

This article was downloaded by: [Don Lofgren]

On: 08 November 2011, At: 11:02

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

Partial skull of Zygodolophodon (Mammalia, Proboscidea) from the Barstow Formation of California

Don L. Lofgren^a & Rajsavi S. Anand^b

^a Raymond M. Alf Museum of Paleontology, Claremont, California, 91711, U.S.A

^b The Webb Schools, Claremont, California, 91711, U.S.A

Available online: 08 Nov 2011

To cite this article: Don L. Lofgren & Rajsavi S. Anand (2011): Partial skull of Zygodolophodon (Mammalia, Proboscidea) from the Barstow Formation of California, *Journal of Vertebrate Paleontology*, 31:6, 1392-1396

To link to this article: <http://dx.doi.org/10.1080/02724634.2011.605192>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

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

DON L. LOFGREN^{*1} and RAJSAVI S. ANAND²; ¹Raymond M. Alf Museum of Paleontology, Claremont, California 91711, U.S.A., dlofgren@webb.org; ²The Webb Schools, Claremont, California 91711, U.S.A.

The first proboscideans in North America are from the family Mammutidae represented by *Zygodolophodon*, which evidently arrived via Asia in the late Hemingfordian (Webb, 1992; Tedford et al., 2004; Prothero, Davis, and Hopkins, 2008). *Zygodolophodon* 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 *Zygodolophodon*, 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. metachinjensis*, 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 *Zygodolophodon* 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*.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; F:AM, Frick Collection, American Museum of Natural History, New York; NMC, Canadian Museum of Nature, Ottawa, Ontario; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California; SMNH, Royal Saskatchewan Museum, Regina, Saskatchewan.

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

ZYGLOPHODON Vacek, 1877

ZYGLOPHODON 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 glenoid 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 the basicranium taken at lateral borders of glenoid 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 (postentocone, third postrite cusp) are present.

*Corresponding author.

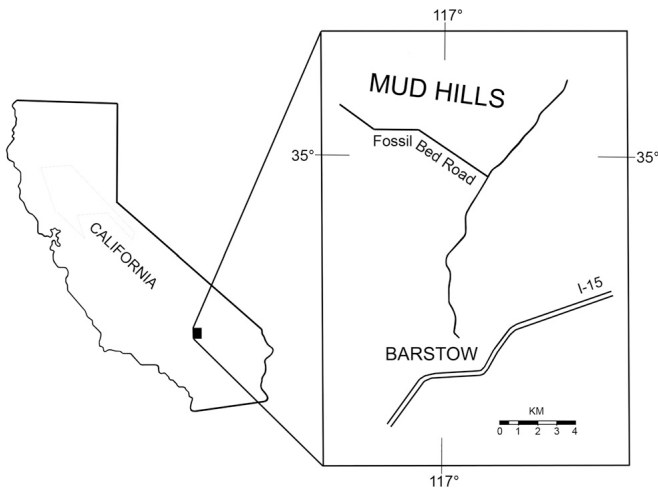


FIGURE 1. Location of the Mud Hills, Mojave Desert, California (adapted from Steinen 1966).

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 *Zygodon*, the M3s of RAM 908 have robust zygodont crests separated by deep valleys. The paracone,

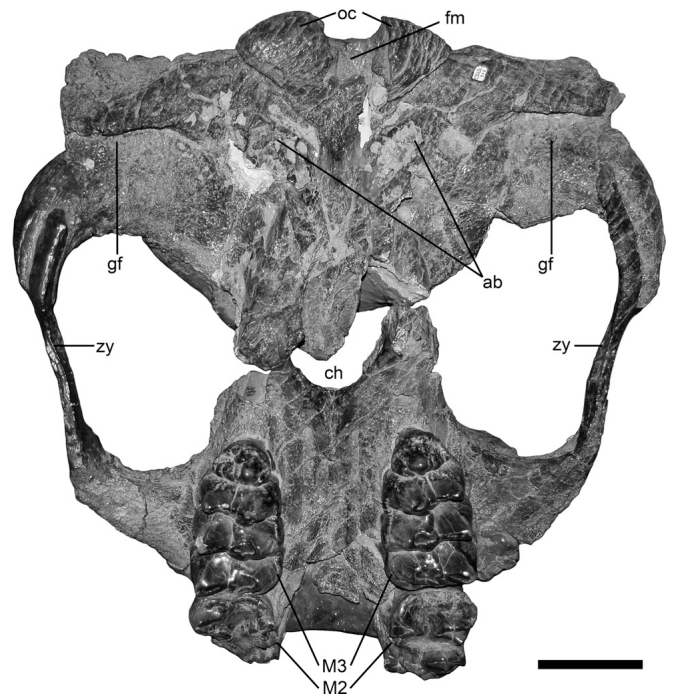


FIGURE 3. Ventral view of RAM 908. **Abbreviations:** ab, auditory bulla; ch, choanae; fm, foramen magnum; gf, glenoid fossa; oc, occipital condyle; zy, zygomatic arch. Scale bar equals 10 cm.

