EVOLUTION OF TERTIARY MAMMALS OF NORTH AMERICA

VOLUME 1:
TERRESTRIAL CARNIVORES, UNGULATES, AND UNGULATELIKE MAMMALS

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28 Oromerycidae

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INTRODUCTION

The Oromerycidae were a middle to late Eocene group of tylopods closely related to camels and protoceratids. They originated in North America in the early Uintan, during the great middle Eocene radiation of artiodactyls, and became extinct during the terminal Eocene extinction crisis at the end of the Chadronian. Of the six valid genera, four are known from the Uintan, three from the Duchesnean, and only two genera occur in the Chadronian. Most were small deer-like animals, the size of musk deer or dik-diks, but the late Eocene *Eotylopus* and *Montanatylopus* reached the size of small antelopes (Figure 28.1). They had no cranial appendages or locomotory specializations. Indeed, they are so primitive in skull, dentition, and skeleton that they have long been confused with primitive camels and protoceratids. Although *Oromeryx* was described by Marsh in 1894, the family was not formally named until 1955 (Gazin, 1955).

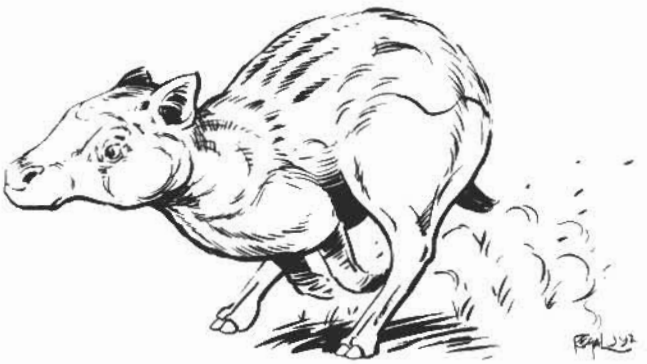


Figure 28.1. Restoration of *Protylopus*, by Brian Regal.

DEFINING FEATURES OF THE FAMILY OROMERYCIDAE

CRANIAL

As already noted, the oromerycids have remarkably few derived characters that distinguish them from primitive camels and protoceratids. The skull (Figure 28.2A) is like that of most primitive tylopods, with a short, broad rostrum, incomplete postorbital bar, and no facial or lacrimal vacuities. Like other tylopods, the bulla is inflated and filled with cancellous bone.

DENTAL

The dentition (Figure 28.2B) is relatively low crowned and bunodont for a selenodont tylopod. All of the anterior teeth are present, and there are no diastemata. *Eotylopus* has slightly enlarged canines, but all other oromerycids have equal-sized canines and incisors (if they are known). The first two premolars are simple blades, and the last two premolars are bladelike with a lingual cusp. The molars are bunoselenodont with strong labial cingula and mesostyles. Only two features help distinguish them from primitive tylopods. In the upper molars, the protocones are bifurcate posteriorly (Wilson, 1974; Prothero, 1986), which is found elsewhere only in the most primitive camels. All oromerycids retain this primitive feature. The only uniquely derived feature in the dentition is the deep lingual cleft between the entoconid and hypoconulid on m3.

POSTCRANIAL

Postcranially, oromerycids are known primarily from the nearly complete skeleton of *Eotylopus* (Matthew, 1910) and a partial skeleton of *Montanatylopus* (Prothero, 1986). The vertebrae have the primitive condition of the vertebral artery passing through transverse processes, rather than through the pedicels of the neural arch, as in camels and protoceratids. The limb elements are elongate, like those of most cursorial artiodactyls, but not nearly as slender as those of camels. The only noticeable specialization is the fusion of the radius and ulna, which happened independently in a number of advanced ungulates. The manus has four fully-developed metacarpals, although the central two are more robust. The fibula is

