

The beginning of the Age of Mammals

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Abstract: The paper reviews community evolution of the first million years of the great mammalian expansion, in relation to the herbivores. Origination rates suddenly increased 2 or 3 orders of magnitude and gradually declined. The decline occurred together with an apparent increase in the importance of extinction as herbivore diversity increased to a new and higher equilibrium level characteristic of modern terrestrial communities. Much of this community reorganization happened in an interval of unusually low predation, which implicates competition as the primary organizer of placental communities. Appendices describe new taxa (1 family, 2 subfamilies, 13 genera, 1 subgenus, and 46 species, mostly of Condylarthra), give many other taxonomic changes and several faunal lists, and propose a new North American land-mammal age, the Mantuan. The major classification of the Ungulata is revised, with a phylogeny including all genera of the Arctocyonia.

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The Cenozoic, the Age of Mammals, begins with the Paleocene. Most known early Paleocene mammals are condylarths, the ancestral ungulates, many of which lacked hoofs. Only one species of condylarth (Protungulatum donnae Sloan and Van Valen, 1965) has been described from beds dated earlier than the Puerco (Matthew, 1937) of northwest New Mexico, the classic terrestrial early Paleocene. I here raise that total to 13, by new taxa and correlations, and give several implications of them for the history of the vertebrates and evolutionary theory.

The localities Bug Creek Anthills, Bug Creek West, and Harbicht Hill, all of latest Cretaceous age, are in east-central Montana (Sloan and Van Valen, 1965). Mantua (Jepsen 1930, 1940), in northwest Wyoming, I show to be pre-Puerco Paleocene. Diagnoses and figures of new taxa, and justification of the phylogeny, will be given more fully elsewhere. Here I discuss primarily the first million years of condylarth evolution.

GENERAL PHYLOGENY

All known pre-Puerco condylarths are plausible ancestors of later condylarths. Therefore perhaps none of their lineages become extinct until after Puerco time, although for one lineage this seems likely. We know nothing of such early condylarths elsewhere in the world and large gaps still exist, so the phylogenies are merely permissive. In a discussion of the phylogeny of the earliest radiation of angiosperms, on the basis of their pollen, Doyle (1977) also failed to find evidence of any extinction. He thought some extinction must really have occurred although it was not detectable in his coarse phylogeny. My prejudice agrees with his, but the data in neither case as yet demand this result. Nor do the data distinguish punctuated from gradual evolution at the species level.

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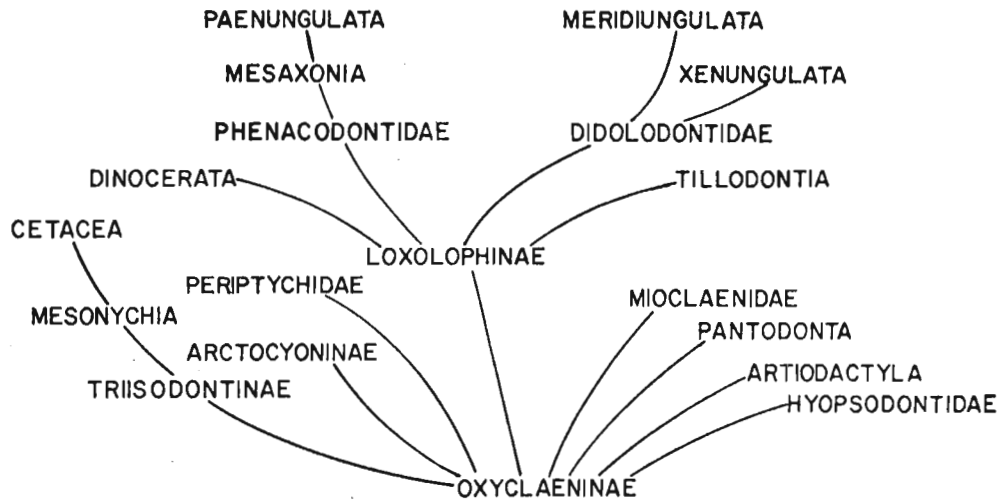


Figure 1. Outline phylogeny of the ungulates. Named subfamilies belong to the Arctocyoniidae and named families to the Arctocyonia. See Appendix 2 for more detail and explanation of names.

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Figure 1 gives a provisional phylogeny of the ungulates, with only enough detail in derived groups to indicate origins as I now see them. I separate the Mioclaenidae from the Hyopsodontidae because these groups seem to have had independent origins. Unfortunately little is yet known of the Mioclaenidae beyond their jaws, although there is a skull and some questionably referred postcranial material for the derived genus *Pleuraspidotherium*. Schaeffer (1947, 1948) referred an astragalus from the Puerco to *Choeroclaenus*, but this was merely because the astragalus and a partial jaw had been found together. Such co-occurrence of elements of different genera are common in the Puerco. True association in this case is possible but unproved, as Matthew (1937) had noted.

The early members of all four condylarth families differentiated by Puerco time were similar to each other and boundaries within the phylogeny are in part arbitrary. Only the Periptychidae had diverged enough by the Puerco to warrant familial status on the basis of genera then alive. In fact three genera present at Harbicht Hill and referred to different orders (Insectivora, Primates, and Condylarthra) are similar enough to be placed in the same family except for their descendants (Van Valen and Sloan, 1977).

ADAPTATIONS AND SIZE

By the early Paleocene, the smaller periptychids and oxyclaenine arctocyoniids emphasized tooth shear, in different ways and with different jaw movement. These periptychids wore their molar protocones down from almost the labial side, a unique feature involving horizontal shear, while oxyclaenines retained some vertical embrasure shear. Loxolophine arctocyoniids, mioclaenids, and large periptychids emphasized grinding. Hyopsodontids were intermediate. Triisodontine arctocyoniids were large crushers.

Table 1. Numbers of species of presumptive herbivores in several sequential vertebrate faunas.

Puerco	Multituberculata	6	total 35
	Taeniodonta	2	
	Condylarthra	27	
Mantua	Multituberculata	2	total 11
	Taeniodonta	1	
	Condylarthra	8	
Harbicht Hill	Ornithischia	3	total 15
	Multituberculata	6	
	Primates	1	
	Condylarthra	5	
Bug Creek West	Ornithischia	3	total 13
	Multituberculata	7	
	Condylarthra	3	
Bug Creek Anthills	Ornithischia	3	total 12
	Multituberculata	8	
	Condylarthra	1	
<u>Triceratops</u> community	Ornithischia	5-6	total 12-13
	Multituberculata	7	

The sample of multituberculates from Mantua may well be too small.

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Except for Eoconodon, all condylarths through Mantua time were rat-sized and differed in estimated weight by no more than a factor of 3 or 4. Eoconodon was about 8 times the size of the next largest. Several animals this size evolved by Puerco time, but the largest was no more than a meter long. Larger ungulates arrived in the middle Paleocene and herbivorous dinosaurs regionally vanished between the times of Harbicht Hill and Mantua. In the early Paleocene small herbivores began to get large but didn't get very far. An equilibrium distribution of body sizes had been destroyed and another was being evolved.

THE FIRST MILLION YEARS

In Montana, the Cretaceous ended about 10^5 years after Bug Creek Anthills (Van Valen and Sloan, 1977), with Harbicht Hill midway to the boundary. Mantua is a channel sandstone into Cretaceous rocks but just postdates dinosaur extinction in northern Wyoming. Puerco is less than 2×10^6 years after Bug Creek Anthills (Butler et al., 1977; Lindsay et al., 1978) and probably is only about 1 million years later (Rigby and Lucas, 1977). These intervals are necessarily only approximate.

The condylarths invaded the northern United States as part of a warm-temperate community that gradually replaced the indigenous subtropical flora and fauna (Van Valen and Sloan, 1977). The proportion of local evolution and immigration during the transition is unknown, but the immigrants themselves were evolving rapidly because almost all special appear in phylogenetic order. They rapidly escaped from the temperate community and their descendants populated the earth.

The final extinction of dinosaurs in North America occurred during the interval studied. There is evidence (Van Valen and Sloan, 1977) that the explosive radiation of condylarths was a major cause of the extinction, acting by diffuse competition.

At the same time the herbivorous placental mammals were in first flower, the multituberculates were doing what they could to keep up with their new competitors. They declined in abundance of individuals from the Cretaceous to their final extinction in the Oligocene, but their maximum species diversity, even when corrected for degree of ignorance, was in the middle Paleocene (Van Valen and Sloan, 1966; contra Fox, 1968a). This curious situation seems to have come about by a narrowing of the average width of adaptive zones of species, to accommodate the herbivorous placentals, while more narrowly adapted multituberculates were able to squeeze in for a while. Condylarths, primates, and rodents successively predominated in competition. The competition itself, though, was not as one might think. A species lineage of multituberculate that was able to establish itself had as long a life expectancy as a species lineage of the competing placentals. The competitive inferiority of multituberculates, whatever its causes, manifested itself in a lower ability to establish new species lineages.

PREDATION AND COMMUNITY STRUCTURE

The fitting of species together into any community is sometimes ascribed to the effects of predation (Connell, 1975). The placental explosion provides a natural experiment in this subject, and indeed a counterexample. For a geologically short but critical interval (the early Paleocene) predation on mammals seems to have been much reduced, yet this had no detectable effect on their community evolution. Thus competition, rather than predation, was the main factor in the initial organization of Cenozoic terrestrial communities.

Before dinosaur extinction in an area, predation was undoubtedly important for mammals as well as for other animals. Any of the several species of predaceous dinosaurs may have eaten mammals when young, and coelurosaurs may have done so even as adults. There were also large lizards, a cursorial xiphodont crocodile, and a primitive snake or two. When the world changed, only the crocodile (a small pristichampsine), the snake (a booid), and about three middle-sized varanoid lizards survived. In early Paleocene faunas the cursorial crocodile is known from one tooth (Princeton Univ. 17074) from Mantua. One specimen of a snake has been reported from the Puerco. These two specimens, of thousands recovered from the several described early Paleocene faunas, represent the only trace of terrestrial predators large enough to prey on mammals.

Other potential predators did exist at this time, however. The varanoid lizards reappear later in the Paleocene and may have been regionally present, in unsampled sites or as rare elements in known sites, in the early Paleocene. The Varanidae, active predators today, disappeared in North America with the dinosaurs. So did the large non-varanid varanoids. The non-varanid varanoids are represented today by Heloderma and Lanthanotus. These are sluggish animals and at least Heloderma rarely or never eats mammals old enough to move from the nest (Bogert and Martín del Campo, 1956).

Cursorial birds undoubtedly flourished, at least in the Southern Hemisphere, during the early Paleocene (cf. Cracraft, 1973). They are unknown in North America until about the end of the Paleocene. The oldest known owl occurs in the late Paleocene of Colorado (Rich and Bohaska, 1976); when owls originated is unknown. Hawks and vultures have not been found earlier than the Eocene London Clay (Fisher, 1967).

The great placental radiation seems to have been concentrated near streams, as suggested by the absence of the Protungulatum community and its descendants from non-channel deposits until beyond the base of the Paleocene. Therefore semi-aquatic predators may sometimes have eaten mammals. Alligator teeth are common in all early Paleocene faunas, although the posterior teeth suggest clam-eating habits. Semi-aquatic turtles and shorebirds were also present. However, this aquatic and semi-aquatic community survived the great extinction unscathed (Sloan, 1970; Van Valen and Sloan, 1977) and showed no evolutionary response to the mammalian radiation. Moreover, the mammals show no indication of other than strictly terrestrial (with perhaps arboreal and fossorial) habits.

Carnivorous mammals (Mesonychidae and the larger Miacidae) appeared in the middle Paleocene, so one may ask about the diets of their ancestors. Unfortunately, in each case there are no suitable lineages. The most primitive middle Paleocene miacids were minute and probably still insectivorous. Mesonychids seem to have radiated predominantly in Asia, from where they may have come to North America. However, triisodontine arctocyonids were ancestral to mesonychids, and this subfamily does occur in the early Paleocene of North America.

Like other arctocyonids, triisodontines had reduced their embrasure shear between the molars. They had not yet evolved the efficient centrocrista-talonid shear characteristic of mesonychids (and, convergently, of oxyaenids, which retained embrasure shear from their insectivorous ancestors). Their teeth and jaws were massive, but the teeth nevertheless suffered extensive wear, apical rather than shearing. As in other arctocyonids, the canines were unreduced and the mandibular condyle was still in its primitively low position.

Following an oral suggestion from Karen Hiiemae, I looked at the widths of the zygomatic arches of some primitive condylarths to see what room remained for expansion of the temporalis musculature. Periptychids (including Maiorana), the primitive arctocyonids Ragnarok and Loxolophus, and the triisodontine Eoconodon all have narrow arches. Deltatherium has a wide arch, and Arctocyonides (including Claenodon) and Arctocyon are intermediate. Deltatherium is thus the best candidate among arctocyonids for predaceous habits, as its slicing teeth also suggest, but it seems to be closely related to the herbivorous Pantodonta. Hiiemae also noted that most of the movement vector of the temporalis is vertical rather than toward the rear. The temporalis is unreduced in insectivorous bats (Storch, 1968) even though they have little danger of jaw dislocation from struggling prey (cf. Maynard Smith and Savage, 1959).

The retention of unreduced canines by arctocyonids (and their enlargement in several lineages) may itself have selected for retention of a large temporalis. Large canines require a large gape. Why the canines remained unreduced is unclear but may well have been related to social interactions, as it is in muntjacs and other artiodactyls. Sexual

dimorphism in canine size of some species could occur, as it does even for the small canines of modern horses.

Comparison with the ancestral artiodactyl Diacodexis is also instructive (cf. Van Valen, 1971). Diacodexis retains unreduced canines in both jaws, has a large ascending mandibular ramus and an apparently large temporalis, and its mandibular condyle is no higher than that of Arctocyon. Its teeth are also quite similar to those of fairly primitive arctocyonids. However, its astragalus was fully developed in the artiodactyl manner, for straight and rapid rather than shifty running, and Diacodexis presumably had hoofs.

Bakker (1977) has noted the complete absence of terrestrial carnivores larger than about 1 kg. in the middle and upper parts of the Lystrosaurus zone in South Africa, in the early Triassic. The common herbivore Lystrosaurus was large, and large carnivores had occurred with it earlier (and re-evolved later). Lystrosaurus, being the only large herbivore and having semi-aquatic adaptations, may have been able to cause its predators' extinction. It then had its world to itself. However, it soon became extinct too, perhaps because of the evolution of new predators and competitors. This is the only other case I know of an animal community with negligible predation. However, in the Vendian there are also no clear predators; medusae were the only pelagic animals and therefore may have fed by filtering phytoplankton.