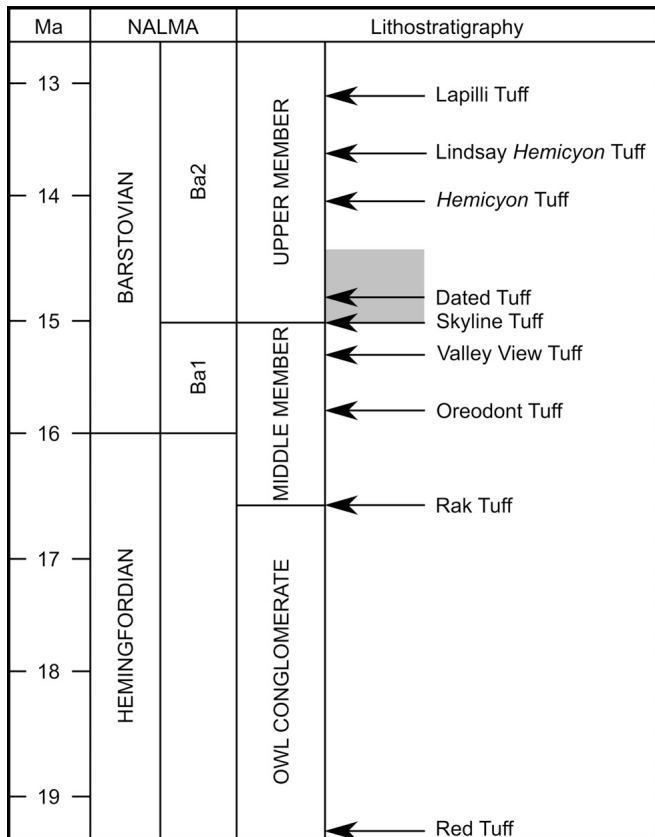


FIGURE 2. Geochronology and biostratigraphic subdivision of the Barstow Formation, with shaded area representing the approximate stratigraphic position of RAM 908. **Abbreviations:** Ba1, early Barstovian biochron; Ba2, late Barstovian biochron; Ma, million years; NALMA, North American Land Mammal Age (adapted from Pagnac, 2009).

metacone, third postrite cusp, protocone, hypocone, and postentoconule are large and exhibit little or no wear. Pretrite cusps are more worn than postrite cusps and the third postrite cusp is unworn. The median sulcus is weakly developed. Posteriorly, the sulcus is offset progressively labially at each successive interloph. Mesoconelets are present on the third loph, with the pretrite mesoconelet being much smaller than the postrite mesoconelet.

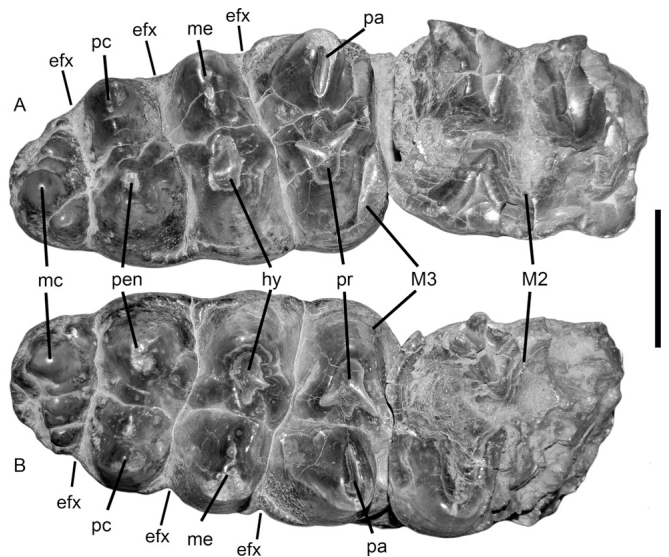


FIGURE 4. Occlusal view of (A) right M2-3 and (B) left M2-3. **Abbreviations:** efx, ectoflexus; hy, hypocone; mc, main cupsule; me, metacone; pa, paracone; pc, third postrite cusp; pen, postentoconule; pr, protocone. Scale bar equals 5 cm.