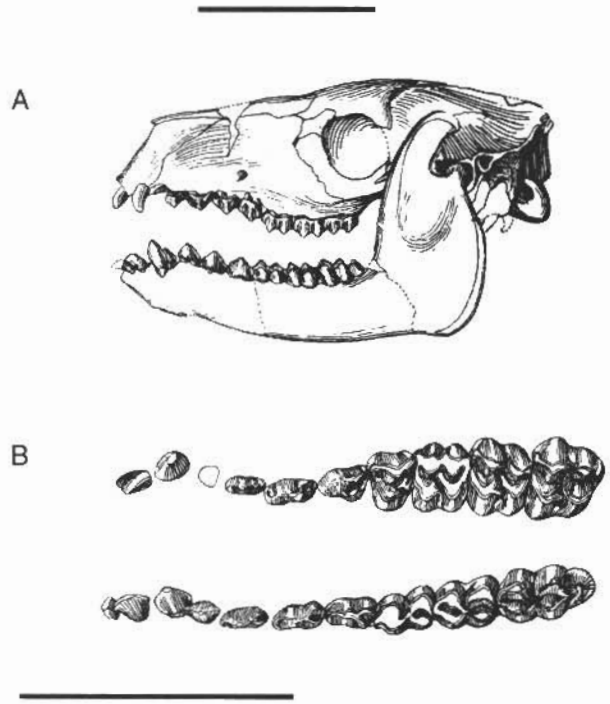


Figure 28.2. A. Skull and jaws of *Eotylopus reedi* (UW 216), a representative and relatively completely known oromerycid (scale bar = 5 cm). B. Crown view of dentition of *Eotylopus reedi* (scale bar = 5 cm). (Modified from Prothero, 1986.)

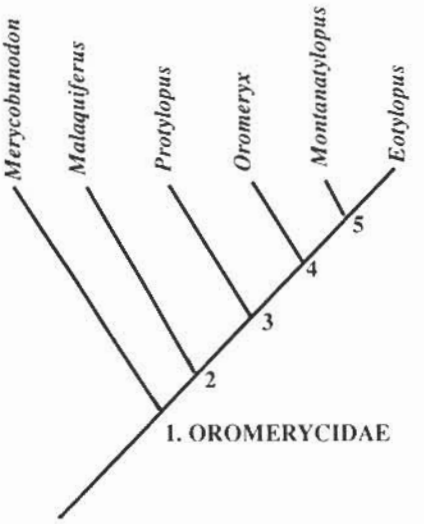


Figure 28.3. Interrelationships within the Oromerycidae. Characters at the nodes are as follows: (1) OROMERYCIDAE: Deep lingual cleft separating metaconid from entoconid on m3. (2) Lose hypocone; weak upper molar cingula; plicate enamel. (3) Stronger selenes; higher crowned, more rectangular upper molars. (4) Upper molars narrow posteriorly. (5) Much larger size; lose enamel plications.

reduced to a nodule. The lateral metatarsals have been so reduced that the foot is essentially didactyl.

SYSTEMATICS

SUPRAFAMILY

Although the teeth of *Oromeryx* were described by Marsh in 1894, and the complete skeleton of *Eotylopus* was described by Matthew in 1910, oromerycids remained poorly understood. Some taxa (e.g., *Oromeryx*) were considered primitive ruminants; others (e.g., *Protylopus*, *Eotylopus*) were considered ancestral to the camels (Scott, 1899, 1940, 1945; Simpson, 1945). The oromerycids were recognized as distinct from camelids by Matthew in 1910, but were not formally named until Gazin did so in 1955. Subsequent authors (Wilson, 1974; Golz, 1976; Black, 1978; Prothero, 1986) have upheld the validity of the group, although Wilson (1974) placed them as a subfamily of the Camelidae.

INFRAFAMILY

Six valid genera of oromerycids are recognized (Fig. 28.3). Their temporal and geographic distribution is shown in Figures 28.4 and 22.5. *Camelodon arapahovius* (Granger, 1910) from the Beaver Divide locality in central Wyoming (CP39IIB) is based on a left mandible with such a worn dentition that there is no recognizable crown pattern. Its only unique feature is a diastema between p2 and p3, which does not place it with any group. The affinities of this taxon are indeterminate.