EQUILIBRIAL DIVERSITY

By Puerco time an evolutionary equilibrium was becoming established (Table 1). The numbers of species and genera of presumptive herbivores are almost as large as those of later Cenozoic faunas. Extinction became important as new lineages could rarely enter without older ones vanishing. At least 6 early Paleocene condylarth genera lack known descendants. The increase in diversity probably started at about the time of Harbicht Hill. Until then the number of species of herbivores had hardly changed despite some turnover attributable mostly to diffuse competition. Then, for a million years or so, adaptive zones of species were narrowed and energy per species probably therefore declined. This new equilibrium has persisted ever since.

The change from one equilibrial diversity to another may reflect a competitive advantage of more narrowly adapted species. The large body size of dinosaurs would not have permitted as fine a partitioning in the Cretaceous as occurred in the Cenozoic, and dinosaurs seem to have been competitively superior to the mammals underfoot until the evolution of the Protungulatum community, without dinosaurs (Van Valen and Sloan, 1977).

EVOLUTIONARY RATES

Rapid evolution continued past Puerco time but its rate declined. The Mantua fauna is subjectively more different from that of the Puerco than the Puerco is from middle Paleocene. At the family level, origination rates for mammals have declined exponentially throughout the Cenozoic, by two orders of magnitude (Van Valen, 1973) although regulated equilibria came to exist for body size (Van Valen, 1975), genera (Webb, 1969; Van Valen, 1975), and presumably species.

Table 2. Numbers of condylarth taxa in the earliest faunas, and origination rates for each interval between faunas.

		Families	Genera	Species	Interval (years, very approximate)	Origination rates in millimacarthurs ¹	
						Genera	Species
Later ↑ Earlier	Puerco	3	21	29			
					10 ⁶	2	3
	Mantua	2	8	9			
					2 x 10 ⁵	5	4
	Harbicht Hill	2	4	5			
				2 x 10 ⁴	50	30	
	Bug Creek West	2	2	3			
					2 x 10 ⁴	50	100
	Bug Creek Anthills	1	1	1			

¹Macarthurs (Van Valen, 1973) apply to rates of discrete phenomena generally; for originations, one macarthur equals one origin per thousand years per potential ancestor.

Some species, now unknown, probably evolved and disappeared between Mantua and Puerco time. For this reason the true origination rate for at least species between Mantua and the Puerco should perhaps be somewhat higher than that shown. However, the relatively low turnover (cf. D.E. Russell, 1967) between the two levels of the Puerco, which are separated by 10⁵ years or probably more (Butler et al., 1977; Lindsay et al., 1978), indicates values no larger than those in the table. The numbers of genera and species for Mantua and Puerco include respectively 1 and 2 lineages known both before and after the respective fauna but absent from existing collections there. Vertical lines signify taxa known from more than one fauna. Their pattern, and the intermediate morphology of Mantua species, determine the relative position of the Mantua fauna.

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Origination rates for genera and species declined by an order of magnitude between Bug Creek Anthills and the Puerco (Table 2), despite several kinds of inaccuracies. The rates at Puerco time are still an order of magnitude higher than the characteristic extinction rates, and therefore origination rates at equilibrium, of Cenozoic mammals (Van Valen, 1973). These in turn are appreciably higher than the turnover rates of Mesozoic tetrapods. Turnover rates in the western United States therefore increased by two to three orders of magnitude with the arrival and evolution of the Protungulatum community, and gradually decreased by about two orders of magnitude during the Paleocene.

The approach to an equilibrium species density in the early Paleocene therefore slowed the evolutionary explosion, but general and special adaptations continued to cause unusually rapid reassortments of the resource space among taxa at all levels for several million years afterwards.

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APPENDIX 1: Condylarths

Here I describe the new taxa on which the foregoing analysis is based. Also, at a referee's suggestion, I make available some other taxa and note some synonymies and other changes, accumulating for 20 years. Species synonymies are based on observed variation, not on extrapolation. This is a progress report, with results only. I still need to make many relevant comparisons and expect further modifications and additions as well as documentation. Abbreviations: ACM, Amherst College Museum; AMNH, American Museum of Natural History; KU, University of Kansas Museum of Natural History; NMNH, (U.S.) National Museum of Natural History, Smithsonian Institution; PU, Princeton University; ROM, Royal Ontario Museum; UCMP, University of California (Berkeley) Museum of Paleontology; UM, University of Minnesota; l, maximum proximodistal length; tald w, talonid width; trd w, trigonid width; w, maximum width perpendicular to labial border of tooth. All measurements are in millimeters and are of the type specimens. Names and dates in parentheses refer to first publication of a concept now called by the name given.

Order Condylarthra Cope, 1881
 Suborder Arctocyonia Van Valen, (1966) 1969
 Family Arctocyonidae Giebel, 1855 (Murray, 1866)
 Subfamily Oxycloeninae Scott, 1892

Protungulatum gorgun, new species.

Type: AMNH 35987, right mandible with M_2 , Harbicht Hill (species also at Bug Creek West). Plate 1, Figure 4.

Diagnosis: Larger than P. donnae Sloan and Van Valen (1965); hypoconid enlarged relative to entoconid, paraconid projects proximally; upper molars with rather massive protocone. Suitable ancestor for Triisodontinae and Oxycloenus. $M_2l, 5.5$; trd w, 3.8; tald w, 3.7.

Etymology: Gorgun, the Woses' name for orcs in The Lord of the Rings, with reference to the Cretaceous Hell Creek Formation.

Protungulatum sloani, new species

Type: UM VP1456, left mandible with M_{1-3} , Purgatory Hill. Plate 1, Figure 3.

Diagnosis: Size of P. donnae but molar talonid somewhat longer and wider, base of enamel lower labially; conules of upper molars farther apart. $M_2l, 3.6$; trd w, 2.8; tald w, 2.8.

Etymology: Robert E. Sloan, my collaborator on these faunas.

Oxyprimus, new genus

Type species: Oxyprimus erikseni, new species.

Diagnosis: Trigonid walls nearly vertical; P_4 rather narrow; molar talonids larger than in Protungulatum; upper molars rather rectangular. Includes the smallest known arctocyonids.

Etymology: Oxys, Greek, sharp; primus, Latin, first. Reference is to morphology, primitiveness, and Oxyclaenus.

Oxyprimus erikseni, new species

Type: UM VP1561, right M_1 , Harbicht Hill. Plate 1, Figure 5.

Diagnosis: Molar metaconid conical; M^1 transverse. M^1_1 , 3.5; trd w, 2.1; tald w 2.2.

Etymology: Richard Erikson, who preserved the map which led to the rediscovery of Harbicht Hill, and who assisted in collecting the material which contains the type specimen of O. erikseni.

Oxyprimus galadrielae, new species

Type: PU 16866, left maxilla with P^3-M^3 , Mantua. Plate 1, Figure 1.

Diagnosis: Molar metaconid elongate; M^1 transverse. Same as Loxolophus sp. of Jepsen (1930, Plate IV, Figure 9). M^2_1 , 3.8; w, 6.1.

Etymology: Galadriel (Sindarin [Elvish], radiantly garlanded woman), wise elf-queen of The Lord of the Rings and The Silmarillion.

Oxyprimus putorius, new species

Type: PU 16704, right maxilla with P^3-M^3 , Mantua. Plate 1, Figure 2.

Diagnosis: M^1 not transverse. M^2_1 , 3.4 ± 0.2 ; w, 4.8 ± 0.1 .

Etymology: Putorius, subgenus of Mustela containing the Old World polecats; for Polecat Bench, Wyoming, where the Mantua channel occurs.

Oxyprimus albertensis (Fox, 1968)

Prothryptacodon albertensis Fox (1968b) belongs to Oxyprimus and is conspecific with Carcinodon aquilonius Russell (1974). The species occurs also at Purgatory Hill and is the largest known species of the genus. M_2 of the type is 3.8 mm. long, not 4.7 mm. as published.

Deltatherium durini, new species

Type: AMNH 102161, left $M^{?1}$, Crazy Mountain Field, Montana, locality not in field book but from the time of collection very probably somewhere in the Melville Formation. Plate 1, Figure 6.

Diagnosis: Two-thirds the size of D. fundaminis, conules much larger, tooth less transverse. $M^{?1}_1$, 5.3; w, 5.6.

Etymology: Name of many dwarf-kings in The Lord of the Rings; Durin I began Khazad-Dûm. Allusion is to size.

Chriacus Cope, 1883

Synonyms include Spanoxyodon Simpson, 1935; Tricentes Cope, 1883; Metachriacus Simpson, 1935. The type specimen of the type species of Tricentes even has four premolars, by new preparation, although the name was given in the belief that P^1 was absent.

Chriacus calenancus, new species

Type: UM VP1472, left M_2 , Purgatory Hill. Plate 2, Figure 3.

Diagnosis: Steeper postvallid than C. baldwini, and smaller entoconid. M_2_1 , 5.5; trd w, 4.5; tald w, 4.5. C. calenancus can alternatively be regarded as a temporal subspecies of C. baldwini.

Etymology: Sindarin (Elvish) calen, green; anca, jaws. Reference is to inferred herbivory.

Chriacus orthogonius Russell, 1929

Metachriacus punitor Simpson, 1935, is a synonym.

Chriacus katrinae, new species

Type: PU 13949, right mandible with M_{1-3} , Rock Bench Quarry. Plate 2, Figure 2.

Diagnosis: Slightly larger than C. pelvidens, jaw half again as deep, upper molars less transverse. Same as Chriacus sp. of Jepsen (1930, Plate IV, Figure 4). M_2^1 , 8.1; trd w, 5.7; tald w, 5.9.

Etymology: Katrina, my daughter.

Chriacus baldwini (Cope, 1882)

Synonyms include Tricentes crassicollidens Cope, 1884; Chriacus truncatus Cope, 1884; Chriacus schlosserianus Cope, 1888; Metachriacus provocator Simpson, 1935; Spanoxydon latrunculus Simpson, 1935. The type specimen contains P_3-M_1 , as Cope thought, not P_{2-3} , DP_4 as Matthew thought in 1897 or DP_{2-4} as in Matthew (1937). Most referred specimens of C. baldwini belong to C. pelvidens, as E. Manning discovered.

Chriacus oconostotae, new species

Type: PU 20782, left mandible with P_4-M_2 , Cedar Point Quarry, northern Big Horn Basin, Wyoming. Plate 2, Figure 1.

Diagnosis: P_4 protoconid both low and short, molar trigonids taller than in C. pelvidens and paraconid weaker. M_2^1 , 7.9; trd w, 5.5; tald w, 5.8.

Etymology: Oconostota, Cherokee leader.

Chriacus metocometi, new species

Type: AMNH 17194, right M_2^2 , Mason Pocket, Tiffany, southern Colorado. Plate 2, Figure 4.

Diagnosis: Small species with relatively low cusps and a large, distolingually projecting hypocone. M_2^1 , 5.4; w, 6.8.

Etymology: Metocomet ("King Philip"), Wampanoag leader.

Prothryptacodon Simpson, 1935

Synonyms include Pantinomia Van Valen, 1967, and Landenodon Quinet, 1968 ("1966").

Prothryptacodon ambiguus (Van Valen, 1967)

Distinctions from P. furens include the shorter P_4 protoconid and the more blade-like paraconid of M_2 (shown also in AMNH 93218).

Prothryptacodon europaeus (Quinet, 1968 ["1966"])

Synonyms are Landenodon woutersi Quinet, 1968, and Landenodon luciani Quinet, 1968. The type is a DP^4 .

Thryptacodon demari Gazin, 1956

Thryptacodon belli Gazin, 1956, is a synonym.

Thryptacodon antiquus Matthew, 1915.

Synonyms are Thryptacodon olseni Matthew, 1915, and Thryptacodon loisi Kelly and Wood, 1954. Thryptacodon pseudarctos Simpson, 1928, is perhaps better placed here than as a senior synonym of T. australis.

Oxyclaenus Scott, 1892

Carcinodon Scott, 1892, is a synonym.

Oxyclaenus cuspidatus (Cope, 1884)

The type specimen is atypical, but each of its oddities can be matched in the variation of the rest of the sample.

Oxyclaenus simplex (Cope, 1884)

Mioclaenus filholianus Cope, 1884, is a synonym. The maxilla Simpson (1936) figured as O. simplex belongs to Choeroclaenus turgidunculus. The P^4 of O. simplex is close to that of O. cuspidatus.

Thangorodrim, new genus

Type species: Thangorodrim thalion, new species

Diagnosis: Most similar to Oxyclaenus; lower teeth broad but not bunodont; P₄ with large metaconid and a talonid basin; M₁ talonid much wider than trigonid; P₄ with large protocone directly lingual of paracone; upper molars with large conules, moderate hypocone, and no pericone.

Etymology: Thangorodrim, the mountainous triple fortress of Morgoth in The Silmarillion. Reference is to Purgatory Hill.

Thangorodrim thalion, new species

Type: UM VP1473, left M₁, Purgatory Hill. Plate 1, Figure 7.

Diagnosis: Differs from T. pugnax (Simpson, 1935), the only other known species, in having a shorter talonid and a considerably steeper labial slope of the hypoconid. M₁l, 6.8; trd w, 4.8; tald w, 5.6.

Etymology: Sindarin (Elvish) thalion, strong. Reference is to the massive morphology and the generic name.

Subfamily Arctocyoninae Giebel, 1855

Colpoclaenus Patterson and McGrew, 1962

Claenodon silberlingi Gidley, 1919 (synonym: Claenodon vecordensis Simpson, 1935) appears referable to Colpoclaenus and is perhaps specifically different from Neoclaenodon procyonoides Matthew, 1937, also a probable member of Colpoclaenus.

Arctocyonides Lemoine, 1891

Claenodon Scott, 1892, is a synonym of Arctocyonides rather than of Arctocyon, which is restricted to Europe. Procyonictis Lemoine, 1885, is a senior synonym. As the International Commission on Zoological Nomenclature has acted on only one of several proposals I submitted to them more than 10 years ago, and some are still unpublished by them, I prefer to use the well-known junior synonym without applying for its validation.