TABLE 1. Lengths and loph widths (both in mm) of M2s and M3s of *Zygalophodon*.

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

Measurements of NMC 9999 from Madden and Storer (1985:table 1).
*Estimated.

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 postrite cuspules 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 labially, 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 cuspules 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 *Zygalophodon* should be used with caution if employed in phylogenetic analysis of mammutids.

DISCUSSION

North American species of *Zygalophodon* 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-

gary was tentatively included as well. *Miomastodon* was considered a strictly North American zygodont mammutid, except for possible inclusion of the species from Hungary (Osborn, 1936).

In revising the Paleomastodontidae, Madden (1980) considered *Miomastodon* a junior synonym of *Zygalophodon* but did not provide an anatomical basis for his reclassification. This synonymy has persisted (McKenna and Bell, 1997; Shoshani and Tassy, 2005; but see Saunders, 1996), but *Zygalophodon* is usually classified within the Mammutidae, not the Paleomastodontidae (McKenna and Bell, 1997; Shoshani and Tassy, 2005). Madden (1980) also considered *Zygalophodon* to be monotypic, with *Z. tapiroides* having priority. This interpretation was abandoned by its proponent only 5 years later when Madden and Storer (1985) described a specimen of *Z. proavus* from Saskatchewan, Canada. In the most recent review of North American Proboscidea, Lambert and Shoshani (1998) only recognize *Z. proavus* (equals *Z. merriami*, *Z. tapiroides* nomen nudum).

Comparison of RAM 908 to the sample of *Zygalophodon* from North America is limited by rarity of specimens. No other skull of the genus is known. Thus, the point of comparison between RAM 908 and other specimens of the genus is limited to the M3 and only three have been described. All are referred to *Z. proavus*; one each from the Wood Mountain Formation of Saskatchewan (Madden and Storer, 1985), the Pawnee Creek Formation of Colorado (Frick, 1933), and the Deep River Formation of Montana (Madden, 1980). These occurrences, as well as that of RAM 908 (Barstow Formation of California), are all from Barstovian assemblages (Woodburne, Tedford, and Swisher, 1990; Tedford et al., 2004; Pagnac, 2009). The most complete upper dentition of *Zygalophodon* from North America is F:AM 23337, left upper tusk, left partial maxilla with M2–M3, and associated right M2–M3 of *Z. proavus* from the Pawnee Creek Formation of Colorado (Frick, 1933); same formation as holotype of *Z. proavus*, a P4, AMNH 8523 (Cope, 1873). The right M3 of F:AM 23337 is similar in loph morphology and in the development of the lingual cingulum (Frick, 1933:fig. 24) to M3s of RAM 908. Differences are the presence of small pretrite central conules developed anterior to the hypocone and postentoconule in F:AM 23337. In RAM 908, only a thickening of the enamel is seen on the anterior slopes of the hypocone and postentoconule; although with moderate wear, the second and third loph wear facets on RAM 908 and F:AM 23337 would be indistinguishable. F:AM 23337 also differs from RAM 908 as the fourth loph of the Pawnee Creek specimen has three cusps of similar size, with a closely appressed pretrite pair separated from a single postrite cusp by a deep valley. Also, a small cusp is positioned posterior to the pretrite pair, which makes the posterior margin of the tooth asymmetrical, as the lingual half of the loph extends further posteriorly than the labial half.

A well-preserved right M3 (AMNH 8137) from the Deep River Formation of Montana (Schlesinger, 1917; Madden, 1980:fig. 3) is moderately worn and is also similar to RAM 908 and F:AM 23337 in loph and cingulum development. The wear facets on the second and third lophs indicate that small pretrite conules may have been present anterior to the hypocone and postentoconule as seen in F:AM 23337, or that the enamel is thickened in these areas of the tooth as seen in RAM 908. The fourth loph of AMNH 8137 has three cusps with a pretrite pair separated from a single postrite cup by a deep valley and the lingual half of the loph extends further posteriorly than its labial half, features very similar to those seen in F:AM 23337. Unlike any other *Zygalophodon* M3 from North America, the second loph of AMNH 8137 is significantly wider than the first loph (Table 1). The Deep River Formation specimen was referred to *Zygalophodon* "*tapiroides*" by Madden (1980), now *Z. proavus* (Lambert and Shoshani, 1998).

