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A NEW SPECIES OF *BENSONOMYS* (RODENTIA, CRICETIDAE) FROM THE LATE EARLY HEMPHILLIAN (LATE MIOCENE), COAL VALLEY FORMATION, SMITH VALLEY, NEVADA

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ABSTRACT

A new species of sigmodontine rodent, *Bensonomys lindsayi*, is described from the late Miocene (late early Hemphillian North American Land Mammal age, Hh2) Coal Valley Formation of Smith Valley, Nevada. The sample of *B. lindsayi* is one of the best known for the genus, including the most complete cranial material definitely associated with a lower dentition. *Bensonomys* possesses a myomorphous zygomasseteric cranial structure, similar to that of other sigmodontine rodents (e.g., *Calomys*). This is the first record of *Bensonomys* from west central Nevada and extends the paleogeographic range of the genus.

INTRODUCTION

Small mammal fossil bearing matrix in the collection of the Natural History Museum of Los Angeles County from locality LACM 7685 has been recently prepared and yielded 20 partial dentaries, a partial skull and associated partial dentary, and two partial maxillae of the small sigmodontine rodent *Bensonomys*. This sample, especially the partial skull, represents some of the most complete specimens of *Bensonomys* known. The specimens come from the late early Hemphillian (Hh2) portion of the Coal Valley Formation exposed along the eastern side of Smith Valley, Nevada, and represent a new species of *Bensonomys*. This is the first record of *Bensonomys* from west central Nevada and extends the paleogeographic range of the genus about 450 km northwestward from southern Nevada. The purpose of this paper is to document this new species.

MATERIALS AND METHODS

Measurements of specimens were taken using an optical micrometer to the nearest 0.01 mm. All measurements are in millimeters and all teeth were measured at their greatest dimensions. Dental formulae and nomenclature follow standard usage (e.g., Shotwell, 1967; Korth, 1994). Upper and lower teeth are designated by uppercase and lowercase letters, respectively. Line drawings were made using a camera lucida. All specimens are in the vertebrate paleontology collection of the Natural History Museum of Los Angeles County and detailed locality data are on file at this repository.

Abbreviations and Institutional acronyms are as follows: A-P, greatest anteroposterior dimension; ^{40}Ar/^{39}Ar, Argon-Argon; IGCU, Instituto de Geologia, Universidad Nacional Autónoma de México; K-Ar, Potassium-Argon; L, left; LACM, Natural History Museum of Los Angeles County; Ma, million years before present; R, right; TR, greatest transverse dimension; UNR, University of Nevada, Reno.

BIOSTRATIGRAPHY AND PROVENACE

The Coal Valley Formation of Smith Valley, Nevada, has been long recognized for its Hemphillian mammals comprising the Smith Valley Fauna (Wilson, 1936; Macdonald, 1959; Gilbert and Reynolds, 1973; Tedford et al., 1987, 2004; Kelly and Secord, in press). Further south, in the type area of Coal Valley, the lower portion of the Coal Valley Formation has yielded the Clarendonian Coal Valley Flora and Fauna (Axelrod, 1956; Tedford et al., 1987, 2004). Evernden et al. (1964) dated biotite from a tuff underlying the Smith Valley Fauna in Smith Valley at 9.6 Ma (K-Ar method, corrected for new constants). Swisher (1992) dated plagioclase from the Wilson Canyon Tuff (WCT) at 7.52 ± 0.08 Ma (corrected for new Fish Canyon Tuff constants) using the more accurate single-crystal laser-fusion ^{40}Ar/^{39}Ar dating method. The WCT occurs within the fossil bearing strata of the Coal Valley Formation that yielded the Smith Valley Fauna (Swisher, 1992; Kelly and Secord, in press). Tedford et al. (1987, 2004: see fig. 6.2 and appendix, p. 220), apparently using the older 9.6 Ma date, place the Smith Valley Fauna in their correlation charts in the beginning of the Hemphillian (Hh1). Kelly and Secord (in press) re-evaluated the biostratigraphy of the Coal Valley Formation that yielded the Smith Valley Fauna in Smith Valley. They recognize three mammalian assemblages in the Smith Valley Fauna spanning the early to late Hemphillian (Hh1 to Hh3) as follows; a lower assemblage from below the WCT (Hh1), a middle assemblage from between the WCT and the marker shale (Hh2), and an upper assemblage from above the marker shale (Hh3). They also reported two new $^{40}Ar/^{39}Ar$ dates of 7.08 ± 0.01 and 6.98 ± 0.01 Ma run by Chris Henry (Nevada Bureau of Mines and Geology, UNR) on sanidines from two tuffs that occur between the WCT and the marker shale (130 and 160 m above the WCT, respectively). Thus, based on the new dates and biostratigraphy, the Smith Valley Fauna appears to span the early to late Hemphillian (Hh1-Hh3), or about 8.5 - 6.5 Ma.

The *Bensonomys* sample reported on herein is part of the middle assemblage of the Smith Valley Fauna, which is estimated to span the interval of 7.5-6.7 Ma (Kelly and Secord, in press) or early late Hemphillian (Hh2). Specifically, locality LACM 7685, which yielded the *Bensonomys* sample, occurs about 30 m above the tuff dated at 6.98 Ma, limiting the age of the sample to younger than this date.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Family Cricetidae Rochebrune, 1883
Subfamily Sigmodontinae Wagner, 1843
Bensonomys Gazin, 1942
Bensonomys lindsayi new species
(Figures 1-3, Tables 1-3)

Holotype—Partial left dentary with i-m3, LACM 153284.