Arctocyonides montanensis (Gidley, 1919)

Claenodon latidens (Gidley, 1919) is a synonym.

Arctocyonides mumak, new species

Type: PU 17406, left mandible with P₄-M₃. East border of Section 10, T56N, R99W, north of Powell, Wyoming. Plate 3, Figure 1.

Diagnosis: Largest known arctocyonid. Derived from A. ferox but upper molars more squarish, cusps lower, and paracone and metacone closer together. Somewhat parallel to the incipiently crown-hypsodont genus Arctocyon. I have seen specimens from 11 localities in PU and AMNH, all from the middle to late Tiffanian and possibly the Clarkforkian. M₂l, 16.5; trd w, 14.8; tald w, 13.6.

Etymology: Mûmak, name used in Ithilien for the animal hobbits called an oliphaunt, resembling a large elephant. Reference is to size.

Mentoclaenodon Weigelt, 1960

Claenodon acrogenius Gazin, 1956, belongs to Mentoclaenodon.

Subfamily Loxolophinae, new

Diagnosis: Arctocyonids with relatively low-crowned and transverse lower molars, trigonid basins without central crest (as in Arctocyoninae), M₁ paraconid not projecting forward (as in Thryptacodon).

Included genera: Ragnarok, Baiocanodon, Platymastus, Loxolophus, Mimotricentes, Deuterogonodon, and Desmatoclaenus.

Ragnarok, new genus

Type species: Ragnarok harbichti, new species

Diagnosis: Molars moderately low-crowned and bulbous; upper molars and lingual lobe of P₄ transverse.

Etymology: The twilight of the gods, from the Eddas, with reference to the extinction of the dinosaurs, which occurred while Ragnarok lived and in which

it probably assisted (Van Valen and Sloan, 1977).

Ragnarok harbichti, new species

Type: AMNH 35983, right mandible with M_{1-3} , Harbicht Hill. Plate 3, Figure 4.

Diagnosis: Molar talonids smaller than those of R. nordicum (Jepsen, 1930), from Mantua, the only previously described species. See Plate 3, Figure 5. M_2^1 , 5.8; trd w, 5.1; tald w, 4.5.

Etymology: Darwin Harbicht (later Harbin) discovered the first Cretaceous condylarths and collected the type specimen of R. harbichti in 1938.

Ragnarok wovokae, new species

Type: PU 17304, right $M^?2$, the complete tooth in this number, Leidy Quarry (see Appendix 3). Plate 3, Figure 2.

Diagnosis: Size of R. nordicum but base of hypocone projects lingually; molar more triangular in outline than rectangular. $M^?2_1$, 5.8; w, 8.4.

Etymology: Wovoka, the Paiute prophet of the Ghost Dance.

Platymastus, new genus

Type species: Platymastus palantir, new species.

Diagnosis: Occlusal surfaces rather flat; molar protocone central, broad, and massive, expanded lingually, paracone and metacone small; molar paraconid small, central, proximal.

Etymology: Platys, Greek, flat or broad; mastos, Greek, breast. Reference is to the unusual morphology of the protocone and to the finding of the type specimen at a breast-shaped hillock informally but widely known as Mammelon Hill.

Platymastus palantir, new species

Type: AMNH 58034, right M^2 ; Hemithlaeus facies of Puerco, Mammelon Hill, Betonnie Tsosie Arroyo. Plate 2, Figure 6.

Diagnosis: Upper molar protocone more lingual than in P. mellon; metacrista extends distolabially. M^2_1 , 4.2; w, 6.3.

Etymology: Quenya (Elvish) palantir, distant watcher, one of 7 globes made by Fëanor that gave visions through spacetime. Reference is to the long duration of the genus.

Platymastus mellon, new species

Type: AMNH 56293, left M^1 or 2 ; Tiffany, southern Colorado, about 50 m. stratigraphically above Mason Pocket. Plate 2, Figure 7.

Diagnosis: Upper molar protocone more labial than in P. palantir; stylar shelf reduced; metacrista extends distolingually. M^1_1 , 3.8 ± 0.2 ; w, 5.5 ± 0.2 .

Etymology: Sindarin (Elvish) mellon, friend, the password of the west gate of Khazad-dûm in The Lord of the Rings. Reference is to similarity to P. palantir, presumptive diet of plants, and obliquely to the English word melon and Greek mellēsis, delay, from mello.

Loxolophus Cope, 1885

Synonyms include Protogonodon Scott, 1892, and Paradoxodon Scott, 1892 (preoccupied, =Paradoxodonta Strand, 1943). Protogonodon kimbetovius Matthew, 1937, belongs here.

Loxolophus hyattianus (Cope, 1885)

Chriacus priscus Cope, 1888, is a synonym.

Loxolophus pentacus (Cope, 1888)

Synonyms are Chriacus ruetimeyerianus Cope, 1888; Protogonodon stenognathus Matthew, 1897; Protogonodon grangeri Simpson, 1936.

Loxolophus spiekeri (Gazin, 1938)

Protogonodon biatheles Gazin, 1941, is a synonym.

Mimotricentes Simpson, 1937

The concept of this genus includes that of Tricentes of all original workers from Cope (1884) up to Van Valen and Sloan (1965).

Mimotricentes subtrigonus (Cope, 1881)

Synonyms include Mimotricentes latidens Gidley in Simpson, 1935, and Mimotricentes angustidens Simpson, 1937. The population from Rock Bench is polymorphic for the presence of P_1 and variable in the position of the molar paraconid.

Mimotricentes mirielae, new species

Type: AMNH 58219, right mandible with M_{2-3} ; Hemithlaeus facies of Puerco, Mammelon Hill, Bitonitsoseh Arroyo. Plate 3, Figure 3.

Diagnosis: Smaller than M. subtrigonus, with slightly higher trigonid more vertical postvallid, and slightly stronger paraconid. M_{31} , 5.5; trd w, 3.6; tald w, 3.2; M_2 tald w, 3.8.

Etymology: Miriel (Quenya, jewel-woman), Númenorian queen in The Silmarillion, forced into marriage and the loss of her throne.

Desmatoclaenus Gazin, 1941

Mioclaenus protogonioides Cope, 1882, belongs here. Eodesmatodon Zheng and Chi (1978) seems unrelated; it may perhaps be a paroxyclaenid insectivoran.

Desmatoclaenus diana, new species

Type: AMNH 23177, right M^2 , probably Hemithlaeus facies of Puerco, near Kimbeto. Plate 3, Figure 6.

Diagnosis: Small species with conules distinctly farther apart than paracone and metacone; M_1 talonid relatively short. M^2_1 , 5.8 ± 0.1 ; w, 7.0.

Etymology: Diana, my daughter.

Desmatoclaenus mearae, new species

Type: UCMF 114308, right $M1-2$, Saddle locality, Bison Basin. Plate 2, Figure 5.

Diagnosis: Smaller than D. hermaeus and with larger hypocone. Perhaps conspecific with Tetraclaenodon sp. of Simpson (1936), from Scarritt Quarry. Closest known ancestor for perissodactyl group. M^2_1 , 6.0; w, 7.9.

Etymology: Meara, any one of the great horses of Rohan in The Lord of the Rings.

Baioconodon Gazin, 1941

Chriacus antiquus belongs here, as E. Manning discovered. It becomes the latest known species of its genus.

Deuteronogonodon noletil, new species

Type: AMNH 17078, right maxilla with P^4-M^3 , Section 3, T27N, R11W, Kutz Canyon, Torrejon. Plate 4, Figure 1.

Diagnosis: Somewhat smaller than D. montanus; mesostyle nearly or quite absent. M^2_1 , 9.5 ± 0.1 ; w, 13.2 ± 0.1 .

Etymology: Quenya (Elvish) nóle, knowledge, and til, horn. Reference is to the apparent relationship of D. noletil to uintatheres.

Subfamily Triisodontinae Scott, 1892.

Andrewsarchinae Szalay and Gould, 1966, need not be separated now that they are not considered mesonychids.

Eoconodon copanus, new species

Type: PU 13290, left M_{71} , Mantua. Plate 4, Figure 3.

Diagnosis: Lower molars elongate, entoconid small and distal. Same as Eoconodon sp. of Jepsen (1930, Plate IV, Figure 5.) M_{71} , 10.4, trd w, 5.6; tald w, 5.4.

Etymology: Greek kopanon, pestle, with reference to the robust morphology suitable for pounding, and with reference to Edward Drinker Cope, who described the first two known species of the genus.

Eoconodon nidhoggi, new species

Type: UM VP1471, left M_3 , Purgatory Hill. Plate 4, Figure 6.

Diagnosis: Smallest known species of Eoconodon. Lower molars moderately elongate, entocristid complete, trigonid walls rather vertical; upper molars very transverse. M_{31} , 7.4 ± 0.1 ; trd w, 4.4; tald w, 3.7. There is also a larger species of Eoconodon at Purgatory Hill, the size of E. gaudrianus.

Etymology: Nidhogg, the adder (or dragon) that gnaws on a root of the great ash Yggdrasil which extends into Nifflheim, the region of darkness and cold in the Eddas. Reference is to Purgatory Hill and to a rattlesnake which occupied its top the day the first Eoconodon tooth was found there.

Eoconodon coryphaeus (Cope, 1885)

The type specimen of Triisodon heilprinianus Cope, 1882, is an unworn molar referable to the taeniodont Conoryctes comma of the Torrejon. The next available name is Sarcothraustes coryphaeus Cope, 1885, the type of which contains at least two individuals. I choose the skull as type. Despite a note circularized incorrectly under my name, coryphaeus is the type species of Eoconodon by original designation.

Goniacodon Cope, 1888

Conoryctes crassicuspis Cope, 1882, appears to belong here rather than in Triisodon.

Goniacodon hiawathae, new species

Type: UCMF 47254, right M^2 and left M^{1-2} , Wagonroad, central Utah. Plate 4, Figure 2.

Diagnosis: Almost as large as G. crassicuspis but the molar hypoconid is not yet at the distolabial corner of the talonid. M^1 , 10.2; w, 11.3.

Etymology: Hiawatha, Mohawk leader.

Triisodon quivirensis Cope, 1881

Sarcothraustes antiquus Cope, 1882, is a synonym.

Andrewsarchus Osborn, 1924

Paratriisodon Chow, 1951, is a synonym.

Andrewsarchus mongoliensis Osborn, 1924

Paratriisodon gigas Chow, Li, and Chang, 1973, is a synonym.

Family Phenacodontidae Cope, 1881

Subfamily Meniscotheriinae Cope, 1881

Recognition that the Pleuraspidotheriinae are only convergent to Meniscotherium permits the special similarities of the latter to Ectocion to indicate ancestry.

Ectocion parvus Granger, 1915

Meniscotherium(?) priscum Granger, 1915, is a synonym, as Earl Manning discovered.

Phenacodus Cope, 1873

Almogaver Crusafont Pairó and Villalta Comella, 1954, is a synonym.

Phenacodus primaevus Cope, 1873

P. grangeri Simpson, 1935, is a synonym, as M.C. McKenna discovered.

Family Didolodontidae Scott, 1913

Asmithwoodwardia Ameghino, 1901

Synonyms include Ernestokokenia Ameghino, 1901, and Archaeohyracotherium Ameghino, 1906. Figure 4 gives a long chain from this genus in presumptively too little time, but the known morphology doesn't require earlier branchings.

Didolodus Ameghino, 1897

Synonyms include Paulogervaisia Ameghino, 1901, Enneoconus Ameghino, 1901, and Argyrolambda Ameghino, 1904.

Family Mioclaenidae Osborn and Earle, 1895

Subfamily Mioclaeninae Osborn and Earle, 1895

Promioclaenus Trouessart, 1904

Tiznatzinia Simpson, 1936, is a synonym. I recognize P. vanderhoofi (Simpson, 1936), P. wilsoni, P. acolytus (Cope, 1882) [with P. aquilonius (Simpson, 1935)], P. lemuroides (Matthew, 1897), and P. pipiringosi Gazin, 1956.

Promioclaenus wilsoni, new species

Type: KU 9446, rostrum with left P⁴-M³ and right P³-M², right mandible with ?P₁, P₃-M₂, left mandible with P₂₋₃, left M₁ trigonid; Taeniolabis facies of Puerco, Ojo Alamo. Plate 4, Figure 8.

Diagnosis: Teeth relatively uninflated; upper molars with postcingulum interrupted labially by metacingulum and extending more lingual than the protocone apex, not rising toward the latter; P₄ with distinct metaconid and with tall paraconid adnate to protoconid, as in Ellipsodon but more separate. Litaletes-like species of Wilson (1956). M²₁, 3.9; w, 5.4.

Etymology: Robert W. Wilson organized the collecting of this specimen, recognized its affinities despite my name change, and re-established the genus Promioclaenus.

Litaletes Simpson, 1935

Jepsenia Gazin, 1939, is a synonym. If distinction of Litaletes from Promioclaenus as an exgroup is adaptively warranted, this is best done by the massively enlarged protocone of M² and the correspondingly large lingual concavity of the talonid basin of M₂.

Litaletes sternbergi (Gazin, 1939)

Ellipsodon shepherdii Gazin, 1939, and Jepsenia mantiensis Gazin, 1939, are synonyms.

Litaletes ondolinde, new species

Type: PU 17479, left mandible with P₃-M₃, Rock Bench. M₂₁, 5.3; trd w, 4.0; tald w, 3.7. Plate 5, Figure 5.

Diagnosis: Lower molars absolutely and relatively longer than in L. disjunctus, and P⁴ protocone smaller.

Etymology: Quenya (elvish) ondo, rock, and lindë, song. Reference is to Rock Bench and to the hidden city Ondolinde or Gondolin of The Silmarillion. The Rock Bench specimens and others were formerly as hidden (and unsorted).

Bomburia, new genus

Type Species: Ellipsodon priscus Matthew, 1937.

Diagnosis: Moderately inflated teeth, molar talonids very short, M₂ with moderate entoconid, P₄ with basal paraconid but no metaconid, P⁴ with relatively large but uninflated protocone and no metacone.

Etymology: Bombur, a fat dwarf in The Hobbit and The Lord of the Rings. Reference is to size and morphology.

Ellipsodon yotankae, new species

Type: ACM 6359, right M²; Torrejon, Section 17, T23N, R8W, 3/4 mile south of Route 44, 3.3 miles east of Nageezi, New Mexico. Plate 4, Figure 5.

