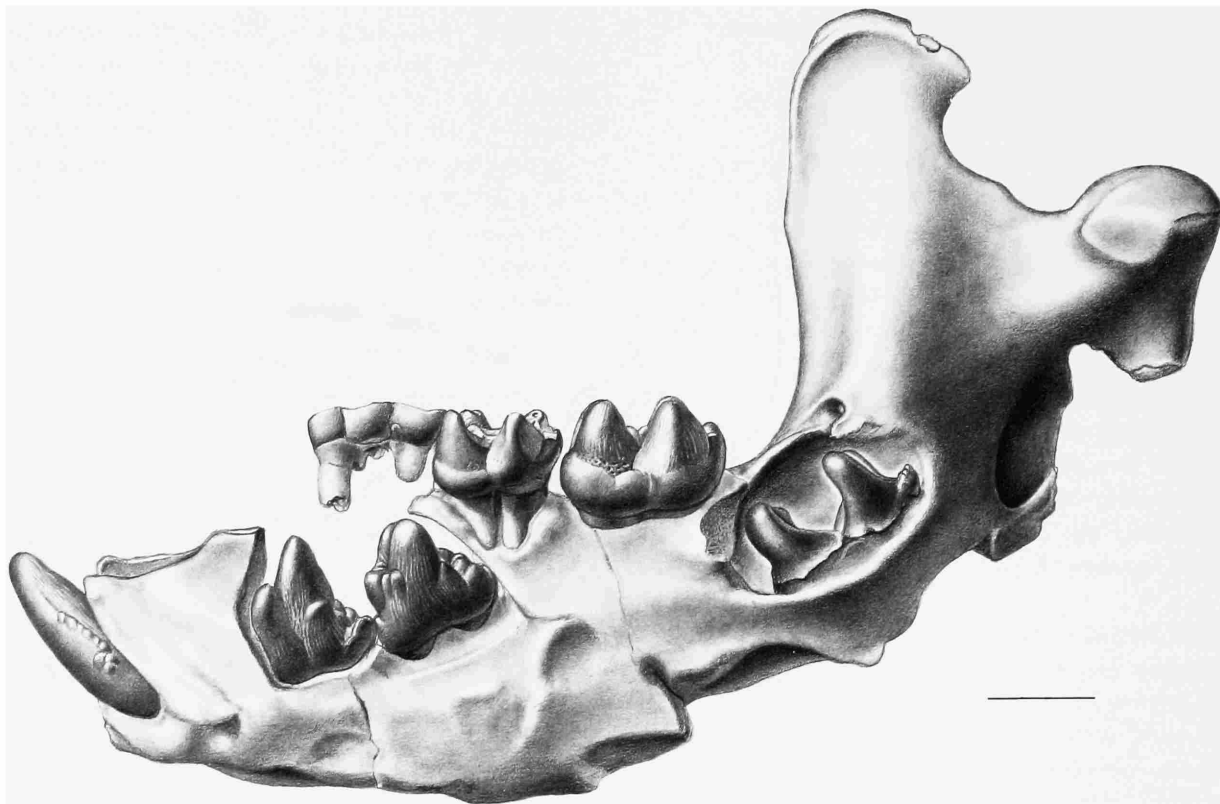


FIGURE 5.—*Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington, right mandibular ramus, in lingual aspect. DP₄ in original position as found, prior to preparation of specimen; P₃ and P₄ shown in present state of specimen with bone removed dorsal and lateral to teeth; compare Figure 8. Note opening of coronoid canal above crypt of M₃. Scale approximately 2 cm.

between Durham's (1944:113, figs. 5 and 6) localities A 3683 and A 3684, in a section that he explicitly assigned to the lower part of the Twin River Formation (Twin Rivers formation of Durham) and to his *Echinophoria rex* Zone. (The *Echinophoria rex* Zone should now be called the *Liracassis rex* Zone, and the *Echinophoria apta* Zone, the *Liracassis apta* Zone, according to Moore, 1984a:719. In the following discussion we retain the older notation of the references cited.) However, Brown and Gower (1958:2502, fig. 5) redefined the Twin River Formation so that the reference section for their upper member, between East Twin River and Murdock Creek, includes our locality. Nevertheless, they noted (1958:2510) without disagreement that their upper member included strata assigned by

Durham (1944) both to his *Echinophoria apta* and to his *E. rex* zones. Our locality lies approximately 366 meters (1200 feet) east of USGS foraminiferal collecting locality f 11802 and 91 meters (300 feet) west of f 11803 (= Durham's 1944, locality A 3684), both of which localities were assigned to the upper member of the Twin River Formation and their faunas to the upper part of the Zemorrian Foraminiferal Stage by Rau (1964:G9, G27, table 6, pls. 1 and 4).

On the basis of molluscan biostratigraphy of another rock unit, the Lincoln Creek Formation of southwestern Washington, Armentrout (1975:25–29) established the Matlockian molluscan stage, which he divided into a lower and an upper zone, equivalent, respectively, to the *Echinophoria rex* and overlying *E. apta* zones of

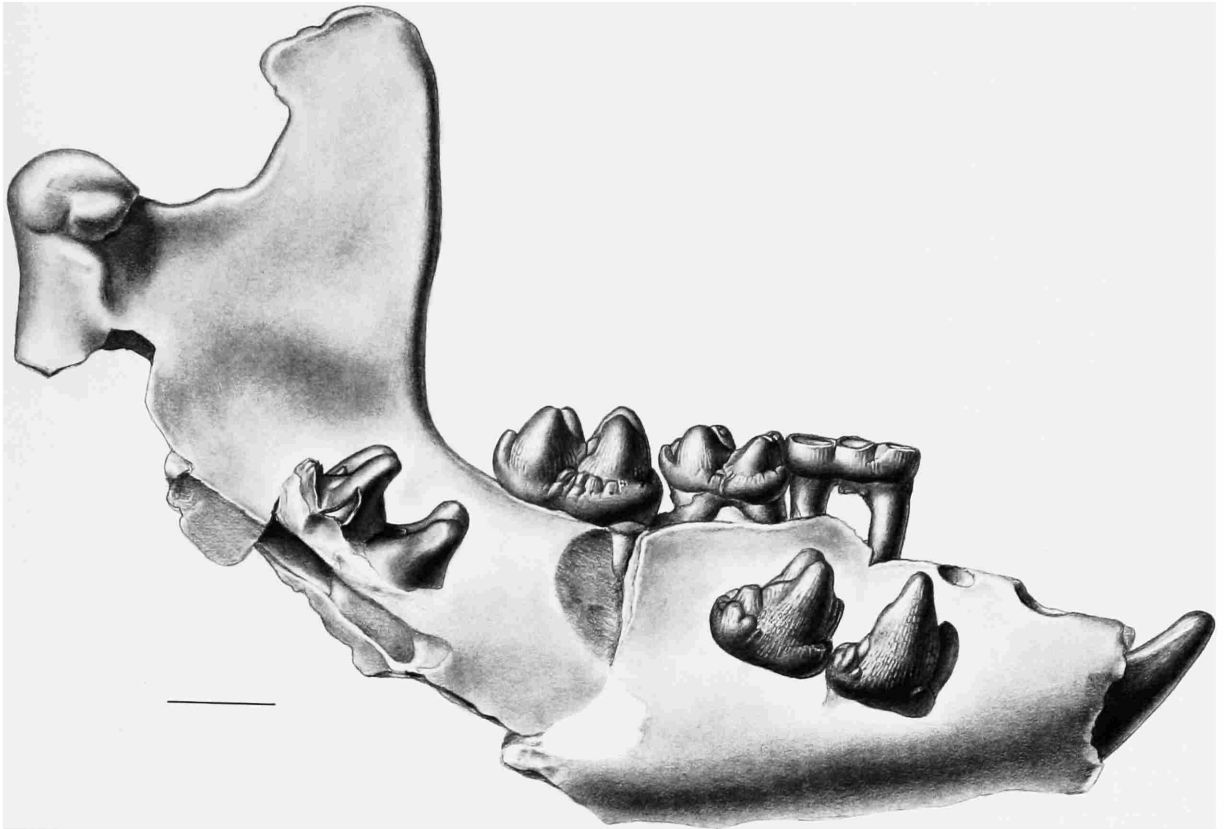


FIGURE 6.—*Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington, right mandibular ramus, in labial aspect. DP₄ in original position as found, prior to preparation of specimen; bony ramus shown at stage of preparation of Figure 9; P₃, P₄, and M₃ shown as visible in present state of specimen with bone removed to show teeth in labial aspect. Scale approximately 2 cm.

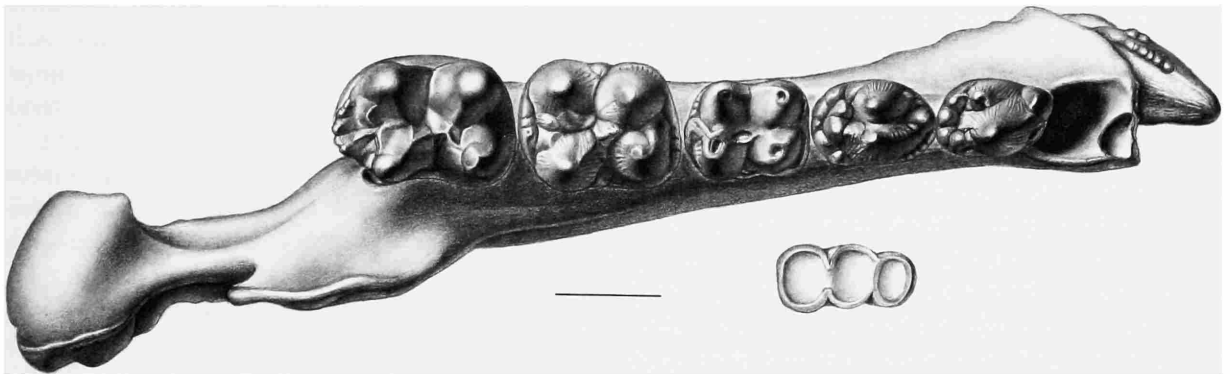


FIGURE 7.—*Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington, right mandibular ramus, in occlusal aspect. DP₄ shown adjacent; P₁ (or DP₁), P₃, P₄, and M₃ shown as if fully erupted and in occlusal position; compare Figures 4, 5, and 8–10, for true position of these teeth. Opening of coronoid canal, adjacent to posterolabial corner of M₃, shown only to indicate its presence, as it would have shifted in position through remodeling of bone as M₃ erupted. See Figure 5 for true location as preserved. Scale approximately 2 cm.

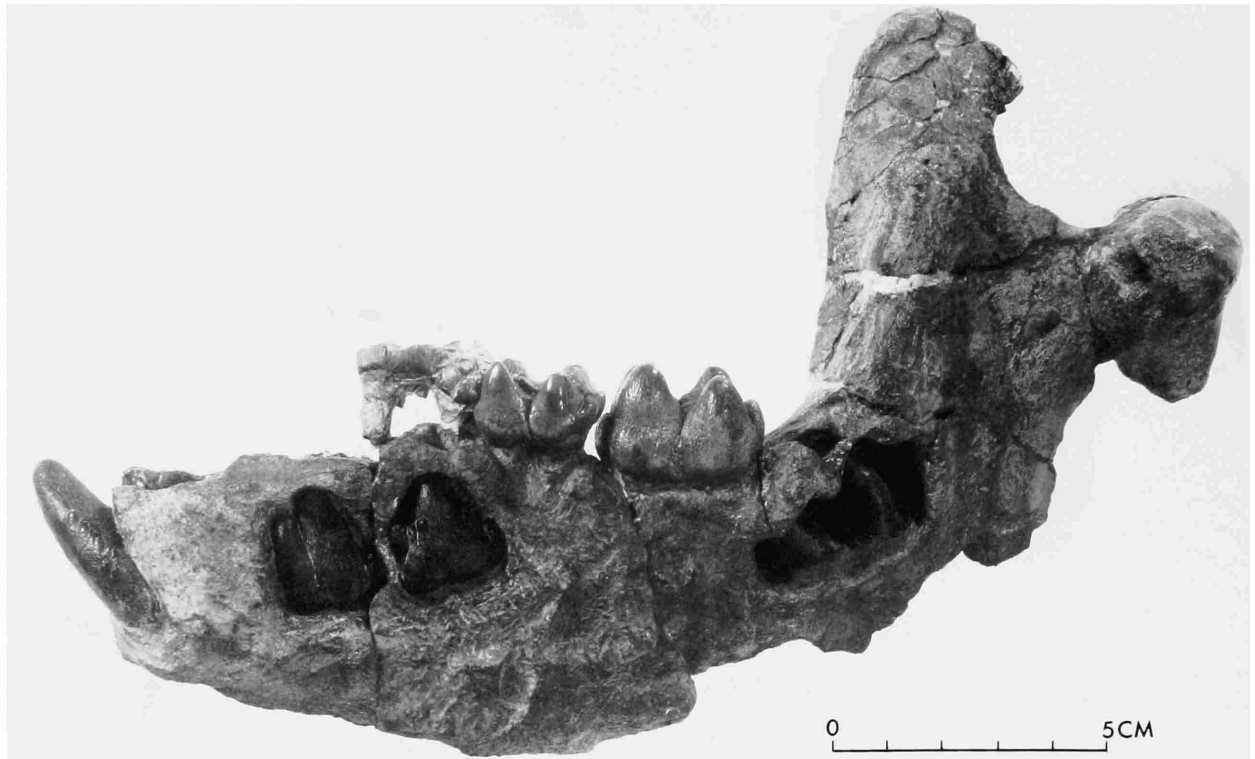


FIGURE 8.—*Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington, right mandibular ramus, in lingual aspect. Specimen photographed prior to removal of any detectable bone in preparation, and prior to exposure of mandibular foramen and additional preparation on opening of coronoid canal.

the Olympic Peninsula. Addicott (1976a) established molluscan stages for the Neogene of Oregon and Washington. His earliest stage, the Juanian, shares its type section with the *E. apta* Zone, and has its base in the sea cliff approximately 2 km east of the mouth of East Twin River (not 3 km as stated erroneously in Addicott, 1976a:97, 98; Addicott, pers. comm. to Ray, 21 Sep 1978), between UCMP localities A 3680 and A 3691 (see Durham, 1944, fig. 6). Addicott's (1976b, fig. 2) generalized section of the upper member (= Pysht Formation) of the Twin River Formation erroneously includes the lower half of the upper member of the Twin River Formation in the *Echinophoria apta* Zone (Addicott, pers. comm. to Ray, 8 Mar 1982). The section from locality A 3691 downward should be referred to the *E. rex* Zone, including all localities numerically between A 3681 and A

3691, inclusive, and geographically between A 3691 on the west and A 3690 on the east (Durham, 1944, fig. 6). Our locality lies some 1.6 km east of locality A 3691 in westerly dipping strata, thus well below the base of the Juanian Stage and within the reference section of the *E. rex* Zone.

A sample of the enclosing matrix from the holotype of *B. proteus*, USNM 244035, was processed for Foraminifera by Kristin McDougall of the USGS, yielding one planktonic and 27 benthic taxa, indicative of an Oligocene, late Zemorrian age. She stated, "This fauna is quite similar to that found by Rau (1964) in samples f 11801 and f 11802. The faunas suggest cool temperatures in a protected upper bathyal to outer neritic environment" (USGS Report on Referred Fossils, shipment number 0-76-8M, sample Mf 3256, 24 Aug 1976). Snavely et al.

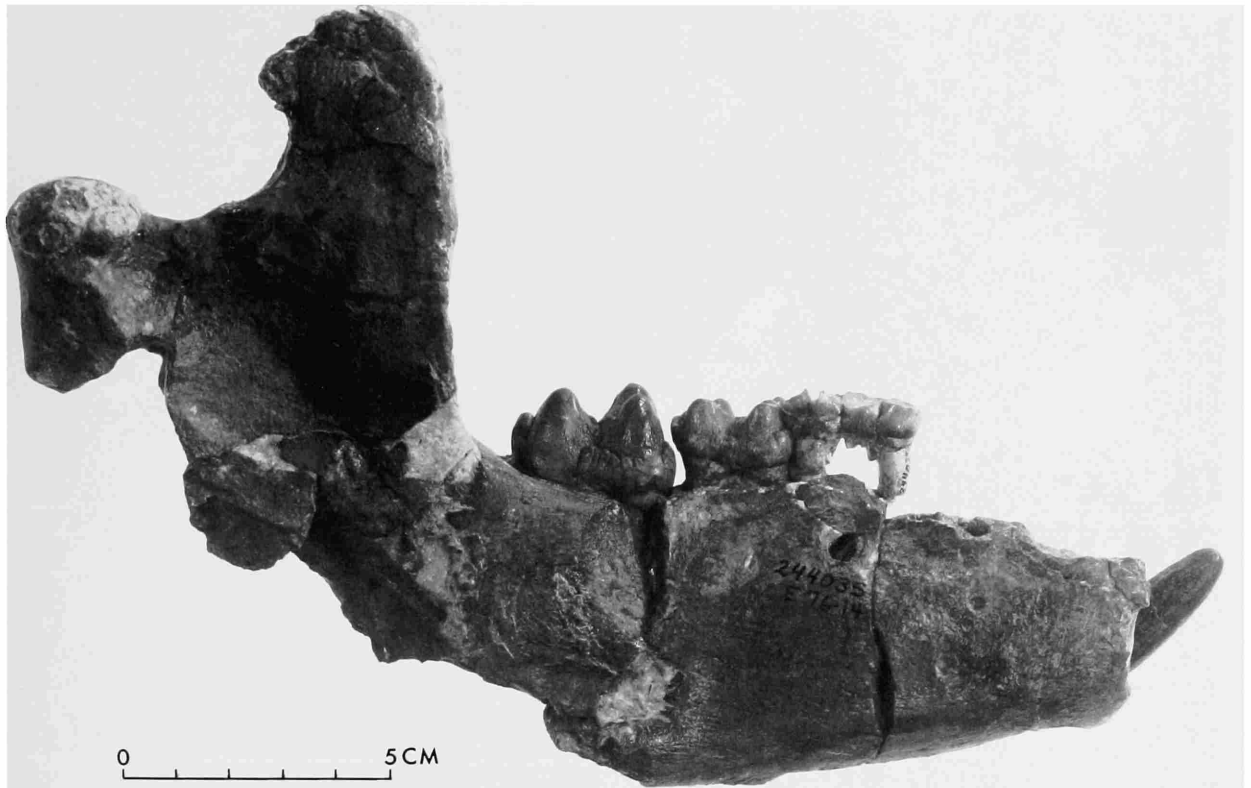


FIGURE 9.—*Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington, right mandibular ramus in labial aspect. Specimen photographed prior to removal of any detectable bone in preparation.

(1980, fig. 15) have presented a paleogeographic map showing the distribution of late Eocene and Oligocene shelf and deep-water marginal seas in the Pacific Northwest during the time of deposition of the Makah, Pysht, Alsea, and other broadly correlative formations of the region.

The regional geology of the Olympic Peninsula, including major, previously unpublished results of mapping by Snively and associates in the area of concern herein, has been portrayed in a map at the scale of 1:125,000, with a synopsis and bibliography (Tabor and Cady, 1978). The relevant strata are therein mapped as the upper member of the Twin River Formation. Snively et al. (1978) raised the Twin River to group rank and named formations for its upper members, of which the Pysht Formation is uppermost. The type-locality of the Pysht Formation is the section exposed for some 18 km in the cliffs and on the

shore from Pillar Point State Park eastward to 3.5 km west of Low Point. This eastern limit is in the SE corner (not SW as stated erroneously in Snively et al., 1978:A118), Sec. 19, T. 31 N, R. 9 W, whereas our fossil locality is in the SW corner, in the lower part of the Pysht Formation.