Hypodym—Partial right dentary with m1-3, LACM 153274; Partial right dentary with m1-2, LACM 153275; Partial right dentary with m1, LACM 153276; Partial right dentary with i-m3, LACM 153277; Partial left dentary with i-m2, LACM 153278; Partial left dentary with i-m3, LACM 153279; Partial left dentary with i-m3, LACM 153280; Partial right dentary with i-m3, LACM 153281; Partial left dentary with m1-2, LACM 153282; Partial right dentary with i-m2, LACM 153283; Partial left dentary with i-m3, LACM 153284; Partial left dentary with i-m3, LACM 153285; Partial right dentary with m1-3, LACM 153286; Partial right dentary with m1-3, LACM 153287; Partial right dentary with i-m2, LACM 153288; Partial right dentary with m1-3, LACM 153289; Partial left dentary with m1-2, LACM 153290; Partial left dentary with i and m2-3, LACM 153294; Partial right dentary with m1, LACM 153295; Partial left dentary with m2, LACM 153296; Lm2, LACM 153297; Partial left dentary with m2, LACM 153298; Partial skull with right and left I-M3 and associated partial right dentary with i-m3, LACM 153293; Partial right maxilla with M1-2, LACM 153291; Partial left maxilla with M1, LACM 153292.

Type Locality—LACM 7685, between dated pumice levels (~7.0 Ma) and overlying marker shale, Coal Valley Formation, Upper Petrified Tree Canyon, Smith Valley, Lyon County, Nevada.

Age and Fauna—Early late Hemphillian (Hh2), middle assemblage of Smith Valley Fauna.

Diagnosis—A small species of *Bensonomys*: similar in size to *B. winklerorum* (Carranza-Castañeda and Walton, 1992); slightly smaller than *B. gidleyi* (Baskin, 1978); smaller than *B. arizonae* (Gidley, 1922), *B. coffeyi* (Dalquest, 1983), *B. hershkovitzi* Martin et al., 2002a, and *B. meadensis* Hibbard, 1956; much smaller than *B. baskini* (Lindsay and Jacobs, 1985), *B. eliasi* (Hibbard, 1938), and *B. stirtoni* (Hibbard, 1953); and larger than *B. yazhi* (Baskin, 1978) and *B. elachys* (Lindsay and Jacobs, 1985). Differs from *B. arizonae*, *B. baskini*, *B. coffeyi*, *B. elachys*, *B. gidleyi*, and *B. yazhi* by having distinct parastyle on M1 anterolabial cingulum that forms an occlusal wear surface with opposing well-developed m1 anterolabial cingulid and differs from *B. arizonae*, *B. eliasi*, *B. meadensis*, and *B. stirtoni* by having less anteroposterior expansion of m1 anteroconid and less alignment of lower molar primary cusps (protoconid-metaconid and hypoconid-entoconid more offset). Further differs from *B. arizonae* by having m1 relatively wider transversely and m2 width usually exceeds that of m1. Further differs from *B. baskini* by having M2 anterior cingulum lacking midline cuspule, M2 cingular shelf between paracone and metacone lacking cuspules, M2 and m1-2 lacking any development of mesolophs/mesolophids, and m3 posterior labial valley not quite as deep. Further differs from *B. coffeyi* by having m1 anteroconid cuspids (lobes) more distinct (better separated) and m3 anterolabial cingulid less developed. Further differs from *B. elachys* by having m1 anteroconid cuspids better developed (more completely bilobed), m1 posteroconulid (small cuspid on posterior cingulid) lacking, m2 anterior cingulid less developed, and m2 width usually exceeds that of m1. Further differs from *B. gidleyi* by having M1-2 lacking mesolophs and mesostyles, M1 posterior cingulum slightly less developed, m1 anteroconid cusps less offset, m1 posterior cingulid lacking median posteroconulid, and m3 with distinct small entoconid present during early wear. Further differs from *B. hershkovitzi* by having lower molar mesolophids lacking, m1 anteroconid cuspids better developed, m1 anterolabial cingulid slightly less developed, and bulbous termination of masseteric crest does not extend quite as far anteriorly (in *B. hershkovitzi* it is almost fused with mental foramen). Further differs from *B. meadensis* by having M1 posterior cingulum and M2 anterior cingulum better developed, and m1 posterior cingulid lacking any labial extension. Further differs from *B. stirtoni* by having m1-2 labial cingulids between protoconids and hypoconids and m3 anterolabial cingulid less developed. Further differs from *B. yazhi* by having M1 anterolabial cingulum present and well developed, M1 mesoloph lacking, m1 anteroconid more transversely expanded (relatively wider), m1 lingual valley between anteroconid and metaconid deeper, m1-2 posterior cingulids lacking a median posteroconulid, m3 entoconid present, and m3 less reduced relative to m1-2. Further differs from *B. winklerorum* by having M1 anterocone more strongly bilobed and relatively more bulbous, M2 posterior cingulum less developed and lacking distinct basin between cingulum and metaconid, M2-3 smaller (anteroposteriorly and transversely), m1 anteroconid distinctly bilobed, and m1 wider transversely relative to A-P length. *B. lindsayi* can also be distinguished from all species of the closely related genus *Symmetrodontomys* by having: 1) slightly more brachydont cheek teeth; 2) slightly more alternation of the m1-2 molar cusps, especially on m2; 3) lack of the X-shaped occlusal pattern of the anteroconid, protoconid, and metaconid due to greater separation of the m1 anteroconid from the protoconid and metaconid with the protoconid positioned relatively further posteriorly; 4) m3 more reduced relative to m1-2; and 5) smaller size.

Etymology—Named in honor of Everett H. Lindsay, Professor emeritus, of the University of Arizona for his extensive contributions to our knowledge of fossil rodents.