Diagnosis: Large species, M² transverse, molar protocone massive; lower molars almost (M₂) or quite (M₁) as broad as long. M²₁, 4.9; w, 8.6.

Etymology: Tatanka Yotanka ("Sitting [buffalo] Bull"), leader of the Hunkpapa Sioux.

Ellipsodon witkoi, new species

Type: AMNH 811a, right maxilla with P⁴-M², Taeniolabis facies of Puerco, Barrel Spring Arroyo. Several lines of evidence suggest that it really is from this horizon, but skepticism is appropriate until more specimens are found. Plate 4, Figure 7.

Diagnosis: Large species, protocone smaller than in E. yotankae, upper molars more transverse than in E. grangeri. M^2_1 , 4.9; w, 8.2.
Etymology: Tasunke Witko ("Crazy Horse"), leader of the Oglala Sioux.

Mioclaenus turgidus Cope, 1881

Mioclaenus lydekkerianus Cope, 1888, is a synonym.

Subfamily Pleuraspidothereiinae Zittel, 1892

Protoselene Matthew, 1897

Dracoclaenus Gazin, 1939, is a synonym.

Protoselene bombadili, new species

Type: NMNH 23285, left maxilla with M^2 , Hemithlaeus facies of Puerco, near Mammelon Hill. Plate 8, Figure 7.

Diagnosis: Smallest known species; lacks mesostyle and hypocone. M^2_1 , 4.8; w, 6.2.

Etymology: Tom Bombadil, the Hobbit name for a simple, powerful, and very old being. Reference is to these three traits.

Family Hyopsodontidae Trouessart, 1879 (Lydekker, 1889)

Lemuravidae Marsh, 1875, is an unused senior synonym.

Subfamily Hyopsodontinae Trouessart, 1879

Included genera: Litomylus Simpson, 1935; Haplaletes Simpson, 1935; Haplomylus Matthew, 1915; Aletodon Gingerich, 1977; and probably one or more species now placed in Oxyprimus. Decoredon Xu, 1977, is probably a primate, perhaps a plesiadapid.

Haplaletes andakupensis, new species

Type: UM 2050, left M^2 , Purgatory Hill (species also at Wagonroad). Plate 4, Figure 4.

Diagnosis: Upper molars relatively transverse, hypocone small, conule wings interrupt cingula, protocone lingual; P^4_4 relatively transverse; lower molars with little deflection of labial border. M^2_1 , 3.2; w, 4.1.

Etymology: Andhakupa (or Andakupa), as described in the fifth book of the Bhāgavata Purāna, is the hell for those who kill mosquitoes and other blood-sucking insects. Reference is to Purgatory Hill and the proximity of Bug Creek.

Litomylus Simpson, 1935

Oxytomodon Gazin, 1941, is a synonym.

Litomylus dissentaneus Simpson, 1935

Litomylus scaphicus Gazin, 1956, and Litomylus scaphiscus Gazin, 1956, are synonyms.

Litomylus osceolae, new species

Type: AMNH 16039, right mandible with M_{1-3} , Torrejon, Torrejon Arroyo. Plate 5, Figure 2.

Diagnosis: Larger than L. dissentaneus, L. aequidens, and L. perissus, and smaller than L. ishami. Proximal part of P^4_4 relatively rotund. M^2_1 , 3.9; trd w, 3.1; tald w, 3.4.

Etymology: Osceola, Seminole leader.

Litomylus aequidens (Matthew, 1937)

Plate 5, Figure 1 (AMNH 16720), shows what Matthew's enigmatic Ellipsodon aequidens is, apparently a descendant of L. perissus (Gazin, 1941). M^2_1 , 3.0; trd w, 2.0; tald w, 2.2.

Litomylus(?) alphamon, new species

Type: ROM 05631, left mandible with M_{1-2} , Swan Hills, Locality 1 of L.S. Russell (1967). Plate 5, Figure 3.

Diagnosis: Small species, M_2 smaller than M_1 , entocristid strong, M_1 paralophid unusually proximal. Tooth ratio suggests Adapisoricidae, but relatively low crown and paraconid and talonid morphology are hyopsodontine. Same as "oxyclaenine?" of L.S. Russell (1967, p.24). M^2_1 , 2.4; trd w, 2.0; tald w, 2.0.

BEGINNING OF THE AGE OF MAMMALS

Etymology: Sindarin (Elvish) *alph*, swan, and *amon*, hill. Reference is to the locality, with allusion also to *Alph*, the sacred river of Xanadu; *Amon*, usually the chief Egyptian god; *alpha*, the letter; and Greek *monos*, single.

Subfamily Tricuspidontinae Simpson, 1929 (Teilhard, 1921)

Dipavali, new genus

Type species: Paschatherium petri Russell, 1964.

Diagnosis: Upper molars quadrate, with large hypocone and no postprotocrista. Molar entoconid higher than hypoconid. The type species of Paschatherium, Adapisorex dolloi Teilhard de Chardin, 1927, is an adapisoricid, sensu lato (McKenna, 1960; Van Valen, 1967; contra Russell, Louis, and Savage, 1975). Dipavali is generically and probably ordinaly distinct; see D.E. Russell (1967) on a possible P₄ of Dipavali.

Etymology: The Hindu festival of lights, by analogy to the Christian festival Easter, which prompted the name Paschatherium. The gender is feminine.

Microhyus Teilhard de Chardin, 1927

Louisina Russell, 1964, is a synonym.

Family Periptychidae Cope, 1882

Subfamily Periptychinae Cope, 1882

Maiorana, new genus

Type and only known species: Maiorana noctiluca, new species.

Diagnosis: Upper molars only weakly transverse, protocone apex tall and central, hypocone small, its base not projecting lingually; molar paraconid and entoconid large; canines small; mandibular condyle high.

Etymology: Middle Latin *maiorana*, marjoram, with allusion to Latin decompositions as *larger* or *May* frog, and things pertaining to the *larger*, or to the gold of *Maia* or *May*. Quenya (Elvish), *wandering angel*. Allusion is to the pleasantly spicy *Maiorana* family.

Maiorana noctiluca, new species

Type: PU 16667, skull fragment with left C, P³-M³; Mantua. Plate 6, Figure 4.

Diagnosis: As for genus. Probably the "forme intéressante" of Russell (1964, p.247). M²₁, 4.5; w, 6.2.

Etymology: Latin, a light in the darkness, for the phylogeny and especially for Virginia.

Tinuviel, new genus

Type and only known species: Tinuviel eurydice, new species.

Diagnosis: Upper molars weakly transverse, pericone as large as hypocone and placed symmetrically lingual to protocone; molar paraconid nearly as large as metaconid; cingular cusp lingual of paraconid; cusps rather blunt, protocone wearing from apex rather than from labial surface.

Etymology: Sindarin (Elvish) *tinúviel*, daughter of twilight, or nightingale, Beren's name for Lúthien in *The Silmarillion*.

Tinuviel eurydice, new species

Type: UM 2226, left M₃, Purgatory Hill. Plate 8, Figure 4.

Diagnosis: As for genus. M₃₁, 5.0; trd w, 3.3; tald w, 2.8.

Etymology: *Eurydice* vanished just before being led from Hades. Reference is to Purgatory Hill, the late occurrence of this species, Lúthien's rescue of Beren from Sauron's dungeon, and their escape from Morgoth's deep tunnels with a *silmaril*.

Fimbrethil, new genus

Type and only known species: Fimbrethil ambaronae, new species.

Diagnosis: Crests rather weak, molar paraconid small and central, entoconid large; premolars plesiadapid-like. Upper teeth not definitely known. Fimbrethil may possibly be a primate despite its molars, but it is easier to derive from Maiorana than from Purgatorius.

Etymology: Fimbrethil, entwife loved by Fangorn in The Lord of the Rings. Reference is to partly primate-like morphology and the disappearance of both Fimbrethils.

Fimbrethil ambaronae, new species

Type: AMNH 58054, left mandible with M_{1-2} , Hemithlaeus facies of Puerco, Mammelon Hill. Plate 6, Figures 1-3.

Diagnosis: As for genus. M_2 l, 2.9; trd w, 2.2; tal d w, 2.2.

Etymology: Quenya (Elvish) ambarona, one of Fangorn's shorter names for his forest. Reference is to the dimness of the forest and of the affinities of this species.

Ectoconus ditrignonus (Cope, 1882)

Ectoconus majusculus Matthew, 1937, is a synonym.

Periptychus Cope, 1881

Carsiptychus Simpson, 1936 (Matthew in Simpson, 1936), is best treated as a subgenus.

Periptychus coarctatus Cope, 1883

Plagiptychus matthewi Simpson, 1936, is a synonym.

Subfamily Anisonchinae Osborn and Earle, 1895

Mimatuta, new genus

Type species: Mimatuta morgoth, new species

Diagnosis: Primitive periptychids: upper molars quite transverse, protocone apex central, hypocone absent to moderate, its base not projecting lingually; molar paraconid large, entoconid small.

Etymology: Sindarin (Elvish) mir, jewel, and Matuta, Roman goddess of dawn. Reference is to ancestral position, with allusion to Latin mius, imitator, and tuta, safe, and to Mim, dwarf of The Silmarillion, and Latin tuta, examined.

Mimatuta morgoth, new species

Type: UM 1560, right maxilla with M^2 , Harbicht Hill (species also at Bug Creek West). Plate 7, Figure 5.

Diagnosis: Upper molars rather triangular; P_4 metaconid relatively weak. M^2 l, 4.4; w, 6.5.

Etymology: Morgoth (Quenya [Elvish] mor, dark, and goth, universal enemy). Feanor's name for Melkor, the power-lustful Vala of The Silmarillion. Reference is to the Hell Creek Formation.

Mimatuta minuial, new species

Type PU 14211, left maxilla with P^3 - M^3 , Mantua. Plate 7, Figure 4.

Diagnosis: Upper molars rather quadrate; P_4 metaconid rather strong. M^2 l, 3.8; w, 6.1.

Etymology: Sindarin (Elvish) minuial, the time at dawn when the stars fade. Reference is to the dawn of the Cenozoic and the fading of the Mesozoic stars.

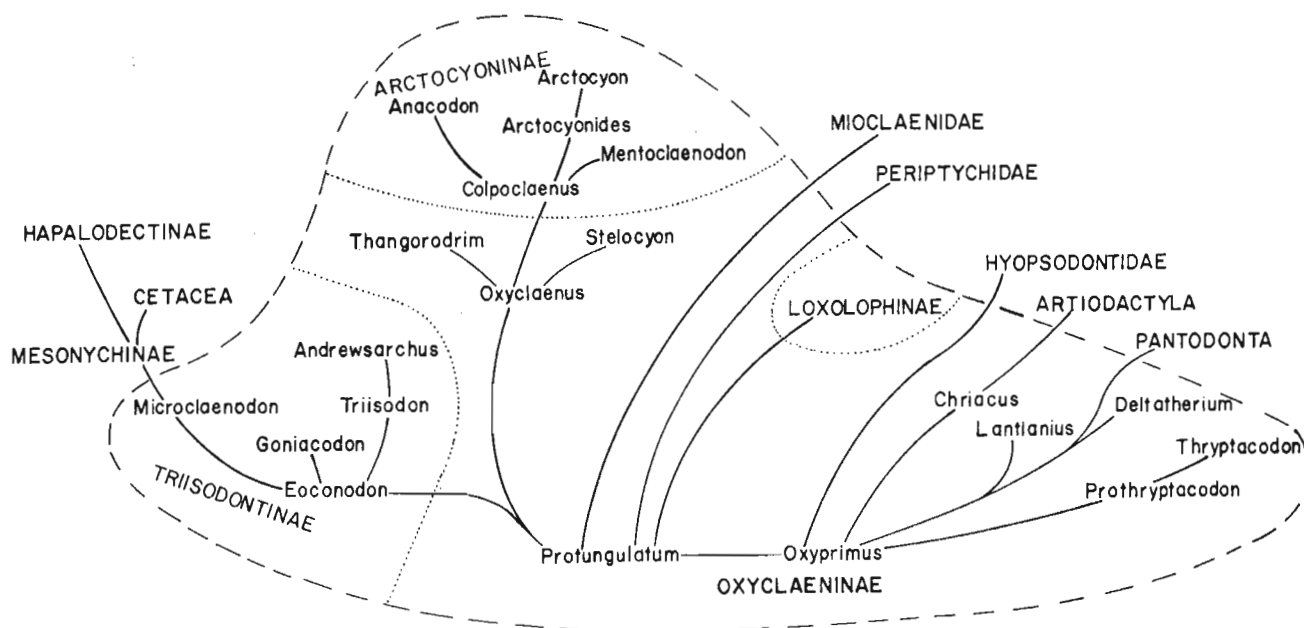


Figure 2. Provisional phylogeny of the Arctocyonidae. Dotted lines are subfamily boundaries and dashed lines are family boundaries. In this figure and others, derivation from a taxon does not imply derivation from a known species of that taxon. All valid taxa (except probably the Tubulidentata) omitted from all these figures I exclude from the Ungulata.

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Minatuta makhialutae, new species

Type: PU 17305, right mandible with M₂₋₃, Leidy Quarry. (see Appendix 3). Plate 7, Figure 1.

Diagnosis: Lower molars relatively elongate, paraconid rather isolated, sharp postmetacristid on M₂. M₂l, 3.9 ± 0.1; trd w, 2.9; w, 2.8.

Etymology: Makhialuta ("Red Cloud"), Oglala Sioux leader.

Earendil, new genus

Type and only known species: Earendil undomiel, new species

Diagnosis: Upper molars moderately transverse, protocone apex labial, hypocone moderate, its base projecting lingually. Possible ancestor of Haploconus. M²l, 3.9; w, 5.9.

Etymology: Earendil, who (in The Silmarillion) sailed with a silmaril to get the aid that defeated Morgoth.

Earendil undomiel, new species

Type: PU 14205, left maxilla with P²-M³, Mantua. Plate 7, Figure 2.

Diagnosis: As for genus.

Etymology: Quenya (Elvish) undómíel, evening star, which Earendil with his silmaril became.

Anisonchus Cope, 1881

Anisonchus (Anisonchus)

Diagnosis: Postcingulum of M² not interrupted by postmetaconule wing.

Included species: A. athelas, new species; A. eowynae, new species; A. dracus Gazin, 1939; A. sectorius Cope, 1881. These species form a lineage.