Armentrout (1977; 1978; 1981:140) restricted his Matlockian Stage to the *E. rex* Zone, leaving the succeeding *E. apta* Zone for the Juanian Stage, thus eliminating the overlap between the two stages. As now restricted, the Matlockian Stage is wholly beneath the Juanian Stage.

As originally proposed, the Juanian represented the basal Neogene, lower Miocene molluscan stage in the Pacific Northwest, with its base at the Oligocene-Miocene boundary, at 23–24 million years ago, within the upper part of the Zemorrian Benthic Foraminiferal Stage (Ad-

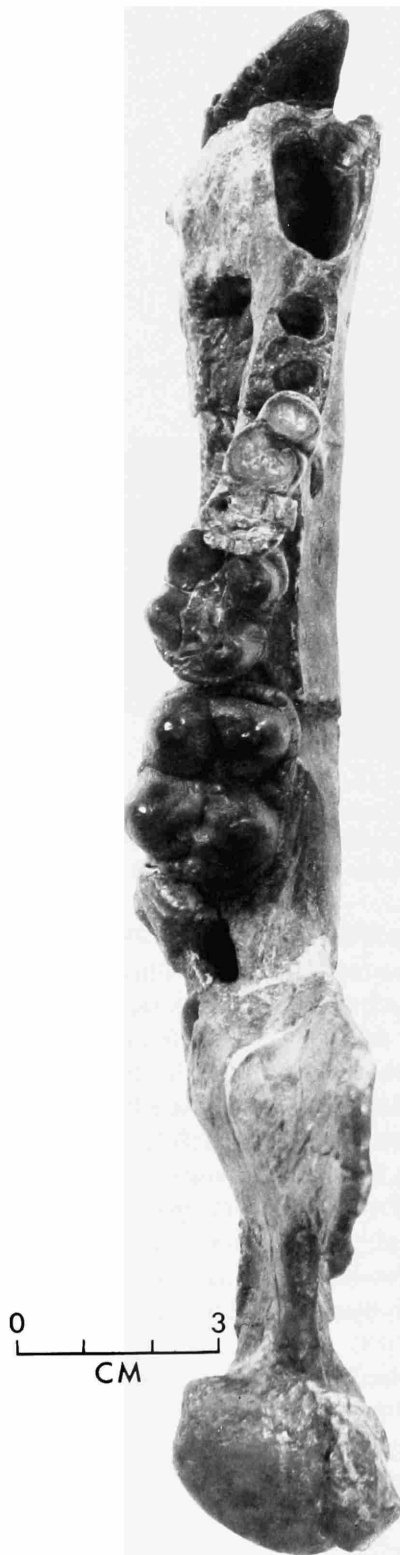
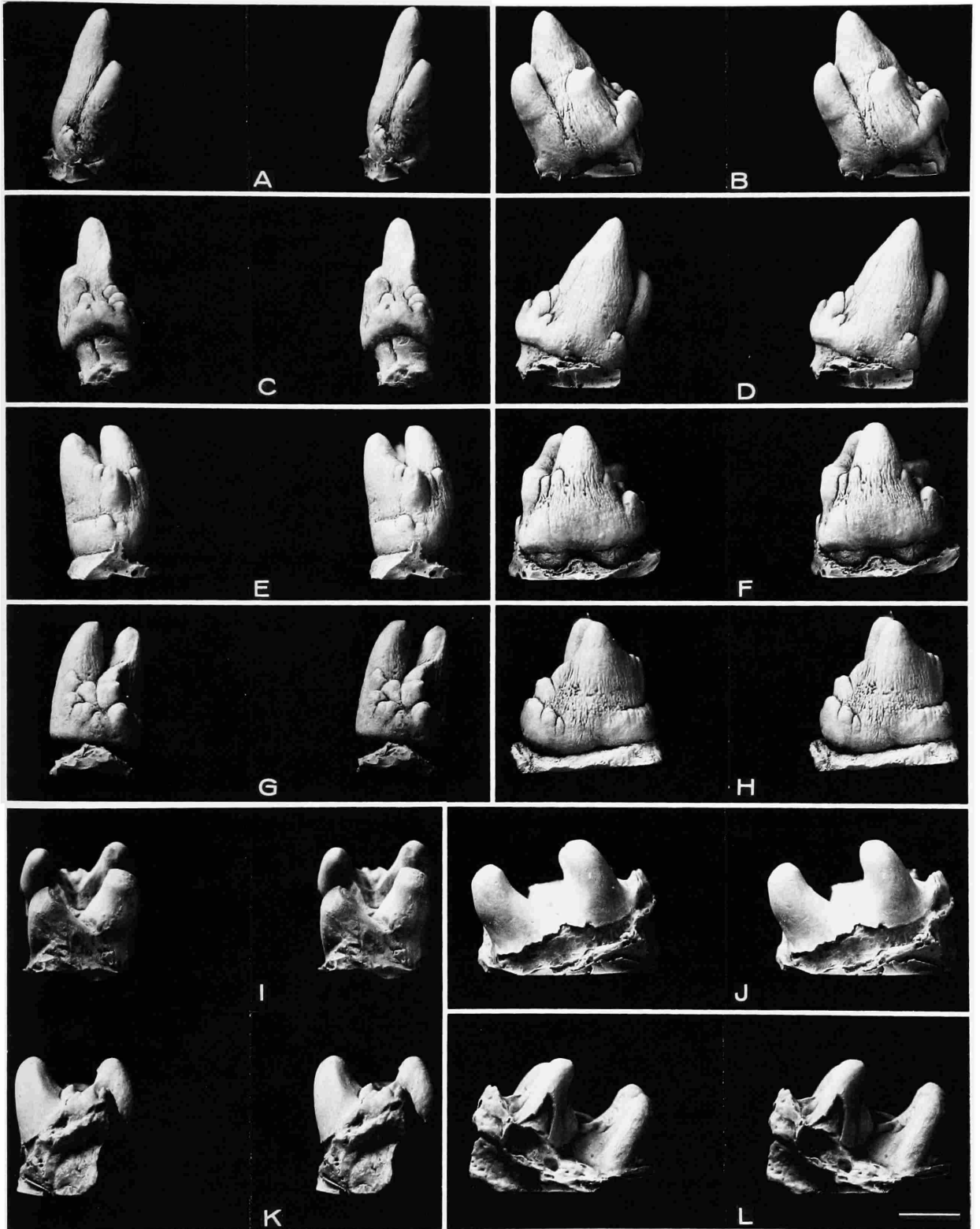


FIGURE 10.—*Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington, right mandibular ramus in occlusal aspect. Specimen photographed prior to removal of any detectable bone, and prior to additional preparation on opening of coronoid canal.

dicott, 1976a:98). Subsequently, however, the upper boundary of the Juanian has been regarded as almost or exactly coeval with that of the Zemorrian Stage, with the bases of both at 29 or more million years ago. Thus, the Juanian Stage is now usually regarded as late Oligocene (pre-Aquitania) in age (Addicott, 1977:163, fig. 3; Allison, 1977:876; Armentrout, 1981:140, 142, 145; Armentrout et al., 1983), although Allison (1976; 1978), Allison and Marincovich (1981:4), and Moore (1984b:4) regard the Juanian as mostly late Oligocene and partly early Miocene in age. Armentrout's restricted Matlockian molluscan stage (= *E. rex* Zone, = below the uppermost part of the Zemorrian Foraminiferal Stage), representing time from some 29 to 32 million years ago, is thus earlier in age than latest Oligocene (Armentrout, 1981:145), or is in fact early Oligocene, 33–38 million years old (Armentrout et al., 1983, chart; our Figure 3).

ASSOCIATED FAUNA.—Douglas Emlong discovered numerous specimens of vertebrate fossils in the Pysht Formation. The majority of these are skulls of archaic cetaceans under study by R. Ewan Fordyce and others and as yet alluded to only briefly in the literature (Whitmore and Sanders, 1977:310, 311, fig. 2; Fordyce, 1981:1028, 1033). A single specimen from the same area has provided the basis for a new genus and species of penguin-like peleciform bird, *Tonsala hildegardae* Olson, 1980. This material is thought to be similar in age to *B. proteus*, but

FIGURE 11.—Stereophotographs of casts (whitened) of some postcanine teeth of *Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington: A–D, RP₃ in anterior (A), medial (B), posterior (C), and lateral (D) aspects. E–H, RP₄ in anterior (E), medial (F), posterior (G), and lateral (H) aspects. I–L, RM₃ in anterior (I), medial (J), posterior (K), and lateral (L) aspects. Scale 1 cm.



faults introduce an element of uncertainty, as the direction of throw of the faults and the relationship of the residual accumulation of fossils to the bedrock and the faults are unresolved. There is in any case no basis to suppose that any of the material postdates the Pysht Formation.

MEASUREMENTS.—The following measurements of the holotype right mandibular ramus of *Behemotops proteus* (USNM 244035), are in millimeters. Those in parentheses are approximate, based on incomplete, damaged, or incompletely accessible parts. Those for all alveoli or dental crypts are as preserved, in all cases at least somewhat below the real alveolar border. See "Description, Dental Formula" for identification of dental loci.

Maximum length of specimen as preserved	235
Depth of ramus below M ₁	56.5
DP ₂ Maximum diameter of crypt (alveolus?)	(8.4)
Minimum diameter of crypt (alveolus?)	(5.5)
DP ₃ Maximum anteroposterior dimension of combined alveoli	(16.3)
DP ₄ Anteroposterior length of crown	(26.8)
Width of anterior lobe of crown	10.2
Width of medial lobe of crown	11.8
Width of posterior lobe of crown	(15.1)
P ₁ (or DP ₁) Maximum height of crown, measured on medial surface	39.9
Maximum diameter of crown	(19.7)
Minimum diameter of crown at same level	(12.2)
P ₂ Maximum diameter of crypt	(23.3)
Minimum diameter of crypt (alveolus?) at edge	(14.2)
P ₃ Maximum height of crown	26.0
Anteroposterior diameter of crown	20.8
Transverse diameter of crown	14.4
P ₄ Maximum height of crown	21.5
Anteroposterior diameter of crown	23.1
Transverse diameter of crown	15.8
M ₁ Maximum height of crown (metaconid)	14.5
Length of crown	24.1
Anterior width of crown	(18.0)
Posterior width of crown	(17.5)
M ₂ Maximum height of crown (metaconid)	21.2
Length of crown	31.7
Anterior width of crown	23.7
Posterior width of crown	23.6
M ₃ Maximum height of crown (base of crown)	(15.5)

incompletely formed), as preserved (metaconid)	(31.7)
Length of crown	(19.0)
Anterior width of crown	(21.0)
Posterior width of crown	

DESCRIPTION.—The holotype, USNM 244035, is generally well preserved, with sharply defined surfaces on the bones and all teeth. For the teeth the only exception is some fracturing in the posterior lobe of DP₄ (Figure 10) and a single, major, anteroposterior fracture with some offset and compression in the crown of M₁ (Figures 10, 12C). For the bones, the lingual surface of the horizontal ramus of the mandible (Figure 8) and the caudal surface of the femur (Figure 14A) and much of the tibial surface are curiously eroded (chemically?) and pitted. This destruction of bone apparently removed the thin lingual walls of the crypts of the unerupted P₃, P₄, and M₃, creating windows through which the initial preparation was done to expose these teeth. The phenomenon seems to have affected exactly the parts of the specimen that remained covered by the remnant of a primary concretion of slightly different color and texture than the enclosing secondary concretion.

Further preparation was done to expose more of the crowns of the unerupted teeth, by removing much of the labial and dorsal walls of their crypts. The unerupted teeth have been maintained in their original positions as found, and casts have been prepared of their crowns to enable viewing in direct occlusal aspect.

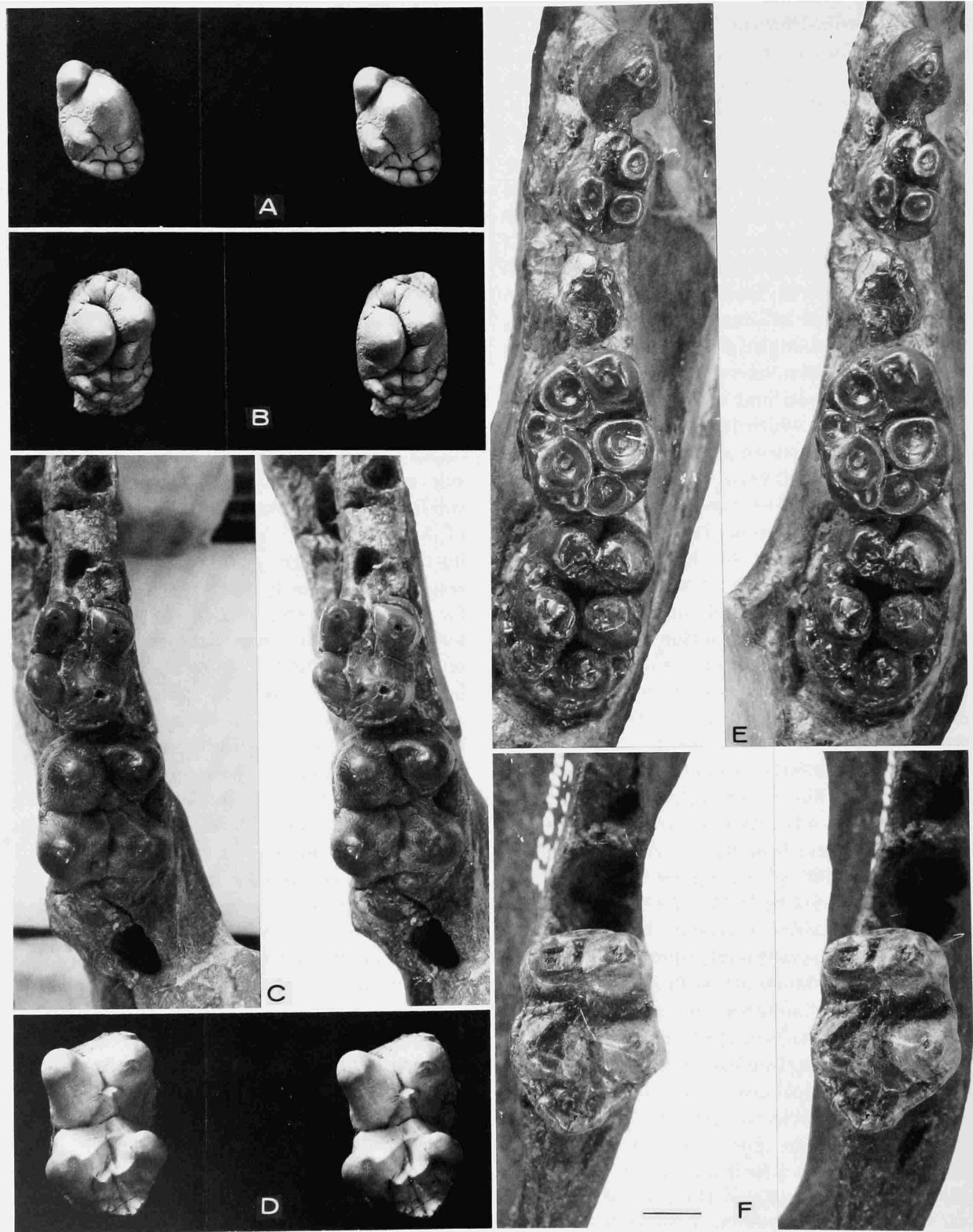
Dental Formula (Figure 4): Considerable phylogenetic significance attaches to the identification of dental loci in *Behemotops proteus*, in part because of divergent specializations and emphasis or de-emphasis of given loci in related taxa. For example, inferior tusks are developed from second incisors in moeritheres and other proboscideans, but from canines in desmostylians. Sirenians are less critical for such comparisons because their retention of five premolars in the known Eocene taxa, unique among Tertiary placental mammals (Domning, Morgan, and Ray, 1982), sets them phylogenetically apart from desmosty-

lians and proboscideans, which primitively retained only four premolars. The interpretations of *B. proteus* presented herein rest in part on evidence from *B. emlongi* from the Yaquina Formation of Oregon, described later in this paper.

Some aspects of the dental formula and succession in the holotype of *Behemotops proteus* seem certain. There is no reason to question the identification of M_1 – M_3 as conventionally understood (but see below, "Implications for Eutherian Dental Homologies"). M_1 is considerably smaller than M_2 and M_3 , and is already substantially worn, whereas M_2 , although fully in occlusal position, is virtually unworn, and the crown of M_3 is incompletely formed and remains in its crypt (a small window to which had opened in the bone above it). The early emplacement and attrition of a relatively small M_1 is a common feature in bunodont herbivores, and is strongly pronounced in the desmostylian genus *Paleoparadoxia* (Figures 12E, 19). The identification of DP_4 is also definite, because it was found, deeply worn, in place immediately anterior to and in contact with M_1 . Its posterior root, although broken, is still in place anterior to M_1 . Moreover, DP_4 is trilobate, again as in many herbivorous mammals, for example artiodactyls (see Figure 20), phenacodonts (West, 1971, fig. 1), some specimens of *Moeritherium* (YPM 34764) but not especially so in the specimen figured by Andrews (1906:110, fig. 43), *Phiomia serridens* (Andrews, 1906, pl. 18), and *Deinotherium* and *Gomphotherium* (Lartet, 1859, pl. 13: fig. 4c; pl. 14: fig. 4c. See also Frick, 1926; 1933). If DP_4 and M_1 – M_3 have been identified correctly, then the tooth occupying the crypt directly under DP_4 (and the anterior part of M_1) must be P_4 and the tooth in the crypt immediately anterior to it must be P_3 . The two alveoli, subequal in size and circular in cross section, lying one each anterior and posterior to the principal cusp of P_3 , are for the two roots of DP_3 . Between and slightly lingual to these alveoli is what appears at first sight to be a third alveolus but which may be in reality the apex of the P_3 crypt below (Figure 10). A similar resorption window can be seen in a specimen

(AMNH CA 2423) of the living pygmy hippopotamus, *Hexaprotodon liberiensis*, that died at a comparable stage in its ontogeny. Thus, the DP_3 of *Behemotops proteus* was probably double-rooted. Only the deepest apical parts of the DP_3 alveoli are preserved, because a considerable, although unknown, amount of bone is missing anterior to DP_4 along the dorsal, alveolar-marginal edge of the horizontal ramus.

Anterior to the P_3 locus the situation becomes less clear because of the loss of bone and the absence of all teeth except one (interpreted below as P_1 or DP_1). We regard the large, simple alveolus anterior to the P_3 locus as in fact the ventral remnant of the crypt for a large, fully formed, but probably unerupted P_2 . There is at depth a slight vertical crest in the bone on each side of the alveolus, suggestive of incomplete subdivision into anterior and posterior moieties of the root that occupied it. On the anterolabial border of this large crypt or alveolus is an apical remnant of a much smaller alveolus, probably for the anterior root of DP_2 . The anteriormost tooth present (forming the anteriormost preserved part of the specimen) is a large, procumbent, essentially caniniform tooth, with its crown and at least much of its root fully formed but lying in its crypt deep within the mandible at the time the animal died. This tooth, which we regard as P_1 or DP_1 , looks as if it would also fit the crypt of P_2 reasonably well, suggesting that the P_2 also was a relatively simple tooth. Unfortunately, the holotype of *B. proteus* retains no vestige of the canine or incisive loci. Enough bone of the horizontal ramus remains beneath P_1 (or DP_1) to demonstrate that the canine or any other enlarged anterior tooth could not have extended to the rear past P_1 (or DP_1) at the stage of ontogeny represented by the holotype. There is apparently no room for such a tooth, and, further, there is no hint of growth of the mandibular ramus in anticipation of the eventual emplacement of such a tusk. Rather, the symphyseal region may have resembled that of *Hexaprotodon*, with the P_1 (or DP_1) of *B. proteus* occupying the position of the canine in *Hexaprotodon*.