Description—The 21 partial dentaries in the sample are consistent in their morphology (Figure 1). The masseteric crest terminates below the anterior portion of m1 as a well-developed knoblike process. This process is separated from the mental foramen by 0.60 mm (mean for ten specimens). The mental foramen occurs high on the dentary, along the dorsal edge of the diastema, just anterior to the m1. A moderately developed sulcus is present between the capsular and coronoid processes. The anterior enamel of the lower incisor is smooth. The lower incisor mean transverse width at midpoint of ten specimens is 0.61 mm.

The lower molars are brachydont with the primary cusps alternating or offset from each other, that is the metaconid and entoconid are anterior to the protoconid and hypoconid, respectively (Figures 2B-F). The molars progressively decrease in size from the m1 to m3 with the m3 significantly reduced in size relative to m1-2. All of the m1s in the sample are in their alveoli within the dentaries, so the number of roots could not be determined without damaging the specimens. Measurements of the holotype dentition and a summary of the lower molar dental statistics for the entire sample are presented in Table 1.

The m1 has an elongated oval occlusal outline due to the presence of a large anteroconid (Figure 2B-F). In early to moderate wear (Figure 2B, C, E and F), the anteroconid is strongly bilobed (two-cusped) by a well-developed and relatively persistent median cleft. The labial lobe of the anteroconid is equal to, or slightly larger, than the lingual lobe. In very late wear (Figure 2D), the bilobed structure of the anteroconid is obliterated, so that the anterior occlusal outline becomes crescent shaped. The lingual lobe of the anteroconid is usually slightly anterior to the lingual lobe. A high, well-developed anterolabial cingulid is present and well connected to the labial lobe of the anteroconid from which it extends posteriorly to connect with the anterolabial side of the protoconid. With wear, the occlusal wear surface of the anterolabial cingulid joins the occlusal wear surface of the anterolabial lobe of the anteroconid. This results from the occlusion of these surfaces with the opposing well-developed M1 anterolabial lobe of the anterocone and anterolabial cingulum, respectively. The valley between the anterolingual lobe of the anteroconid and metaconid is deep. The metaconid is separated from the entoconid by a wide valley and, in all specimens, no mesolophids or mesostylids are present between these cusps. The metaconid and entoconid are narrower anteroposteriorly and higher than the protoconid and hypoconid. Moderately developed cingular shelves are present lingually between the anteroconid and metaconid, and between the metaconid and entoconid. A moderately developed cingular shelf is present labially, between the protoconid and hypoconid. A moderately developed posterior cingulid is present that extends lingually from the hypoconid to about the middle of the posterior side of the entoconid. In all specimens, a protoconulid (accessory cuspid or posterostylid of Baskin [1978]) is lacking along the posterior cingulid.

The m2 has a subrectangular occlusal outline. The anterolabial cingulid is well developed. It extends labially from the anterior side of the metaconid and then turns posteriorly to join with the anterolabial side of the protoconid. As in m1, a distinct valley separates the m2 metaconid and entoconid. Mesolophids and mesostylids are completely lacking in all specimens. The cingular shelfs between metaconid and entoconid, and between the protoconid and hypoconid, are moderately developed. The m2 width usually exceeds that of m1 (in only two specimens out of 17 is the

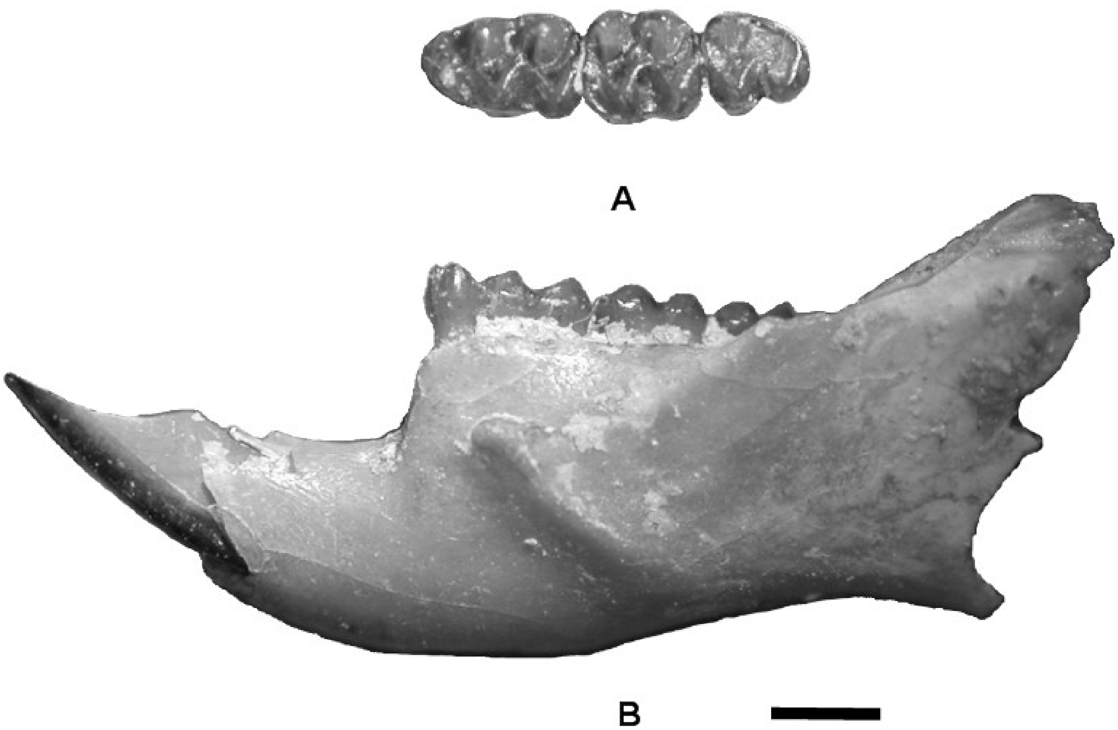

FIGURE 1. Holotype of *Bensonomys lindsayi* new species, partial left dentary, LACM 153284. A, m1-3, occlusal view. B, dentary, lateral view. Scale = 1 mm.

width of m2 equal to or slightly smaller than the m1 width). The m2 posterior cingulid is similar in size and shape to that of m1.

