Merychus verrucomalus, a New Species of Oreodont (Mammalia, Artiodactyla) from the Middle Miocene Runningwater Formation

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INTRODUCTION

Among the oreodonts in the extensive Childs Frick Collection in the American Museum of Natural History are seven skulls, or partial skulls, with well-developed tuberosities on the anterior part of the zygomatic arch below the orbit. Although similar in other characters to Merychys of comparable size, these specimens represent a distinct species within the genus as based on unique zygomatic structure. Merychys verrucomalus is the only oreodont known to have a large tuberosity on the zygomatic process of the jugal.

The following abbreviations are used: Frick Laboratory, the American Museum of Natural History (F:A.M.) and the University of Nebraska State Museum (U.N.S.M.).

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the Department of Vertebrate Paleontology, the American Museum of Natural History, for providing stratigraphic information, for reading the manuscript, and for giving helpful suggestions. Mr. Ted Galusha recognized most of these specimens as unusual and separated them from his other oreodont collections.

SYSTEMATICS
CLASS MAMMALIA
ORDER ARTIODACTYLA
FAMILY MERYCOIDODONTIDAE THORPE, 1923
SUBFAMILY MERYCHYINAE SIMPSON, 1945
MERYCHYUS LEIDY, 1858

Merychys verrucomalus,1 new species
Figures 1–4; table 1

HOLOTYPE: F:A.M. No. 32919, skull, jaws, and front limbs.
REFERRED MATERIAL: F:A.M. No. 32918, skull, jaws, partial post-cranial skeleton with front and hind limbs from the NE ¼, Sec. 6, T. 29 N., R. 49 W., Dawes County, Nebraska; F:A.M. No. 32917, partial skull, jaws, miscellaneous bones from the NE ¼, SE ¼, Sec. 16, T. 29N., R. 52 W., Dawes County, Nebraska; F:A.M. No. 32967, skull, jaws, cervical vertebrae, from the NE ¼, Sec. 21, T. 29 N., R. 49 W., Dawes County, Nebraska; F:A.M. No. 32916, skull lacking part of cranium, jaws, miscellaneous bones, from NW ¼, Sec. 14, T. 30 N., R. 48 W., Dawes County, Nebraska; F:A.M. No. 32966, skull, jaws, and front limb, from 5–7 miles NE of Agate, Sioux County, Nebraska; F:A.M. No. 34312, anterior part of skull, from Sec. 29, T. 30 N., R. 47 W., Dawes County, Nebraska; and U.N.S.M. No. 2-10-8-36, skull, jaws, partial skeleton.

STRATIGRAPHIC POSITION AND TYPE LOCALITY: Main fork of Cottonwood Creek, NE ¼, NW ¼, Sec. 31, T. 30 N., R. 49 W., approximately 12 feet below “upper wavy-bedded sandstone zone,” Middle Hemingfordian Runningwater Formation (“Upper” Marsland of Schultz and Falkenbach, 1947, 1968; Runningwater Formation, Cook, 1965; McKenna, 1965; and the present paper, see fig. 5), Middle Miocene, Dawes County, Nebraska. The stratigraphy is that as interpreted by Ted Galusha, who has worked in this area for many years. All but one of the specimens

1 Verruca, Latin, wart; mala, cheekbone.
reported herein were collected by Ted Galusha and his associates.

**Diagnosis:** *Merychys verrucomalus* differs from similar-sized *M. elegans* Leidy and all other species of the genus in having a distinct tuberosity on the anteroventral-lateral side of the zygomatic arch, ventrolateral to the orbit.

**Description:** The type specimen, F:A.M. No. 32919, is an uncrushed skull lacking part of the left zygomatic arch and basicranial region, associated with jaws and a partial skeleton (figs. 1A, B; 2A–D; 4C, D). The skull is mesocephalic, has slightly retracted nasals and shallow facial fossae. The sagittal crest is moderately prominent, but it varies from slight to very prominent on referred skulls, depending on their individual age as based on tooth wear and sex. Supraoccipital “wings” are fan-shaped and are incorporated into the remainder of the lambdoidal crest (fig. 2C). The exoccipital pits are round and enclose a small exoccipital foramen. The anterior part of the zygomatic arch is unique and is discussed below, the posterior part is somewhat robust but otherwise comparable with those of other species of *Merychys* (fig. 2A). The teeth of *M. verrucomalus* are subhypodont, especially $M_3$. Auditory bullae are not preserved in the holotype because they have been broken away, but a medium-sized and medially depressed bulla is preserved in specimen F:A.M. No. 32967. The bulla is not nearly so inflated as it is in *Merychys crabilli* Schultz and Falkenbach, (see F:A.M. No. 45384), from the Harrison Formation of Nebraska, nor is it so transversely “pinched” as in the later *M. relictus* Matthew and Cook (1909; see F:A.M. Nos. 43078, 43079), from the “Lower Snake Creek” assemblage. Bullae within *Merychys* tend to decrease in size and become “pinched” through time.