INCLUDED GENERA IN THE FAMILY OROMERYCIDAE

The locality numbers listed for each genus refer to the list of unified localities in Appendix I. The acronyms for museum collections are listed in Appendix III.

The locality numbers may be listed in a couple of alternative ways. Parentheses around the locality (e.g., [CP101]) mean the taxon in question at that locality is cited as an "aff." or "cf." the taxon in question. Parentheses are usually used for individual species, thus implying the genus is firmly known from the locality, but the actual species identification may be questionable. Question marks in front of the locality (e.g., ?CP101) mean the taxon is questionably known from that locality, thus implying some doubt that the taxon is actually present at that locality, either at the genus or the species level.

Merycobunodon Golz, 1976

Type species: *Merycobunodon littoralis* Golz, 1976.

Type specimen: LACM 27351.

Characteristics: Most primitive of the oromerycids, with teeth intermediate between the bunodont and selenodont conditions. Differs from all other oromerycids in having lower-crowned upper molars with weaker crests, stronger cingula, and more squared occlusal outline.

The m2 is unknown. M2 length = 8.1 mm.

Included species: *M. littoralis* only, known from locality CC4 only.

***Malaquiferus* Gazin, 1955**

Type species: *Malaquiferus tourteloti* Gazin, 1955.
Type specimen: USNM 20588.
Characteristics: *Malaquiferus* also has very low crowned teeth, with squared upper molars and small protoconules on M1–M3. It is distinguished from most other oromerycids in having highly wrinkled enamel and lacking lingual upper molar cingula.
Average length of m2: 6.8–7.8 mm.
Included species: *M. tourteloti* only (known from localities SB43A, SB43B, CP29C).

***Protylopus* Wortman, 1898**

Type species: *Protylopus petersoni* Wortman, 1898.
Type specimen: AMNH 2076.
Characteristics: *Protylopus* is slightly more advanced than *Merycobunodon* and *Malaquiferus* in having higher crowned, more rectangular molars with stronger selenes. Unlike more advanced oromerycids, the molars do not narrow posteriorly. As used by Golz (1976, Figure 15), *Protylopus* is essentially a wastebasket genus for all oromerycids that have reached a certain grade of evolution. Not all of the species are referable to this genus on the basis of shared derived characters.
Average length of m2: 7.0–10.6 mm.
Included species: *P. petersoni* (= *P. minor*, *P. parvus*) (known from localities CC7C, [CC9AA], CP5A, CP6A, CP6B, CP38C); *P. pearsonensis* (localities CC9B, CC9BB); *P. stocki* (localities CC7C, [CC8], CC9B); ?*P. robustus* (localities CC7C, CC9AA); ?*P. annectens* (CP6B).

Protylopus sp. is also known from localities CC7B, ?SB43B, ?CP38D.

***Oromeryx* Marsh, 1894**

Type species: *Oromeryx plicatus* Marsh, 1894.
Type specimen: YPM 14571
Characteristics: *Oromeryx* is slightly larger than most *Protylopus* and has posteriorly tapered upper molars. It is considerably smaller and less hypsodont than *Eotylopus* or *Montanatylopus*.
Average length of m2: 7.9 mm.
Included species: *O. plicatus* only (known from localities SB44B, CP6A, CP6B).

***Eotylopus* Matthew, 1910**

Type species: *Eotylopus reedi* Matthew, 1910.
Type specimen: UW 216.
Characteristics: *Eotylopus* has slightly higher crowned teeth than other oromerycids except *Montanatylopus* and lacks the enamel plications seen in most other oromerycids. It is also larger than any other oromerycid except *Montanatylopus*. It differs from *Montanatylopus* in being smaller and much less hypsodont.
Average length of m2: 9.8–11 mm.
Included species: *E. reedi* (known from localities SB26B, SB43D, SB44C, SB44E, CP39B, CP39C, CP39F, CP40A, CP41A, CP68B, CP98C); *E.* n. sp. A (described but not named by Golz, 1976) (locality CC9D); ?*E.* n. sp. B (Tabrum and Fields, 1980) (locality NP24C).