The m3 has a subtriangular occlusal outline with the transverse width of the metaconid and protoconid greater than that of the entoconid and hypoconid. The metaconid, protoconid, and hypoconid are well-developed cusps. The entoconid is a small distinct cusp in unworn teeth, much reduced in size and height as compared to those on m1-2. It is worn down to a smooth surface by moderate wear. The anterolabial cingulid is a distinct crest along the anterolabial side of the protoconid, but is not as well developed as on the m2. A moderately developed cingular shelf is present between the protoconid and hypoconid. With wear, the m3 occlusal wear surface forms the typical sigmoidal or S-shaped sigmodontine pattern.

The upper molars, like the lowers, are brachydont and decrease in size from M1 to M3, with M3 significantly reduced in size relative to M1-2 (Figure 2A). The primary cusps are offset with the protocones and hypocones anterior to the paracones and metacones, respectively. In all specimens, mesostyles and mesolophs are lacking. Measurements of the upper dentition are presented in Table 2.

The M1 has an elongated oval occlusal outline with a well-developed, bilobed anterocone. The anterocone is slightly offset labially from the anteroposterior axis of the tooth. A well-developed anterolabial cingulum is present that extends posteriorly from the anterolabial lobe of the anterocone to the anterolabial side of the paracone. In all specimens, about midway along the anterolabial cingulum, a distinct cusp (parastyle) is present that forms an occlusal wear surface with the opposing anterolabial cingulid of m1 (Figure 2A). Moderately developed cingular shelfs are present between the anterolingual lobe of the anterocone and protocone, the protocone and hypocone, and the paracone and metacone. A distinct, small posterior cingulum is present in teeth that are unworn or in very early wear, but it is obliterated during early to moderate wear wherein its wear surface joins with that of the metacone.

The M2 is subrectangular in occlusal outline. The anterior cingulum is well developed and extends

TABLE 1. Measurements (in mm) of holotype (LACM 153284) and summary of measurements of lower dentition and rami of all specimens of *Bensonomys lindsayi* new species. Abbreviations are N = number of specimens, OR = observed range, X = mean, SD = standard deviation, and CV = coefficient of variation.

Summary of all specimens Measurement	Holotype	N	OR	X	SD	CV
m1 A-P	1.44	18	1.32 – 1.44	1.37	0.04	2.9
m1 TR	0.98	18	0.91 - 0.98	0.95	0.02	2.1
m2 A-P	1.15	21	1.00 –1.15	1.06	0.06	5.7
m2 TR	1.03	21	0.85 – 1.04	0.98	0.05	5.1
m3 A-P	0.95	11	0.92 - 0.98	0.94	0.05	5.3
m3 TR	0.89	13	0.77 - 0.91	0.81	0.05	6.2
m1-3 A-P	3.44	12	3.20 – 3.44	3.33	0.07	2.1
Depth of ramus below m1	2.87	12	2.56 – 2.91	2.70	.12	4.4

lingually along the anterior border from a level about equal to the middle of the paracone to the anterolingual side of the protocone. Moderately developed cingular shelfs are present between the paracone and metacone, and between the protocone and hypocone. The posterior cingulum is slightly better developed than that of M1 and its wear surface also joins with that of the metacone during early to moderate wear.

The M3 is subtriangular in occlusal outline. The anterior cingulum is well developed and extends lingually from anterolabial corner of the tooth to the anterolingual side of the protocone. The paracone is the highest cusp and is only moderately offset from the protocone, being positioned slightly posterior to the protocone. The paracone, protocone, and metacone are distinct, well developed cusps, whereas the hypocone is reduced to a small cusp just lingual to the middle of the posterior side of the tooth. A weakly developed cingular shelf is present between the paracone and metacone and the valley between these cusps is well developed and deep. The posterior cingulum is moderately developed and distinct in teeth that are unworn or in very early wear, but with further wear, its wear surface joins that of the hypocone and metacone.

A single specimen (LACM 153293) was recovered that included a partial skull and associated partial right dentary in occlusion. The partial dentary was slightly damaged when removed from the skull and includes a partial incisor and m1-3. The occlusal patterns and structure of the teeth in this specimen along with the dentary morphology (knoblike process at the anterior termination of the masseteric crest and mental foramen situated high on the diastema crest, anterior to m1) are indistinguishable from those in all the other dentaries referred herein to *B. lindsayi*. This fact allows unequivocal assignment of the skull to *B. lindsayi*. The partial skull is represented by the nasals, premaxillae, maxillae, anterior portions of the zygomatic arches, small portions of the frontals and lacrimals, and a complete dentition (Figure 3A-B). There is some distortion, with the nasals being rotated anteriorly and the left half of the skull displaced posteriorly and dorsally relative to the right half of the skull. A reconstruction of the skull (lateral and anterior views) with the posterior portions hypothesized based on other closely related sigmodontine rodents (e.g., *Calomys*) is shown in Figure 3C-D.

