INTRODUCTION

The primitive tylopod family Oromycidae was first recognised by Gaaz in 1955. Except for Eotylosus and Prototylosus, most oromycids are known only from teeth and jaws. Oromycids are remarkably rare in the fossil record and are currently known from only five genera: Meromycolodon Golj, 1976; Malagaosaurus Gaaz, 1955; Prototylosus Wortman, 1898; Oromycolos Marsh, 1894; and Eotylosus Matthew, 1910. Except for Eotylosus, oromycids are restricted to the middle and late Eocene (Uintan-Duchesnean) of North America. Eotylosus is known from the latest Eocene (Duchesnean) of California and Texas, and ranges to the mid-Oligocene (late Chadronian) of the High Plains. Previously, Eotylosus was the only Oligocene oromycid known.

Because they are rare, incompletely known, and primitively similar to other late Eocene selodont artiodactyls, oromycids have long been poorly understood. Scott (1899, 1940, 1943) originally considered them to be camels, but Matthew (1910) recognized that they were a different group. Gaaz (1955) formally created the Family Oromycidae, and its distinctiveness was recognized by subsequent authors (Wilson, 1974; Golz, 1976; Black, 1978). The derived feature that distinguishes oromycids from all other selodont artiodactyls is the deep lingual notch separating the entoconid from the metaconid on lower M3. Oromycids can also be recognized by their retention of the primitive condition of bifurcate protocones on the upper P4-M3, which is also found on the most primitive camels (Wilson, 1974).

In 1938, J. Leroy Kay of the Carnegie Museum found this new oromycid at the McCarty's Mountain locality, near the town of Glen, Madison County, Montana (Figure 1). This locality was first described by Douglass (1905, p. 209-211). According to Wood et al. (1941, p. 25), "it is merely a locality term for Oligocene exposures on its slopes or at its base, in northwestern Madison County, Montana. Douglass divided the exposures into several successive fossiliferous levels, but his unpublished notes have not yet been located; much or all of the Oligocene may be represented." According to Emry, Bjork and Russell (personal communication), the McCarty's Mountain fauna is probably early medial Chadronian in age, slightly younger than the Yoder local fauna of Wyoming (earliest Chadronian), and slightly older than the Pipestone Springs local fauna (medial Chadronian) of nearby Jefferson County, Montana (Figure 1). This would make the McCarty's Mountain local fauna about 56 Ma in age (Prothero, 1985).

Abbreviations used in this paper are as follows: CM, Carnegie Museum of Natural History; Ma, million years before present; UW, University of Wyoming Museum of Geology. For ease of word processing, the system of dental abbreviations follows Jepson (1966), with upper teeth indicated by upper case P and M for upper premolars and molars, lower case p and m for lower premolars and molars.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Suborder Tylopoda Illiger, 1811
Family Oromerycidae Garaz, 1955

**Montanatylus n. gen.**

*Montanatylus matthewi* n. sp.

**Diagnosis.**—Distinguished from all other oromyrecids by its much larger size (M1-3 length = 50 mm) and relatively hypsodont teeth.

**Montanatylus matthewi** n. sp.

**Etymology.**—In honor of William Diller Matthew, premier student of the Tyloropoda, who first recognized the distinctiveness of the oromyrecids.

**Holotype.**—CM 9918, a nearly complete skeleton. See Table 1 for dimensions.

**Horizon and locality.**—From the type locality, McCarty’s Mountain, Madison County, Montana. A jaw fragment from the Eocene-Oligocene Rubio Peak Formation, southwest New Mexico, may be referable to this taxon (S. Lucas, personal commun.).

**Description.**—Same as for genus.

**Description.**—The skull of *Montanatylus* (Figures 2.1, 3.1-3.3) lacks only the zygomatic arches and a few anterior teeth. The skull is nearly twice the size of that of *Eotylopus* (Figure 2.4), the largest oromyrecid previously known. The cranium has the same basic shape and curvature of that of *Eotylopus*, although it is a bit broader transversely. The premaxilla extends posteroilaterally to the level of P2. There is no facial fossa, and apparently no lacrimal vacuity, although this is difficult to judge, since the anterior portion of the skull is badly fractured, with some bone missing. The infraorbital foramen lies immediately above M1. The orbits flare widely from the side of the skull. The supraorbital ridge projects laterally, and then abruptly tapers back just posterior to the orbit. Weak supraorbital canals are visible near the midline of the skull between the orbits. The braincase is relatively small and tapered posteriorly. The sagittal crest is quite weak, as in *Eotylopus*. The lambdoid crest and occiput are more posteriorly elongated than in *Eotylopus*, even though they are partially broken in CM 9918.