Dentition: The terms developed by Tobien (1978 and elsewhere) for the description of mastodont molars, including *Moeritherium*, can be applied readily to the molars of *Behemotops*, and are noted herein throughout the description.

All teeth except M_3 show finely to coarsely crenulated enamel, wrinkled or pustulose, except where smoothed by wear.

The only deciduous tooth preserved is the deeply worn, trilobate DP_4 (Figures 4–10). Wear has reduced the occlusal plan to a series of three interconnected, subcircular rings of enamel, increasing in size posteriorly. The cusps of the upper deciduous premolars of *Moeritherium* (Schlosser, 1911, pl. 13: fig. 9) have a similar round outline at the stage of wear demonstrated; an only minimally trilobate lower deciduous premolar has been reported by Andrews (1906:110, fig. 43). However, DP_4 of YPM 34764 is trilobate. The anterior lobe of DP_4 in *B. proteus* is bordered anteriorly by a distinct precingulid.

P_1 (or DP_1) (Figures 4–10) is represented by a well-formed but unerupted tooth. The tooth is simple, unicusped, essentially caniniform, single-rooted, robust, and has a bluntly rounded tip reminiscent of the principal cusp of P_3 in the same specimen. There are faint longitudinal crests on opposite sides of the crown from approximately 7 to 13.7 mm down from the tip of the tooth, from which point the crests each give way to a single row of small cusps or coarse crenulations of subequal size, best exposed on the medial surface of the crown where the cusps are some six in number. These crests divide

the crown into two unequal sections, a narrower, flattened, posteromedial one and a broader, rounded, anterolateral one. Later in ontogeny this tooth almost certainly would have rotated clockwise (as viewed dorsally) more than 45° about its longitudinal axis, so that the crests would have become anterior and posterior, the smaller, flatter surface lingual, the larger, more convex surface labial, and the greatest diameter anteroposterior. It would have stood much higher than P_3 (and perhaps somewhat higher than P_2) when fully erupted.

P_2 (Figures 4, 7, 10) is represented only by its crypt (alveolus). The crypt is similar enough to the shape of P_1 (or DP_1) to suggest a very similar tooth. However, its orientation, if that of P_1 (or DP_1) resembled it, would imply rotation of P_1 (or DP_1) as suggested above. A single root was present, but traces of fusion of two roots, perhaps separated at some earlier phylogenetic stage, are indicated on the alveolar walls.

P_3 (Figures 4–8, 11A–D, 12A) is dominated by a single, high, bluntly conical cusp (protoconid), with a weak posterior crest. Low on its anterolingual slope is a well delimited, subcylindrical, somewhat recurved cusp (paraconid); on its posterolingual slope is a weaker, lower, less independent cusp (metaconid); at its anterolabial base, labial to the paraconid, is a small cingular cusp, which, with a meager shelf at the anterior base of the paraconid, represents a precingulid. Small cusps on the posterior slopes of the protoconid and metaconid near their bases may represent the hypoconid and entoconid, respectively. Posterior to that and spanning almost the breadth of the tooth is a strong postcingulid consisting of some five small cusps, the labialmost three of which are largest and subequal to one another in size. A tiny, marginal, basal cusp occupies the base of the crease delimiting the protoconid and possible hypoconid. The anterior and posterior roots are separate, in contrast to those of *B. emlongi*.

P_4 (Figures 4–8, 11E–H, 12B) is slightly larger than P_3 , but not so tall. It is dominated by two bluntly conical cusps of almost exactly equal

FIGURE 12.—Stereophotographs in occlusal aspect of some inferior postcanine teeth of *Behemotops proteus* from lower part of Pysht Formation of Washington, *Paleoparadoxia tabatai* from Izumi locality, Japan (Shikama, 1966:12), and *Behemotops emlongi* from lower part of Yaquina Formation of Oregon: A–D, *Behemotops proteus*, holotype, USNM 244035: A, RP_3 ; B, RP_4 ; C, RM_1 – RM_2 ; D, RM_3 . A, B, and D are photographs of casts (whitened), because original teeth cannot be viewed in exact occlusal aspect; compare Figures 4–10. E, *Paleoparadoxia tabatai*, cast of neotype, USNM 26375, LP_3 – M_3 . F, *Behemotops emlongi*, holotype, USNM 24033, LM_3 . Scale 1 cm.

height. The lingual of these (metaconid) lies slightly posterior to a point directly medial to the labial cusp (protoconid), and is simple, with only two minor subsidiary cusps, one each at the base of its anterolingual and posterolingual slopes; the metaconid is not twinned. The metaconid is embraced labially by the more complex protoconid, with its strong, cuspidate paracristid and protoconid curving about the anterolabial and posterolabial parts of the base of the metaconid. The paracristid terminates in a poorly differentiated and somewhat bifid paraconid near the middle of the anterior wall of the crown. A well-marked and cuspidate precingulid lies below the paracristid along the anterolabial base of the crown. Posterior to the metaconid and protoconid are two low cusps (entoconid and hypoconid), the latter the larger, lying posterior to the termination of the protoconid. The entoconid and hypoconid together are bordered posterolingually, posteriorly, and posterolabially by a strong postcingulid consisting of five to six low cusps of varied size, shape, and height. The anterior and posterior roots are apparently still separate, in contrast to those of *B. emlongi*.

M_1 (Figures 4–10, 12c) is by far the smallest of the molars, being only slightly larger in crown area than P_4 but more nearly rectangular. The basic plan of the bunodont, brachydont tooth is simple; it consists of four independent, subequal, major low conical cusps, the protoconid, metaconid, hypoconid, and entoconid, each occupying a quadrant of a square, to which attach strong pre- and postcingulids. The cingulids are not continued on the lingual and labial walls of the tooth, although suggested by a bulbous expansion of the anterolabial part of the base of the protoconid and by a pustulose shelf at the labial outlet of the valley between the protoconid and hypoconid. The conical shape of the protoconid is modified slightly by a very weak paracristid (anterior crescentoid of first pretrite, a. cr. 1) that extends anterolingually but lacks an identifiable paraconid. The metaconid is not twinned. A cristid obliqua (a. cr. 2) occupies an analogous position on the anterolingual slope of the hypo-

conid. A low, worn, independent cusp occupies the center of the occlusal surface of the crown. This cusp lies adjacent to the anterolingual termination of a. cr. 2 and on the anterior slope of the transverse valley. It may represent a conelet subsidiary to the metaconid but, if so, it is posteriorly displaced. A low, broad hypolophid extends down the labial slope of the entoconid. The presence of the hypolophid, together with the nature of the wear on the crown, excessive on the anterior walls of the hypoconid and entoconid and on the posterior walls of the protoconid and metaconid, impart a mildly lophodont character to this tooth, not clearly evident in the little-worn M_2 and even less so in the unerupted M_3 . The crenulated postcingulid rises from its lingual and labial extremities to a central hypoconulid. The anterior and posterior roots are well separated labially, but are closer together lingually.

M_2 (Figures 4–10, 12c) is almost an exact but enlarged replica of M_1 . It is almost unworn and therefore reveals the features of the crown clearly. The base of the crown forms a bulbous collar, especially distinct on the anterior half of the tooth. The cingulid, although variably developed, is interrupted only lingual to the entoconid and labial to the hypoconid. The metaconid is not twinned. Anterior to the postcingulid and side by side posterolabial to the entoconid and posterolingual to the hypoconid are two small cusps on either side of the midline of the crown (at least the worn labial member of the pair is identifiable in M_1 , and the lingual member could be present but obscured by wear and faulting of the tooth). These cusps are similar to the conelets of *Gomphotherium* (Tobien, 1978, fig. 1) but are not placed quite so far forward. The cristid obliqua (a. cr. 2) of M_2 supports two small cusps separated by a notch representing the transverse valley. These cusps are similar to those of M_1 , but unworn. The anterior of the two lies at the base of the posterolabial slope of the metaconid, and might be regarded as its conelet, analogous in position to that of the entoconid. The postcingulid rises to a median apex as in M_1 . Insofar as

can be seen, the roots are as in M_1 .

M_3 (Figures 4–8, 11I–L, 12D) is basically similar in construction to M_1 and M_2 insofar as its incompletely formed enamel cap reveals. Its roots had not formed at the time of the animal's death. However, the crown does show some uniquely interesting features. For example, all four principal cusps are simpler, higher, more nearly cylindrical than bluntly conical, and thus more widely separated from one another. The metaconid is not twinned. There is no evidence of a paraconid or paracristid (a. cr. 1). The cristid obliqua (a. cr. 2) is sharply defined, as is a complementary crest (hypolophid?) extending anterolabially from the entoconid. The anteriormost of the two low cuspules seen on the cristid obliqua is a low, trihedral cusp, similar in position to a more rounded cuspule in the same position on M_2 , and to the worn cuspule on M_1 , but less clearly tied to the metaconid. The postcristid is sharply defined, and posterolabial to the entoconid it possesses a low, sharply pointed conelet. A small crest descends along the posterolingual base of the hypoconid. The crenulated postcingulid shelf is broader anteroposteriorly than in M_1 or M_2 , and lends an angular, V-shaped outline to the posterior end of the tooth. The crown is not sufficiently formed to show the condition of the cingulid elsewhere.

Apparently, the odd "bunostylodont" nature of the M_3 of *Behemotops proteus* must be attributed to its incomplete ontogenetic development; at maturity it would presumably have had more swollen cusps like those of the other molars. This is indicated by two pieces of evidence. First, M_3 contrasts with all other teeth of the specimen in not having wrinkled or crenulated enamel; this suggests that the outer layers of enamel had not yet been deposited. Second, at least in *Desmostylus* it is certain that the columns of the molars attained nearly their full height long before reaching their final diameter. The developing molar, therefore, consisted of a group of high, slender columns, initially not connected at their bases and often found isolated. Only in later stages of development was sufficient enamel deposited on

each column to fill the spaces between the columns. The clearest example of this that we have seen is in NSM 5600, the skull and mandible of *Desmostylus* described by Yoshiwara and Iwasaki (1902). On plate 2 of their paper an unerupted right upper molar (" M_2 ") is shown. Examination of the actual specimen, now further prepared, discloses the condition described above, the tooth consisting of separate, very slender columns (Figure 13). Thus, there is no reason to doubt that a similar although less extreme process of cusp thickening took place during the dental ontogeny of *B. proteus* and no reason to suppose that the difference in M_3 cusp thickness between the latter and *B. emlongi* is of any major taxonomic importance. Due allowance for additional enamel deposited on the sides (and to a lesser extent, on the tips) of the cusps of *B. proteus* would bring the dimensions of its M_3 into tolerable agreement with those of *B. emlongi*.

Osteology: The mandible of the holotype, USNM 244035, is robustly proportioned; its horizontal ramus was certainly thicker than immediately suggested by the specimen as preserved, in view of the postmortem loss of bone over much of its lingual surface. A remnant of bone below the posterolingual corner of M_2 and the thickness of the ramus at P_1 (or DP_1) and P_2 indicates that the horizontal ramus was originally several millimeters thicker over much of its expanse (Figures 8 and 10). The ventral margin of the mandible is essentially straight as far as it is preserved. Two small mental foramina open adjacent to the crypt of P_3 (Figure 9); undoubtedly others were present more anteriorly. The ostensible foramen midway below DP_4 (Figure 9) is in fact a window adjacent to the tip of the crown of P_4 . The ascending ramus of the mandible has its anterior and (as far as preserved) posterior margins nearly vertical. The rounded articular condyle is elevated well above the plane of occlusion; the anterior margin of the ascending ramus is nearly straight and approximately perpendicular to the plane of occlusion. The coronoid process is broad, smoothly curved, and has a posterior hook. The mandibular foramen lies midway be-



FIGURE 13.—*Desmostylus hesperus*, NSM 5600, from Togari, Gifu Prefecture, Honshu, Japan, originally described by Yoshiwara and Iwasaki (1902); right upper molars in labial aspect. Note slender and distinctly separated enamel columns of unerupted and incompletely formed posterior molar, in contrast to thick, appressed columns of fully formed and erupted anterior molar.

tween the anterior and posterior margins of the ascending ramus and directly posterior to the crypt for M_3 (Figure 5). The mandibular canal passes forward from the foramen, under the ventrolateral edge of the developing M_3 , and less than 4 mm from it. A coronoid foramen (coronoid canal) passes through the base of the coronoid process at the rear of the developing alveolus of M_3 (Figures 5 and 8).

Very little can be said about the postcranial skeleton, represented only by a few pieces

thought to be part of the holotype. The distal half of the femur (Figure 14A,C) displays an anteroposteriorly narrow shaft expanding distally into a broadly flattened extremity with a broad patellar facet; the narrowness of the shaft is strongly reminiscent of the condition in *Paleoparadoxia*. Its incompleteness and the erosion of the bone on its caudal surface make precise assessment of its proportions impossible. The distal epiphysis was not coossified with the diaphysis, as it is slightly displaced. The tibia is represented

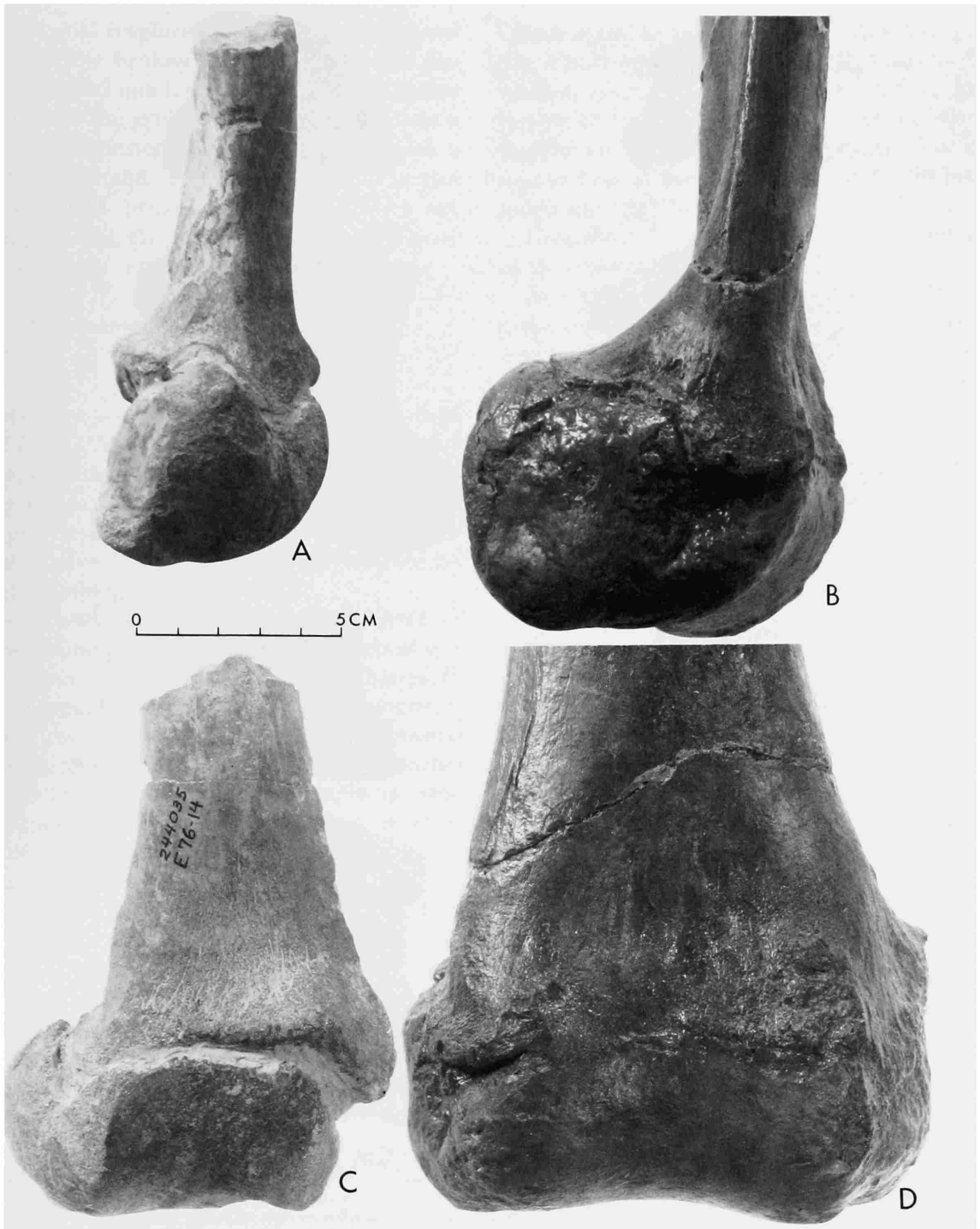


FIGURE 14.—*Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington, distal part of right femur, in lateral (A) and cranial (C) aspects; *Paleoparadoxia tabatai* from Izumi locality, Japan (Shikama, 1966:12), cast of neotype, USNM 26375, distal part of right femur, in lateral (B) and cranial (D) aspects.

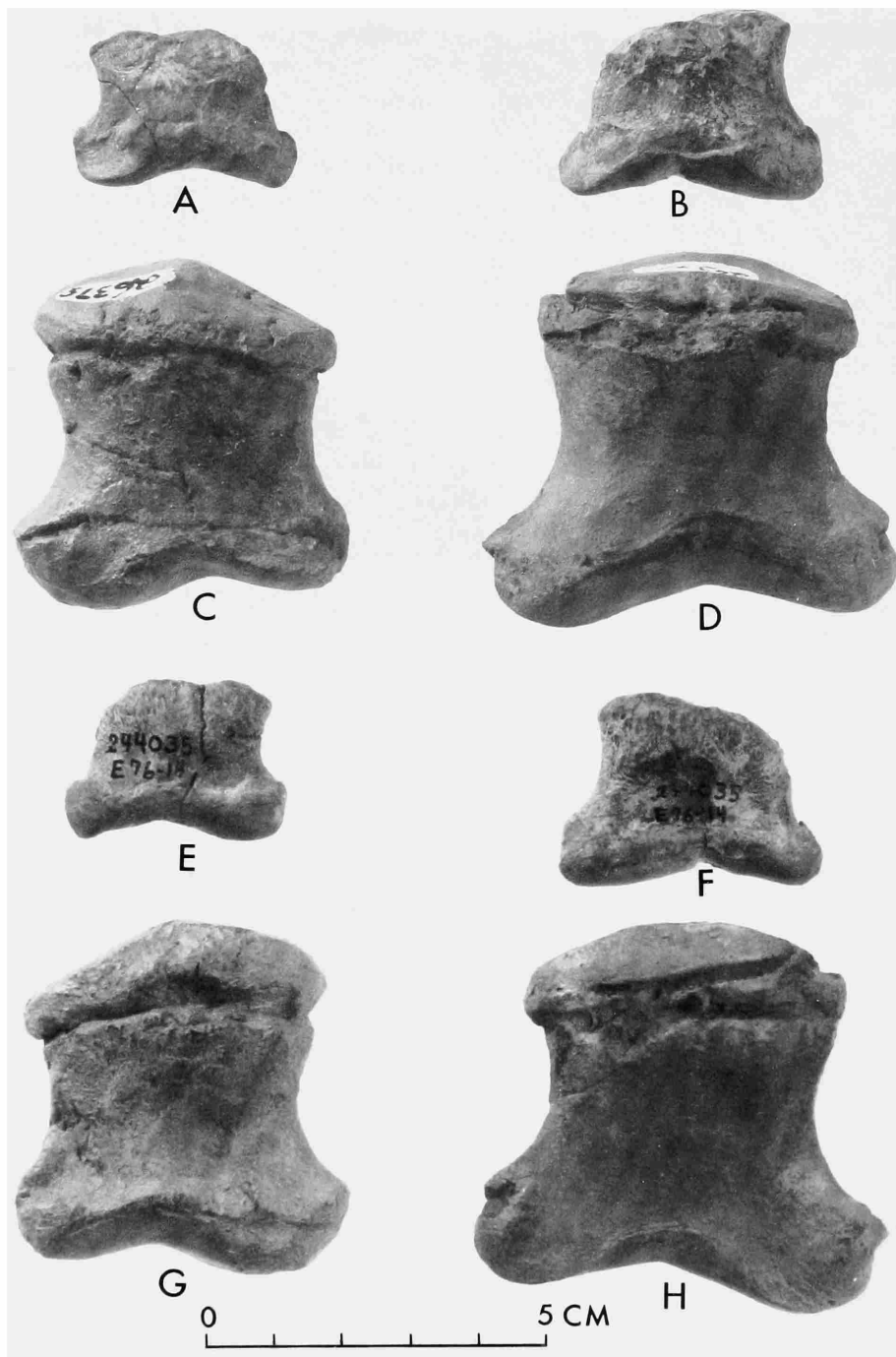


FIGURE 15.—*Behemotops proteus*, holotype, USNM 244035, from lower part of Pysht Formation of Washington, phalanges, lacking proximal epiphyses, in dorsal (A, B) and palmar (E, F) aspects; *Paleoparadoxia tabatai* from Izumi locality (Shikama, 1966:12), cast of neotype, USNM 26375, phalanges, in dorsal (C, D) and palmar (G, H) aspects.

by a proximal fragment with separate proximal epiphysis. The broken cross section of the diaphysis, some 60 mm from its proximal end (some 80 mm with the epiphysis in place), indicates a broad, anteroposteriorly flattened tibia with a low tibial crest and very shallow fossae. The two phalanges lack proximal epiphyses. They are strikingly broad, flat, and splayed distally (Figure 15A,B,E,F), also reminiscent of *Paleoparadoxia*.