The nasals narrow posteriorly and extend to a position past the posterior margin of the infraorbital foramen. The upper incisor is acutely curved as in other sigmodontine rodents, with the enamel extending across the anterior surface and wrapping slightly around the anterolateral side (about ¼ the A-P width) of the tooth. The enamel is smooth with no grooving present. The transverse width of the upper incisor at midpoint is 0.72 mm. A diastema of 5.16 mm is present between the incisor and the anterior root of M1 on the left side. The diastema on the right side is distorted by some compression of maxilla. Although slightly damaged, the incisive foramina are elongated and narrow, about 4.1 mm in A-P length, and extend from 0.95 mm posterior to the incisors to a level just anterior to the m1 protocone. The infraorbital foramen has its dorsal portion expanded laterally whereas it is transversely compressed ventrally by the zygomatic plate. A distinct process that projects anteriorly is present along the lateral edge of the infraorbital foramen where the anterior root of the zygomatic arch meets the foramen border. An additional small, but distinct, accessory nutrient foramen is present on the zygomatic plate between the ventral portion of the infraorbital foramen and the anterior root of M1. The zygomatic plate is moderately expanded and is ventrally tilted posteriorly. The entire zygomasseteric structure is myomorphous, similar to the extant sigmodontine *Calomys*.

Discussion—*Symmetrodontomys* Hibbard, 1941, exhibits certain dental and mandibular characters that are very similar to those of *Bensonomys*, so comparison of the Smith Valley form to both genera was necessary to determine a correct generic assignment. *Bensonomys* is characterized by the following (Gazin, 1942;

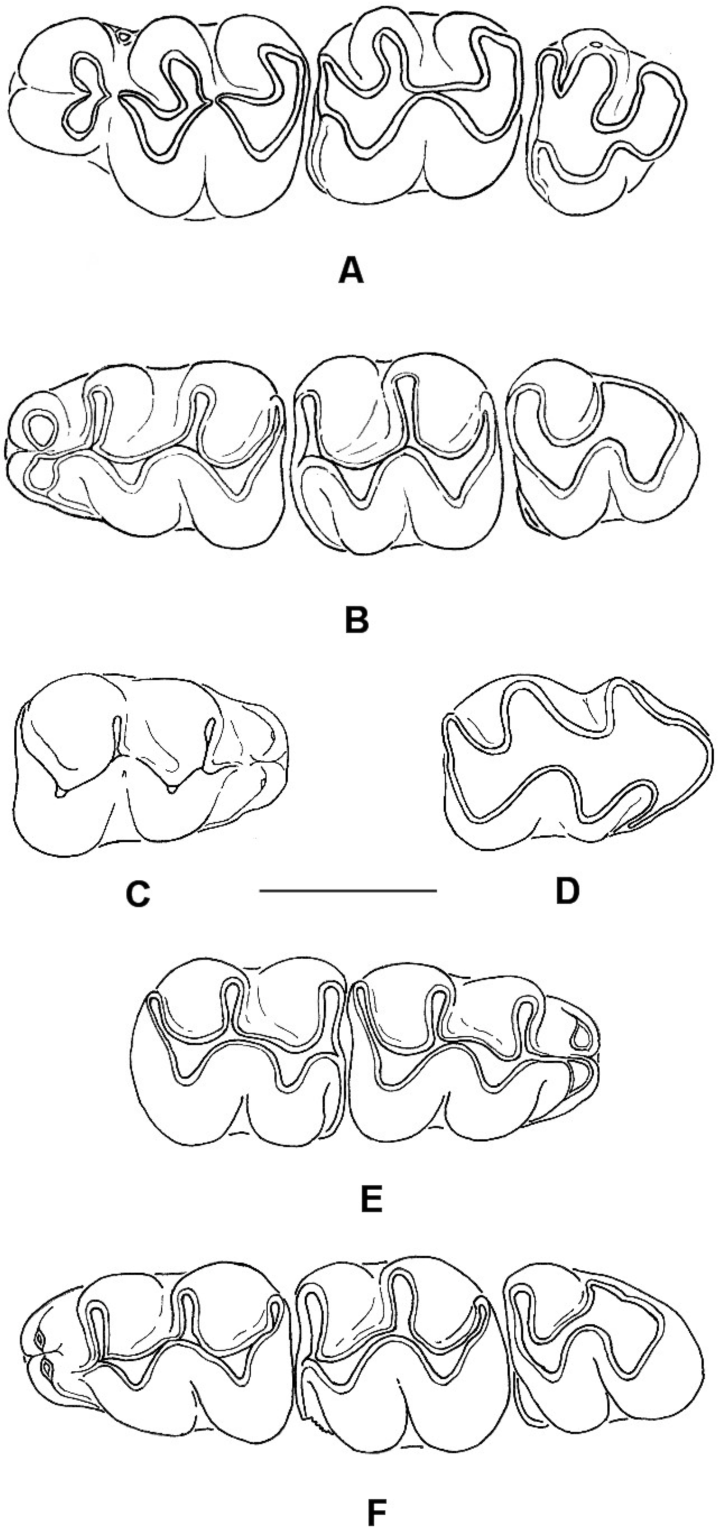

FIGURE 2. Upper and lower molars of *Bensonomys lindsayi* new species. A, LM1-3, LACM 153293. B, Lm1-3, Holotype, LACM 153284. C, Rm1, LACM 153277, very early wear. D, Rm1, LACM 153295, late wear. E, Rm1-2, LACM 153293. F. Lm1-3, LACM 153280. All occlusal views, scale = 1 mm.