Anisonchus athelas, new species

Type: NMNH 23279, left maxilla with P⁴-M², Gas Tank Hill (NE 1/4 Sec 20 [?], T20S, R6E, Emery County, Utah), correlative with Puerco. Plate 8, Figure 5.

Diagnosis: Upper molars transverse, appreciably shorter lingually than labially, with moderately large hypocone and weak precingulum; P⁴ protocone elongate proximodistally. Probable ancestor of Haploconus. M²l, 3.9 ± 0.1; w, 6.0 ± 0.1.

Etymology: Sindarin (Elvish) athelas, kingsfoil, a healing plant in The Lord of the Rings. Reference is to the joining of phylogenies.

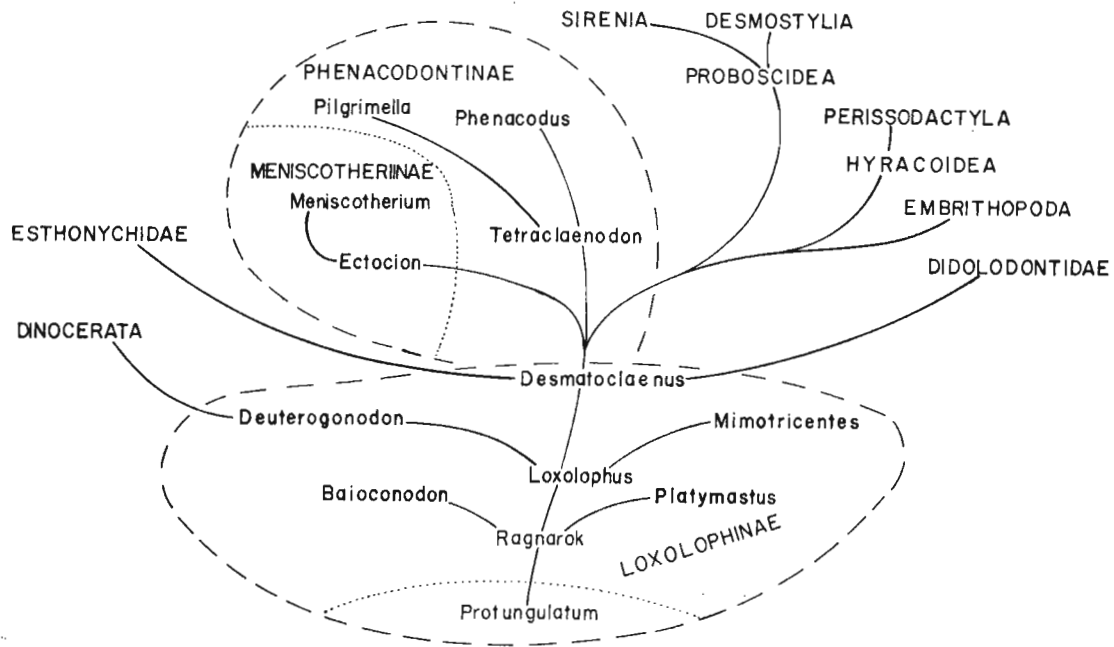


Figure 3. Provisional phylogeny of the Loxolophinae and Phenacodontidae. See Figure 2.

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Anisonchus eowynae, new species

Type: UCMP 69260, right maxilla with M^1-3 , Wagonroad. Plate 8, Figure 6.

Diagnosis: Upper molars transverse, with large hypocone, weak precingulum, and nearly parallel proximal and distal borders. M^2_1 , 3.9; w, 6.5.

Etymology: Éowyn, woman of Rohan in The Lord of the Rings, who killed the chief of the Nazgûl and was cured of his poison by athelas.

Anisonchus sectorius Cope, 1881

Synonyms include Zetodon gracilis Cope, 1883.

Anisonchus (Mithrandir), new subgenus

Type species: Anisonchus oligistus Gazin, 1941.

Diagnosis: Postcingulum of M^2 interrupted by postmetaconule wing.

Trigonid less elongate, especially M_1 , and hypoconulid less lingual than in A. (Anisonchus).

Included species: Haploconus gillianus Cope, 1882; A. oligistus; A. onostus Gazin, 1939; A. fortunatus Simpson, 1932. Except possibly for A. gillianus, these species form a lineage.

Etymology: Mithrandir (Sindarin, gray wanderer), Elvish name for Olórin, wisest of the Istari in The Lord of the Rings. Reference is to the subtleness of the differences between the subgenera.

Haploconus elachistus Gazin, 1941

I restrict the type to the upper molars figured by Gazin (1941, p.51.).

Oxyacodon Osborn and Earle, 1895

Escatepos Reynolds, 1936, is a synonym. Anisonchus cophater Cope, 1884, is probably better referred to Oxyacodon than to Conacodon. Cope referred O. agapetillus to Anisonchus when he described it in 1884; I return the genus to the Anisonchinae.

Revised diagnosis: Crests sharp; upper molars quite transverse, protocone apex labial, hypocone moderate to large, its base projecting lingually; molar paraconid rather small, entoconid as large as hypoconid; M_2 talonid unusually transverse; P_4 relatively elongate.

Oxyacodon josephi, new species

Type: PU 21087, right maxilla with M^1-3 , Mantua. Plate 6, Figure 5.

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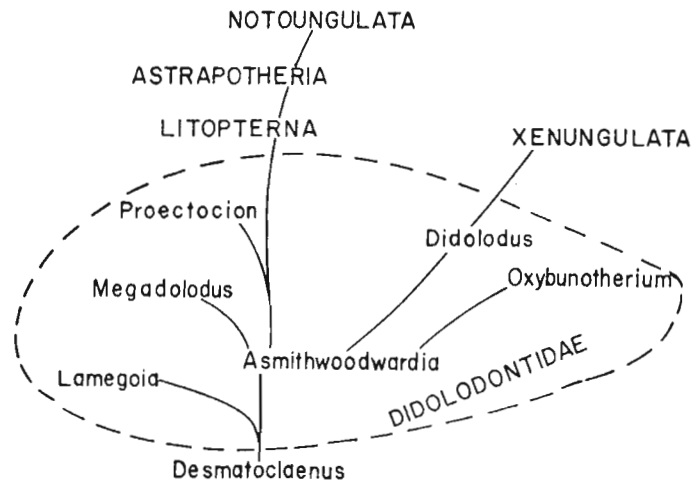


Figure 4. Provisional phylogeny of the Didolodontidae. See Figure 2.

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Diagnosis: Hypocone not as lingual as later species; hypoconulid of M_{1-2} small. Same as Oxyacodon sp. of Jepsen (1930, Plate IV, Figures 2-3).
 M_2^1 , 3.5 ± 0.2 ; w, 5.0 ± 0.1 .

Etymology: Joseph, Nez Percé leader.

Oxyacodon agapetillus (Cope, 1884)

I restrict the type to the specimen with M_{1-2} and sharper crests. The other specimen with the same number (AMNH 3557) belongs to Fimbrethil ambaronae.
Oxyacodon priscilla Matthew, 1937, and Escatepos campi Reynolds, 1936, are synonyms of O. agapetillus.

Oxyacodon marshater, new species

Type: AMNH 36068, left M_2 , Wagonroad (species also at Purgatory Hill).
 Plate 8, Figure 2 .

Diagnosis: M_2 transverse, paraconid a small cusp, metacristid present, entoconid as large as relatively large hypoconulid. M_2^1 , 3.6; trd w, 3.2; tald w, 3.2.

Etymology: For Edward Drinker Cope, by analogy to his Anisonchus cophater (now also placed in Oxyacodon), the only species he ever named for his rival Marsh. Marsh + hater (English).

Oxyacodon tecumsae, new species

Type: AMNH 2378, mandibles with left M_{1-2} and right P_4-M_3 , Torrejon, Torrejon Arroyo. Plate 8, Figure 1.

Diagnosis: M_2 transverse, paraconid bladelike, no metacristid, entoconid considerably larger than hypoconulid. M_2^1 , 3.8; trd w, 3.0; tald w, 3.2.

Etymology: Tecumsah, Shawnee leader.

Perutheriinae, new subfamily

Type and only known genus: Perutherium Thaler in Grambast, Martinez, Mattauer, and Thaler, 1967.

Diagnosis: Periptychids with strong metastylid and metacristid.

Suborder Mesonychia Van Valen, 1969 (1966; Matthew, 1909)
 Family Mesonychidae Cope, 1875

Ancalagon, new genus

Type and only known species: Dissacus saurognathus Wortman in Matthew, 1897.

Diagnosis: Canine and molar cusps massive, M_1 without metaconid, M_{2-3} with strong metaconid, protocone lobes P^4-M^3 longer than wide, pollex complete.

Etymology: The mightiest dragon of Morgoth, in The Silmarillion.

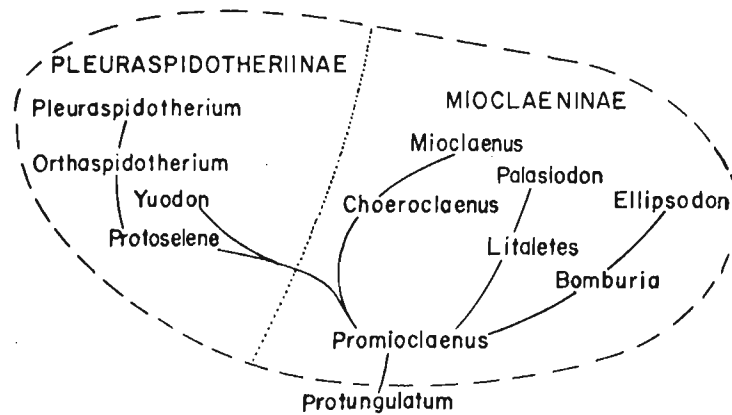


Figure 5. Provisional phylogeny of the Mioclaenidae. See Figure 2.

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APPENDIX 2: Non-condylarths

A rather extensive subject. I describe the two namable insectivorans from Purgatory Hill and a later condylarth-like insectivoran, and make several proposals in the major classification of ungulates.

Cohort Unguiculata Linnaeus, 1766

Order Insectivora Cuvier, 1817 (Illiger, 1811)

Suborder Proteutheria Romer, 1966 (Van Valen, 1967, MS used by Romer)

Family Palaeoryctidae Winge, 1917 (McDowell, 1958)

Subfamily Procerberinae Sloan and Van Valen, 1965

Procerberus plutonis, new species

Type: UM VP1464, right M_1 or M_2 , Purgatory Hill. Plate 7, Figure 3.

Diagnosis: Upper and lower molars a little lower crowned and more transverse than in P. formicarum and protocone longer proximodistally. M_2 , 2.8; trd w, 1.8; tald w, 1.7.

Etymology: Pluto, with reference to Purgatory Hill.

Family Pantolestidae Cope, 1884

Niphredil, new genus

Type and only known species: Niphredil radagasti, new species

Diagnosis: P_4 with small but definite distolingual metaconid; M_1 talonid small, narrower than the apically worn trigonid; M_1 protoconid and metaconid rather bulbous, their bases confluent in middle of trigonid; mental foramina under M_1 trigonid and P_1 ; mandibular condyle almost at level of toothrow; angle hook-shaped.

Etymology: Sindarin (Elvish) niphredil, white-flowering forb of open woods in Neldoreth and Lothlorien.

Niphredil radagasti, new species

Type: PU 21416, left mandible with P_2 , P_4 - M_1 ; Cedar Point Quarries, middle Tiffanian of northern Bighorn Basin, Wyoming. Plate 5, Figure 4.

Diagnosis: As for genus; as large as Palaeosinopa veterima. M_1 , 5.3; trd w, 3.4; tald w, 3.1.

Comment: Possibly a synonym of Palaeosinopa simpsoni Van Valen, 1967. However, the latter (based on upper teeth) shows no generic distinction from

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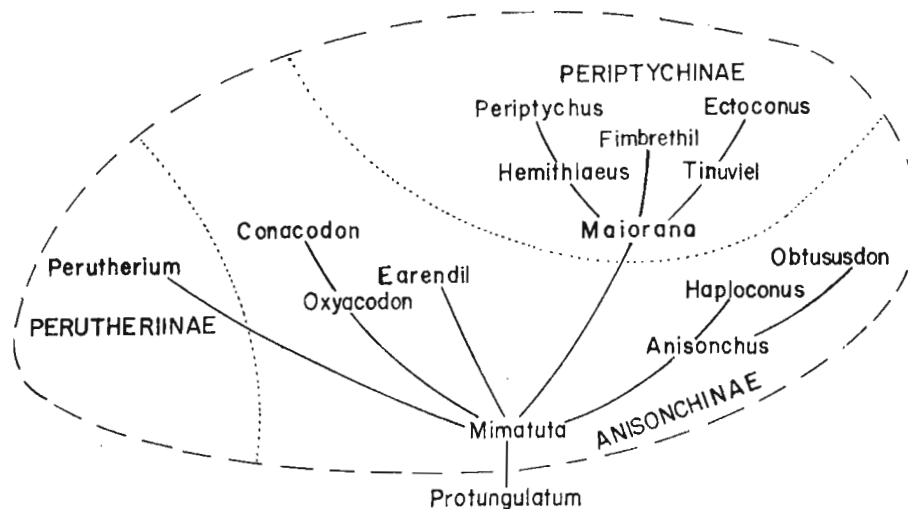


Figure 6. Provisional phylogeny of the Periptychidae. See Figure 2.

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Palaeosinopa. I would prefer to leave the present specimen as tentatively referable to P. simpsoni, but a genus must be based on a species name rather than on a specimen, and Niphredil is important in consideration of pantolestid phylogeny.

Etymology: Radagast, naturalist of the Istari in The Lord of the Rings.

Suborder Erinaceota Van Valen, 1967

Family Adapisoricidae Schlosser, 1887 (Van Valen, 1967)

Subfamily Nyctitheriinae Simpson, 1928

Leptacodon proserpinae, new species

Type: UM VP1595, right P₄, Purgatory Hill. Plate 8, Figure 3.

Diagnosis: P₄ extremely narrow, nearly three times as long as wide; metaconid large; molar talonid distinctly narrower than trigonid, postvallid nearly vertical, trigonid relatively tall; M₃ relatively small. Closest to L. munusculum. P₄l, 2.3; w, 0.8.

Etymology: Proserpina, who was carried down into Hades. Reference is to the extension downwards of the range of Leptacodon (and the Adapisoricidae) into the fauna of Purgatory Hill.