Zygalophodon proavus is also represented in the Wood Mountain Formation of Saskatchewan by joined dentaries (SMNH P1665) and a right M3 (NMC 9999) described by Madden and

Storer (1985). NMC 9999 appears to be nearly unworn, 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 loph of NMC 9999 is more complex than in RAM 908, F:AM 23337, and AMNH 8137, with mesoconelets present on the first three loph; small central conelets 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 loph has four small cusps (Madden and Storer, 1985) and its anteroposterior length is much less than the fourth loph 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 loph width of AMNH 8137 from the Deep River Formation are 150.2 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 loph 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 loph width (Table 1), about 16–19% shorter and 17–21% narrower (first loph) than those of F:AM 23337 and AMNH 8137. Using the scale provided in the illustration of NMC 9999 (Madden and Storer, 1985: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 *Zygodolophodon* is that size differences based on sex in Proboscidea have long been recognized; for example, study of extant African elephants by Blumenbach (1797). Recognizing sexual dimorphism in extinct groups of Proboscidea 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 *Zygodolophodon* M3s; RAM 908, in comparison to F:AM 23337 and AMNH 8137 (Table 1). A second specimen of *Zygodolophodon* 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 *Zygodolophodon*, 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 *Zygodolophodon* species in North America. We favor the single-species hypothesis and tentatively refer RAM 908 to *Zygodolophodon* cf. *Z. proavus*.

CONCLUSIONS

Specimens of the upper dentition of *Zygodolophodon* 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 *Zygodolophodon* 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 loph in the M3 of *Zygodolophodon* is probably not a useful taxonomic indicator because there is significant variation in the development of the fourth loph between the right and left M3s of RAM 908.

ACKNOWLEDGMENTS

We thank R. Tedford, M. Woodburne, and D. Pagnac for helpful discussions, A. Farke, G.-S. Kim, and J. Taylor for help with figures, J. Meng and J. Galkin from the AMNH for access to specimens, G. Jorgenson, D. Lawler, and J. Shearer of the California Bureau of Land Management for field work permits, the Mary Stuart Rogers Foundation and the David B. Jones Foundation for financial support, and J. J. Saunders and D. Pagnac for their helpful suggestions.

LITERATURE CITED

- Averianov, A. O. 1996. Sexual dimorphism in the mammoth skull, teeth and long bones; pp. 260–267 in J. Shoshani and P. Tassy (eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, U.K.
- Blumenbach, J. F. 1797. *Handbuch der Naturgeschichte*. 5th edition. Dieterich, Gottingen.
- Cope, E. D. 1873. Synopsis of New Vertebrata from the Tertiary of Colorado Obtained during the Summer of 1873. Government Printing Office, Washington, D.C., 19 pp.
- Frick, C. 1933. New remains of trilophodont-tetrabelodont mastodons. *Bulletin of the American Museum of Natural History* 59:505–652.
- Hay, O. P. 1922. Further observations on some extinct elephants. *Proceedings of the Biological Society of Washington* 35:97–101.
- Illiger, C. D. 1811. *Prodromus Systematis Mammalium et Avium Additis Terminis Zoographicis Uttriusque Classis*. Salfeld, Berlin, 301 pp.
- Lambert, W. D., and J. Shoshani. 1998. Proboscidea; pp. 606–621 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary Mammals, Volume 1: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge University Press, Cambridge, U.K.
- Lister, A. M. 1996. Sexual dimorphism in the mammoth pelvis: an aid to gender determination; pp. 254–259 in J. Shoshani and P. Tassy (eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, U.K.
- Madden, C. T. 1980. *Zygodolophodon* from Sub-Saharan Africa, with observations on the systematics of paleomastodontid proboscideans. *Journal of Paleontology* 54:57–64.
- Madden, C. T. 1989. New and dwarf species of mastodon *Miomastodon* from the middle Miocene of Barstow, Southern California. *Geological Society of America Abstracts with Programs* 21, Number 5:109–110.

