

FIRST PLEISTOCENE JUMPING MOUSE (*ZAPUS*, ZAPODINAE, RODENTIA) FROM UTAH

Dennis R. Ruez, Jr.,¹ and Christopher J. Bell¹

ABSTRACT.—Two of the Little Dell Dam fossil localities produced the 1st Pleistocene records of the jumping mouse *Zapus* from Utah. We describe these teeth in detail and compare their morphology with both extinct and extant jumping mouse taxa. Although it is not possible to confidently assign these specimens to a particular species, the Little Dell Dam fossils are clearly distinct from the only living jumping mouse (*Zapus princeps*) currently known from Utah. The paracone is attached to the rest of the occlusal surface of the upper 1st and 2nd molars in modern *Z. princeps* from Utah; the paracone is isolated in the molars from Little Dell Dam. The fossils from Little Dell Dam are the 1st reported records of Pleistocene *Zapus* west of the Rocky Mountains.

Key words: Little Dell Dam, Utah, Pleistocene, *Zapus*, Zapodinae.

Pleistocene vertebrates from Utah are mainly limited to isolated fossils from sediments associated with Ice Age Lake Bonneville (Nelson and Madsen 1980, 1987, Miller 1982, Jefferson et al. 1994, Gillette and Miller 1999). The fauna from Little Dell Dam Locality 2 (LDD2; Salt Lake County, UT) consists of at least 14 species of mammals (Gillette et al. 1999), a diversity only exceeded in the Pleistocene of Utah by Crystal Ball Cave (49 spp.; Heaton 1984, 1985), Silver Creek Junction (26 spp.; Miller 1976), Rock Springs Cave (17 spp.; Jefferson et al. 1994), and Bechan Cave (17 spp.; Jefferson et al. 1994). These more taxonomically diverse assemblages differ from LDD2 in being Rancholabrean (late Pleistocene) in age. Based on arvicoline rodents, the LDD2 fauna was assigned to the Irvingtonian land mammal age (middle Pleistocene), making it the first-known, and oldest, taxonomically diverse Irvingtonian vertebrate fauna known from Utah (Gillette et al. 1999). The less diverse Little Dell Dam Locality 1 (LDD1) fauna contains only 7 taxa and was also estimated to be Irvingtonian in age but younger than LDD2 (Gillette et al. 1999).

Among the LDD2 specimens are 5 complete teeth of the jumping mouse *Zapus* (Zapodinae, Rodentia). Additionally, LDD1 and LDD2 each yielded a single, unidentified, fragmentary zapodine tooth. These 7 specimens constitute the 1st Pleistocene records of *Zapus*

from Utah. Here we describe these teeth in detail and compare them with the known dentition of modern and extinct zapodine species. In Utah there is a single Holocene locality with records of *Zapus*; 2 teeth assigned to *Z. princeps* were recovered from the Stevens Creek fauna (Smith et al. 1999). *Zapus princeps* is the only zapodine that occurs in Utah today (Durrant 1952), although *Z. hudsonius* does extend into eastern Colorado and Wyoming (Clark and Stromberg 1987, Fitzgerald et al. 1994). A 3rd species, *Z. trionatus*, occurs today in coastal regions of California, Oregon, Washington, and British Columbia (Hall 1981).

MATERIALS AND METHODS

Dental terminology follows that employed by Martin (1989) for advanced zapodines and is supplemented with additional topographic names utilized by Wang (1985) for brachyodont zapodine molars (Fig. 1). Neither Martin (1989) nor Wang (1985) provided names for all the reentrant folds. Those not labeled by Martin (1989) are provided names (Fig. 1) in a manner that is consistent with his conventions. Additionally, we follow the usage of entolophid as employed by Reig (1977), which corresponds to the hypolophid of Wang (1985) and “hypolophulid I” of Wood and Wilson (1936). Hypolophulid is retained in this paper for the direct

¹Department of Geological Sciences, Jackson School of Geosciences, The University of Texas at Austin, Austin, TX 78712-0254.