Cohort Ungulata Linnaeus, 1766

The phylogeny (Figures 1-7), together with considerations of major adaptation, suggest that the ungulates can be divided into about six major groups, or superorders. Existing names can be used for each. A taxon is an adaptively unified part of a phylogeny (Van Valen, 1978).

Superorder Protungulata Weber, 1904, including Condylarthra, Pantodonta, Dinocerata, Xenungulata, and probably Tubulidentata.

Superorder Meridiungulata McKenna, 1975, including Litopterna, Astrapotheria (including Trigonostylopoidea) and Notoungulata (the latter including Pyrotheria: Patterson, 1977).

Superorder Paenungulata Simpson, 1945 (Blainville, 1834), including Proboscidea, Sirenia, and Desmostylia.

Superorder Mesaxonia Marsh, 1884, including Embrithopoda, Perissodactyla, and Hyracoidea (if the latter are maintained distinct from Perissodactyla).

Superorder Paraxonia Marsh, 1884, including Artiodactyla.

Superorder Mutica Linnaeus, 1766, including Cetacea.

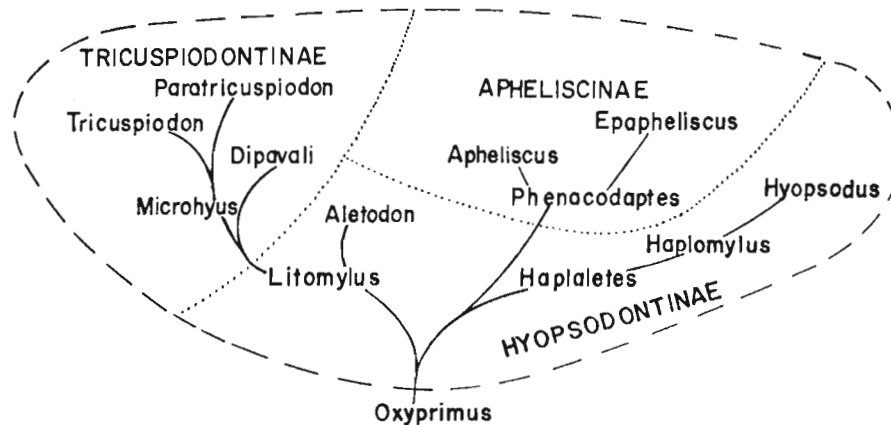


Figure 7. Provisional phylogeny of the Hyopsodontidae. See Figure 2.

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Order Pantodonta Cope, 1873

Paleocene pantodonts are oversplit at the family level. In the Pantolambdidae I include the Barylambdidae, Titanoideidae, Pantolambdodontidae, and presumably Pastoralodontidae Chow and Qi, 1978. The Bemalambdidae Chow, Chang, Wang, and Ting 1973 (see Zhou, Zhang, Wang, and Ding [same authors], 1977) are distinct but may well not be pantodonts. I suspect they are anagalid or perhaps didelphodontine derivatives.

Order Embrithopoda Andrews, 1906 (1904)

Phenacolophidae, new family (Szalay and McKenna, 1971)

Diagnosis: Brachyodont embrithopods retaining a centrocrista on their upper molars. McKenna and Manning (1977) referred Phenacolophus (the only known genus) to the Arsinotheriidae, a placement indefensible adaptively.

APPENDIX 3: Faunas

The Mantua fauna appears to be at least as different from that of the Puerco as the Puerco is from the Torrejon. Moreover, this difference seems to be primarily a result of evolution rather than environment or geography, because of the phyletic relations. I therefore propose the Mantuan land-mammal age for North America. Such provincial ages are based on faunal differences rather than on elapsed time, so it appears irrelevant that the Mantuan was very short. It was also very distinctive and will have some significance in comparative evolution.

The Mantuan can be defined as consisting of primitively low-diversity faunas characterized by primitive periptychids such as Maiorana, Mimatuta, and Earendil, together with primitive arctocyonids such as Ragnarok, Oxyprimus, Eoconodon, and Protungulatum. Mioclaenids, hyopsodontids, taeniodonts, phenacodontids, large periptychids, Eucosmodon, Taeniolabis, Ptilodus, and the more derived arctocyonids and anisonchines are absent and may not have originated yet. (However, only 1 tooth shows that this is untrue for primates.) Dinosaurs, pterosaurs, stagodontids, pEDIOMYINES, Glasbius, and Gypsonictops are absent and presumably regionally extinct.

Possibly the Mantuan doesn't exist as far south as New Mexico, where its time-correlative may contain a community with dinosaurs and other Maestrichtian-type animals.

Only two Mantuan faunas are yet reported, Mantua and Leidy Quarry, both in the Bighorn Basin, Wyoming. Leidy Quarry is 1 mile NNE of the SE corner of Section 5, T44N, R94W, Hot Springs County, at the southern end of the Bighorn

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Basin. According to the geological map of Wyoming, this locality is in the lower part of the "Fort Union" (=Polecat Bench) Formation. It contains the two mammalian genera most common at Mantua and deserves further field investigation. I list the known condylarths (or all placentals, for Purgatory Hill) for several faunas:

Bug Creek West: Protungulatum donnae, P. gorgun, Mimatuta morgoth.

Harbicht Hill: Protungulatum donnae, P. gorgun, Oxyprimus erikseni, Ragnarok nordicum, Mimatuta morgoth.

Mantua: Oxyprimus galadrietae, O. putorius, Ragnarok nordicum, Eoconodon copanus, Maiorana noctiluca, Mimatuta minuiat, Earendil undomiel, Oxyacodon josephi.

Leidy Quarry: Ragnarok wovokae, Mimatuta makpialutae.

Puerco (H if known specimens restricted to Hemithlaeus facies even if [as with most] too rare to indicate a real restriction, and similarly T for Taeniolabis facies): Oxyclaenus simplex, O. cuspidatus, Baioconodon antiquus, Platymastus palantir (H), Loxolophus hyattianus, L. kimbetovius (H), L. pentacus (T), Mimotricentes mirielae (H), Desmatoclaenus protogonioides (H), D. diana (H), Eoconodon gaudrianus, E. coryphaeus, Hemithlaeus kowalevskianus (?H), Ectoconus ditrignonus, Periptychus coarctatus, Anisonchus gillianus, Oxyacodon agapetillus (H), O. apiculatus (T), O. cophater, Fimbrethil ambaronae (H), Promioclauenus wilsoni (T), P. vanderhoofi, Bombur priscus, Ellipsodon witkoi (T), Choeroclaenus turgidunculus, Protoselene bombadili (H).

Gas Tank Hill: Loxolophus sp., Ectoconus ditrignonus, Anisonchus athelas.

Purgatory Hill: Procerberus plutonis, cf. Gelastopus sp.; cf. Pararyctes sp., Prodiacodon crustulum Novacek (1977), cf. Aphronorus sp., Leptacodon proserpinae, about 5 other insectivorans, Purgatorius unio, undescribed plesiadapid, Protungulatum sloani, Oxyprimus albertensis, Chriacus calenancus, Thangorodrim thalion, Eoconodon nidhoggi, E. sp. (larger), Haplaletes andakupensis, Tinuviel eurydice, Anisonchus oligistus, Oxyacodon josephi.

Rock Bench: Chriacus katrinae, C. orthogonius, Prothryptacodon furens, Colpoclaenus ?silberlingi, Arctocyonides montanensis, Mimotricentes subtrigonus, Goniacodon levisanus, Promioclauenus acolytus, Litaletes ondoline, Anisonchus sectorius, Litomylus dissentaneus, Haplaletes disceptatrix, Tetraclaenodon puercensis, Microclaenodon assurgens, Dissacus navajovius.

Cedar Point: Chriacus oconostotae, Thryptacodon australis, Colpoclaenus keeferi, Mentoclaenodon acrogenius, Mimotricentes fremontensis, Phenacodus primaevus, Ectocion wyomingensis, cf. Haplaletes serior, Dissacus cf. D. praenuntius.

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- Zhou: see Chow.

Note on plates: Figures are of types unless specimen numbers are given. For scale, measurements are given of lengths (in mm.) of parts photographed, as preserved.

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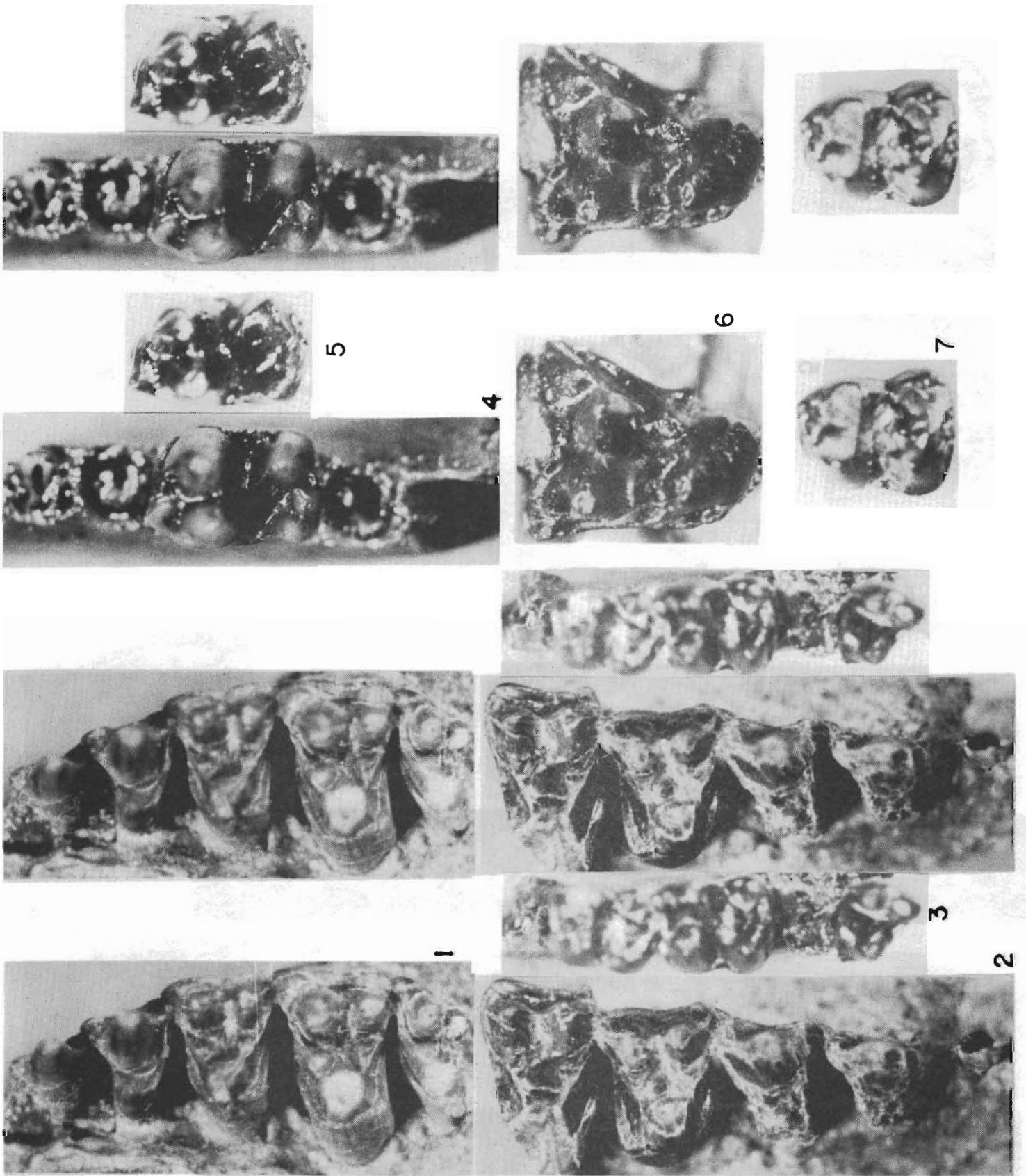


PLATE 1. 1: Oxyprimus galadrietae; P³-M³, 14.6. 2: Oxyprimus putorius; P³-M², 11.0.
 3: Protungulatum sloani; M₁₋₃, 10.7. 4: Protungulatum gorgun; M₂, 5.4.
 5: Oxyprimus erikseni; M₁, 3.5. 6: Deltatherium durini; M¹, 5.3. 7: Thangorodrim thalion; M₁, 6.8.