The basicranium is moderately well preserved. The auditory bullae are broken, but were apparently quite small, and may have been filled with porous bone (as in camels). However, this is difficult to judge because of the poor state of preservation. The hypoglossal foramen is well preserved. There is no sign of the “winglike” basioccipital processes seen in camels and protoceratids. A large groove which apparently represents the medial and posterior lacerate foramina passes medial to the bulla. The external auditory meatus is just slightly above the level of the
basicranium. It is closed ventrally by the bulla. A large postglenoid foramen and foramen ovale are visible just anterior to the bulla. The glenoid itself is shelllike, but much narrower than in camels. The basisphenoid has a very prominent ventral “keel” that narrows anteriorly. The pterygoid processes are long and flare slightly posterolaterally. The anterior border of the internal nares is at the level of anterior M3.

The upper dentition (Figure 4.1) is remarkably robust and hypsodont for an oromerycid. It is clearly oromerycid, however, since it shows the bifurcate protocones characteristic of that family. 11 and 12 are small and spatulate. There is no trace of the I3 alveolus, and both III’s are missing. Judging from the lack of space for them, they may have been absent. There is a large alveolus for the upper canine, although the canin itself is not preserved. There are no significant diastemata between the anterior teeth, or between the cheek teeth. P1 is biauricate, with a bifurcate anterior ridge. P2 is also biauricate, with simple ridges. P3 has a slightly bifurcate anterior ridge and a distinct posterolingual cusp. The posterior ridge is flared slightly laterally, and has a faint posterior cingulum. P4 is seladont and very broad transversely, with a posteriorly bifurcate lingual scleve, and faint anterolingual and posterolingual cingula.

The molars are relatively hypsodont compared to those of other oromerycids. They are well worn, so their seladonty resembles that of camels. Wear has obliterated the bifurcation of the protocones on M1–2, but it is still distinct on M3. The mesostyles are progressively stronger on more posterior molars. The protocones have weak anterolingual cingula, and a faint trace of a lingual cingulum can be seen on the metaconules of M3. The ectolophs are alinate as in Equus, but not as straight as in camels. The metastyles of M2–3 have a distinct posterolingually deflected process that nearly touches the posterior lingual scleve of the metaconule, and closes the gap between them. The parastyles have a similar lingual process, which abuts the metastyle of the adjacent tooth with wear.