Behemotops emlongi, new species

FIGURES 12F, 16–18

HOLOTYPE.—USNM 244033 (Emlong field no. E77-21), nearly complete left mandibular ramus, considerably damaged in region of symphysis and posterior border of ascending ramus and condyle; only M_3 present, but with partial or complete alveoli of all adult teeth; collected by Douglas Emlong, 25 March 1977.

DIAGNOSIS.—Lower incise alveoli three in number, subequal in size, with round cross sections; lower canine (probably unlike that of *B. proteus*) greatly enlarged, tusk-like, procumbent, laterally compressed; longest diastema between P_2 and P_3 , shorter than anteroposterior diameter of either tooth; P_3 and P_4 alveoli simple, housing single-rooted teeth, unlike *B. proteus*; anterior half of mandible massive; symphyseal region broad, shovel-like.

ETYMOLOGY.—For the late Douglas R. Emlong, collector extraordinary.

TYPE-LOCALITY.—183 meters (200 yards) south-southeast of Elephant Rock (Figure 2c), Seal Rock State Wayside, Lincoln County, Oregon; Sec. 25, T. 12 S, R. 12 W, Waldport Quadrangle, 15-minute series, USGS (Figure 2); intertidal bench 76 meters (250 feet) west of the cliff face.

REFERRED SPECIMEN.—USNM 186889 (Emlong field no. 555), much fragmented, poorly preserved anterior part of right mandibular ramus with root of P_3 and essentially complete canine tusk; collected by Douglas Emlong, April 1969. Seal Rock State Wayside, Lincoln County, Oregon; Sec. 25, T. 12 S, R. 12 W, Waldport

Quadrangle, 15-minute series, USGS (Figure 2). Same horizon as USNM 244033, Yaquina Formation, from the foot of the sea cliff, approximately 43 meters (140 feet) north of the isthmus joining Tourist Rock to the mainland. The isthmus to Tourist Rock lies at latitude $44^{\circ}29'50''N$, longitude $124^{\circ}05'00''W$.

HORIZON.—In coarse grit layer of lower part of the Yaquina Formation (Snively et al., 1976).

AGE AND CORRELATION (FIGURE 3).—The holotype and referred specimens of *Behemotops emlongi*, USNM 244033 and 186889, are from the Yaquina Formation of western Oregon, assigned to the Juanian Stage (Addicott, 1976a:99; Armentrout, 1981:141) and are somewhat younger than the holotype of *B. proteus* from the lower part of the Pysht Formation of northwestern Washington. The area has been mapped by Snively et al. (1976), who noted that the only formation exposed in the area is the lowermost part of the Yaquina Formation.

Most of the Yaquina Formation is usually assigned to the Zemorrian Stage, with only the uppermost part possibly referable to the Saucian Stage (Snively et al., 1969:38; Rau, 1981:81; Armentrout et al., 1983, chart). The exposures in the vicinity of Seal Rock have been identified explicitly as the lower part of the Yaquina Formation (Emlong, 1966:2; based on pers. comm. from Snively) and thus pertain to the Zemorrian part of the formation.

ASSOCIATED FAUNA.—The Yaquina Formation in Lincoln County, Oregon, has produced, in addition to the two specimens of *Behemotops emlongi*, a fairly rich fauna of pinnipeds, desmostylians, and cetaceans (Ray, 1977:428, 429). One of the cetaceans, *Aetiocetus cotylalveus* Emlong, 1966, was collected from the upper part of the Yaquina Formation, approximately 0.8 km (0.5 mile) north of Seal Rock State Wayside, and additional skulls are now known from the Yaquina Formation but are not as yet described (Whitmore and Sanders, 1977:317; L.G. Barnes, pers. comm.). Other Desmostylia from the Yaquina Formation include specimens of *Cornwallius*, under study by Reinhart (1975; 1982:550,

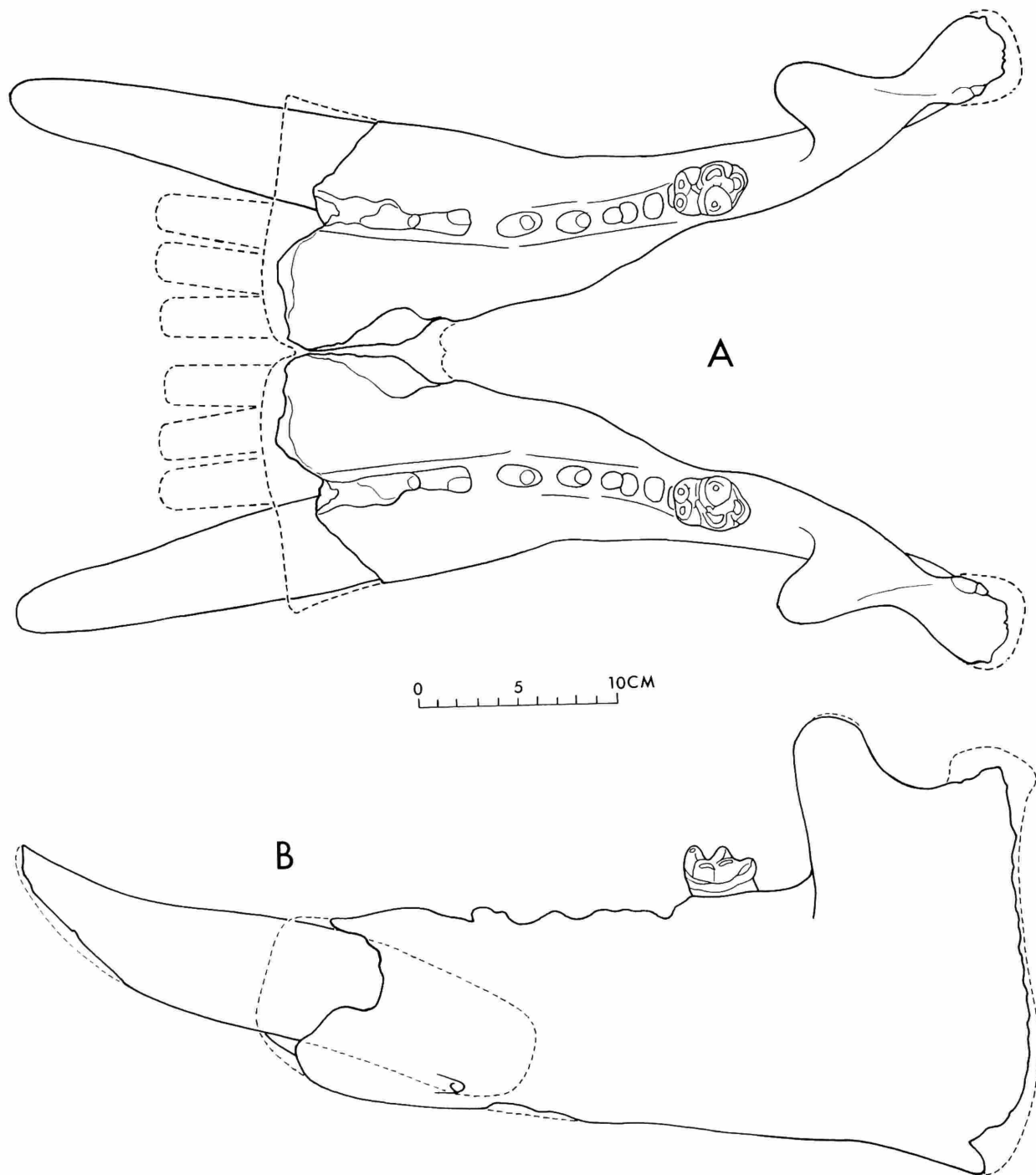


FIGURE 16.—Diagrammatic representation of mandible of *Behemotops emlongi* from lower part of Yaquina Formation of Oregon, mature individual, in occlusal (A) and left lateral (B) aspects; based on both the holotype, USNM 244033, and referred specimen, USNM 186889. Degree of posterior divergence of mandibular rami and length and shape of incisors (but not the fact of their presence as indicated by alveoli) are based primarily on analogy with *Paleoparadoxia*.

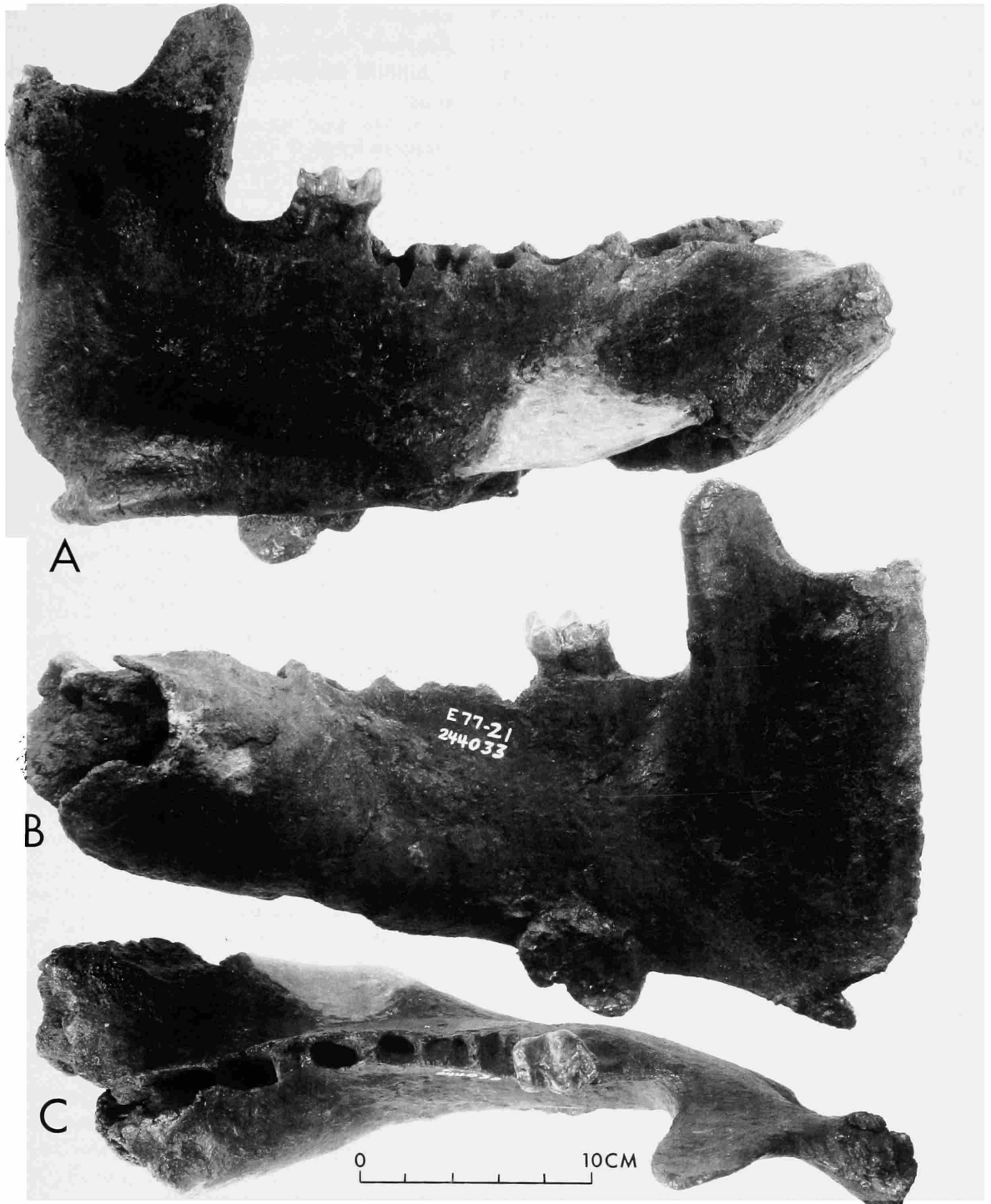


FIGURE 17.—*Behemotops emlongi*, holotype, USNM 244033, left mandibular ramus from lower part of Yaquina Formation of Oregon, in lingual (A), labial (B), and occlusal (C) aspects.

fig. 1), collected from the same area and horizon (lower part of the Yaquina Formation) near Seal Rock as the specimens of *Behemotops emlongi*. The original material of *Cornwallius sookensis* is from the Sooke Formation on Vancouver Island, in large part at least coeval with the Yaquina Formation (Durham, 1944:113; Addicott, 1976a:99).

Also from the same horizon in the lower part of the Yaquina Formation is the only land mammal known thus far from the formation, a fragment of a maxilla with deeply worn M^2 and M^3 (USNM 187125; Emlong field no. 291) of an anthracothere (Ray, 1977:431). Richard H. Tedford has examined this specimen and has provided us with the following statement (7 Apr 1983).

The teeth, although worn and broken, retain the diagnostic divided mesostyle and loss of paraconule found in only the genus *Arretotherium* among known North American anthracotheres. The dimensions of the M^3 of USNM 187125 are: length, 24.6 mm; width across the mesostyle, 25.8 mm. All three of the described species of *Arretotherium* [*A. acridens* Douglass, 1902; *A. leptodus* (Matthew, 1909); and *A. fricki* Macdonald and Schultz, 1956] have upper molars of similar size and proportions, so it is not possible to determine the precise affinities of the Yaquina anthracothere without further evidence. It is closest in size to the holotype of *A. leptodus* from the late Arikarean. As now recognized (Macdonald, 1956, 1963), the genus is confined to the early Miocene (late Arikarean through early Hemingfordian) and seems to succeed the closely related late Oligocene (Whitneyan through early Arikarean) genus *Elomeryx*. However, an extension of the geological range of the genus, in the form of a species like *A. leptodus*, into the early Arikarean seems indicated by unpublished material from Nebraska, South Dakota, and Wyoming contained in the Frick Collection at the American Museum of Natural History. These records would push the range zone of *Arretotherium* into the late Oligocene, in agreement with the assignment of a late Oligocene age for most of the Zemorrian and approximately equivalent Juanian stages.

MEASUREMENTS.—The following measurements of the holotype and referred specimen of *Behemotops emlongi* are in millimeters. Those in parentheses are approximate, based on incomplete or damaged parts of specimens. Those for all alveoli are as preserved, in all cases at least

somewhat damaged. See "Description, Dental Formula" for identification of dental loci.

USNM 244033, holotype, left mandibular ramus:

Maximum length of specimen as preserved	396
Maximum height of mandible at coronoid process	222
Depth of horizontal ramus below M_1	114.1
Depth of horizontal ramus behind M_3	128.3
Maximum width of jaw at symphysis as preserved	(119.3)
Breadth of jaw behind M_3	(35)
Canine tusk alveolus, maximum dorsoventral diameter	(75.9)
Canine maximum transverse diameter	(29.4)
Alveolar length	
P_1 (or DP_1)– M_3	(208?)
P_2 – M_3	(176)
P_3 – M_3	(135)
M_1 – M_3	87.8
P_1 (or DP_1) (alveolus strongly inclined forward)	(36.7)
P_2	24.9
P_3	21.5
P_4	16.1
M_1	20.3
M_2	23.0
M_3	40.6
Alveolar width	
P_1 (or DP_1)	(18.6)
P_2	15.6
P_3	(12.3)
P_4	11.4
M_3 (anterior)	6.9
M_3 (posterior)	18.0
Diastema between P_2 and P_3	17.0
M_3	
Maximum height of crown (metaconid)	18.0
Length of crown	37.6
Anterior width of crown	24.2
Posterior width of crown	28.6

USNM 186889, referred anterior fragment of right mandibular ramus:

Combined breadth of alveoli of the three incisors	(63)
Maximum depth (as preserved) of I_2 alveolus	(55)
Maximum mediolateral diameter of I_3 alveolus	(17.9)
Maximum anteroposterior diameter of I_3 alveolus	(14.8)
Maximum depth (as preserved) of I_3 alveolus	(33.5)
Canine tusk	
maximum length (as preserved)	267
maximum dorsoventral diameter (near alveolar margin)	(63.5)
maximum transverse diameter (near alveolar margin)	(43.1)

P ₃ root	
anteroposterior diameter	(23.8)
transverse diameter	(15.7)
maximum length (as preserved)	43.1

DESCRIPTION.—The holotype and referred specimen of *Behemotops emlongi*, USNM 244033 and 186889, as well as specimens of other taxa from the same horizon in the Yaquina Formation, exhibit a peculiar preservation. The bone is weak and, especially in USNM 186889, has grit from the enclosing matrix pressed into its surface as if to become almost an integral part of the bone (Figure 18). The alveolus of the canine tusk of USNM 244033 may well have been compressed laterally after burial. A part of the lingual wall of the alveolus had disintegrated; for this reason during preparation the mandible was strengthened in that area with fiberglass (Figure 17A,C). The poor preservation of surface detail in both specimens leaves some doubt as to the detailed character of the anterior premolar alveoli (Figures 17C, 18C), and makes illustration of the incisive alveoli impractical.

