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PARTIAL SKULL OF ZYGOLOPHODON (MAMMALIA, PROBOSCIDEA) FROM THE BARSTOW FORMATION OF CALIFORNIA

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The first proboscideans in North America are from the family Mammutidae represented by Zygolophodon, which evidently arrived via Asia in the late Hemingfordian (Webb, 1992; Tedford et al., 2004; Prothero, Davis, and Hopkins, 2008). Zygolophodon is known from Barstovian assemblages from California, Colorado, Oregon, Montana, Nebraska, Wyoming, Nevada, and Saskatchewan (Tedford et al., 1987; Lambert and Shoshani, 1998; Tedford et al., 2004).

In May 1965, while prospecting outcrops of the Barstow Formation in the Mud Hills a few miles north of Barstow, California (Fig. 1), Mr. Ken Monroe found a partial proboscidean skull. Shortly thereafter, it was collected by a crew from the Raymond M. Alf Museum of Paleontology (RAM) led by Dr. Raymond Alf. The skull is referred to Zygolophodon, which has been reported from Miocene to Pliocene strata in Europe, Africa, Asia, North America, and South America (Osborn, 1936; Shoshani and Tassy, 1996; McKenna and Bell, 1997). The genus may consist of as many as eight species, Z. proavus, Z. aegyptensis, Z. morotoensis, Z. gobiensis, Z. turicensis, Z. tapiroides, Z. metachinjienensis, and Z. gromovae (Madden and Storer, 1985; Tobien, 1996; Tassy, 1996a) but only Z. proavus is definitely known from North America (Lambert and Shoshani, 1998). The partial skull of Zygolophodon from the Barstow Formation is of particular interest due to its rarity and size, because it represents the only skull of the genus from North America and its teeth are significantly smaller than those of Z. proavus.


Proboscidean dental terminology follows that advocated by Tassy (1996b:fig 3.3). Dental measurements were made using a Mitutoyo micrometer.

SYSTEMATIC PALEONTOLOGY
PROBOSCIDEA Illiger, 1811
MAMMUTIDAE Hay, 1922
ZYGOLOPHODON Vacek, 1877
ZYGOLOPHODON cf. Z. PROAVUS Cope, 1873 (Figs. 3–4)

Referred Specimen—RAM 908, a crushed partial skull preserving the ventral portion of the palate, zygomatic arches, and basicranium, with complete RM3 and LM3 and damaged RM2 and LM2.

Locality and Horizon—RAM 908 is from RAM locality V201006, described in the RAM locality database as approximately 1 mile east of Owl Canyon. This vague information does have value, because about 1 mile east of Owl Canyon, the Skyline Tuff and the lower part of the unnamed upper member of the Barstow Formation crop out in the north half of Section 29, Township 11 North, Range 1 West (Woodburne, Tedford, and Swisher, 1990). This is the only area east of Owl Canyon where the unnamed upper member is exposed and these strata contain numerous beds of green mudstone, the rock type that filled pore spaces in RAM 908. Because proboscidean remains have only been recovered from the unnamed upper member of the Barstow Formation (Woodburne, Tedford, and Swisher, 1990; Pagnac, 2005, 2009) and Section 29 is the only area where the unnamed upper member is exposed east of Owl Canyon, RAM 908 is most likely derived from this area and its corresponding stratigraphic level. At least one attempt was made to relocate the site: Dr. Alf was taken to this area in the mid-1980s by Mr. Grant Meyer (then Director of the RAM) but he did not recognize the locality. However, Woodburne, Tedford, and Swisher (1990:475) describe the stratigraphic occurrence of RAM 908 as being collected “just beneath the Dated Tuff.” This reference is problematic because data supporting this precise stratigraphic placement couldn’t be found (M. Woodburne, pers. comm., December 2010). Based on available evidence, RAM 908 is most likely from the unnamed upper member, but the exact location may never be determined. The estimated stratigraphic placement of RAM 908 is shown in Figure 2.