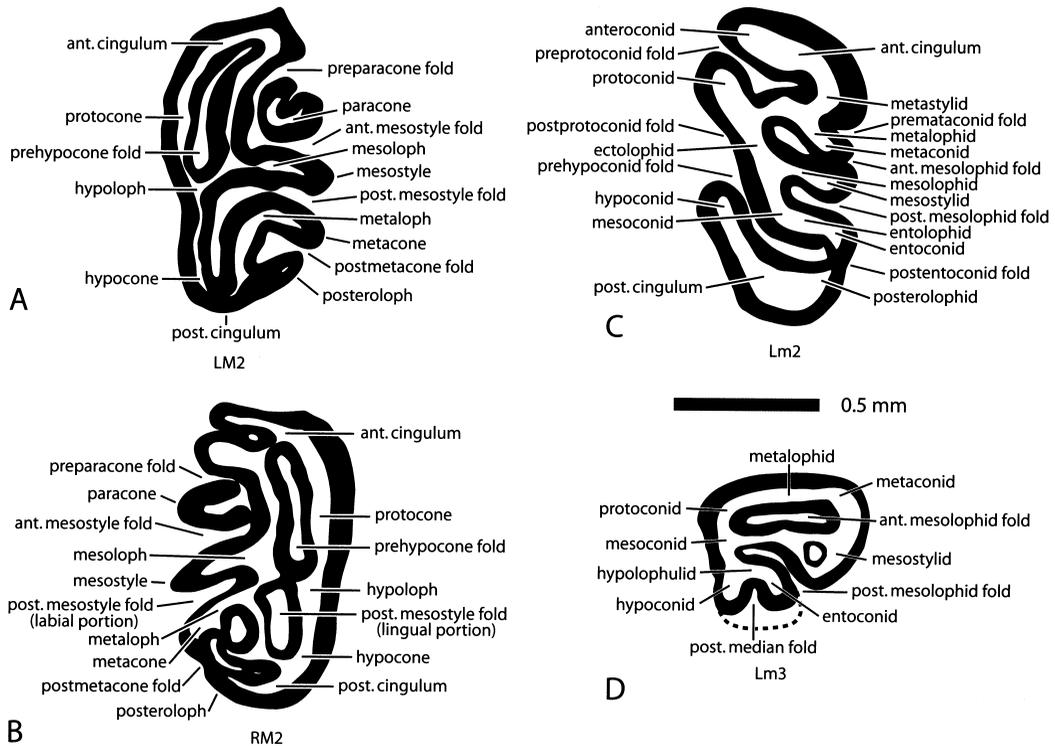


Fig. 1. Occlusal patterns of *Zapus* molars from Little Dell Dam 2, Utah. The thickness of the black areas indicates the thickness of the enamel expressed on the occlusal surface. A, UMNH VP 12324, LM2; B, UMNH VP 12325, RM2; C, UMNH VP 12326, Lm2; D, UMNH VP 12327, Lm3. For all teeth pictured, anterior is toward the top of the page. Labial is toward the right for A and toward the left for B, C, and D. The dashed line on UMNH VP 12327 indicates the approximate outline of the posterior portion of the tooth if not for the aberrant wear. Abbreviations: ant. = anterior; post. = posterior.

connection between the hypoconid and entoconid and is the equivalent of “hypolophulid II” of Wood and Wilson (1936). We treat *Zapus* as a member of Zapodinae but do not address the taxonomic status of the Zapodidae, namely, whether Dipodidae exclusive of zapodines is monophyletic, because the issue is not germane to our paper.

All fossils are curated in the University of Utah Museum of Natural History (UMNH). Six were recovered from the lower peat layer of LDD2, and a single partial molar is known from LDD1. The zapodine tooth fragments from LDD1 (UMNH VP 12329) and LDD2 (UMNH VP 12328) are too incomplete for confident taxonomic allocation and are not described here. Camera lucida drawings were made with an Olympus S2X9 binocular microscope. Abbreviations: M, upper molar; m, lower molar; L, left; R, right.