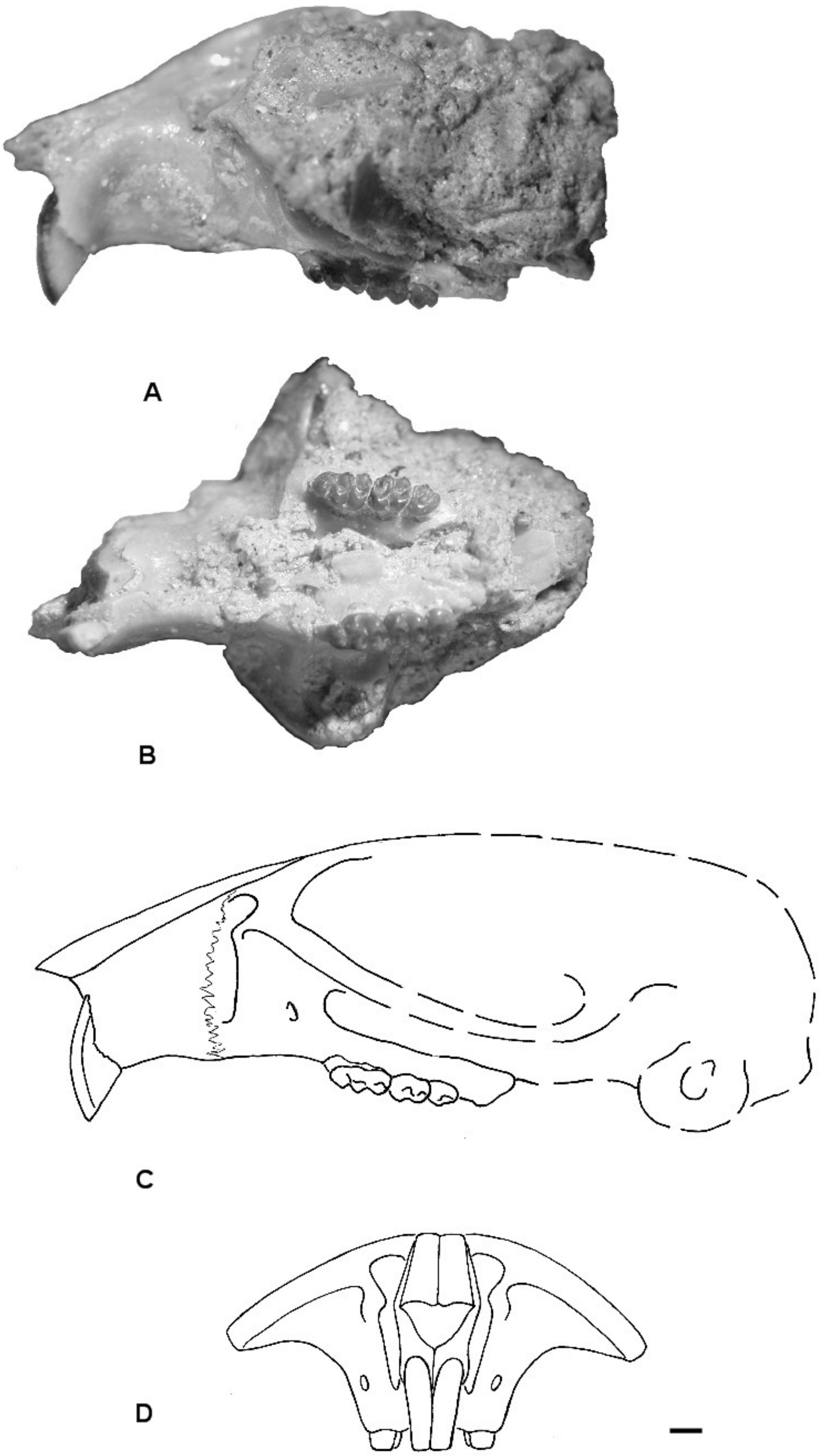

FIGURE 3. Skull of *Bensonomys lindsayi* new species. A, partial skull, LACM 153293, right lateral view (reversed). B, partial skull, LACM 153293, ventral view. C, reconstructed lateral view of skull with posterior portion hypothesized from other closely related sigmodontine rodents. D, reconstructed anterior view of skull showing myomorphous zygomasseteric structure in *Bensonomys*. Scale = 1 mm.

TABLE 2. Measurements (in mm) of upper dentition of *Bensonomys lindsayi* new species.

Specimen number	Measurement	Right	Left
LACM 153293	M1 A-P	1.56	1.55
	M1 TR	1.05	1.05
	M2 A-P	1.01	1.00
	M2 TR	0.86	0.86
	M3 A-P	0.72	0.73
	M3 TR	0.85	0.85
LACM 153291	M1 A-P	1.58	
	M1 TR	1.06	
	M2 A-P	1.00	
	M2 TR	0.95	
LACM 153292	M1 A-P		1.59
	M1 TR		1.00

Hibbard, 1950, 1956, 1972; Dalquest, 1978; Baskin, 1978, Harrison, 1978; Czaplewski, 1987; Tomida, 1987; Martin, 2000; Martin et al., 2002a, 2002b): 1) small, brachydont sigmodontines; 2) the M1 anterocone and m1 anteroconid are elongated anteroposteriorly and usually bilobed (two-cusped); 3) the masseteric crest is robust with an anterior bulbous termination occurring at or near the anterior base of m1; 4) the mental foramen is situated high on the dentary, along the diastema and anterior to m1; 5) the M3 and m3 are reduced in size relative to the M1-2 and m1-2, respectively; 6) the M1 usually with three roots and m1 usually with two roots (exceptions, some *B. yazhi* and *B. eliasi* with four-rooted M1 and *B. yazhi* with three-rooted m1 [see Baskin, 1978, 1986; Martin, 2000]); and 7) the primary cusps of M1-2 and m1-3 alternate, especially m1-2, that is the metacone (id)-protocone (id) and metacone (id)-hypocone (id) are offset. The number of roots on m1 could not be determined for the Smith Valley form because all of the m1s are in their respective dentaries.