Dental Formula (Figures 4 and 16): The holotype and referred specimen of *Behemotops emlongi* are compatible with the interpretation of the dental formula of *B. proteus* and add information on the permanent incisors and canine. USNM 244033 has its well-worn M₃ in place. Its broadly exposed roots consist of a transversely widened anterior root and a larger posterior root, triangular in cross section with the apex of the cross section posterior, under the talonid. Some of the weak, thin-walled bone of the alveolar margins of all teeth has been lost in preservation or preparation, making their size and character somewhat conjectural. The alveoli of M₂ and M₁ indicate transversely widened anterior and posterior roots subequal in size but with the anterior root longer in M₂ and the posterior longer in M₁. The alveoli of the roots of M₁ are comparatively small, shallow, and convergent apically, indicating a small, possibly senescent M₁. The P₄ alveolus is shallow, simple, and ovoid in cross section; that of P₃ somewhat deeper, more elongate anteroposteriorly, and with the sugges-

tion of crests on each side. There is a short diastema anterior to P₃, perhaps resulting from the progressive forward tilting of P₂ and P₁ (or DP₁) in accommodation to their position dorso-medial to the alveolus of the massive canine tusk. The alveolus of P₂ is larger than those of P₃ and P₄, anteroposteriorly elongate, simple, and has crests on its lingual and labial walls, reflecting indentations in the root of P₂. The alveolus of P₁ (or DP₁) is similar in size to that of P₂, strongly inclined forward, and simple, with no indication of subdivided roots. The alveolus of the canine tusk is very large, laterally compressed (possibly in part postmortem), and extends posteriorly to a point at least below M₁. There are vestiges of the deepest parts of the simple alveoli of I₁ and I₂, and possibly of I₃, but the amount and quantity of the bone preserved in this region would be inadequate for secure interpretation were it not for the existence of USNM 186889. If correctly interpreted, the apices of the alveoli of these three teeth converge in a triangular arrangement.

The bone in USNM 186889 is poorly preserved and meager, but is just sufficient to provide a reliable basis for establishment of the anterior mandibular dental formula. P₃ is represented by a remnant of a robust, forwardly tilted, simple root, 43.1 mm long as preserved, and transversely subdivided into subequal anterior and posterior moieties by slight lateral indentations. There is no indication of a diastema anterior to P₃, but the adjacent shattered, poorly preserved bone is very likely displaced lingually. If this bone and the tooth were swung labially into line with the P₁ (or DP₁) and P₂ alveoli, a diastema would open anterior to P₃. The alveoli of P₂ and P₁ (or DP₁) are essentially similar to their counterparts in USNM 244033, as far as preserved. Each lies anteriorly inclined along the dorsolingual surface of the canine and separated from it only by a thin alveolar wall. The alveolus of P₂ is very incomplete, and inadequate to reflect subdivision of the root if such is the case. The alveolus of P₁ (or DP₁) indicates a much smaller, shorter root than in P₁ (or DP₁) of

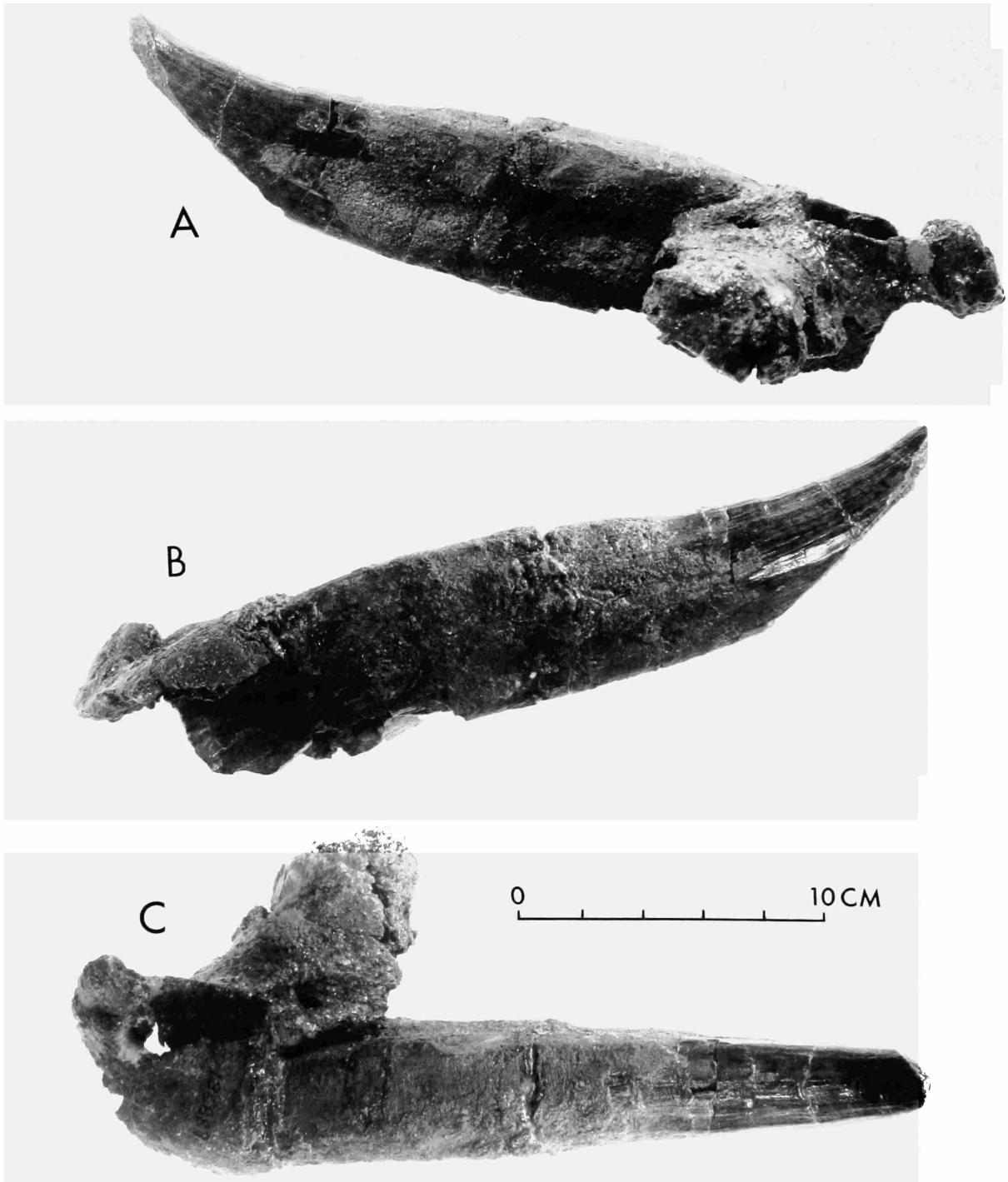


FIGURE 18.—*Behemotops emlongi*, referred anterior fragment of right mandibular ramus from lower part of Yaquina Formation of Oregon, USNM 186889, in lingual (A), labial (B), and dorsal (C) aspects.

USNM 244033. Perhaps the most important feature of USNM 186889 is the presence of alveoli of three incisors, strongly indicating that the tusk is a canine as in *Paleoparadoxia* (Figure 19). The alveolus of the first incisor is much fractured and obscured by matrix; that of I_2 , although highly incomplete, is 55 mm deep as preserved and suggests a straight, robust tooth of rounded cross section. The alveolus of I_3 is similar, but its preserved part is only some 33.5 mm deep, indicating a shorter tooth.

Thus, *Behemotops emlongi* from the lower part of the Yaquina Formation of Oregon retained a complete, inferior, adult dentition of three incisors, one canine, four premolars, and three molars. We infer that *B. proteus* from the lower part of the Pysht Formation of Washington did so as well. *Paleoparadoxia*, a more derived desmostylian, had one less premolar.

Dentition: As in *Behemotops proteus*, all preserved teeth of both specimens of *Behemotops emlongi* show the enamel finely to coarsely crenulated, wrinkled, or pustulose, except where smoothed by wear.

The inferior incisors are known only from their incomplete alveoli in USNM 244033 and 186889. These indicate three incisors, approximately similar in size, straight and subcylindrical in shape, perhaps 15–20 mm in their maximum diameters.

The inferior canine, actually preserved in USNM 186889 and represented by its incomplete alveolus in USNM 244033, is a greatly enlarged, strongly procumbent, laterally compressed tusk. It is widest dorsally (anatomically, posteriorly) and narrowest ventrally (anatomically, anteriorly). The ventral narrowing is effected largely by development of single, complementary, broad longitudinal channels on either flattened surface, deeper on the medial side. The tusk is essentially straight in dorsal or ventral aspect, but gently curved in an open S-shape in lateral or medial aspect, with the alveolar end downturned and the extruded end upturned (Figures 16 and 18). The base of the tusk is open, with a deep, conical pulp cavity, indicative of

persistent growth, maintained at least into old adulthood. The tusk has a thin (perhaps 0.5 mm) sheath of enamel extending entirely around its circumference, from the worn tip proximally for some 95 mm. The exact proximal limit of the enamel crown is difficult to define because the deposition of enamel apparently terminated irregularly in streaky continuations of longitudinal ribs and wrinkles, which are apparent on the crown wherever wear facets or polishing have not removed them. There is a large, subplanar wear facet truncating the crown obliquely. This facet would have been produced, not by occlusal wear, but by wear against a substrate, presumably in feeding. There is on the dorsal part of the medial surface of the crown at its widest part what appears to be a facet of occlusal wear (presumably produced by shearing action with a superior incisor), recognizable over a length of some 47.5 mm and a maximum width of 7.5 mm. There is no evidence of cementum on the tusk.

Except for the root of P_3 in USNM 186889, P_1 – M_2 are represented only by alveoli in *Behemotops emlongi*. For information on the size of these teeth, see the discussion of the dental formula and the measurements (pages 26, 27).

A rather heavily worn M_3 is the only tooth preserved in USNM 244033 (Figure 12F). It is essentially similar to the molars of the type specimen of *Behemotops proteus*, especially M_1 and M_2 , but differs from the incompletely formed M_3 of that specimen in having less stylodont principal cusps. As is demonstrated by M_1 of the holotype of *B. proteus*, USNM 244035, thickened enamel can be seen in M_3 of *B. emlongi*, USNM 244033. Its cingulid is continuous labially, being especially strong adjacent to the hypoconid. Two small conelets are present near the posterolingual base of the hypoconid and the posterolabial base of the entoconid, respectively, but are heavily worn. Before wear, the heel was evidently a transverse crest composed of several small crenulations. The metaconid apparently is not twinned.

Osteology: The remnant of the bony ramus of USNM 186889 is osteologically useful primarily in revealing the procumbency of the canine tusk

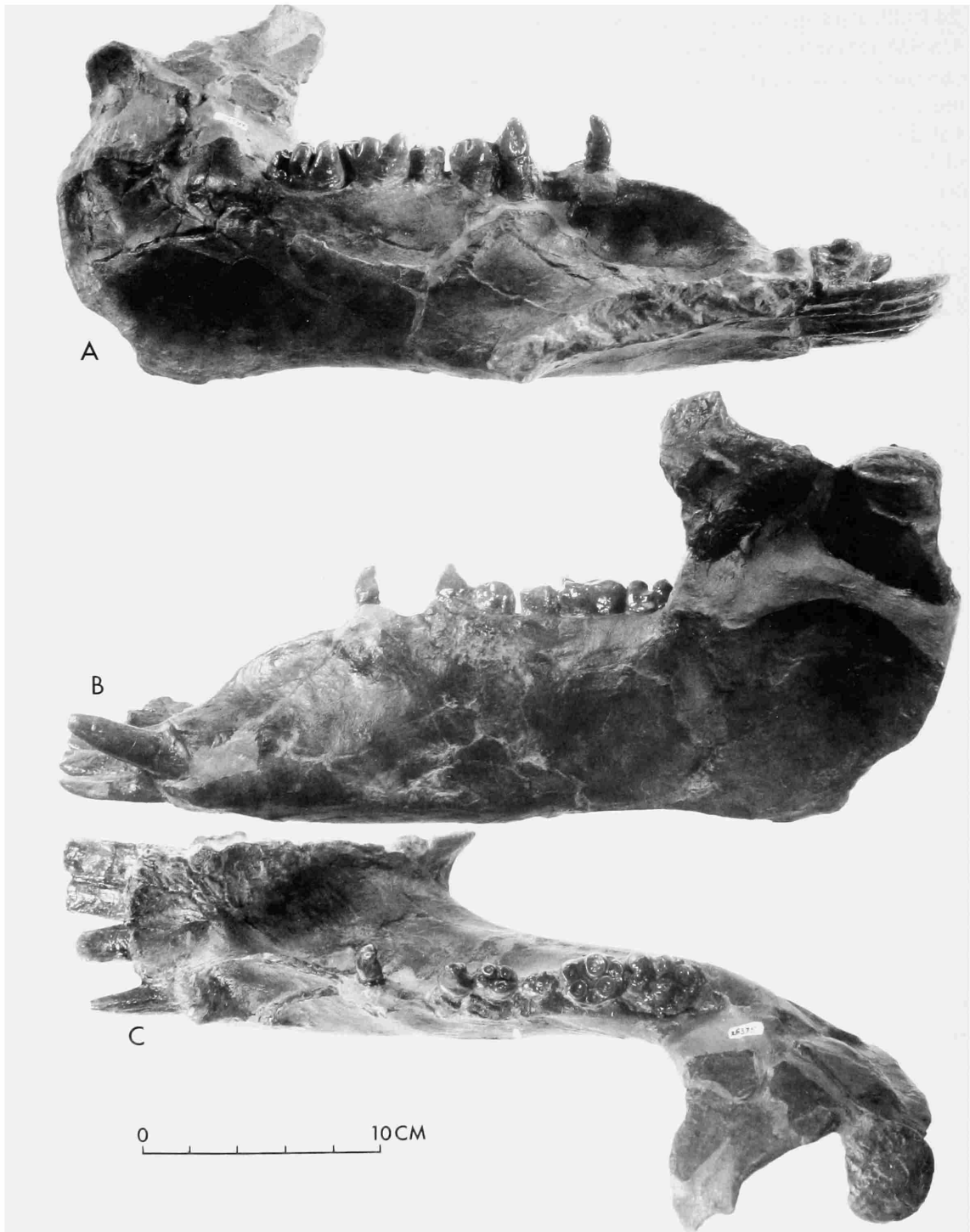


FIGURE 19.—*Paleoparadoxia tabatai*, cast of neotype, USNM 26375, from Izumi locality (Shikama, 1966:12), middle Miocene of Japan, left mandibular ramus, in lingual (A), labial (B), and occlusal (C) aspects.

and the incisors, and the broadly scoop-like symphyseal region. Both of these characteristics are confirmed in USNM 244033, which preserves most of the bony ramus. The most conspicuous character of the ramus is the massively expanded anterior end (Figure 16), reflecting the relatively huge canines and battery of six incisors. The under-surface of the symphyseal region is broadly flattened, almost planar. If this surface is oriented perpendicular to the sagittal plane, as it almost inevitably was in life, then the canine was compressed almost exactly in the vertical plane and the postsymphyseal body of the jaw was canted strongly inward dorsally, as in *Hexaprotodon*. There is a single, large, mental foramen adjacent to the canine alveolus and lying ventral to the P₂ alveolus (Figures 16B, 17B). The postsymphyseal ventral margin of the horizontal ramus is nearly straight, but the angular margin is missing, as is the thin posterior margin of the ascending ramus. If one assumes that little of this latter margin is lost, the anterior and posterior margins are essentially parallel and inclined slightly forward. The condyle is incomplete but its position well above the plane of postcanine occlusion is clear. The mandibular foramen opens just above the level of the dorsal border of the bony horizontal ramus and approximately midway between the anterior and posterior margins of the ascending ramus. The coronoid canal (which descends from the rear of the tooth row to open above the mandibular foramen), if present, is tiny and obscured by poor preservation. The coronoid process is broad, flattened, smoothly rounded in profile, and inclined somewhat anteriorly. The bony ramus posterior to the base of the canine tusk is relatively thin, and the postcanine dentition of modest size, in contrast to the massive, broad, scoop-like muzzle with large teeth indicated anterior to that point.

Relationship between *Behemotops proteus* and *B. emlongi*

Unfortunately, there are few points of anatomy on which the present specimens of *Behemo-*

tops proteus and *B. emlongi* can be directly compared. However, these include the size and morphology of M₃, the postcanine dental formula, the form of the ascending ramus, and to a certain extent the form of the symphyseal region of the mandible. As discussed at length above, the dental formulae of the two species are not demonstrably different except for the fusion of the roots of P₃ and P₄ exhibited by *B. emlongi* (and by more advanced desmostylians). However, the peculiar M₃ morphology of *B. proteus* is attributable at least in large part to incomplete development; the ascending rami are not significantly different; and the symphyseal region of *B. proteus* could well have been broad and scoop-like as in *B. emlongi*. The length of the incomplete M₃ crown in *B. proteus* is 31.7 mm, compared with 37.6 mm for the complete M₃ crown in *B. emlongi*; the difference is even within reasonable limits of intraspecific variation.

Only four differences, two of which are inferred rather than clearly demonstrated by the specimens at hand, suggest to us that specific distinction is warranted: greater adult mandible size, size and position of the canine tusk, and fusion of the roots of P₃ and P₄ in *B. emlongi*. In each of these characters *B. emlongi* is more derived than *B. proteus*, but the matter is clouded by the immature condition of the only known individual of *B. proteus*.

We base our conclusions about projected mandible size in part on growth of this bone in Recent Hippopotamidae, the closest living morphological analogs of desmostylians. An immature *Hexaprotodon* (USNM 271019, Figure 20) with M₂ partly erupted and DP₄ heavily worn (therefore dentally slightly younger than the type of *Behemotops proteus*) has a mandible 20 cm long, compared to 27.5 cm in an adult (USNM 302054) with worn M₃. An immature *Hippopotamus* (USNM 162976) with M₂ completely erupted and DP₄ heavily worn (comparable to the type of *B. proteus*) has a mandible 46 cm long; the largest adult mandible we measured (USNM 123387) was 59 cm long. If a similar relationship between growth and tooth eruption existed in *B. emlongi*

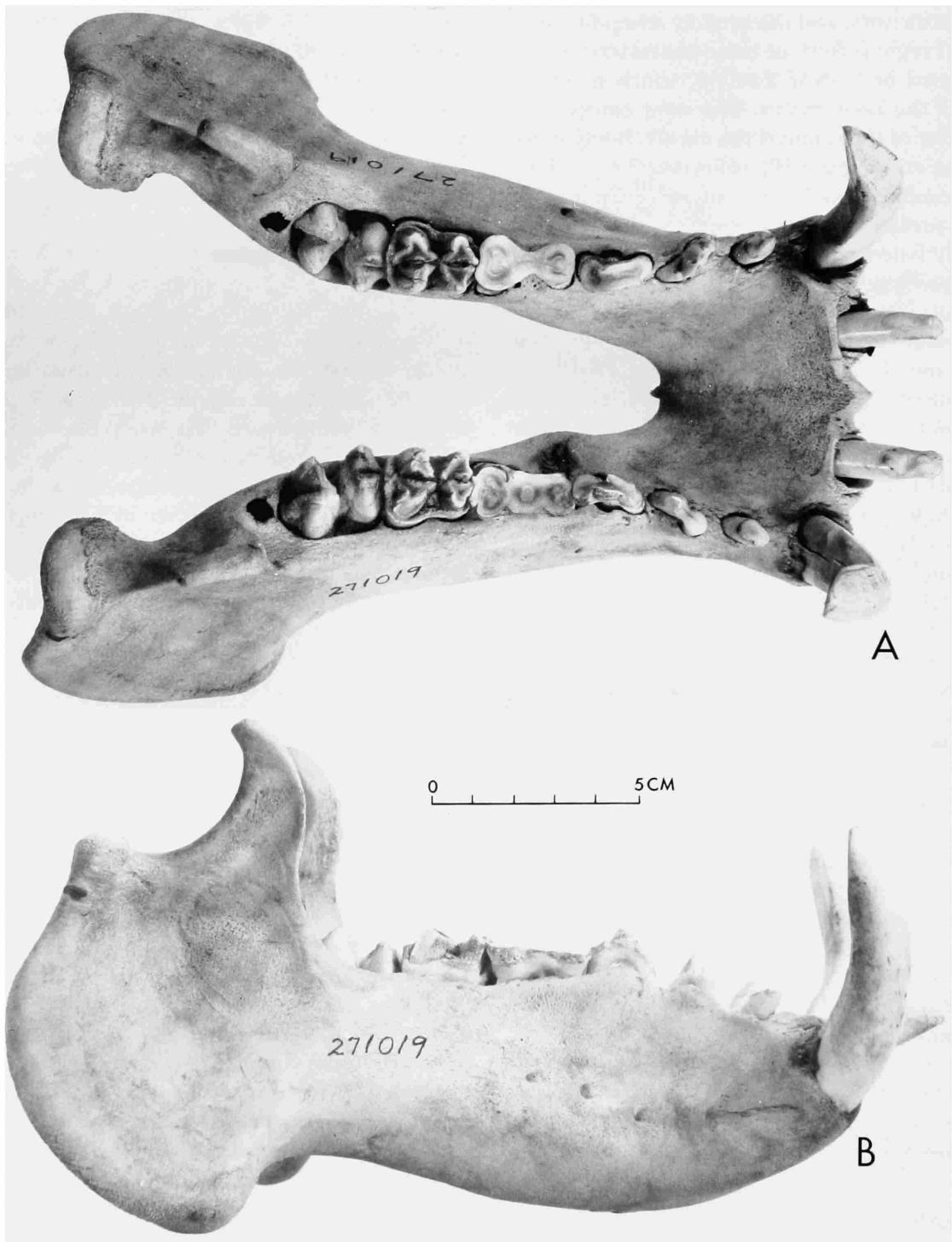


FIGURE 20.—*Hexaprotodon liberiensis*, modern pygmy hippopotamus, USNM (Division of Mammals) 271019 from the National Zoological Park, mandible of immature individual, in occlusal (A) and right lateral (B) aspects.