Description—RAM 908 is a partial skull preserving most of the ventral surface of the cranium posterior to the M2s (Fig. 3). The thin zygomatic arches, broad gnoid fossae, robust occipital condyles, and well-preserved M3s are the most distinctive features of RAM 908. The partial skull is dorsoventrally flattened, with minor lateral displacement of cranial elements. The surface texture of bone is rugose and pitted, and there are a generally parallel series of en echelon fractures oriented obliquely to the anteroposterior axis of the skull that are most prevalent in the occipital region. Spacing of fractures is about 1.0 cm, with a vertical displacement of 1.0–3.0 mm. Both tympanic bullae are broken and green mudstone has filled their inner regions. Diagenetic distortion of the skull from crushing is most evident when the surface areas of the left and right pterygoid-occipital regions are compared, left being greater in area (Fig. 3). Additionally, the skull is fractured and slightly offset laterally just posterior to the M3s. The left zygomatic arch was missing but has been reconstructed based on the intact right zygomatic arch. Skull measurements are as follows: internal width of palate (at fourth loph of M3), 100.0 mm; palatal length from M2 anterior edge to choanae, 239.0 mm; maximum cranium width at zygomatic arches, 543.0 mm; skull length from occipital condyles to M2 anterior edge, 560.0 mm; length of basicranium from choanae to foramen magnum, 260.0 mm; width of basicranium taken at lateral borders of gnoid fossae, 435.0 mm.

RAM 908 has both M2s and M3s (Fig. 3). The crowns of the M2s are heavily damaged but the crowns of the M3s are complete. The left M2 and M3 are closely appressed, but the right M2 and M3 are slightly separated as a result of crushing of the cranium. The M2s have three heavily worn and incomplete lophs that provide little information. However, a median sulcus and the basic cusps of the first (paracone, protocone), second (hypocone, metacone), and third lophs (postentoconule, third postrite cusp) are present.

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In contrast to the M2s, crowns of the M3s are well preserved (Fig. 4). Four lophs are present. The first three lophs narrow posteriorly, and the fourth loph is much less developed. As diagnostic of *Zygolophodon*, the M3s of RAM 908 have robust zygodont crests separated by deep valleys. The paracone,

metacone, third postcusp, protocone, hypocone, and postentococone are large and exhibit little or no wear. Pretrite cusps are more worn than posttrite cusps and the third posttrite cusp is unworn. The median sulcus is weakly developed. Posteriorly, the sulcus is offset progressively labially at each successive interloph. Mesococonelets are present on the third loph, with the pretrite mesococonelet being much smaller than the posttrite mesococonelet.
TABLE 1. Lengths and loph widths (both in mm) of M2s and M3s of *Zygolophodon*.

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>Tooth</th>
<th>Length</th>
<th>Loph 1</th>
<th>Loph 2</th>
<th>Loph 3</th>
<th>Loph 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>RAM 908</td>
<td>LM2</td>
<td>84.3*</td>
<td>70.8*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RM2</td>
<td>84.2*</td>
<td>68*</td>
<td>69.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>LM3</td>
<td>127.3</td>
<td>73.8</td>
<td>74.4</td>
<td>66.1</td>
<td>45.8</td>
</tr>
<tr>
<td></td>
<td>RM3</td>
<td>128.2</td>
<td>76.0</td>
<td>75.8</td>
<td>67.4</td>
<td>48.3</td>
</tr>
<tr>
<td>NMC 9999</td>
<td>RM3</td>
<td></td>
<td></td>
<td>83.0</td>
<td></td>
<td>68.0</td>
</tr>
<tr>
<td>F:AM 23337</td>
<td>LM2</td>
<td>109.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RM2</td>
<td>105.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>LM3</td>
<td>153.5</td>
<td>89.1</td>
<td>84.7</td>
<td>73.3</td>
<td>56.7</td>
</tr>
<tr>
<td></td>
<td>RM3</td>
<td>150.2</td>
<td>92.3</td>
<td>88.8</td>
<td>78.8</td>
<td>61.0*</td>
</tr>
<tr>
<td>AMNH 8137</td>
<td>RM3</td>
<td>150.2</td>
<td>87.6</td>
<td>95.8</td>
<td>85.3</td>
<td>60.6</td>
</tr>
</tbody>
</table>