Based on eight partial dentaries from Rexroad Locality 3 and one partial dentary from Rexroad Locality 2 (Blancan, or about 3.6 – 3.3 Ma), Kansas, Hibbard (1941) named *Symmetrodontomys* and designated *S. simplicidens* as the type species. Included in his diagnosis of *S. simplicidens* were the following characteristics: simple broad cusps, wide valleys, and poorly developed cingulae; m1 with well-developed groove on anteroconid giving the appearance of two distinct cusps; m1 protoconid and metaconid not alternating as in *Peromyscus*, more nearly opposite; m1 hypoconid and entoconid relation the same as that of the above cusps; m2 cusps more nearly opposite, with valleys opposite; m3 not as reduced as *Peromyscus*, but better developed than in *Akodon*, with valleys opposite and not alternate; mental foramen close to anterior root of m1 and nearly joined with masseteric ridge; and ramus strong and deep. Hibbard (1941: fig. 12) regarded the opposing lower molar cusps, especially on m2, as an important defining characteristic of his new genus and species. Two additional early Blancan species are assigned to *Symmetrodontomys*, *S. beckensis* (Dalquest, 1978, 1980) from Beck Ranch, Texas and *S. daamsi* Martin et al., 2000a, from Pipe Creek, Indiana. Martin (2000) referred the type and topotypic material of *Peromyscus sawrockensis* Hibbard, 1964, to *Symmetrodontomys simplicidens*, although he left open the possibility that this material could differ from *S. simplicidens* due to the relatively wider transverse widths of m2-3 in the Saw Rock sample.

In *Symmetrodontomys* from Saw Rock (latest Hemphillian or earliest Blancan, or about 5.0 Ma), the major lower molar cusps alternate, but slightly less so than in most Hemphillian species of *Bensonomys*, especially on m2 (Hibbard, 1964; Dalquest, 1983; Lindsay and Jacobs, 1985; Martin, 2000). In the later samples of *S. simplicidens* from Rexroad, Hornet (early Blancan, or about 3.5 Ma), and Deer Park (middle Blancan, or about 3.0 Ma), the lower molar cusps exhibit less alternation (more opposing), again especially on m2 (Hibbard, 1941; Martin et al., 2000a, 2000b). The same is true for *S. beckensis* and *S. daamsi* (Dalquest, 1978, 1980; Martin et al., 2000a). In the Smith Valley form, the alternation of the lower molar cusps is more distinct, like those of other Hemphillian species of *Bensonomys*, especially on m2. In summary, the early sample of *Symmetrodontomys* from Saw Rock appears to have the lower molar cusps alternating more than the younger samples of *S. simplicidens* from Rexroad, Hornet, and Deer Park. In the Smith Valley form, the lower molar cusps alternate to a degree equal to other Hemphillian species of *Bensonomys* (e.g., Dalquest, 1983: fig. 9; Lindsay and Jacobs, 1985: fig. 8).

In *Symmetrodontomys*, the m1 anterior occlusal surface wears to a "butterfly-shaped" or X-shaped pattern because of the proximity of the bilobed anteroconid to the protoconid and metaconid, and due to the more opposing positions of the protoconid and metaconid. Although the m1 X-shaped occlusal pattern is present in *Symmetrodontomys* from Saw Rock, it is not as well developed as in later samples of *S. simplicidens* from Rexroad, Hornet, and Deer Park (Hibbard, 1941, 1964; Martin, 2000; Martin et al., 2000a, 2000b). This pattern is also present in *S. beckensis* (Dalquest, 1978) and *S. daamsi* (Martin et al., 2000a: fig. 3). In the Smith Valley form, the m1 protoconid is positioned further posteriorly from the anteroconid and metaconid, resulting in an occlusal pattern more similar to those of *Bensonomys* than to those of *Symmetrodontomys*.

Martin's (2000) referral of *P. sawrockensis* to *Symmetrodontomys* appears justified, but whether it is unequivocally synonymous with *S. simplicidens* will require a much larger topotypic sample to determine.

The Saw Rock specimens are currently the oldest known sample of the genus, at about 5.0 Ma or slightly younger (latest Hemphillian or earliest Blancan, Bell et al., 2004). The Saw Rock sample appears less derived than the later Blancan samples of *S. simplicidens* by having slightly more alternation of the molar cusps and a slightly less developed X-shaped occlusal pattern of the m1 anteroconid, metaconid, and protoconid, indicating that the Saw Rock *Symmetrodontomys* may be closer to the ancestry of the genus than previously recognized. The Smith Valley form is at least 1.7 Ma older than the Saw Rock *Symmetrodontomys*, and, judging from its stratigraphic occurrence within the section at Smith Valley, more likely about 1.8 Ma older.