(an animal intermediate in size between *Hexaprotodon* and *Hippopotamus*), its juveniles should have reached 75%–80% of the adult mandibular length by the stage of tooth eruption seen in the type of *B. proteus*. However, the mandible of the latter is only about 55% as long as that of the adult *B. emlongi*.

As noted in our description of *Behemotops proteus*, there does not appear to have been space in the mandible below P_1 (or DP_1) for an enlarged canine tusk like that of *B. emlongi*. Rather, any canine or incisor tusks that were present must have been medial to P_1 (or DP_1). It seems highly unlikely that enough tusk growth or mandibular remodelling could have taken place in the time remaining until eruption of M_3 for *B. proteus* to take on the form of *B. emlongi*.

Principally for the latter reason, we prefer to regard the Washington and Oregon animals as representing separate species of a single genus, pending additional knowledge of their anatomy and ontogeny.

As Hirota (1981), Reinhart (1982:554), and Shikama (1966:131) suggested, and as Reinhart (1959:92) hinted but then denied, some or all desmostylians probably were sexually dimorphic. Writing about the proboscidean allies of the desmostylians, Osborn (1936:183) claimed the same.

In all the known Proboscidea there is a marked disparity between the male and female incisive tusks both in length and in diameter. The adult female tusks never fully attain the length of the adult male tusks, but a still more striking difference is their slenderness of proportion and diameter.

Frick (1933:507, 574, 581, 632, 650) also mentioned sexual dimorphism in gomphotheres and mammoths. Nevertheless, in spite of these examples in proboscideans, we believe that the observed differences in morphology between *Behemotops proteus* and *B. emlongi* are too great to be of sexual origin alone.

History of Desmostylian Systematics

VanderHoof (1937:170–177) thoroughly reviewed the desmostylian literature, and his work

should be consulted for details to that date. We present only a synoptic coverage here.

The desmostylians were first made known by O.C. Marsh (1888) on the basis of some material of *Desmostylus* itself from marine Neogene deposits of Alameda County, California. Marsh referred *Desmostylus* to the Sirenia. Flower and Lydekker (1891), on the basis of Marsh's work, next placed *Desmostylus* in the Halicoridae (= Dugongidae) and from then until 1953 *Desmostylus* was generally regarded, sometimes with a query, as a sirenian.

The second major find of a desmostylian fossil was reported from Japan by Yoshiwara and Iwasaki (1902), who described and figured the anterior part of a skull and both lower jaws of a specimen of *Desmostylus*. They believed their find to be some sort of proboscidean, based in part on a letter from H.F. Osborn. Osborn had examined photographs of the specimen and had read a brief description of the skull, sent to him by Yoshiwara and Iwasaki. In their paper Yoshiwara and Iwasaki made no mention of Marsh's description of *Desmostylus*, so presumably they were unaware of it. They believed their find to represent a new genus, but did not supply a new name. Although Osborn had "informed" them that the skull belonged to a proboscidean, Yoshiwara and Iwasaki demonstrated that it was not like deinotheres or elephantids and therefore would have to represent a branch from the primitive proboscideans, near the origin of that order from among the other ungulates. They also mentioned some similarities to Sirenia. In the same year, however, both Osborn and J.C. Merriam recognized that the Japanese specimen was referable to Marsh's *Desmostylus* (Osborn, 1902). Schlosser (1904) regarded the Japanese specimen as definitely sirenian.

Osborn (1905:109) placed *Desmostylus* in a monotypic family Desmostylidae and stated that it belonged in either the Sirenia or the Proboscidea. Merriam (1906; 1911:412) regarded *Desmostylus* as a sirenian, possibly requiring its own family, and reinforced the suggestion of relationship between sirenians and proboscideans.

Abel (1914:213; 1919:830; 1920:445), in contrast to his later work, concluded that *Desmostylus* was more closely related to the Proboscidea than to the Sirenia, although it is not clear why he did so. Later Abel (1922:381; 1923) abandoned his view of proboscidean affinities of *Desmostylus* in favor of a bizarre notion that it belonged to the mammalian subclass Allotheria (= Multituberculata). He persisted in this belief even after examining a skull of *Desmostylus* at the NMNH (Abel, 1926); then, and later (in Weber, 1928:xiii, 44, 85), he placed the family Desmostylidae in the Monotremata, suggesting a possible relationship between them and multituberculates. Still later Abel (1933:875) elevated them in rank, naming an order Desmostyloidea within the subclass Multituberculata. He evidently regarded them as multituberculates to the end of his career (Abel, 1944). Although it has priority over Desmostyilia Reinhart, 1953, Abel's ordinal name apparently has been overlooked completely during the more than 50 years since its creation. No useful purpose would be served by resurrecting it. Adherence to priority in names of suprafamilial taxa is not required, and in this case it would not be in the interest of stability. Therefore, we strongly recommend retention of the shorter, more euphonious, and entrenched name Desmostyilia.

Hay (1915), followed by Matsumoto (1918), placed the Desmostylidae in the Sirenia, although he emphasized that the Desmostylidae were very different from other (true) sirenians. Later Hay (1923:109) created a suborder Desmostyliformes to contain the Desmostylidae alone among sirenians, placing all other sirenians in a suborder Trichechiformes. In the same paper and in a succeeding one (Hay, 1924:7) he corrected in detail the misinterpretations of cranial sutures on which Abel's assertion of multituberculate affinities were largely based.

Winge (1924:187, 188; 1942:214) regarded *Desmostylus* as "undoubtedly a lateral offshoot of the oldest manatids." Winge also provided some pithy comments about Abel's theory of multituberculate affinities of the desmostylians.

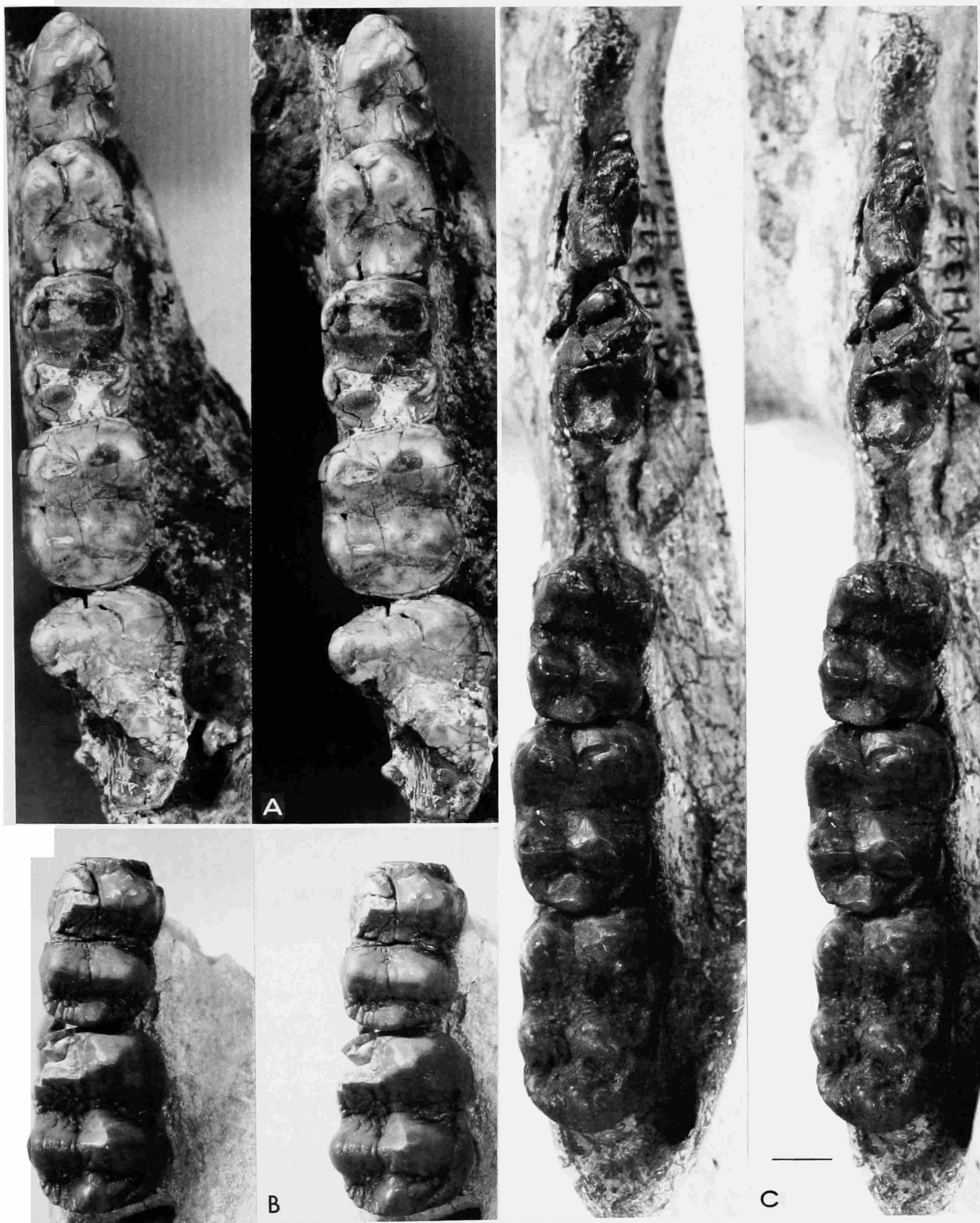
VanderHoof (1937) countered Abel's interpretations in detail and supported inclusion of desmostylians in the Sirenia as the suborder Desmostyliformes. Sickenberg (1938), however, argued strongly against a desmostylian-sirenian relationship. Gregory (1951:428, 801–803) retained *Desmostylus* in the Sirenia but gingerly suggested "remote derivation from such a primitive proboscidean as *Moeritherium*."

According to Shikama (1966:151), an earlier publication by H. Kishida (1924) assigned *Desmostylus* to the Marsupialia. We have not seen Kishida's work.

Ijiri (1939) considered *Desmostylus* to be an ungulate "in the broadest sense" but not a monotreme, multituberculate, marsupial, or sirenian.

Reinhart (1953) proposed the order Desmostyilia, essentially an elevation of Osborn's Desmostylidae and Hay's Desmostyliformes to still higher taxonomic rank. Reinhart's (1959) revision of the Desmostyilia led him to believe that the desmostylians, sirenians, and proboscideans are closely related paenungulates, but that the desmostylian stem separated from the other two orders in the Paleocene. On the basis of postcranial evidence, Reinhart noted that the desmostylians could not be descended from known sirenians because desmostylians were still capable of locomotion on land. Similarly, dental evidence led him to conclude that *Moeritherium* (Figure 21) was already too advanced along the proboscidean path to have been a desmostylian ancestor. Thus, the Desmostyilia were shifted from their former status as a sirenian subdivision and were given taxonomic equality with both the Proboscidea and the Sirenia. McKenna (1975:42) later dubbed this unresolved trichotomous group of paenungulate orders the mirorder Tethytheria. The cladistic analysis given below (Figure 22) resolves the trichotomy and indicates that

FIGURE 21.—Stereophotographs in occlusal aspect of inferior postcanine teeth of *Moeritherium trigodon* from Djebel-Qatrani Formation of Egypt: A, YPM 18181, RP₃–M₃; B, YPM 18098, RM₁–M₂; C, AMNH 13437, RP₂, P₃, M₁–M₃. Scale 1 cm.



Minkoff (1976) suggested that desmostylians should be placed with the Amblypoda rather than the Paenungulata.

Characters Used in Phylogenetic Analysis

The following list of characters was used in the construction of the cladogram depicted in Figure 22. The numbers correspond to those characterizing the various clades of the cladogram.

1. Anterior border of orbit lies forward of M¹
2. Zygomatic process of squamosal bone expanded far laterally.
3. Pachyostosis and osteosclerosis.
4. Bilophodonty incipient.
5. I¹ enlarged to become tusk. (See Savage, 1977, for postulated parallelism in this character in Sirenia.) In trichechids and some dugongids the tusk is secondarily lost.
6. Rostrum deflected.
7. Petrosal separate from skull anteriorly and posteriorly.
8. Atlas vertebra modified (Savage, 1977:347).
9. Mandibular dental capsule exposed posteroventrally.
10. DP₃² (= M₁¹ new) retained without replacement in adults.
11. Hind limbs reduced. (Condition unknown in *Prorastomus*, *Sirenavus*, and some other fossil taxa. *Protosirenia* still apparently retained a large functional femur. However, *Eotheroides libycum* had a reduced pelvis (Andrews, 1906:119; Sickenberg, 1934:94).)
12. External auditory meatus wide.
13. M₃ with hypoconulid shelf transversely broad, but the hypoconulid still central. A small entoconid II (a new entoconid situated behind the true entoconid) can be present adjacent to it lingually (*Minchenella*) and tiny cuspules can be present labially.
14. Former last molars lost.
15. External auditory meatus high, nearly enclosed ventrally by mutual contact of squamosal post-tympanic and postglenoid processes.
16. M₃ with two definite cuspids at rear: a labially displaced hypoconulid and a large entoconid II.
17. M₃ entoconid II somewhat posterolabially shifted.
18. P₄ with enlarged, high hypoconid and entoconid.
19. P₁ (or DP₁) double-rooted.
20. I₂ enlarged.
21. P¹ (or DP¹) and P₁ (or DP₁) lost.
22. C¹ reduced.
23. C₁ lost.
24. I² enlarged.
25. Anterior end of jugal bone reduced (condition unknown in Dor el Talha barythere skull).
26. Base of coronoid process of mandible shifted far forward to arise labial to M₂ (coronoid process not preserved in Dor el Talha barythere).
27. Ascending process of palatine bone disappears from orbitotemporal fossa (bones fused and poorly preserved in Dor el Talha barythere).
28. Condylod foramen lost (not preserved in Dor el Talha barythere skull). The position of this character on the cladogram is uncertain, but close to the point indicated.
29. Front end of skull much shortened, with orbits forward, anterior to P². Infraorbital foramen under orbit.
30. Lacrimal bone lost.
31. Postorbital process of frontal reduced.
32. Cranium tubular.
33. I₃ lost.
34. Nasal opening retracted and proboscis developed (interpretation).
35. Frontal/premaxillary contact occurs (nearly does so in *Moeritherium*; probably does so in Dor el Talha barythere skull).
36. I³ lost (not determinable in Fayum type of *Barytherium grave*, but so interpreted in Dor el Talha barythere skull; Savage, 1969:170).
37. Size larger (and still larger).
38. C¹ lost (not determinable in Fayum type of *Barytherium grave*, but shown in Dor el Talha barythere skull; Savage, 1969:170).
39. I₁ lost.
40. I₂ more enlarged.
41. Scapula with enlarged coracoid process.
42. Stance graviportal.
43. Mandibular ramus with ventral protuberance anterior to the level of P₂ (protuberance faint in Dor el Talha barythere).
44. P³ and P⁴ crowded. P⁴ transverse, lacking metacone (not determined in Dor el Talha barythere).
45. Scapular spine either loses acromion and metacromion or they are short (Dor el Talha barythere). Supraspinous fossa greatly reduced.
46. Distal end of humerus expanded (not determinable in Dor el Talha barythere).
47. I¹ lost.
48. Ethmoid foramen shifted rearward beneath crista orbitotemporalis (ethmoid not preserved in Dor el Talha barythere skull).
49. Cranium pneumatized (possibly this character is misplaced; it may also characterize barythere-like proboscideans).
50. M¹ and M₁ trilophodont.
51. P₂ (but not DP₂) lost.
52. P² (but not DP²) lost.
53. Lower tusks and mandible sharply downturned.
54. Skull with deep rostral trough.
55. Scapular acromion and metacromion reduced. (See character 45.)
56. Paroccipital process enlarged.

57. Paroccipital process further enlarged.
58. Occipital condyles highly placed.
59. Postmetaloph ornamentation of M^2 and M^3 reduced.
60. Metapodials long. Femur shortened. Foot functionally tetradactyl.
61. Skull roof shorter and narrower.
62. Subsidiary median styles occur on P^3 and P^4
63. I^2 more enlarged.
64. External auditory meatus ventrally closed (see character 15).
65. M^2 , M_2 , and M_3 trilophodont.
66. Horizontal component occurs in tooth replacement.
67. P_2 roots fuse.
68. Passage (postzygomatic foramen of VanderHoof, 1937:178, figs. 9, 11) present through squamosal from external auditory meatus to roof of skull.
69. P_3 roots fuse.
70. P_4 roots fuse. Ijiri and Kamei (1961) state that X-ray photographs of the Izumi specimen of *Paleoparadoxia tabatai* show P_3 and P_4 to be double-rooted. Although that might be the case at depth in the mandible, the roots of each tooth are fused at the level of their emergence from the alveolus at the base of each premolar crown. X-ray photographs of the roots of P_3 and P_4 of a specimen of *Paleoparadoxia* from the lower Miocene of Point Arena, California (Phillips et al., 1976:152; Clark, in prep.) show a longitudinal differentiation interpretable as a relic of fusion (A. Panofsky, pers. comm. to the authors).
71. Canines enlarged further to form procumbent tusks. C_1 enormous.
72. C_1 somewhat angular in cross section rather than suboval.
73. P_1 lost. (This and the following two characters apply to all previously recognized desmostylians.)
74. P_2 reduced.
75. All cusps on posterior cheek-teeth become desmostylodont.
76. P_3 paraconid lost.
77. P_4 - M_3 hypoconulid and entoconid II enlarged, especially entoconid II.
78. Lower incisors become rectangular and flat.
79. M_2 with extra cuspid between and labial to protoconid and hypoconid.
80. Molar cingula reduced.
81. Mandibular symphysis becomes elongate.
82. Sagittal crest reduced.
83. At most, only canine tusks and one pair of lower incisors remain.
84. Remaining premolars lost in adults (but in young individuals 3 upper loci and at least 1 lower locus are occupied by deciduous or permanent premolars).
85. Medially positioned bony swelling occurs at the rear of the dentition.
86. Cusp height increases.
87. Molar cingula lost.
88. Suprasymphysial depression reduced.
89. Rear molars very high-crowned, with enamel extending below gum line and into alveolus.
90. Zygomatic process broadened.
91. Sagittal crest lost.
92. Extra cusps occur on molars.