The lower jaws (Figures 3.4, 4.4) show the typical tylopod condition of the long, slender
<table>
<thead>
<tr>
<th>Skull length (in occipital condyle)</th>
<th>191.8</th>
<th>p3 width</th>
<th>3.9</th>
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<tr>
<td>Facial length (l1+M3)</td>
<td>115.4</td>
<td>p4 length</td>
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<tr>
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<td>Rostral width at P1</td>
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<td>m1 length</td>
<td>15.0</td>
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<tr>
<td>Maximum width at orbit</td>
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<td>m1 width</td>
<td>7.8</td>
</tr>
<tr>
<td>Length upper canine alveolus</td>
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<td>m2 length</td>
<td>16.5</td>
</tr>
<tr>
<td>P1-M1 length</td>
<td>90.0</td>
<td>m2 width</td>
<td>8.9</td>
</tr>
<tr>
<td>P1-4 length</td>
<td>41.1</td>
<td>m3 length</td>
<td>25.0</td>
</tr>
<tr>
<td>M1-3 length</td>
<td>50.5</td>
<td>m3 width</td>
<td>9.7</td>
</tr>
<tr>
<td>P1 length</td>
<td>8.8</td>
<td>Atlas length</td>
<td>39.5</td>
</tr>
<tr>
<td>P2 width</td>
<td>4.2</td>
<td>Atlas width</td>
<td>43.3</td>
</tr>
<tr>
<td>P2 length</td>
<td>1.0</td>
<td>Axis width</td>
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</tr>
<tr>
<td>P3 length</td>
<td>3.7</td>
<td>Scapula length</td>
<td>12.8</td>
</tr>
<tr>
<td>P3 width</td>
<td>12.1</td>
<td>Scapula, width at neck</td>
<td>20.5</td>
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<tr>
<td>P4 length</td>
<td>9.7</td>
<td>Scapula, maximum width blade</td>
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<tr>
<td>N1 length</td>
<td>11.4</td>
<td>Humerus length</td>
<td>152.3</td>
</tr>
<tr>
<td>M1 length</td>
<td>14.1</td>
<td>Humerus midshaft width</td>
<td>20.4</td>
</tr>
<tr>
<td>M2 width</td>
<td>14.8</td>
<td>Humerus distal width</td>
<td>26.3</td>
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<tr>
<td>M2 length</td>
<td>17.0</td>
<td>Ulna length</td>
<td>217.8</td>
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<tr>
<td>M2 width</td>
<td>16.9</td>
<td>Radius length</td>
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<tr>
<td>M3 width</td>
<td>18.4</td>
<td>Radius-ulna diaphysis width</td>
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<tr>
<td>M3 width</td>
<td>23.5</td>
<td>Radius-ulna diaphysis midshaft width</td>
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<tr>
<td>Depth of jaw below p2</td>
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<td>Metacarpal III length</td>
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<tr>
<td>Jaw length, r to angle</td>
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<td>Metacarpal III midshaft width</td>
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<td>Height jaw, condyle-base</td>
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<td>Metacarpal III midshaft midshaft width</td>
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<td>Length of mandibular symphysis</td>
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<td>Pelvis, sacral width</td>
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<td>p2-m1 length</td>
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<td>Pelvis, width at acetabulum</td>
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<td>p2-4 length</td>
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<td>Pelvis, anterior sacrum to pubic symphysis</td>
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<tr>
<td>m1-3 length</td>
<td>55.3</td>
<td>Femur, distal width</td>
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<td>Patella, length</td>
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<tr>
<td>p1 width</td>
<td>3.9</td>
<td>Patella, width</td>
<td>21.0</td>
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<tr>
<td>p1 length</td>
<td>15.1</td>
<td>Metatarsal III length</td>
<td>114.4</td>
</tr>
<tr>
<td>p2 length</td>
<td>9.7</td>
<td>Metatarsal III midshaft width</td>
<td>91.3</td>
</tr>
</tbody>
</table>

coronoid process and the high, rounded anterointernally deflected articular process. The angular process lacks the characteristic dorsal "hook" seen in most camels. The mastoid fossa is very shallow. The symphysis is short, and extends to the level of p1. The ramus is otherwise quite slender and narrow. No men tal foramina are preserved. The three lower incisors and the canine are spatulate in shape, with distinct lingual ridges. They flare from the symphysis without any diastema. The p1 is missing. The p2 is a bulbous blade, with a divided posterior crest, both wings of which bend lingually. The third lower premolar is similar to p2, except that it is narrower and the posterolingual crest is stronger and more anteriorly oriented. The fourth lower premolar is less blade-like, and has a distinct trigonid ridge formed by the crests that branch lingually off the central cusp. It also has a distinct talonid ridge with a faintly twisted entoconid. The molars are much more hypodont than in any other oromerycid. The first lower molar is so highly worn that it shows nothing beyond the typical se- lendont condition. The second lower molar is also very worn, but does show a distinct groove separating the entoconid and hypoconid, another distinctive oromerycid feature. The third lower molar is transversely, and shows the entoconid-hypoconid groove even better than do the other molars. The hypoconid is separate from the rest of the tooth at the apex, although with greater wear it would merge. The trigonid is open anteriorly, but completely closed posteriorly. The hypoconulid is ridgelike, with a slight lingual curl at its posterior end. Lingual to the hypoconulid two tiny cusps occupy the gap between the entoconid and the hypoconulid.