Central conules are not present, but the protocone wear facet extends onto a thickening of enamel developed on its anterior and posterior slopes. This gives the false impression that the posterior and anterior extensions of this wear facet indicate that weakly developed central conules were present. This thickening of the enamel is also seen on the anterior and posterior slopes of the hypocone and anterior slope of the postentoconule. In general, the labial slopes of the lophs are much steeper than their lingual slopes, whereas the anterior and posterior slopes of the lophs are about equal. An ectoflexus is present on all three interlophs. A well-developed lingual cingulum is present anterior to the protocone that extends to the ectoflexus of the third interloph. A labial cingulum is only present on the anterior and posterior parts of the paracone and posterior to postcuspules in the fourth loph.

Fourth lophs are unworn and the right and left M3s differ in their cusp development. The fourth loph of right M3 has a large main cuspule positioned on the posterior margin of the tooth, with a smaller cuspule developed anterolingually and four progressively smaller ones developed labi-ally, with the most labial one being very small and positioned on the cingulum. The right M3 also has a small cuspule on the anterior slope of the main-cuspule. The main cuspule of the left M3 is slightly larger and is positioned more lingually than the main cuspule of the right M3. Four cuspsules are developed labial to the main cuspule on the left M3 that get progressively lower labially and another cuspule is positioned anterolingual to the main cuspule. A small cuspule is developed posterolingual to the main cuspule on the left M3, unlike the right M3, which has a small cuspule anterior to the main cuspule. Measurements of the dentition of RAM 908 are given in Table 1.

Differences in cusp development in the fourth lophs of M3s from RAM 908 are significant because they show that fourth loph morphology can vary within a single individual. This indicates that the development and positioning of cusps on the fourth loph of the M3 in *Zygolophodon* should be used with caution if employed in phylogenetic analysis of mammutids.

**DISCUSSION**

North American species of *Zygolophodon* have a complex taxonomic history. *Mastodon proavus* was named by Cope (1873) based on AMNH 8523 from Pawnee Creek, Colorado. Decades later, *Mastodon merriami* was described by Osborn (1921). Soon thereafter, Osborn (1922) erected *Miomastodon*, named *Miomastodon merriami* the genotypic species, and placed *"Mastodon" proavus* (Cope, 1873) and *"Mastodon" matthewi* (Osborn, 1921) from western Nebraska in *Miomastodon; "Mastodon" tapiroides americanus* (Schlesinger, 1922) from Hun-
Storer (1985). NMC 9999 appears to be nearly un worn, but damaged, because part of the labial, lingual, and anterior margins of the tooth are missing (Madden and Storer, 1985:fig.1). The cusp pattern on the loths of NMC 9999 is more complex than in RAM 908, F:AM 23337, and AMNH 8137, with mesoeocelets present on the first three loths; small central cones may also be present but this is unclear, because the illustration of NMC 9999 (Madden and Storer, 1985:fig.1) lacks sufficient detail. A major difference between the Wood Mountain Formation M3 and the others is that its fourth loth has four small cusps (Madden and Storer, 1985) and its anteroposterior length is much less than the fourth loths in RAM 908, F:AM 23337, and AMNH 8137.