Comparisons with Early Proboscidea and *Minchenella*

From early in the history of their study, desmostylians were generally considered to be odd sirenians. Sirenians themselves were considered to be related to Proboscidea, a concept that dates back at least to de Blainville (1816, 1836 [1834]) and perhaps to Linnaeus (1758). Linnaeus (1758:33, 34) had placed *Elephas* and *Trichechus* next to one another within his order Bruta, but of course he had also added sloths, anteaters, and pangolins to the mix. Unlike Cuvier and most authors of the succeeding century, Linnaeus did not ally the Sirenia with the Cetacea. Gervais (1855) pointedly abandoned de Blainville's scheme of a sirenian-proboscidean special relationship, emphasizing aquatic habitus and neglecting the shared features claimed by de Blainville. Although some workers in the late nineteenth century championed sirenian-proboscidean affinity (e.g., Kneeland, 1850; Kaup, 1855), most taxonomic treatises made no special attempt to relate the two or in fact argued against the relationship and maintained the cetacean connection (e.g., Owen, 1859; Gray, 1866; Gill, 1871, 1872, 1873; Trouessart, 1879, 1898; Flower and Lydekker, 1891; von Zittel, 1893).

Moeritherium.—A new claim of sirenian relationship to proboscideans was provided when the fossil genus *Moeritherium* was made known from the Fayum deposits of Egypt by Andrews (1901b, 1901c, 1902, 1904a, 1906). Andrews correctly placed *Moeritherium* in the Proboscidea but suggested in his discussion of the pelvis that *Moeritherium* and a primitive sirenian (his "*Eotherium*") with unreduced pelvis and femur might have had

a common ancestor at some earlier time in the Tertiary (Andrews, 1906:119). Sickenberg (1934:94) later referred the sirenian pelvis in question to a different sirenian genus, *Protosiren*. Winge (1906, 1924, 1942:26) arranged the ungulates in a genealogical scheme in which arsinotheres first differentiated from a meniscotheriid source. The arsinotheres were then supposed to have divided into hyracids and elephants, the latter giving rise to the Sirenia. According to Winge (1942:148, 149, 211, 212), the Sirenia are merely aquatic proboscideans. Winge considered *Moeritherium* to be the most primitive then-known proboscidean, with *Barytherium* interposed between it and the deinotheres. Osborn (1907:15) included *Moeritherium* in the Proboscidea and placed the orders Proboscidea and Sirenia next to each other among the nine ungulate orders that he recognized in his classification. In a paper on the feeding habits of *Moeritherium* and *Palaeomastodon*, Osborn (1909:140) suggested that "*Moeritherium* [sic] is an offshoot of the Proboscideo-Sirenian stock, with slightly nearer kinship to the elephants than to the Sirenia [sic]." Osborn took both real and supposed aquatic modifications of *Moeritherium* to imply that it was somewhat more sirenian-like than other Proboscidea, but he did not conclude that *Moeritherium* was a sirenian, although he did state that "*Moeritherium* [sic] is closer to the Sirenia [sic] and less close to the Proboscidea than has hitherto been supposed." Osborn's paper was objected to by Andrews (1909), who was, of course, thoroughly familiar with both *Moeritherium* and the Egyptian Tertiary sirenians. However, based upon what Osborn actually wrote, Andrews (and also, apparently, Gregory, 1920:245) misinterpreted Osborn's point. Andrews noted that sirenians with tusks (i.e., many dugongids) have evidently obtained them by enlarging I^1 , and he also pointed to derived features of the ear region that *Moeritherium* shared with other proboscideans. He argued that the aquatic habitat of *Moeritherium* had produced some similar adaptations, but that the dentition, particularly the enlargement of I^2 and I_2 to become

tusks, was conclusively in favor of genealogical relationship of *Moeritherium* to *Palaeomastodon* and more advanced elephant-like genera, not to Sirenia. This is perfectly true, but Osborn (1909:139) was aware of it and had not claimed otherwise. Possibly influenced by Winge (1906), Osborn (1910:200, 203, 558) retained the Moeritheriidae in the Proboscidea, but (Osborn, 1910:204) took a new tack by claiming that "we may look for other radiations of the proboscidean stock in Africa; possibly the river-living sirenians may prove to be one of these radiations."

Gregory (1910:368) stated:

The genus [*Moeritherium*] represents a very primitive offshoot from the Proboscideo-Sirenian stock. Its dentition and certain other characters indicate a nearer alliance with the Proboscidea than with the Sirenia, but it is far more primitive than any other known representative of either order.

Ten years later Gregory (1920:180, and erratum and addendum) continued to regard *Moeritherium* as a proboscidean, but pointed out that its lacrimal bone, if present, was not like that of later proboscideans and that in this respect *Moeritherium* resembled sirenians. With regard to the origin of the latter, he stated that "the Sirenia, although highly specialized for aquatic life, show special resemblances with *Moeritherium* in the skull (including the orbital region) and dentition, and are generally regarded as a derivative of the proboscidean stem" (Gregory, 1920:245).

Abel (1914:191-213; 1919:826; 1920; 1933:899) not only placed *Moeritherium* in the Proboscidea, but also placed *Barytherium* there as well, stating that *Barytherium* might be some sort of side branch from the early deinotheres. Abel thought that the Proboscidea and Sirenia are closely related, at times (in Weber, 1928:425; 1933:899, 904) following von Zittel (1925:246) in arranging the two groups as suborders, along with hyracoids and embrithopods, within an order Subungulata.

Osborn (1921a:2) strongly supported proboscidean affinities for *Moeritherium* and divided the Proboscidea into Moeritherioidea, Deinotherioi-

dea (sic), Mastodontoidea, and Elephantoidea. These coordinate categories were believed to be of either subordinal or superfamilial rank. Osborn no longer seems to have regarded the sirenians as derivatives of proboscidean stock, although he stated (Osborn, 1921a) that the facial and cranial proportions of *Moeritherium* are analogous to those of the Sirenia. Osborn omitted consideration of the barytheres in his two 1921 papers and two years later specifically excluded them from the Moeritheriidae (as Moeritheriinae; see Osborn, 1923:1).

That *Moeritherium* might not have been so aquatic an animal as had been supposed by various previous authors was suggested by Matsumoto (1923:105). Moreover, an extensive analysis of the similarities between *Moeritherium* and hyracoids, sirenians, and proboscideans brought Matsumoto down heavily in favor of proboscidean relationships for *Moeritherium*.

Petronievics (1923) not only thought *Moeritherium* was a member of the Proboscidea, but also believed it to be ancestral to *Palaeomastodon*. He misinterpreted Osborn (1909) by claiming that Osborn had held that *Moeritherium* was "an offshoot of sirenian stock allied to Proboscidea" (Petronievics, 1923:58). Petronievics (ibid.) also accused Osborn of holding the same views in Osborn's (1919) paper on *Palaeomastodon*. Curiously, Osborn's (1919:266) paper did indeed contain the following statement: "In 1909² Osborn pointed out that *Moeritherium* is to be regarded as a terrestrial form of the Sirenians [sic] (manatees and dugongs) in no way directly related to the Proboscideans." (The footnote to this passage reads "2. Osborn, 1909, 332." Here "332" refers to paper 332 in Osborn's life-long sequence of publications, i.e., Osborn (1909) of the present paper's bibliography, not to some unknown paper of 1909 containing a page 332.) Here, however, Osborn (1919) clearly misquoted himself. We have not been able to find such a statement in Osborn's (1909) publication. The nearest that Osborn had come to such a stance in 1909 was his statement, already quoted, that *Moeritherium* was "closer to the Sirenians [sic] and

less close to the Proboscidea than has hitherto been supposed."

Osborn (1923:1) once more included the moeritheres in the Proboscidea, referring to them (1925:20, 21) as "small, amphibious promastodonts."

Simpson (1931:264) included the moeritheres as one of four superfamilies of the order Proboscidea: Moeritherioidea, Dinotherioidea (sic), Mastodontoidea, and Elephantoidea. The barytheres were maintained at ordinal rank and the order Sirenia was classified in accordance with Hay's (1923) division of the sirenians into two suborders: Trichechiformes and Desmostyliiformes.

Although he did not believe *Moeritherium* to be ancestral to other proboscideans, Osborn (1936:22) maintained the genus in a monotypic suborder of the Proboscidea, Moeritherioidea, coordinate with Deinotherioidea, Mastodontoidea, and Elephantoidea. As he had held fifteen years earlier, Osborn (1936:24, 48) believed the facial and cranial proportions of *Moeritherium* to be analogous, not homologous, to those of the Sirenia. At one point in his monograph Osborn (1936:39) did indeed list the sirenians, moeritheres, and proboscideans as coordinate groups, but elsewhere on the same page he placed *Moeritherium* within the Proboscidea.

In his famous two-volume compendium on the Proboscidea it is noteworthy that Osborn (1936, 1942) omitted the barytheres from consideration. Although mentioned several times (volume 1:51, 53; volume 2:1424) in passing in this enormous and otherwise comprehensive monograph, the barytheres, then known from a single Eocene Fayum species, were evidently considered to belong to a monotypic order, Barytheria Andrews, 1904b, and were therefore excluded from Osborn's work. Osborn had evidently reached this conclusion as early as 1905 (Osborn, 1905:112) and apparently he continued to hold the same view in 1921 (Osborn, 1921a, 1921b, 1921c). In his earliest discussion of *Barytherium* (as "*Bradytherium*" grave; see Andrews, 1901d, erratum) Andrews (1901a) had regarded the an-

imal as a *Deinotherium*-like proboscidean, as did Abel (1914). But in 1904 Andrews viewed the Barytheria as an amblypod subgroup coordinate with the Dinocerata. By 1906, however, Andrews once more considered the barytheres to belong to the Proboscidea as family Barytheriidae, incertae sedis (Andrews, 1906:172). Four years later, Osborn (1910:200, 559; and also 1921a, 1921b, 1921c) continued to regard the barytheres as deserving ordinal rank. It is curious that Osborn, even if in agreement with Andrews (1904b) in that he regarded the barytheres as non-proboscidean, made no attempt to compare them with moeritheres or other proboscideans in his 1936–1942 monograph.

In his masterly classification of mammals, Simpson (1945:132–134) maintained the Moeritherioidea as a monotypic suborder within the Proboscidea, coordinate with Deinotherioidea, Elephantoida (with which Simpson combined Mastodontoidea), and Barytherioidea. The name Barytherioidea was coined by Simpson partly because of a change in rank of Andrews' Barytheria to that of a suborder, partly in order to agree with the suffixes of other proboscidean suborders, and partly because Andrews' name "Barytheria" was preoccupied by Barytheria Cope, 1898 (p. 123), a term that Cope had used for toxodont notoungulates.

Until 1955, *Moeritherium* continued to be regarded as an unquestioned primitive proboscidean, but in that year Deraniyagala (1955:15, 16) separated *Moeritherium* from the Proboscidea and placed the various species of moeritheres in a new order, Moeritheria. This was done because of the presumed lack, in moeritheres, of the trunk, believed by Deraniyagala to characterize Proboscidea alone. Thus, *Moeritherium* was ostracized on the basis of retention of a primitive character, not on the basis of derived features possessed uniquely or shared with any other group of mammals, e.g., Sirenia. Deraniyagala failed to show that *Moeritherium* is anything other than a primitive offshoot from proboscidean ancestors that had not yet become equipped with a trunk and the associated anatomical specializa-

tions of more advanced Proboscidea.

A nearly complete skeleton of *Moeritherium* from the Egyptian Fayum was placed on display at the Yale Peabody Museum in December, 1963, and was figured and discussed briefly by E.L. Simons (1964:14). No detailed description of the specimen has yet appeared, but the skeleton was refigured by Tobien (1976, fig. 8). Simons noted that the elongate skeleton and various features of the skull were suited to aquatic life and he stated that "the creature can hardly have been close to the line of elephant ancestry." However, no attempt was made by Simons to ally *Moeritherium* with any other mammalian group. Thus, Simons' comments about the distinctiveness of *Moeritherium*, like Deraniyagala's remarks, are based upon symplesiomorphies and possible autapomorphy rather than on synapomorphic features. Later, however, Simons (1968:3) alluded to "certain postcranial resemblances" between *Moeritherium* and the Desmostylia.

Similarly, Tobien (1971, 1976) kept *Moeritherium* well away from other proboscidean ancestry, but noted only autapomorphic and symplesiomorphic characters. He implied, but did not document, sirenian relationships for *Moeritherium*. By 1978, however, Tobien no longer suggested sirenian affinities, simply referring to *Moeritherium* as a paenungulate remotely related to *Palaeomastodon* and *Phiomia* (Tobien, 1978:199, 200).

Savage (1971:220) believed that "*Moeritherium* and *Barytherium* are, if not true proboscideans, basically close to the Proboscidea; nothing allied to this order occurs outside of Africa until the Miocene." Savage believed the ancestry of the Proboscidea to have been probably from unknown early Paleocene African condylarths.

Maglio (1973, 1978), Coppens et al. (1978), and (for all intents and purposes) Harris (1978) restricted the Proboscidea to Elephantoida by excluding not only the moeritheres, but also the barytheres and deinotheres. These semantic joint maneuvers served only to obfuscate matters by sweeping the problem of interrelationships of

these animals under the rug, as Deraniyagala had done with *Moeritherium* in 1955.

Coppens and Beden (1978:333) stated that "other authors, such as Tobien (1971), also exclude [moeritheres] from the Proboscidea and classify them among the sirenians." Indeed, Tobien (1976:157) mentioned "many authors" holding such a view. But only Tobien seems to have written anything at all about *Moeritherium* actually being a sirenian; those authors who thought *Moeritherium* to be related to the Sirenia did so because of their belief that the Sirenia originated from early proboscidean stock of some sort. Other authors have remarked only about the difficulty of retaining such an aquatically adapted animal within the Proboscidea.

Stating that their comments were based on a personal communication from one of us (Domning), Coppens and Beden (1978:333) noted that *Moeritherium* does bear some striking similarities to the order Desmostylia. However, these similarities were not discussed by them. Domning himself (1978a:573, 574), in an article published in the same book as that of Coppens and Beden, stated simply that "the desmostylians were formerly included within the Sirenia but are now accorded ordinal status in close alliance with moeritheres, proboscideans, and sirenians." Coppens and Beden briefly considered the question of whether *Moeritherium* should be regarded as a branch from early Sirenia, but they ultimately concluded merely that moeritheres were descended from basic "subungulate" stock. They left the ordinal affinities of moeritheres as an open question.

Van Valen (1978, fig. 3) depicted both Desmostylia and Sirenia as descendants of Proboscidea, but he provided neither evidence nor discussion of his conclusions.

Tassy (1979) reviewed the relationships of *Moeritherium* on the basis of both new and old material. On the basis of cladistic analysis he concluded that *Moeritherium* is more closely related to the Proboscidea than to the Sirenia.

Two years later Tassy (1981) published a detailed description of an Eocene *Moeritherium* skull

from Dor el Talha, Libya, and again attempted a cladistic analysis of the systematic position of *Moeritherium*. Once more he concluded that the genus is more closely related genealogically to the Proboscidea than to Sirenia or Desmostylia. However, he linked Sirenia with Proboscidea on the basis of reduction of the mastoid apophysis and the presence of lophodonty, both weak characters.

In our own analysis, *Moeritherium* is regarded as a primitive proboscidean because it shares ten derived features with barytheres, deinotheres, and elephantoids (characters 4, 20–28 of cladogram: Figure 22).

That *Moeritherium* is not directly ancestral to other proboscideans is suggested by five unique characters that would have to have been reversed if *Moeritherium* were to have given rise directly to proboscideans such as *Palaeomastodon* and *Phiomia* (Characters 29–33 of cladogram: Figure 22). After the departure of the phylogenetic line leading to *Moeritherium*, *Barytherium*, deinotheres, and elephantoids developed nine shared-derived features (characters 34–42 of cladogram: Figure 22). However, the loss of I^1 , I^3 , C^1 , and I_1 had not yet occurred in the earliest known proboscidean, an unnamed taxon (the Brezina animal) from the early Eocene of Algeria (Mahboubi et al., 1984). The Brezina animal is therefore not a barythere; rather, it is the plesiomorphous sister-group of all "higher" proboscideans and could be ancestral to them, in keeping with its age and geographic position.

Moeritherium has been reported from five (possibly six) sites in the northern half of Africa and one in southern Asia (Tobien, 1971; Coppens and Beden, 1978; Tassy, 1981; Coiffait et al., 1984):

1. Fayum Basin, Egypt. Eocene and Oligocene. See Andrews (1906).
2. Dor el Talha, Libya. Eocene. See Arambourg and Magner (1961); Savage (1969, 1971).
3. 60 km NE of Gao, Mali. Eocene. See Arambourg, Kikoine, and Lavocat (1951); Tobien (1978:194, 195).
4. M'Bodione Dadere, Senegal. Lutetian. See Gorodiski and Lavocat (1953).

5. Khenchela, northeastern Algeria. ?Eocene. See Gaudry (1891); Schlesinger (1912).
6. Nementcha Mountains, eastern Algeria. Late Eocene. See Coiffait et al. (1984).
7. Harudi, Kutch, India. Lutetian. See Sahni and Mishra (1975).

At several of the African sites as well as in Asia the identification of specimens as *Moeritherium* may be misleading and might better be stated as "moeritheriid" or "primitive proboscidean-like animal" rather than given as an identification to the generic level. For instance, according to Gorodiski and Lavocat (1953:316), the Eocene animal from Senegal is only about half the size of *Moeritherium gracile*.

Inasmuch as the Harudi specimen on which the Indian identification is based is a small moeritherid-like sacrum, it is likely, as implied by West (1980:520), that it represents *Anthracobune* or a very closely related genus (see below) rather than *Moeritherium*.

A sometimes quoted early reference to another Asian occurrence of *Moeritherium* is in error. Pilgrim (1912:15) referred what he thought was a fragmentary upper molar to *Moeritherium*(?) sp. The specimen was found near Khajuri, Bugti Hills, Baluchistan, Pakistan, in what is presently thought by R.L. Bernor (pers. comm.) to be the continental equivalent of the lower part of the Gaj Formation (early Miocene). Later, Osborn (1936:79) identified the specimen as a P⁴ probably referable to *Trilophodon pandionis* (= *Gomphotherium angustidens* of present terminology), a common Siwalik species. Possibly the animal might represent the poorly known genus *Hemimastodon* Pilgrim, 1912, recently discussed by Tassy (1982:239, 240).

Anthracobune (including *Pilgrimella* and *Jozaria*).—The closest relative of *Moeritherium* and other proboscideans, *Anthracobune pinfoldi* Pilgrim, 1940 (p. 129) (congeneric with *Pilgrimella pilgrimi* Dehm and zu Oettingen-Spielberg, 1958 (p. 33), and *Jozaria palustris* Wells and Gingerich, 1983 (p. 125)), was known for nearly forty years before Earl Manning recognized its true affinities in the late 1970s. In the first stages of study of

the holotype of *Behemotops proteus* in 1976 one of us (Ray), convinced that it was desmostylian but equally convinced that comparison with *Anthracobune* (and "*Pilgrimella*") was warranted, spent much fruitless and frustrating time wandering among the artiodactyls and perissodactyls until a chance conversation with Earl Manning dehorned the dilemma. Manning's identification of *Anthracobune* as a *Moeritherium*-like animal was also generously made known to R.M. West, who was the first to publish on the matter (West, 1980:518; 1983). West placed *Anthracobune* in the Moeritheriidae. During the long interval from 1940 to 1980, *Anthracobune* (with "*Pilgrimella*") had masqueraded as an artiodactyl (Pilgrim, 1940; Gingerich, 1977; Coombs and Coombs, 1977; and most other authors), a perissodactyl (Coombs and Coombs, 1977:303; 1979), and a phenacodontid condylarth (Van Valen, 1978, fig. 3). Wells and Gingerich (1983) assigned it to a new family Anthracobunidae within the Proboscidea, and (based on an examination of the specimens of *Behemotops* reported herein) suggested that the Desmostylia, as well as the Moeritheriidae and the Sirenia, may be derived from anthracobunids. The fact that *Anthracobune* occurs in southern Asia, rather than in Africa, was doubtless a major cause of its long neglect in discussions of the phylogenetic origin of proboscideans and their possible affinities to the desmostylians.