Postcranial skeleton. —Montaquamylus matthewi is known from a postcranial skeleton, which is missing only part of the vertebral column and some of the hind limb bones. The five cervical vertebrae preserved are relatively shorter than those of Poebrotherium. This indicates that Montaquamylus had a much shorter neck than a camel, a neck more like that of Eoceras.
The atlas (Figures 3.3, 3.4) is much broader, heavier, and more rectangular than a camel atlas. The anterodorsal facets for the occipital condyle are very robust in contrast to the anteroventral facets. The ventral surface of the centrum has no axial ridge. There is almost no trace of a neural arch on the dorsal surface, although there appears to be some breakage in this area. The transverse processes are very narrow and straight sided, giving the atlas a rectangular shape in dorsal view. A deep atlantoaxial foramen for the superior branch of the first spinal nerve perforates the anterior margin of the transverse process just posterior to the anterodorsal articulation with the occipital condyle. The posterior articulation for the axis is broad and triangular. The vertebral canal does not seem to enter the atlas from behind (as in Protherohippium), but passes laterally, forming a distinct groove just ventral to the base of the transverse process. It then passes up into a foramen under the anteroventral base of the transverse process.

The centrum of the axis (Figures 2.2, 2.3, 3.3, 3.4) is narrow and laterally compressed, although not as long as in camels. The neural arch and posterior articulations are broken. The atlantoaxial facets flare broadly ventrolaterally and are continuous beneath the odontoid process. A shallow trough posteroventral to the odontoid process indicates that these facets were once separate. The odontoid process is short, dorsoventrally convex and turns slightly dorsally.

The three remaining cervicals have a broad anterior facet on the centrum that is shaped like a dorsoventrally compressed oval. There are also separate anterolateral facets. The ventral surface of the centrum is smooth, with no ridges like those seen in camels. The posterior centrum articulation is broadly convex, with a slight ventral point. Most of the transverse processes and neural arch are badly broken, but the prostylepophyses are broad and posteroventrally flared.

The fourth cervical has an even more dorsoventrally flattened anterior articulation of the centrum. The ventral surface of the centrum has a distinct anteroposterior ridge. The posterior articulation of the fourth cervical is more dome shaped than that of the third cervical. The opening for the vertebrocostal canal passes just lateral to the centrum and slightly ventral to the pedicles of the neural arch. Most of the transverse processes and neural arch are broken, except for the pro- and poststylepophyses. The remaining (right) cervical is similar to the fourth, except that it is more crushed and less well preserved.

A few thoracic and lumbar vertebrae are preserved, but largely as centra with most of the processes and projections broken off. The centra have flat, semicircular anterior articulations and slightly concave, laterally broad posterior articulations. Each has a distinct anteroposterior ridge along the ventral surface. The prostylepophyses flare more laterally and less anteriorly, as seen in the cervicals. The neural arches are badly broken,
but diverge posteriorly into two ridges which terminate in the narrow, slightly knoblike postzygapophyses.

The sacrum and pelvis (Figures 5.1, 5.2) are also known in CM 9918. At least four fused vertebrae compose the sacrum. The anterior sacral articulation with the lumbaris is broadly oval, dorsoventrally compressed, and slightly convex anteriorly. The contact with the pelvis is broad and includes both the first and second sacrals. The iliac blade has a broad, dorsally arched flange above the sa-
cral articulation. A laterally flaring process of
the iliac blade projects anteriorly to the sacral
region. The posterior portion of the ilium is
robust, with a broad lateral flare for the ac-
acetabulum, which has a strong anterodorsal
rim, and a much weaker ventral rim. It is
deply socketed, with a distinct posterior sul-
cus which begins in the center of the socket
and emargi nates the posterior rim. The is-
chial and pubic portions of the pelvis are
poorly preserved and mostly restored in plas-
ter.

The scapula (Figures 6.1, 7.1) is very sim-
ilar in size and shape to the scapula of *Poc-
toatherium*. The glenoid fossa, however, is
more robust, with a blunt, internally flexed
coracoid process. The scapular blade is tri-
angular, with strong lateral ridges. It is broken
dorsally. The scapular spine is long and slen-
der. The long, anteriorly curved scapular
process flares anteriorly from the lateral side
of the neck of the scapula. The scapular spine
is located about a third of the way back from
the anterior edge of the blade. This makes
the spinespina fossa much smaller than the
spine fossa. Dorsally, the spine curves pos-
teriorly as it becomes broader.
The humerus (Figures 6.2–6.4, 7.2, 7.3) is only slightly longer than that of *Poekrotheta*ri*m*, but is much more robust, especially at its proximal end. The head is very massive and knoblike, and faces less posteriorly than in *Poekrotheta*ri*m*. The latera, tuberosity is also very massive, projecting only slightly above the head. The medial tuberosity is short but quite strong, with a distinct postero-medial sulcus. As in most primitive artio-dactyls, the deltoide crest is very weak and the supinator crest is almost absent. The shaft of the humerus is laterally compressed, rather than circular in cross-section. The trochlea is asymmetrical, with the medial condyle larger than the lateral condyle. The ectepicondyle is weak, and lateral to the trochlea there is only a slight depression, with no process. There is almost no intercondylar ridge. The anconeal fossa is short but deep, and is broken through to form a small supratrochlear foramen.