The characteristics of the skull of *Merychys verrucomalus* closely approximate those of skulls of other species or varieties of the genus. A boss or tuberosity on the anteroventral-lateral surface of the zygomatic arch of *M. verrucomalus* is its most notable feature (figs. 1A, B; 2A, D). The tuberosity is variously developed on the seven specimens at hand, but symmetrical and always clearly evident on the zygomatic arch. No evidence exists to indicate that the tuberosity was caused by disease, and it is not a modified muscular attachment, but is lateral to the fossa for origin of *M. masseter superficialis*. This fossa is long and narrow in *M. verrucomalus* and like that in other *Merychys*.

When skulls of *M. verrucomalus* are viewed from the front (figs. 2D; 3A–D) it can be seen that the malar and boss invariably jut ventrolaterally. The sides of the malar are more nearly parallel to the sagittal plane of the skull in all other species or varieties of the genus. Enlargement of the anterior part of the zygomatic arch also causes the arch to
be markedly concave externally and thus it fails to converge anteriorly (fig. 3A–D). This characteristic is also well illustrated by another skull referable to *M. verrucomalus*, U.N.S.M. No. 2-10-8-36 (Schultz and Falkenbach, 1947, p. 272, fig. 4). The arch in other species of the genus may be slightly concave, but it is more usually straight or convex, and converges anteriorly.
Fig. 2. Skull and jaw of *Merychys verrucosus* (F:A.M. No. 32919). A. lateral view of right side of skull. B. lateral view of right mandible. C. posterior view of occiput. D. anterior view of skull. All $\times \frac{1}{2}$.

Morphology of the malar tuberosity varies considerably from a flattened, slightly pitted knob (fig. 3B) to a bulbous, rugose, cancellous-filled structure (fig. 3D). The skulls of three specimens (F:A.M.
Fig. 3. Anterior and ventral views of the malar tuberosity on zygoma of four specimens of *Merychyas verrucomalus*, showing variations in development. The youngest individual, ontogenetically, is on the left, the oldest is on the right. All, except B, are regarded as male animals. A. F:A.M. No. 32917, M₃ is not fully erupted and shows no appreciable wear. B. F:A.M. No. 32916, M₃ is erupted and shows wear on anterior pair of crescents (part of orbit and zygomatic process of squamosal reversed). C. F:A.M. No. 32919, holotype, M₃ is worn. D. F:A.M. No. 32918, advanced wear on M₃. All × ½. E–N, shows method of taking measurements on teeth presented in table 1. E–F, length of M₃ and crown height (unworn teeth only), crown height taken along trace of rib from apex of crown to base of enamel; G–H, M₃, width; I, P₁–M₃; J, M₁–M₃; K, P₁–P₄; L, M₁–M₃; M, P₁–P₄; N, P₁–M₃.
TABLE 1

Basic Statistics of Merychius verrucomalus
(Measurements are in Millimeters*)

<table>
<thead>
<tr>
<th>Number</th>
<th>Observed Range</th>
<th>Mean</th>
<th>Standard Deviation</th>
<th>Standard Error of Mean</th>
<th>Coefficient of Variation</th>
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<tbody>
<tr>
<td>P1-M3</td>
<td>5</td>
<td>74.5-80.2</td>
<td>76.5</td>
<td>2.26</td>
<td>1.01</td>
</tr>
<tr>
<td>P1-P4</td>
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<td>32.2-34.4</td>
<td>33.2</td>
<td>1.14</td>
<td>0.51</td>
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<tr>
<td>M1-M3</td>
<td>6</td>
<td>42.1-51.3</td>
<td>45.0</td>
<td>3.39</td>
<td>1.38</td>
</tr>
<tr>
<td>Length, M3</td>
<td>6</td>
<td>18.5-22.1</td>
<td>19.8</td>
<td>1.32</td>
<td>0.54</td>
</tr>
<tr>
<td>Width, M3</td>
<td>6</td>
<td>14.6-16.1</td>
<td>15.3</td>
<td>0.52</td>
<td>0.21</td>
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<tr>
<td>Height, M3</td>
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<td>18.7-21.8</td>
<td>19.8</td>
<td>1.71</td>
<td>0.98</td>
</tr>
<tr>
<td>Malar depth</td>
<td>6</td>
<td>21.0-31.4</td>
<td>25.0</td>
<td>4.05</td>
<td>1.65</td>
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<tr>
<td>Skull length</td>
<td>3</td>
<td>152.3-161.1</td>
<td>157.1</td>
<td>4.46</td>
<td>2.58</td>
</tr>
<tr>
<td>P1-M3</td>
<td>5</td>
<td>82.3-88.5</td>
<td>84.3</td>
<td>2.50</td>
<td>1.12</td>
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<tr>
<td>P1-P4</td>
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<td>32.2-35.3</td>
<td>33.6</td>
<td>1.35</td>
<td>0.60</td>
</tr>
<tr>
<td>M1-M3</td>
<td>6</td>
<td>48.3-65.7</td>
<td>54.2</td>
<td>7.03</td>
<td>2.87</td>
</tr>
<tr>
<td>Length, M3</td>
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<td>22.1-26.8</td>
<td>24.7</td>
<td>1.68</td>
<td>0.68</td>
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<tr>
<td>Width, M3</td>
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<td>10.0</td>
<td>0.71</td>
<td>0.29</td>
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<tr>
<td>Height, M3</td>
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<td>18.3-21.3</td>
<td>19.4</td>
<td>1.66</td>
<td>0.96</td>
</tr>
</tbody>
</table>