Differences in morphology between M3s of RAM 908 and those referred to Z. proavus from Colorado, Montana, and Canada are relatively minor. Thus, the Barstow Formation skull could be confidently referred to the species except for a disparity in tooth dimensions, because the M3s of RAM 908 and NMC 9999 are much smaller than those of F:AM 23337 and AMNH 8137. The length and first loth width of AMNH 8137 from the Deep River Formation are 130.2 mm and 87.6 mm, respectively, similar to the M3s of F:AM 23337 from the Pawnee Creek Formation; lengths of 153.5 and 150.2 mm and first loths widths of 92.3 and 89.1 mm (Table 1). The M3s of RAM 908 are 127.3 and 128.2 mm in length and 73.8 and 76.0 mm in first loth width (Table 1), about 16–19% shorter and 17–21% narrower (first loth) than those of F:AM 23337 and AMNH 8137. Using the scale provided in the illustration of NMC 9999 (Madden and Storer, 185:fig.1), NMC 9999 would be approximately 115.0 mm in length, about 12–13 mm shorter than RAM 908, but 35–38 mm shorter than AMNH 8137 and F:AM 23337. A size disparity of this magnitude could reflect the presence of a smaller species in the Barstow Formation of California and Wood Mountain Formation of Saskatchewan in comparison to Z. proavus from the type area in Colorado (Pawnee Creek Formation) and the single specimen from the Deep River Formation of Montana. Madden (1989) surmised that RAM 908 represented a new dwarf species of "Miomastodon" based on the small size of the upper dentition. But with so few specimens of upper teeth available for Z. proavus, it’s difficult to assess the range in size variation of M3 within the species.

One aspect to consider when assessing tooth dimensions in Zygolophodon is that size differences based on sex in Proboscoidea have long been recognized; for example, study of extant African elephants by Blumenbach (1797). Recognizing sexual dimorphism in extinct groups of Proboscoidea is much more difficult, but sexual dimorphism has been demonstrated in Pleistocene mammoths (Averianov, 1996; Lister, 1996) and Miocene gomphotheres (Tassy, 1996c). Size variation in M3s of Gomphotherium augustidens from the En Pejouan (Miocene) locality in southwest France is approximately 10–20% (Tassy, 1996c:fig.11.14A), variation interpreted to represent sexual dimorphism. Size differences seen in supposed female versus male M3s at En Pejouan are similar to the size differences (16–21%) seen in the small sample of Zygolophodon M3s; RAM 908, in comparison to F:AM 23337 and AMNH 8137 (Table 1). A second specimen of Zygolophodon from the Wood Mountain Formation (SMNH P1665.1, joined dentaries with incisors, rm2–3, and damaged lm2–3) referred to Z. proavus was interpreted to probably represent a male individual based on its large size in comparison to all known lower dentition specimens (n = 4) of the species (Madden and Storer, 1985). If so, the small M3 (NMC 9999) from the same formation could represent a female. If the concept of sexual dimorphism in a Miocene species of Gomphotherium can be extended to Miocene species of Zygolophodon, RAM 908 and NMC 9999 may represent small individuals of Z. proavus that are a reflection of sexual dimorphism. Again, with so few specimens available, it is difficult to assess whether the 16–21% range in size variation is that of a single species with sexual dimorphism perhaps being a contributing factor, or if the size difference denotes the presence of a second Miocene Zygolophodon species in North America. We favor the single-species hypothesis and tentatively refer RAM 908 to Zygolophodon cf. Z. proavus.

CONCLUSIONS

Specimens of the upper dentition of Zygolophodon are very rare and RAM 908 represents the only known skull of the genus from North America. Comparison of RAM 908 to the only North American species of the genus, Z. proavus, is limited to the M3. RAM 908 M3s are similar in morphology to those of Z. proavus from Colorado, Montana, and Saskatchewan, which implies that they represent a single species. However, there is a significant disparity in size because M3s from California are 16–21% smaller than those from Colorado and Montana. With so few specimens available, it is difficult to determine if a second, smaller species of Zygolophodon is present. The interpretation favored here is that RAM 908 represents a small individual of Z. proavus, which could be a rare example of sexual dimorphism in an extinct species, but this cannot be confidently demonstrated. The morphology of the fourth loth in the M3 of Zygolophodon is probably not a useful taxonomic indicator because there is significant variation in the development of the fourth loth between the right and left M3s of RAM 908.

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LITERATURE CITED


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