The fused radius-ulna (Figures 6.5, 7.4, 7.5) is longer and more slender than in *Eotylopus* but more massive than in camels. The olecranon is short and massive, with a distinct posterior dorsal flange, as in camels. The sigmoid notch is almost a semicircle, with distinct lateral and medial facets. The head of the radius is square and shallowly concave, with only a slight ridge between the medial and lateral facets. It has a distinct massive bicapital rugosity. The shaft of the radius is slightly narrower than the head, and tapers very little. It is semicircular in cross-section, especially where joined by the flat splint of the ulnar shaft. These two bones are completely fused except near the head of the distal end of the radius. The radius has two distinct carpal facets, which are continuous with a small facet at the distal tip of the splint-like ulna.

The preserved carpus (Figures 5.6) consists of a scaphoid, lunar, unciform, and pisiform. The scaphoid is square with a broad proximal facet and a trough-shaped distal facet, and has a distinctly hooked plantar process. The distal surface of the lunar has a broad triangular facet for the magnum. The scaphoid facet of the lunar is broad and flat, and the radial facet is more saddle shaped.

The unciform has a broad, flat metacarpal facet distally, and a saddle-shaped facet for the lunar and the cuneiform. The plantar process is knoblike and ventrally hooked. The pisiform has two small facets for articulation with the cuneiform, and an enlarged plantar knob.

*Montanarctopus* has four metacarpals. The two central metacarpals (III and IV) are the longest and most robust. However, metacarpals II and V are about half as thick as the central metacarpals and almost as long. One isolated phalanx is preserved.

The hind limbs of CM 9918 are poorly preserved. A fragment of the distal end of the femur, and parts of the shaft are known. The rotoral trochlea is broad and saddle shaped, with a slightly longer medial rim. The patella (Figure 2.6) is tear drop shaped, with a sharp proximal point and a flattened distal end. They are irregularly convex on the anterior surface, and nearly flat except for a faint longitudinal ridge on the articular surface.

The tuber is broken from the calcaneum. The sustentacular facet is broad and concave, and the cuboid facet is arcuate, with two distinct surfaces. The tuber facet is large and...
OLIGOCENE OROMERCYCID FROM MONTANA

projects above the calcaneum with the char-
acteristic tylopalp shape. The calcaneum is
more massive and wider in the dorsoplantar
direction than is seen in camels. In this re-
spect, it is similar to *Eomyops*. Metatarsals
III and IV (Figures 5.6, 8.2) are robust, and
about a third longer than their corresponding
metacarpals. They are separate, although they
have a proximal interlocking ball-and-socket
joint. The proximal plantar processes are very
long and robust, compared to those in cam-
els. The distal trochlea have distinct medial
ridges that become more prominent on the
plantar surface. There are distinct dorsal in-
dentations between the shaft and the trocele.

Discussion— *Montanatomyops* is unques-
tionably a new genus of oromercycid, since it
shows a number of striking features which
readily distinguish it from any other known
oromercycid. These include its much larger
size, its relatively gracile skeleton, and es-
pecially its hypodentid dentition. All other
oromercyceans have much lower crowned teeth,
so *Montanatomyops* converges on camels in
its degree of hypodonty.

Several derived features, such as the loss
of the enamelled plications on the molars and
the larger size, show that *Montanatomyops*
is most closely related to *Eomyops* among the
Oromercyidae. In nearly all of its features,*Montanatomyops* is far more derived than any
other oromercycid. Many of these derived fea-
tures converge on the condition seen in cam-
els, so several previous workers misidentified
it as a camel. However, the separate hypo-
coronal and entocoronal on m3, and other de-
rived oromercycid features, show clearly that
it is not a camel. A full discussion of the
relationships of oromercyceans will be pre-
sented elsewhere.

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