***Montanatylopus* Prothero, 1986**

Type species: *Montanatylopus matthewi* Prothero, 1986.
Type specimen: CM 9918.
Characteristics: *Montanatylopus* is readily distinguished from all other oromerycids in its much larger size and its very hypsodont teeth. Indeed, it is so hypsodont that it was long misidentified as a camel. However, it clearly shows the bifurcate protocones and the entoconid-hypoconulid groove that are diagnostic for oromerycids.
Average length of m2: 16.5 mm.
Included species: *M. matthewi* only (known from localities SB27B, CP83A, NP25C).

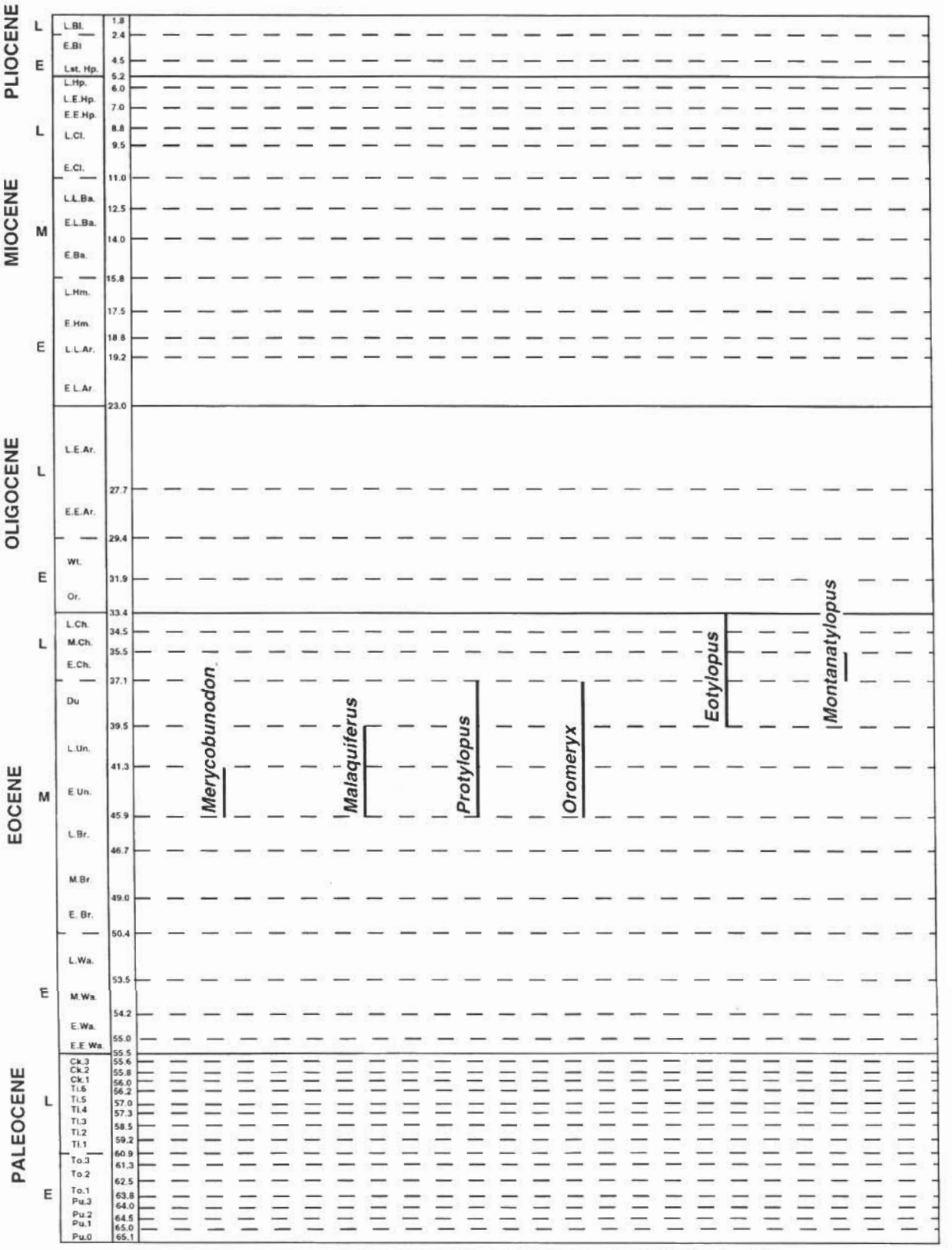
Indeterminate oromerycids

Fragmentary remains ascribed to oromerycids have been reported from localities CP6B, NP8, NP9A.