Anthracobune (sensu lato) shares a derived feature (character 16 of the cladogram: Figure 22) with Moeritherioidea, Barytherioidea, Deinotherioidea, and Elephantoidea and is therefore the sister-group of Proboscidea as classified by Simpson (1945). M₃ has two definite cusps at rear: a labially displaced hypoconulid and a large entoconid II.

That *Anthracobune* itself was not the direct ancestor of the African moeritheres and other proboscideans is attested by three autapomorphic features (characters 17–19 of the cladogram: Figure 22).

Neither could the known anthracobunids have been ancestral to the Sirenia (*pace* Wells and

Gingerich, 1983), whose earliest members retain five premolars as a primitive condition. This condition has nothing to do with the fact that one lineage of sirenians (manatees) much later evolved supernumerary molars (Domning, 1982).

Ishatherium subathuensis Sahni and Kumar, 1980, described as a sirenian, may also be a specimen of *Anthracobune*.

Gingerich and Russell (1981) maintained both *Pilgrimella* and *Lammidhania* as separable from *Anthracobune* and stated that the type specimen of *Ishatherium subathuensis* is similar to an upper molar of *Pilgrimella*. Gingerich and Russell (1981) included *Anthracobune*, *Pilgrimella*, and *Lammidhania* in the Moeritheriidae as proboscideans. West (1983) likewise assigned *Anthracobune* (= *Pilgrimella*) and *Lammidhania* to the Moeritheriidae. Wells and Gingerich (1983), however, placed these three plus *Ishatherium* and their new genus, *Jozaria*, in the Anthracobuniidae. West (1980) had previously regarded *Lammidhania* as an artiodactyl.

Sahni and Mishra's (1975) reference of a fossil proboscidean-like sacrum from the middle Eocene of Kutch, India, to the Moeritheriidae may thus be basically close to the mark, but the genus involved may well be *Anthracobune* or a closely related genus rather than *Moeritherium* itself (West, 1980:521).

Minchenella.—Described as a member of the family Phenacolophidae, *Minchenella* Zhang, 1980 (p. 257) was originally given the name *Conolophus* Zhang, 1978 (p. 268), a junior homonym of a living iguanid lizard of the Galápagos Islands. The type-species, *Minchenella grandis* (Zhang, 1978:268) occurs in the Upper Paleocene Datang Member, Nonshan Formation, Lofochai Group, Datang Commune, Nanxiong County, Guangdong, People's Republic of China. It is known from lower jaws only, so that skull characters and postcranial features do not yet enter into deliberations about its affinities. Zhang (1978) assumed the genus to be a member of the family Phenacolophidae (considered to be condylarths); she made no comparisons with

other, similar mammals. However, phenacolophids are essentially bilophodont mammals in which the M_3 hypoconulid is small and merged with a lingually steeply ascending, wide, posterior cingulum (McKenna and Manning, 1977, fig. 1, legend, character 5). *Minchenella* (as a supposed phenacolophid) was recognized by Gingerich and Russell (1981:237) to be closely related to *Moeritherium* and *Anthracobune*, and was regarded as "the most plausible ancestor of Anthracobuniidae" by Wells and Gingerich (1983).

Comparison of *Minchenella grandis* with *Anthracobune pilgrimi* (identified by West, 1980, as *A. pinfoldi*) has been made possible by means of casts prepared by P.D. Gingerich and R.M. West, respectively. The two species prove to be remarkably close in morphology, the former almost certainly lying close to if not actually within the ancestry of the latter. *Minchenella grandis* lacks the very autapomorphies of *Anthracobune* (sensu lato) that set the latter apart from *Moeritherium* and other, more elephant-like, proboscideans (characters 17–19 of the cladogram: Figure 22; see above). In fact, *Minchenella grandis* also lacks character 16 of the cladogram (Figure 22), which unites *Anthracobune pinfoldi* with its moeritherian and more advanced proboscidean allies: M_3 with both a labially displaced hypoconulid and a large entoconid II.

However, *Minchenella grandis* shares the following character not only with *Anthracobune* and the Proboscidea, but also with *Behemotops* and more advanced Desmostylia (character 13 of the cladogram: Figure 22): M_3 with hypoconulid shelf transversely broadened to form a cuspidate crest in which the hypoconulid is still central. A small entoconid II (a new entoconid situated behind the true entoconid) lies lingually adjacent to the hypoconulid.

For these reasons *Minchenella* appears to us to be a late Paleocene Asiatic possible ancestor of both the Proboscidea (including *Anthracobune*) and the Desmostylia (including *Behemotops*). We see no reason why *Minchenella* should not be regarded as ancestral to both of these mammalian orders (Figure 23). At present, therefore, we

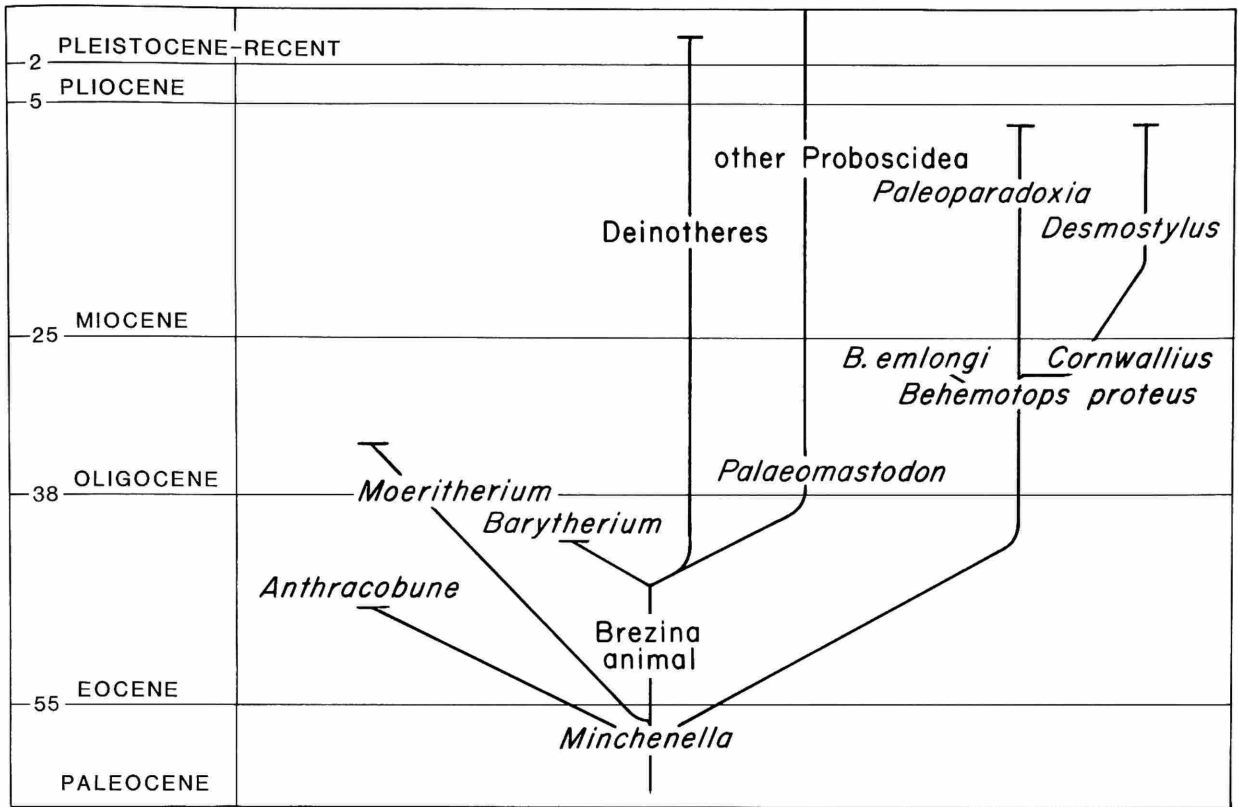


FIGURE 23.—Simplified phylogram of Proboscidea and Desmostylia.

believe the Desmostylia to be more closely related to the Proboscidea than to the Sirenia. The Sirenia appear to us to have branched away from ancestors more primitive than *Minchenella*. The Sirenia, like many other groups of mammals as divergent as marsupial diprotodonts and placental pyrotheres, also became bilophodont early in their history, but early sirenian genera retained five premolars and lacked the peculiar elevated external auditory meatus that characterizes desmostylians and proboscideans in which the skull is known. For a contrary opinion, see Wells and Gingerich (1983).

Implications for Eutherian Dental Homologies

McKenna (1975:37) proposed a new superorder Tokotheria to include all eutherians except

edentates, macroselideans, lagomorphs, pholidotans, possibly rodents, and a few extinct taxa from the Cretaceous and early Cenozoic. He hypothesized that "all tokotheres share or further modify a postcanine dental formula consisting of $dP_1^2 P_2^2 P_3^3 P_4^4 dP_5^5 M_1^1 M_2^2$. DP_5^5 is the tooth usually called M_1^1 ." Domning, Morgan, and Ray (1982) pointed out that primitive sirenians (believed to be tokotheres in McKenna's classification) retained five premolars (contrary to Fox, 1983:21, and others) in addition to three molars. This condition was shown especially clearly in a mandible of *Protosiren* sp. from the middle Eocene of North Carolina (USNM 214596). However, comparison of this specimen and other Eocene sirenians with the holotype of *Behemotops proteus* (USNM 244035) suggests that adult retention of DP_5^5 and DP_5^5 together with loss of the last molar, while not seen in the Sirenia, may yet

be characteristic of the Desmostylia and possibly other groups of tokotheres. Domning, Morgan, and Ray (1982) concluded that McKenna's (1975) hypothesis was false if the Tokotheria were taken to include the Sirenia, but, alternatively, this could also be interpreted to mean that sirenians are not tokotheres.

In USNM 214596, a molariform DP₅ is preceded by a P₃ and P₄ that closely resemble, respectively, the P₃ and P₄ described above for *Behemotops proteus* (USNM 244035). Each P₃ has a single, high, conical cusp flanked by much smaller cusps and pre- and postcingulids. Each P₄, in contrast, has a transversely oriented anterior pair of large cusps and a much smaller posterior pair, together with variously arranged small cusplules and crests.

The DP₄ of *Protosiren* is unknown. However, in *Prototherium veronense* de Zigno, 1875, a sirenian from the late Eocene of Italy, DP₄ is trilobate in outline (Sickenberg, 1934, fig. 28b) and is accompanied by a molariform DP₅ and a double-rooted DP₃ similar to the P₄ described above. The trilobate DP₄ closely resembles that of *Behemotops proteus* (USNM 244035). Domning (1982) has pointed out that the DP₃₋₅ of *Prototherium* also resemble the three anteriormost teeth of living *Trichechus*, which he considers to be their homologues. Trilobate DP₄s are also found in primitive proboscideans, phenacodonts, and artiodactyls as noted in the description of *B. proteus* on page 000. We suggest that these trilobate deciduous teeth in the fourth postcanine position may be homologous in all these taxa. This would imply that the molariform teeth in the fifth postcanine position in most of these groups, traditionally termed M₁, are actually homologues of the sirenian DP₅, and that the sirenian M₃ has no homologue in the other groups. The polarity and distribution of these character states require further study.

Status of the Tethytheria

Simpson (1945) coined the term Paenungulata at superordinal rank for the following orders: Pantodonta, Dinocerata, Pyrotheria (including

the then unnamed Xenungulata), Proboscidea, Embrithopoda, Hyracoidea, and Sirenia (including the desmostylians). Separate superorders coordinate with the Paenungulata were maintained for perissodactyls, artiodactyls, carnivores, and for a scrap-basket group combining condylarths, notoungulates, litopterns, astrapotheres, and aardvarks. That Simpson's (1945) arrangement is unnatural has long been recognized, but progress in understanding the detailed interrelationships of all these mammals has been very slow.

The taxon Tethytheria was created by McKenna (1975:42) for a restricted group drawn from the ranks of Simpson's paenungulates. Tethytheres were defined as comprising the coordinate orders Proboscidea, Sirenia, and Desmostylia. It will be remembered that the desmostylians had been removed from the Sirenia and given ordinal rank by both Abel (1933:875) and Reinhart (1953:187). No attempt was made by McKenna to resolve the trichotomous genealogy implied by the use of three coordinate ordinal taxa, nor was such an attempt made by McKenna and Manning (1977, fig. 1). However, in the present paper (Figure 22) we support the view that Proboscidea and Desmostylia share a more recent mutual ancestor than either of them does with the Sirenia. If our current view is correct, Desmostylia have therefore been shifted from a former special sirenian alliance (e.g., Simpson, 1945) through a neutral position (trichotomy) to a synapomorphous liaison with the Proboscidea and *Minchenella* based upon characters 10, 13, 14, and 15 of the cladogram depicted in Figure 22. Early Sirenia did not share these features and had not yet remodelled their dental formula (characters 10 and 14 of the cladogram). P₅ and the former last molar may have been lost independently in several groups of mammals.

Novacek (1982) united Proboscidea and Sirenia as a monophyletic group whose sister group is the Hyracoidea. However, the characters used are not convincing. For instance, the phenaclophids are not excluded by his character 71 and a squamosal contribution to the glenoid region of the skull (part of composite character 73) is surely plesiomorphous. His incomplete clado-

gram did not include the Desmostylia and did not deal with the presence of five premolars in early sirenians.

Desmostylian Lifestyle

Desmostylians were difficult to visualize as living animals as long as they were regarded as sirenians and until sufficient skeletal material became known. It was long supposed that they lacked functional hind limbs. Even now that extensive skeletal material is available, some question remains regarding the manner in which the limbs could have supported the body (see Inuzuka, 1984, for a critical review and a radical new interpretation). In our opinion, desmostylians were undoubtedly amphibious, but more suited to terrestrial locomotion than pinnipeds.

Analogies have often been drawn between desmostylians and hippopotami, especially after complete skeletons of the former were discovered (e.g., Abel, 1914:212; Matsumoto, 1918; Reinhart, 1953, in diagnosing the order; Thenius, 1960:196; Romer, 1966:254, 1968:201). The remarkable resemblances in size, build, and particularly jaw and dental structure (cf. Figure 20) between desmostylians and hippopotami suggest analogous lifestyles as well.

We believe, however, that to suppose that desmostylians (like hippos) fed mainly on land and resorted to the water chiefly for rest or other activities, would carry the analogy too far. Desmostylians have been found only in marine and never in freshwater or terrestrial deposits; hence they probably never strayed far from salt water. If they fed on the seashore and sought shelter in the water, they would face the problem that the available "shelter" was a much higher-energy environment than the lakes, rivers, and estuaries frequented by hippos. Except for the most protected bays and inlets, coastal waters of the North Pacific would not seem to provide a safe place for such large animals to rest. It is difficult to conceive of a selective regime that would have resulted in terrestrial feeders occupying such a rigorous environment. Rather, it seems more likely that, like pinnipeds, they would rest on

land and venture into the cold water (and possibly the surf) only for some energetic payoff. Further, it seems likely that they would have been tied strongly to the shore for reproduction, again as with pinnipeds, even if they were capable of aquatic copulation as are pinnipeds and hippos.

The desmostylian diet is still controversial. VanderHoof (1937:194) and, more recently, McLeod and Barnes (1984) have supposed that desmostylians fed on mollusks or other benthic invertebrates. This supposition may in part be the basis for the otherwise inexplicable comparison of desmostylians to walruses (Thenius, 1969:586; 1980:49). Walruses do not crush or masticate shells, but feed by suction (Fay, 1982:167–172). Further, there seems no basis in osteology, dentition, or locomotion (cf. Gordon, 1981) of walruses to warrant special comparison to desmostylians.

Most writers, including Reinhart (1959:103) and Domning (1978b:113), have considered desmostylians to be herbivores. Certainly, we see nothing in the dentitions of at least the more primitive, brachydont genera that would suggest a diet radically different from that of proboscideans, hippos, pigs, or other plant-eaters. Shikama (1966:188), while not excluding invertebrates from the diet, suggested that *Paleoparadoxia* and *Desmostylus* were adapted for "browsing" and "grazing," respectively. Domning (1978b:114) extended this idea by speculating that *Desmostylus* specialized on seagrasses such as *Zostera* and especially their rhizome systems, while brachydont taxa primarily ate benthic algae. These food sources should have been available throughout the northern parts of the desmostylians' range (Japan, Sakhalin, Kamchatka, Alaska, British Columbia, Washington, Oregon, and California), even during the relatively cool Oligocene, and thus could have provided a high-road for desmostylian dispersal around the margin of the North Pacific.

If we visualize primitive desmostylians as feeding on benthic algae and other marine plants along North Pacific shores, a major potential adaptation that suggests itself is intertidal feed-

ing. The substantial Pacific tides regularly expose vast amounts of fresh, attached plant material in addition to fragments washed ashore. It would be natural for a moerithere-like herbivore to exploit these resources before swimming out to feed on submerged subtidal plants, with the attendant risks of surf, currents, and hypothermia. Even after desmostylians had evolved their limited adaptations to aquatic locomotion, the intertidal zone would still offer a safer, more accessible, and less energetically costly source of food. The peculiar limb structure of desmostylians (Shikama, 1966, 1968; Inuzuka, 1984) surely indicates something other than purely terrestrial locomotion, but it seems unnecessary to assume that they needed to forage exclusively underwater. We suspect that desmostylians, at least in their earlier evolutionary stages, supplemented their subaqueous diets with intertidal plants. Sheep in certain of the Orkney Islands, which feed principally on intertidal algae (Hall, 1975), may provide an unexpected modern analog for the earliest desmostylians.

The procumbent incisors and canines of desmostylians seem well suited to forking up masses of vegetation, detaching plants from rocks or sand, or uprooting mats of rhizomes as suggested long ago by Matsumoto (1918:66, 70). In particular, the wear on the ventral side of the tusk in the referred specimen of *Behemotops emlongi* suggests frequent contact with abrasive substrates. Microwear on the cheek-teeth, examined by scanning electron microscope, may provide evi-

dence to settle the controversy over diet. Meanwhile, we remain convinced that desmostylians were littoral marine herbivores.

Conclusions

The tethytherian order Desmostylia, although all its known representatives are marine mammals, is the sister-group of the order Proboscidea rather than of the order Sirenia. A new genus and two new species of primitive desmostylians from marine Oligocene rocks of the Pacific Northwest are described in this paper. They help to span the morphological gap between the Proboscidea and Desmostylia, as do the primitive, late Paleocene tethytherian genus *Minchenella* and various primitive Eocene proboscideans described recently from both Africa and Asia. Together with *Minchenella*, the proboscideans and desmostylians thus form an unnamed monophyletic group whose earliest presently known representatives occur in terrestrial late Paleocene rocks of southeast Asia. The relationships of this clade to the Sirenia and to other paenungulates are still not known in detail from paleontological evidence, nor is it known when the desmostylians first entered the sea and spread along the shores of the North Pacific Ocean as far as Mexico. Probably the transition was in the Eocene. In the first stages of assuming their marine habitat these interesting and even bizarre amphibious herbivores probably fed to a large extent on intertidal plants.

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