DESCRIPTIONS

The occlusal surface of UMNH VP 12324 (LM2) is elongate in outline, with wide openings for the labial reentrant folds (Fig. 1A). There is a prominent anterior cingulum with a small, anteriorly pointing projection on the labial half. The preparacone fold gradually arches posteriorly to connect with the anterior mesostyle fold. The lunate paracone is isolated and concave anterolabially. The hypoloph exhibits variable enamel thicknesses along the traverse from the anterior cingulum to the mesoloph to the hypocone. The protocone is connected to the hypoloph, closing the prehyppocone fold and forming a large enamel lake with variable enamel thickness. The mesoloph extends out almost directly labially as a thin finger from the hypoloph. The mesostyle projects laterally farther than the

other labial cusps. The posterior mesostyle fold reaches lingually across the tooth, nearly pinching out the thin band of dentine along the distal portion of the hypoloph, then turns posteriorly and extends to the posterior cingulum, closing the dentine connection between the hypocone and posteroloph-metaloph juncture. Lingual to the metacone and posteroloph, the postmetacone fold is expanded anteroposteriorly. The occlusal surface has a maximum length of 1.06 mm and width of 0.61 mm.

The RM2 (UMNH VP 12325; Fig. 1B) is less worn than the LDD2 LM2 (UMNH VP 12324). As a result there are 4 noticeable differences. The prehyocone fold has 2 interruptions, both more medially placed than in UMNH VP 12324. The paracone does not yet enclose any dentine and is not completely isolated from the rest of the occlusal pattern. The posterior mesostyle fold is split into lingually and posteriorly directed portions by a dentine connection from the mesoloph to the metaloph. Finally, the postmetacone fold is incompletely formed. The occlusal surface has a maximum length of 1.06 mm and width of 0.63 mm.

The LDD2 Lm2 (UMNH VP 12326; Fig. 1C) is slender, tapers slightly posteriorly, and lacks enamel lakes in the anterior and posterior cingula. The anterior cingulum is asymmetrical, protruding much farther anteriorly at the labial edge. The anteroconid is bulbous and lacks any hint of an anterior median fold. From the position of the metastylid, there is a posterolabially trending dentine connection to the arcuate metalophid. The metaconid lies at the end of a posterolingual extension of the metalophid. At the labial edge of the anterior portion of the tooth, the preprotoconid fold opens from a narrow slit between the anteroconid and protoconid into a small horizontal valley bounded by the metastylid lingually and the metalophid posteriorly. The ectolophid shows a very faint postprotoconid fold labial from the position of the anterior mesolophid fold. The mesostylid is slightly expanded compared with the width of the mesolophid and the enamel of the former contacts that of the metaconid. The result is lingual closure of the anterior mesolophid fold to create an enamel lake. The opening of the posterior mesolophid fold is only constricted slightly by the expansion of the mesostylid. The narrow prehyo-

conid fold is oriented almost directly antero-posteriorly and separates the mesoconid from the posterior cingulum. The entoconid turns sharply posteriorly and makes a very slight connection with the posterior cingulum at the lingual edge of the tooth, separating the postentoconid fold from the elongated prehyoconid fold. The central portion of the posterior cingulum is greatly expanded, although it lacks a postcingular enamel lake. The occlusal surface has a maximum length of 1.10 mm and a width of 0.61 mm.

The anterior edge of the Lm3 (UMNH VP 12327) is nearly straight, with the band of dentine within the metalophid of uniform thickness (Fig. 1D). Neither the protoconid nor the metaconid is expanded. The metaconid and mesostylid connect at the lingual edge of the tooth, enclosing the anterior mesolophid fold as an enamel lake. A 2nd, smaller enamel lake occurs near the mesostylid. The triangular mesostylid is greatly expanded and nearly contacts the small entoconid. Those 2 regions bracket a narrow posterior mesolophid fold that penetrates to the mesoconid. The posterior portion of the tooth exhibits aberrant wear. At the occlusal surface a short posterior median fold separates the hypoconid from the entoconid. If this portion of the tooth were worn to the same level as the occlusal surface of the rest of the tooth, no fold would be present. The occlusal surface has a maximum length of 0.49 mm and width of 0.61 mm.