* Measurements on teeth were taken as shown in figure 3E-N.

Nos. 32918, 32919, and 32967) have the largest tuberosities and the most prominent sagittal crests and are interpreted as belonging to male individuals, the other skulls (F:A.M. Nos. 3412, 32917, 32916, 32966 and probably U.N.S.M. No. 2-10-8-36) have smaller bosses and crests, but also have all stages of tooth wear and are probably those of young male, as well as female animals.

The mandible is nearly straight along its ventral border, is markedly concave in the region of the anterior surface of the symphysis (a feature common in oreodonts), and has a large angular process, the size of which, however, varies, depending on individual age (fig. 2B). The apophysis posterior to the condyle is small.

Postcranial material associated with skulls has been recovered. The best skeleton is specimen F:A.M. No. 32918, which includes a partial axial skeleton, partial scapula, pelvis, humeri, radii, and ulnae, a partial femur, tibiae, pes, and manus. These elements are not particularly robust, although they belong to a presumed male individual, and are similar to those of other Merychius of comparable size (fig. 4A-G).

Discussion: Schultz and Falkenbach (1947) referred U.N.S.M. No. 2-10-8-36 and F:A.M. No. 34312 to Merychius elegans, apparently on the basis of size and stratigraphic position, because they lacked knowledge
Fig. 4. Postcranial elements of *Merychys verrucosalis*. A, anterior view and B, external view of humerus, F:A.M. No. 32918; C, anterior view and D, external view of ulna and radius, F:A.M. No. 32919, holotype; E, anterior view and F, posterior view of tibula (with distal end of fibula), F:A.M. No. 32918; G, left innominate bone, F:A.M. No. 32918. All $\times \frac{1}{2}$. 
Fig. 5. Generalized historical review of nomenclature, pertinent to the present report, of rock-stratigraphic units and local faunas used for western Nebraska and adjacent regions. The amount of time indicated between the units is greatly minimized. The spot in Sinclair Draw where Matthew (in Osborn, 1910, p. 354) introduced the term Snake Creek Formation, was relocated by M. F. Skinner during the summer of 1969.
of specimens having maximum development of the malar tuberosity as now known, and simply noted for both skulls that the “. . . zygomatic arches are robust below the orbits and flare outwardly” (Schultz and Falkenbach, 1947, p. 193). Additional specimens collected since 1947 from the Runningwater Formation indicate that the robust zygomatic arches that flare outwardly are not simply variations within Merychys elegans, but that individuals with this character represent a distinct and specialized species within the genus.

The malar tuberosities show remarkable similarity of form to the rugose areas of attachment of the “warts” of Recent African wart hogs, Phacochoerus. The “warts” in these pigs are paired dermal structures situated on the integument of the face, the largest pair occurs below the eyes. This pair overlies a prominent and rugose area on the bone of the zygomatic arch, although the bone does not extend into the “wart” to give it internal support. The rugosities in Phacochoerus, however, are posterior on the arch, and include in their formation the posterior part of the jugal, as well as the anterior part of the zygomatic process of the squamosal. Old male individuals of Phacochoerus have the largest “warts” as they may grow to several inches in length. Female and young male individuals have smaller and less prominent ones. Similarly, male individuals have the most prominent and most rugose bony attachments for these structures. Although there is abundant literature on Phacochoerus no mention is made of the possible use of its “warts.” Because this information is unavailable, an interpretation of the possible use of similar structures in Merychys verrucomalus is impossible.

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