- Madden, C. T., and J. E. Storer. 1985. The Proboscidea from the Middle Miocene Wood Mountain Formation, Saskatchewan. *Canadian Journal of Earth Sciences* 22:1345–1350.
- McKenna, M. C., and S. K. Bell. 1997. Classification of Mammals above the Species Level. Columbia University Press, New York, 631 pp.
- Osborn, H. F. 1921. First appearance of the true Mastodon in America. *American Museum Novitates* 10:1–6.
- Osborn, H. F. 1922. *Dibelodonedensis* (Frick) of Southern California, *Miomastodon* of the middle Miocene, new genus. *American Museum Novitates* 49:1–4.
- Osborn, H. F. 1936. Proboscidea. A Monograph of the Discovery, Evolution, Migration and Extinction of the Mastodonts and Elephants of the World, Volume 1: Moeritherioidea, Deinotherioidea, Mastodontoidea. American Museum Press, New York, 802 pp.
- Pagnac, D.C. 2005. A systematic review of the mammalian megafauna of the middle Miocene Barstow Formation, Mojave Desert, California. Ph.D. dissertation, University of California–Riverside, Riverside, California, 384 pp.
- Pagnac, D.C. 2009. Revised large mammal biostratigraphy and biochronology of the Barstow Formation (Middle Miocene), California. *Paleobios* 29:48–59.
- Prothero, D. R., E. D. Davis, and S. B. Hopkins. 2008. Magnetic stratigraphy of the Massacre lake beds (late Hemingfordian, early Miocene), northwest Nevada, and the age of the “Proboscidean Datum” in North America. *New Mexico Museum of Natural History and Science Bulletin* 44:239–245.
- Saunders, J. J. 1996. North American Mammutidae; pp. 271–279 in J. Shoshani and P. Tassy (eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, U.K.
- Schlesinger, G. 1917. Die Mastodonten des K.K. Naturhistorischen Hofmuseums. *Denkschriften der Naturhistorischen Hofmuseums, I, Geologisch-Palaontologische Reihe* 1, 230 pp.
- Schlesinger, G. 1922. Die Mastodonten der Budapester Sammlungen. *Geologica Hungaria, Editio Separata*, 2, 284 pp.
- Shoshani, J., and P. Tassy. 1996. *The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, U.K., 472 pp.
- Shoshani, J., and P. Tassy. 2005. Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behavior. *Quaternary International* 126–128:5–20.
- Steinen, R. P. 1966. Stratigraphy of the middle and upper Miocene, Barstow Formation, California. M.S. thesis, University of California–Riverside, Riverside, California, 150 pp.
- Tassy, P. 1996a. Who is who among the Proboscidea?; pp. 39–48 in J. Shoshani and P. Tassy (eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, U.K.
- Tassy, P. 1996b. Dental homologies and nomenclature in the Proboscidea; pp. 21–25 in J. Shoshani and P. Tassy (eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, U.K.
- Tassy, P. 1996c. Growth and sexual dimorphism among Miocene elephants: the example of *Gomphotherium angustidens*; pp. 92–100 in J. Shoshani and P. Tassy (eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, U.K.
- Tedford, R. H., T. Galusha, M. F. Skinner, B. E. Taylor, R. W. Fields, J. R. Macdonald, J. M. Rensberger, S. D. Webb, and D. P. Whistler. 1987. Faunal succession and biochronology of the Arikarean through Hemphillian interval (late Oligocene through earliest Pliocene epochs) in North America; pp. 153–210 in M. O. Woodburne (ed.), *Cenozoic Mammals of North America, Geochronology and Biostratigraphy*. University of California Press, Berkeley, California.
- Tedford, R. H., L. B. Albright III, A. D. Barnosky, I. Ferrusquia-Villafranca, R. M. Hunt Jr., J. S. Storer, C. C. Swisher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler. 2004. Mammalian biochronology of the Arikarean through Hemphillian interval (late Oligocene through early Pliocene epochs); pp. 169–231 in M. O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America*. Columbia University Press, New York.
- Tobien, H. 1996. Evolution of zygodons with emphasis on dentition; pp. 76–85 in J. Shoshani and P. Tassy (eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, U.K.
- Vacek, M. 1877. Überösterreichische Mastodonten und ihre Beziehungen zu den Mastodon-Arten Euripas. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 7:1–45.
- Webb, S. D. 1992. A brief history of New World Proboscidea with emphasis on their adaptations and interactions with man; pp. 16–34 in J. W. Fox, C. B. Smith and K. T. Wilkins (eds.), *Proboscidean and Paleoindian Interactions*. Baylor University, Waco, Texas.
- Woodburne, M. O., R. H. Tedford, and C. C. Swisher III. 1990. Lithostratigraphy, biostratigraphy, and geochronology of the Barstow Formation, Mojave Desert, southern California. *Geological Society of America Bulletin* 102:459–477.

Submitted March 8, 2011; revisions received June 16, 2011; accepted July 9, 2011.

Handling editor: Jessica Theodor.