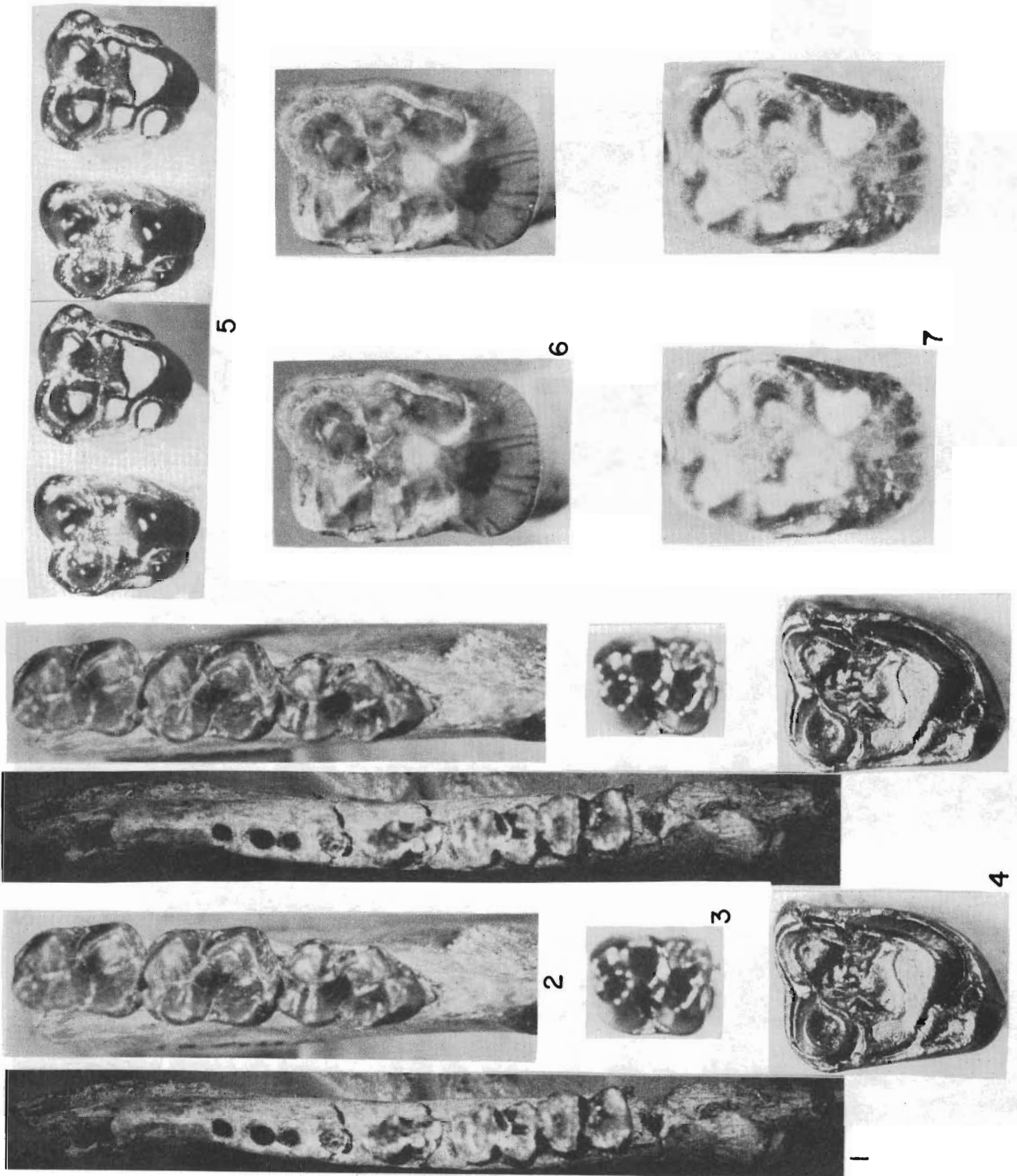


PLATE 2. 1: Chriacus oconostotae; P_4 - M_2 , 22.5. 2: Chriacus katrinae; M_{1-3} , 24.0. 3: Chriacus calenancus; M_2 , 5.5. 4: Chriacus metocometi; M^2 , 5.3. 5: Desmatoclaenus mearae; M^{1-2} , 14.1. 6: Platymastus palantir; M^2 , 4.2. 7: Platymastus mellon; M^1 or 2, 3.6.

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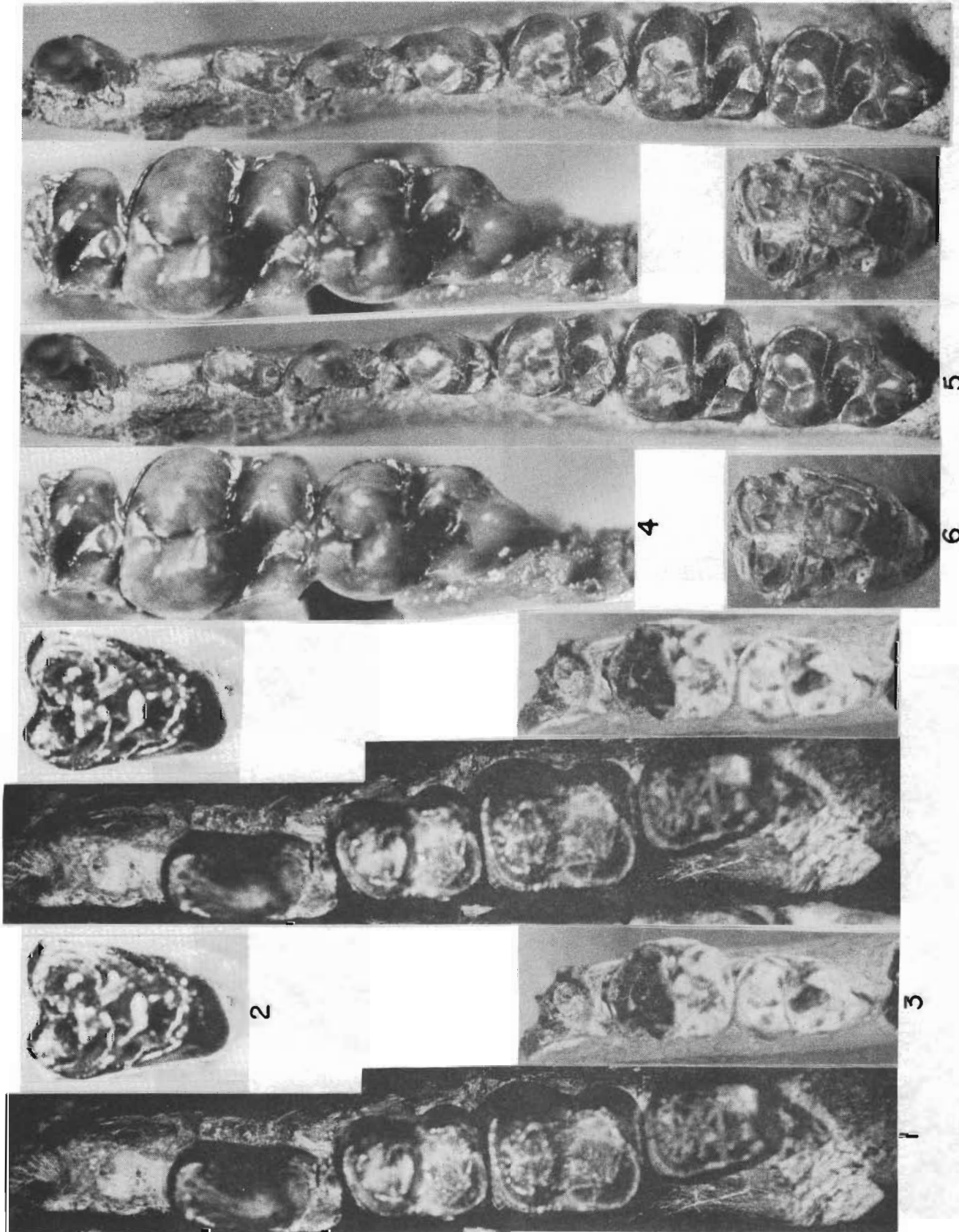


PLATE 3. 1: Arctocyonides mumak; P₄-M₃, 60.6. 2: Ragnarok wovokae; distal width M², 8.5. 3: Mimotricentes mirielae; M₃, 5.4. 4: Ragnarok harbichti; M₁₋₃, 15.0. 5: Ragnarok nordicum, PU 16720; P₂-M₃, 30.6. 6: Desmatoclaenus diana; width M⁴, 6.7.

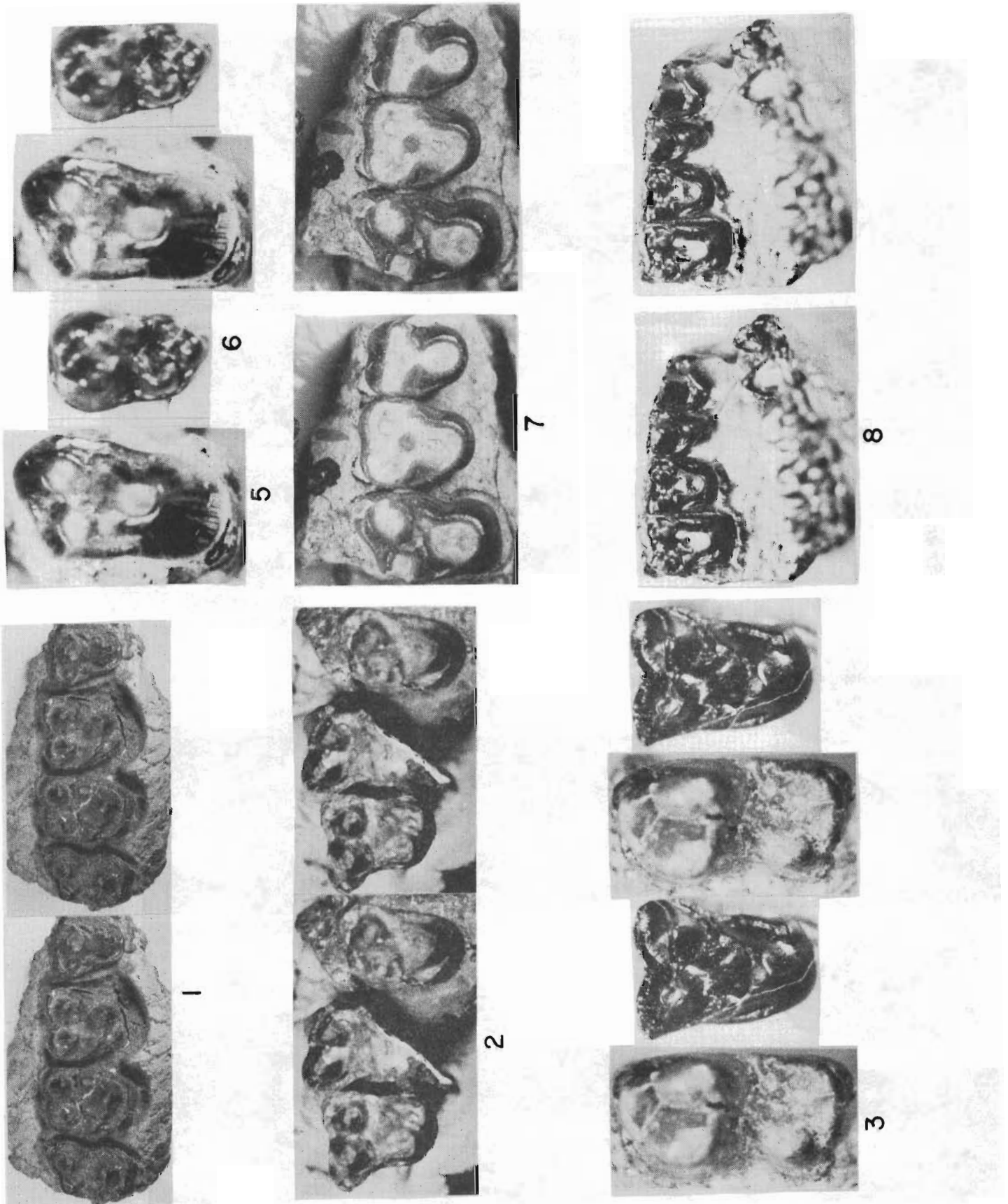


PLATE 4. 1: Deuteronogonodon moletii; P^4-M^3 , 39.9. 2: Goniacodon hiawathae; proximal width right M^2 , 13.2. 3: Euconodon copanus; M^2_1 , 10.4. 4: Haplaletes andakupensis; width M^2 , 4.1. 5: Ellipsodon yotankae; M^2 , 5.0. 6: Euconodon nidhoggi; M^3 , 7.1. 7: Ellipsodon witkoi; P^4-M^2 , 13.5. 8: Promioclænus wilsoni; P^3-M^2 , 13.2.

BEGINNING OF THE AGE OF MAMMALS

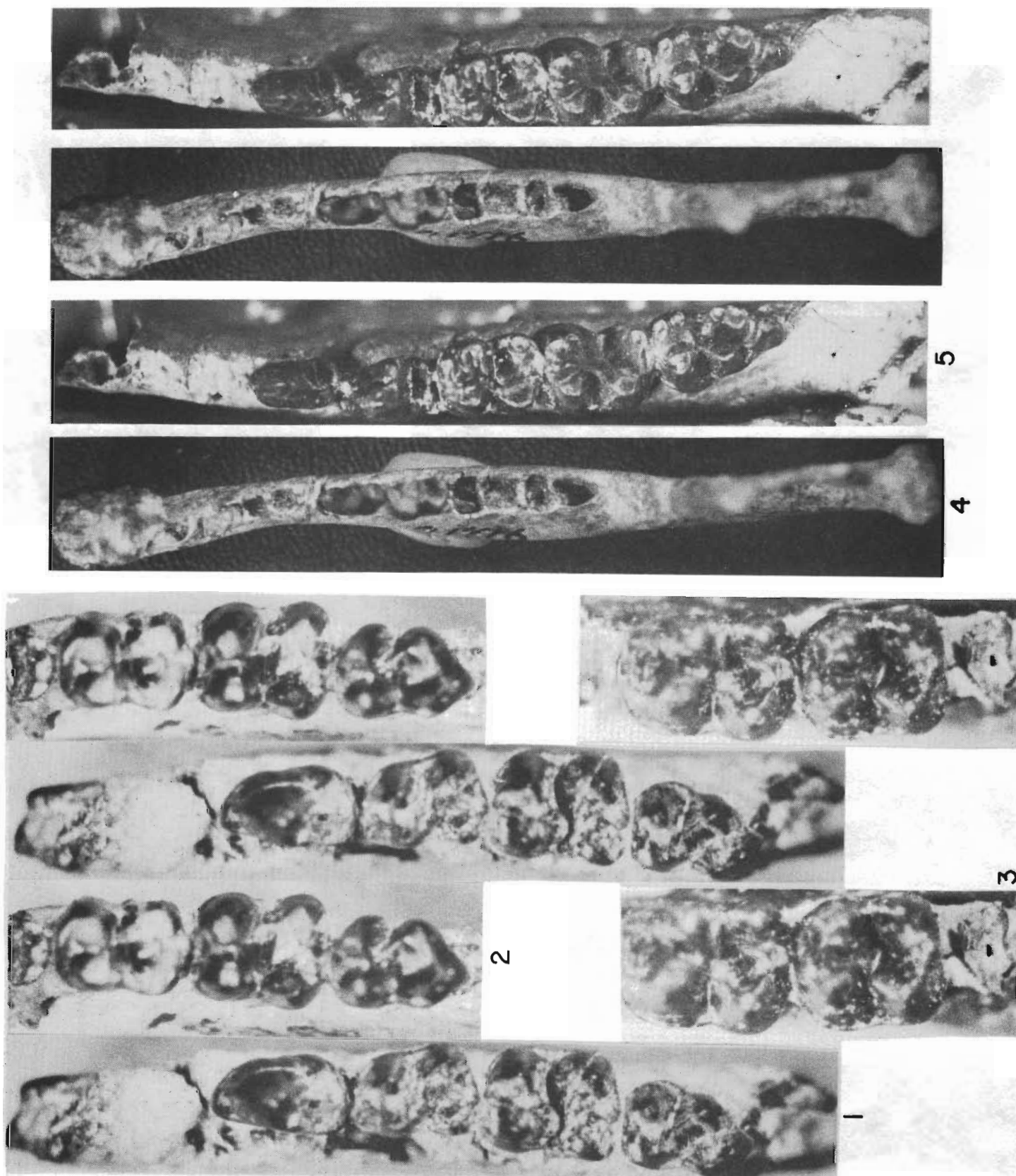
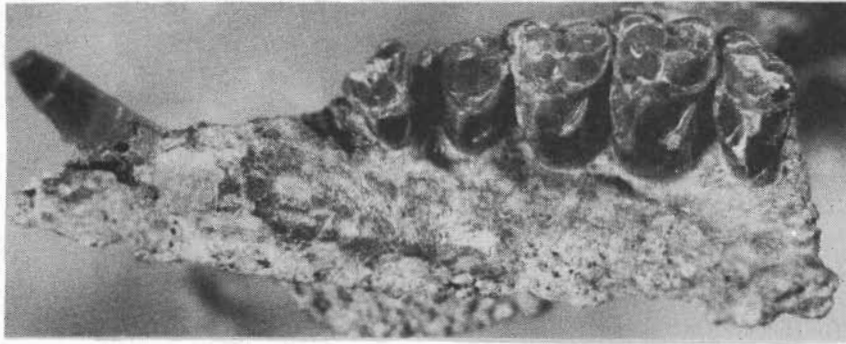