BIOLOGY AND EVOLUTIONARY PATTERNS

Oromerycids were very unspecialized in their skeletons and dentitions, so it is likely they were among the many small, primitive browsing artiodactyls that prowled the forests of the middle and late Eocene. In this regard, they must have shared this niche with primitive protoceratids, oreodonts, agriochoeres, leptomerycids, and homacodonts. By the Oligocene, they had become considerably larger and more cursorial. *Eotylopus* and *Montanatylopus* show signs of greater cursoriality in having a fused radius-ulna, reduced fibula, and a pes reduced to two digits. However, no oromerycid is as gracile as Oligocene camels, protoceratids, leptomerycids, or hypertragulids, which were truly cursorial. *Montanatylopus* did converge considerably on camels in its much larger body size and high-crowned selenodont teeth.

Oromerycids were always rare, so their distribution is largely an artifact of the small sample size. However, there are some distinct geographic trends. *Protylopus* was relatively abundant in the middle Eocene of California, but rare elsewhere; *Malaquiferus* was more common in Wyoming and Texas at the same time; *Oromeryx* was always rare. *Eotylopus* first appeared in the Duchesnean and lasts until the very end of the Chadronian. It is by far the most long lived and widespread of oromerycids, ranging from New Mexico and Texas to Montana and Wyoming. Even so, there are some surprising anomalies in its distribution. It is well known from the Chadronian of Wyoming, Colorado, and Texas, but has so far not been reported from the large Chadronian samples of the South Dakota Badlands. *Montanatylopus* has an unusual distribution: McCarty's Mountain in Montana (Prothero, 1986), the Rubio Peak Formation



Bl.=Blancan, Hp. = Hemphillian, Cl.= Clarendonian, Ba.= Barstovian, Hm.= Hemingfordian, Ar. = Arikareean, Wt. =Whitneyan, Or.= Orellan, Ch. = Chadronian, Du.= Duchesnean, Un. = Uintan, Br. = Bridgerian, Wa. = Wasatchian, Ck. = Clarkforkian, Ti. = Tiffanian, To. = Torrejonian, Pu. = Puercan.

Figure 28.4. Temporal ranges of oromerycid genera.

in New Mexico (Lucas, 1986), and possibly the Ahearn Member of the Chadron Formation in South Dakota (Clark, Beerbower, and Kietzke, 1967), but nowhere else. Clearly, oromerycids occupied a habitat that was not always sampled by Chadronian localities, even when the overall sample size is large.

The diversity trends can be related to the overall picture of faunal and climatic change in the Eocene and Oligocene. Primitive oromerycids, like other primitive selenodont artiodactyls, were fairly abundant in the forested environment of the Uintan and Duchesnean. All of these groups changed or declined during the major climatic change in the Chadronian (Webb, 1977; Prothero, 1986). With the beginning of more mixed forest-grassland habitat in the Chadronian, *Eotylopus* was apparently confined to forest remnants. This may explain its peculiar sampling and distribution. *Eotylopus*, the last of its family, was one of the more important victims of the Chadronian-Orellan extinction event (Prothero, 1994; Berggren and Prothero, 1992), which wiped out a number of archaic, mostly brachydont forest dwellers. The Chadronian-Orellan extinction event was undoubtedly a result of major vegetational changes (Wolfe, 1978, 1992; Retallack, 1983) which in turn was triggered by a worldwide cooling event caused by a pulse of Antarctic glaciation (Berggren & Prothero, 1992; Prothero, 1994).

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