COMPARISONS AND DISCUSSION

Characters allowing generic determination among zapodines were discussed by Preble (1899), Krutzsch (1954), Klingener (1963), and Martin (1989). The LDD2 specimens have a flat occlusal surface and well-developed enamel lophes. Among zapodines these general features are found in the extant *Zapus*, *Napeozapus*, and *Eozapus*, and in the extinct *Pliozapus* and *Javazapus*. Of *Pliozapus*, only the lower dentition is known. Among the 3 living zapodines, the occlusal pattern complexity of the upper and lower 1st and 2nd molars of *Zapus* is intermediate between the simple pattern in *Eozapus* and the numerous additional enamel flexures in *Napeozapus*. In each of the morphological features discussed below, the LDD2 teeth match the occlusal pattern seen in *Zapus*.

The posterior mesostyle fold on the LDD2 M2 fold has a posteriorly directed portion, unlike *Eozapus* and *Javazapus*. The prehypocone fold runs anteroposteriorly, whereas a smaller, but more equidimensional, prehypocone fold (when present) lies diagonally in *Eozapus*; this fold is absent in *Javazapus*. Labial reentrant folds are not closed by the labial cingulum as in *Napeozapus*; the anterior and posterior cingula are more pronounced than in *Napeozapus*. The anterior mesostyle fold and preparacone fold do not extend lingually more than halfway across the tooth as they do in *Eozapus* and *Javazapus*.

The LDD2 m2 has a deep and constricted prehypocnid fold unlike the shallow and broad equivalent in *Eozapus*. The anteroconid is much simpler and smaller than in *Napeozapus*. The LDD2 specimen lacks the cingulum that closes all of the lingual reentrant folds in *Napeozapus*. The mesostylid is connected to the ectolophid via the mesolophid rather than to the metaconid (and lacking a mesolophid) as in *Javazapus*. The entolophid is connected to the posterior cingulum at the lingual border of tooth unlike in *Pliozapus*, *Javazapus*, and *Eozapus*. The LDD2 m2 has a much larger anterior cingulum than *Pliozapus*.

The LDD2 m3 lacks the preprotoconid fold present in *Napeozapus*. The LDD2 tooth has 2 lingual reentrant folds of different lengths, instead of 3 folds of equal lengths as in *Eozapus*. The anterior mesolophid fold of the LDD2 specimen is isolated within a dentine field and should perhaps be more properly termed an enamel lake instead of a fold (Martin 1989).

For species-level comparisons we utilized the descriptions and published illustrations of numerous taxa (Wilson 1936, Hibbard 1941, 1951, Krutzsch 1954, Shotwell 1956, Klingener 1963, Hibbard et al. 1978, Martin 1989, 1994). Comparisons with many taxa are not possible because the upper dentition for several species is not known. Additionally, ontogenetic variation precludes the clear determination of unique diagnostic characters in some cases. The LDD2 *Zapus* molars are unique in being significantly smaller than other described taxa.

The primary difference between the m2 from LDD2 and those from *Zapus sykesae* (Martin 1989) is the absence of anterior and posterior enamel lakes in the former speci-

men. The LDD2 m3 does not close the posterior mesolophid fold into an enamel lake as in 4 of 5 m3's of *Z. sykesae*, but the opening is constricted and may close with additional wear. Each LDD2 M2 has continuous dentine from the anterior cingulum to the hypocone; this is 1 of 3 patterns found in *Z. sykesae*.

Zapus sandersi is known from more specimens and more localities than any other extinct species of the genus (Martin 1989). The anterior cingula of *Z. sandersi* m2's have enamel lakes, unlike the specimen from LDD2. The anterior mesolophid fold is closed in the LDD2 m2 but is not even constricted in *Z. sandersi*. *Zapus sandersi* has no indication of a premetaconid fold like that present in the LDD2 m2. The m3 of *Z. sandersi* has as many as 5 enamel lakes (Hibbard et al. 1978; Fig. 4f) and lacks a posterior median fold, while the LDD2 tooth has 2 enamel lakes and a prominent posterior median fold at the occlusal surface.