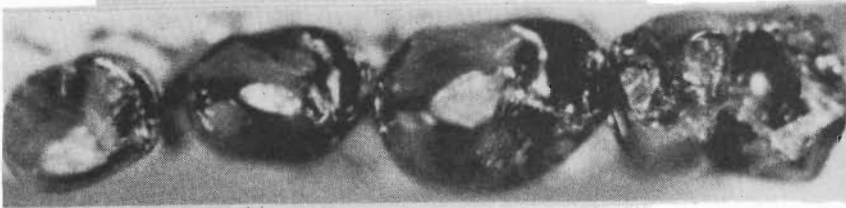
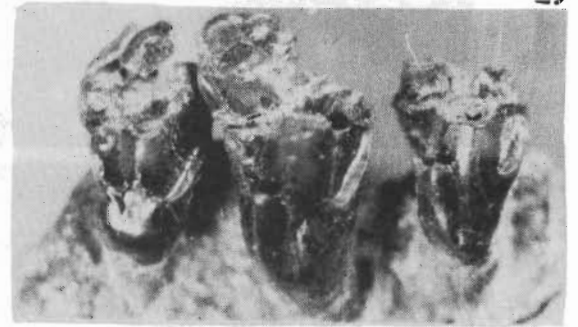
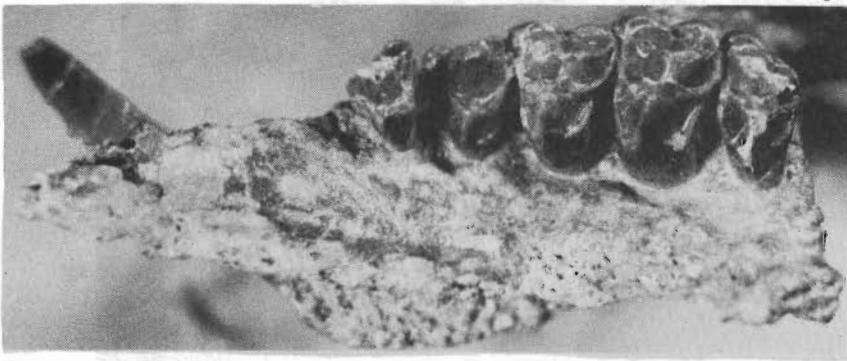
PLATE 5. 1: Litomylus aequidens, AMNH 16720; P₄-M₃, 12.9. 2: Litomylus osceolae; M₁₋₃, 11.5. 3: Litomylus(?) alphamon; M₁₋₂, 5.0. 4: Niphredil radagasti; P₄-M₁, 10.6. 5: Litaletes ondoline; P₃-M₃, 22.8.



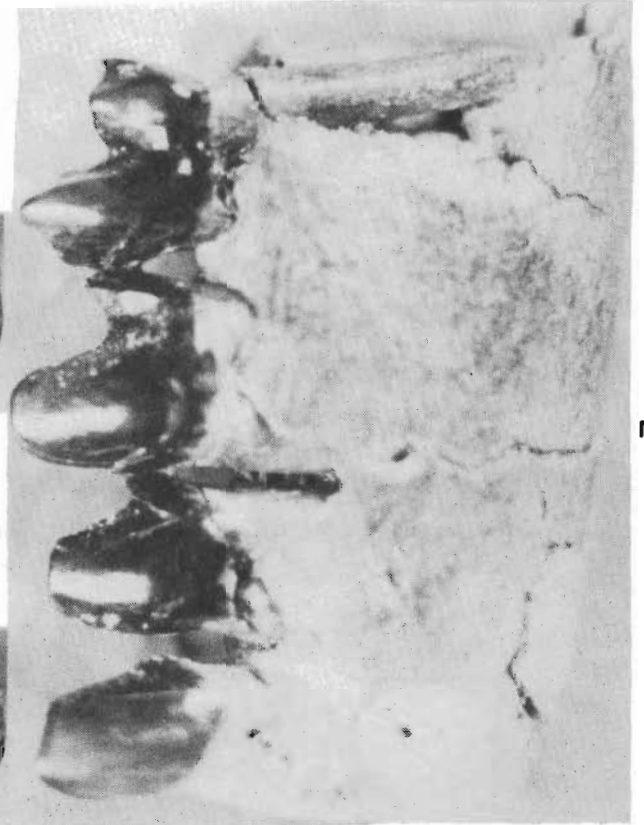
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PLATE 6. 1-3: *Fimbrethil ambaronae*. 2: type; M_{1-2} , 5.6. 1,3: UCMP field number JR-39-70, Mammelon Hill; P_2-M_1 , 9.6. 4: *Maiorana noctiluca*; P_3-M_3 , 17.1. 5: *Oxyacodon josephi*; M^{1-3} , 8.1.

BEGINNING OF THE AGE OF MAMMALS

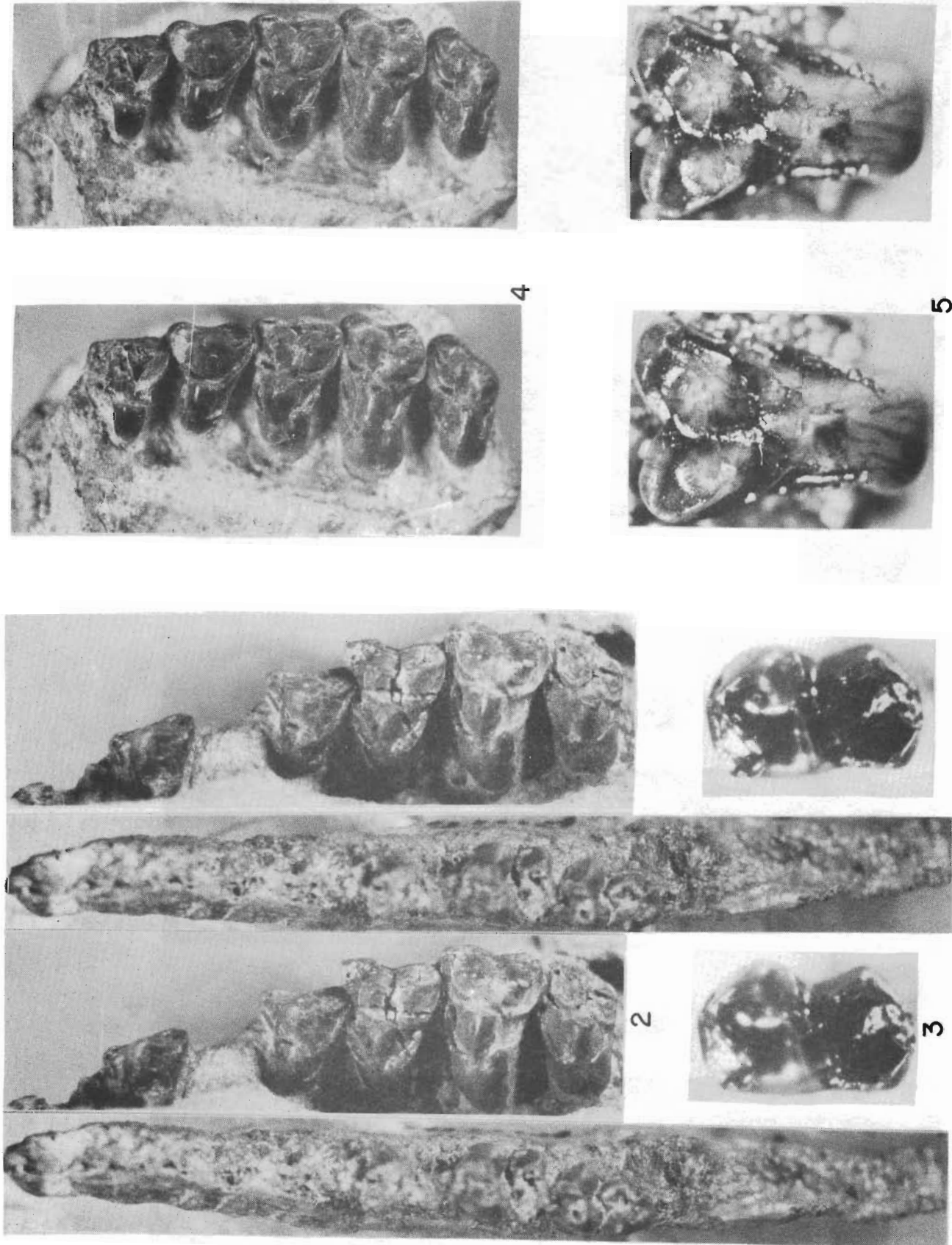


PLATE 7. 1: *Mimatuta makpialutae*; M_{2-3} , 8.1. 2: *Earendil undomiel*; P^3-M^3 , 18.7.
 3: *Procerberus plutonis*; $M_{2,2}$, 2.8. 4: *Mimatuta minuiial*; P^3-M^3 , 16.6. 5: *Mimatuta morgoth*; M^2 , 4.3.

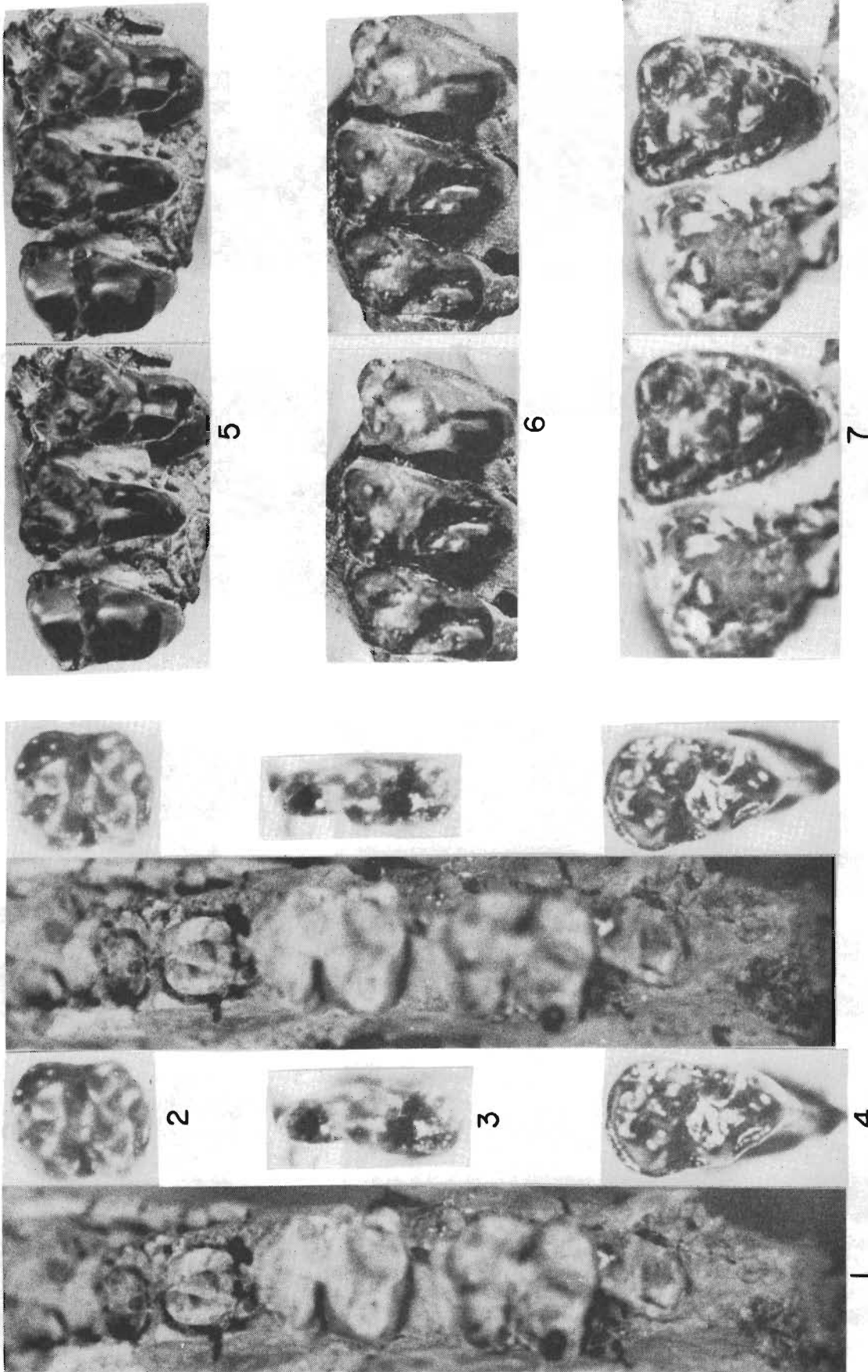


PLATE 8. 1: Oxyacodon tecumsae; M_{1-2} , 7.8. 2: Oxyacodon marshater; M_2 , 3.6.
 3: Leptacodon proserpinae; P_4 , 2.3. 4: Tinuviel eurydice; M_3 , 5.0. 5: Anisonchus athelas; P^4-M^2 , 12.6. 6: Anisonchus eowynae; M^{1-3} , 11.0. 7: Protoselene bombadili; M^2 , 4.8.