Zapus burti is known only from the Borchers fauna in Kansas (Hibbard 1941). The *Z. burti* m2 does not taper posteriorly as does the LDD2 tooth. The m2 anteroconid lies labial to the midline in LDD2 but it is centered in *Z. burti*. Variants in the anterior cingulum of *Z. burti* include the morphology of the LDD2 specimen. The postentoconid fold of *Z. burti* extends beyond the midline of the m2 but is almost absent in the LDD2 tooth. Correspondingly, the prehypocnid fold penetrates further lingually on the LDD2 specimen. Also, the prehypocnid fold is very broad in *Z. burti* but tightly constricted in LDD2. The metalophid in the holotype of *Z. burti* does not reach the metaconid as it does in LDD2. The posterior mesolophid fold of the *Z. burti* m3 is much wider than that in LDD2 *Zapus*.

An early species within the genus, *Zapus rinkerii* is known only from Fox Canyon, Kansas (Hibbard 1951) and was described as possessing several plesiomorphic characters for *Zapus* (Martin 1989). The m2 of *Z. rinkerii* does not taper posteriorly as in the LDD2 specimen. The leading edge of the m2 anterior cingulum is straight in *Z. rinkerii* but slopes posterolingually in LDD2. The posterior expansion of the preprotoconid fold in the LDD2 m2 is not present in *Z. rinkerii*, but differences in lingual folds may be due solely to different ontogenetic ages. The m3 of the holotype of *Z. rinkerii* is too worn to make any valid comparison with

the LDD2 tooth. Klingener (1963) also referred a maxillary fragment and isolated M2 to *Zapus rinkeri*, but, as with most fossil species of *Zapus*, there are no published descriptions or diagnostic characters.

Among the 3 extant species of *Zapus*, the morphology of the m1 anteroconid can be used to separate *Z. hudsonius* from *Z. princeps* and *Z. trionatus* (Martin 1994). To a lesser extent, the same feature of the m2 is also claimed to be useful in a similar manner (Klingener 1963). Klingener (1963:253) stated, "[In] *Z. hudsonius* the anteroconid in m1 and m2 is separated from the metalophid by the confluent preprotoconid and premetaconid folds." This statement may be in error. None of the *Z. hudsonius* m2's illustrated by Klingener (1963) have confluent preprotoconid and premetaconid folds, but both of the illustrated *Z. princeps* and *Z. trionatus* show this morphology.

Recognizing the similarities not only in dental and cranial characters, but also in bacula and sperm morphology, Jones (1981) subsumed *Z. trionatus* as a subspecies within *Z. princeps*. Although this taxonomic change is not currently used in the neontological literature, there are no published characters that permit separation of the dentition of the 2 taxa (Kruttsch 1954, Klingener 1963, Martin 1994). Statements below that refer to the dental morphology of *Z. princeps* are also applicable to *Z. trionatus*.

Based on the morphology of the M1 and M2 paracone, Jones (1981) was generally able to distinguish *Zapus princeps* from *Z. hudsonius*. The paracone on individuals of *Z. hudsonius* is isolated from the rest of the tooth in all populations except those in northern Canada west of Hudson Bay. The paracone of individuals of *Z. princeps* is attached to the rest of the tooth in populations overlying and near the range of *Z. hudsonius*, but more peripheral populations of *Z. princeps* (Arizona, southern New Mexico, and Pacific coast) more commonly have an isolated paracone. Jones (1981) reported *Zapus princeps* from Utah with an attached paracone in all 325 M1's and 329 of 331 M2's examined. Therefore the morphology of the LDD2 *Zapus* teeth is distinct from the pattern currently dominant in the state. Because the modern patterns of *Zapus* teeth vary in areas where *Z. princeps* and *Z. hudsonius* are not sympatric, we are hesitant to refer

the LDD2 specimens to *Z. hudsonius* and to identify the material only as *Zapus*.

We are currently unable to use the presence of *Zapus* in the Pleistocene of Utah to interpret the paleoenvironment. This is not only because we are unable to identify the fossil material to species level, but also because populations of *Zapus*, even of the same species, exhibit a wide range of ecological tolerances, although most have distributions tied to the availability of surface moisture (Whitaker 1972). The fossils from LDD2 are most significant because they represent the 1st Pleistocene records of *Zapus* west of the Rocky Mountains.

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