Table 3 presents examples of the size of m3 relative to that of m1-2 in *Bensonomys* and *Symmetrodontomys*. The mixed sample of *Bensonomys* specimens (probably *B. eliasi* and *B. arizonae*) from Fox Canyon and Rexroad Locality 3 (Hibbard, 1950: plate 10; Martin et al., 2002b) also exhibit reduced m3s (m3 A-P/m1 A-P x 100 = ~60-69%, m3 A-P/m2 A-P x 100 = ~81-89%) comparable to those of the other *Bensonomys* species (Table 3). No m3s have been reported for *B. elachys*, *B. hershkovitzi*, and *B. winklerorum* (Lindsay and Jacobs, 1985; Carranza-Castañeda and Walton, 1992; Martin et al., 2002a). The Deer Park sample of *S. simplicidens* consists of isolated teeth and Martin et al. (2002b) noted that some very worn m3s in this sample might be referable instead to *Onychomys* or *Peromyscus*. In the holotype of *S. simplicidens* from Rexroad Locality 3, the m3 is only moderately reduced in size relative to the m1 and about equal in length to the m2 (Hibbard, 1941). In the samples of *S. simplicidens* from Saw Rock and Hornet, the m3s are also only moderately reduced in size relative to the m1s and the m2 lengths are less than those of the m3s (Martin, 2000: table 1; Martin et al., 2002a: table 2). In *S. daamsi*, the size of m3 relative to m1-2 is comparable to the Saw Rock and Hornet samples of *S. simplicidens* (Martin et al., 2002a). It is unlikely that the five isolated m3s referred to *S. simplicidens* from Deer Park by Martin et al. (2002b) represent this species because they differ significantly in relative and absolute size as compared to those in the samples of *S. simplicidens* from Rexroad, Saw Rock, and Hornet (Table 3; Martin, 2000), and therefore, appear to represent another taxon (possibly *Bensonomys*, *Onychomys*, or *Peromyscus*). Because the m3s referred to *S. simplicidens* from Deer Park cannot be unequivocally assigned to this species, the following observations can be made: 1) species of *Bensonomys* typically have greater reduction in the size of m3 relative to m1 than species of *Symmetrodontomys* (*Bensonomy*s m3 A-P = ~61-69% of m1 A-P, whereas in *Symmetrodontomys* m3 A-P = ~77-81% of m1 A-P); and 2) species of *Bensonomys* typically have the length of m2 significantly greater than that of m3, whereas in species of *Symmetrodontomys* the length of m2 is about equal to or less than that of m3 (*Bensonomys* m3 A-P = ~78-90% of m2 A-P, whereas in *Symmetrodontomys* m3 A-P = ~98-104% of m2 A-P). This characteristic was also noted by Dalquest (1980), wherein he considered the relatively large m3 of *Symmetrodontomys beckensis* to be one of the characters that separates *Symmetrodontomys* from *Bensonomys*. The degree of reduction in m3 size relative to m1-2 in the Smith Valley form is comparable to those of other species of *Bensonomys* (Table 3).

Although the cheek teeth in *Symmetrodontomys*, *Bensonomys*, and *Calomys* are brachydont, Martin (2000) and Martin et al. (2000a) noted that *Symmetrodontomys* is somewhat more hypsodont and the major cusps rise somewhat more vertically than those of *Bensonomys*. Martin et al. (2000a: fig. 4A-B) plotted the crown heights of m1 of *S. simplicidens* and *S. daamsi* to the m1 area (length x width) and to the length of m1. Although Martin et al. (2000a) did not specify the degree of wear of the specimens they plotted, the mean m1 height of *S. simplicidens* from Hornet is 0.78 mm (N= 4, observed range = 0.76-0.80 mm), the mean height for those of *S. daamsi* from Pipe Creek is 0.63 mm (N= 8, observed range = 0.52-0.78 mm), and, estimating from the figures, the observed range for the height of those of *S. simplicidens* from Deer Park is about 0.68-0.73 mm (N= 2). The only plotted sample with a statistically significant number of specimens, albeit still low, is that for *S. daamsi*. In the Smith Valley form, the m1 mean crown height (unworn through early moderate wear) is 0.47 mm (N = 10, observed range = 0.44-0.52 mm), demonstrating that the lower molars of the Smith Valley form are more brachydont than those of *S. simplicidens* and *S. daamsi*. This can be further demonstrated by comparing the ratios of the maximum recorded crown height to the maximum recorded size of m1 in *S. daamsi* (Martin et al., 2000a) and the Smith Valley form. In *S. daamsi*, the ratio is 0.462 (0.78/1.69), whereas in the Smith Valley form, the ratio is 0.361 (0.52/1.44). Thus, the relative maximum crown height is about ten percent greater in *S. daamsi*. This ratio for the Hornet sample (Martin et al., 2000a) of *S. simplicidens* is 0.437 (0.80/1.83), or about seven and a half percent greater than the Smith Valley form. For comparison, the ratios of two barely worn m1s (IGCU 1199 and 1178) of *Bensonomys elachys* from Yepómera are 0.388 (0.49/1.26) and 0.384 (0.48/1.25), respectively. Moreover, when m1 specimens of the Smith Valley form are plotted onto figures 4A-B of Martin et al. (2000a), they clearly reside outside the clustering exhibited by *S. simplicidens* and *S. daamsi*, most were

TABLE 3. Examples of m3 size relative to m1-2 (m3 A-P/m1 or m2 A-P x 100 = %) in *Bensonomys* and *Symmetrodontomys* (for A-P dimensions of samples, see Hibbard, 1941, 1953, 1956, 1964; Baskin, 1978; Dalquest, 1983; Lindsay and Jacobs, 1985; Czaplewski, 1987; Martin, 2000; Martin et al., 2002a, 2002b). [1]Deer Park sample of five isolated m3s referred by Martin et al. (2002b) to *S. simplicidens* appear to represent a different taxon (see text).

m3 A-P/m1 A-P x 100

Symmetrodontomys		*Bensonomys*	
S. simplicidens, holotype	~78%	*B. arizonae,* Verde sample	65.4%
S. simplicidens, Saw Rock sample	81.2%	*B. baskini*	64.7%
S. *simplicidens*, Hornet sample	79.4%	*B. coffeyi*	~69%
S. simplicidens, Deer Park sample[1]	66.9%	*B. gidleyi*	69.1%
S. daamsi	76.7%	*B. lindsayi*	68.6%
		B. meadensis	~65%
		B. stirtoni	68.8%
		B. yazhi	61.3%

m3 A-P/m2 A-P x 100

Symmetrodontomys		*Bensonomys*	
S. simplicidens, holotype	~100%	*B. arizonae,* Verde sample	88.8%
S. simplicidens, Saw Rock sample	104.4%	*B. baskini*	89.7%
S. simplicidens, Hornet sample	102.2%	*B. coffeyi*	~89%
S. *simplicidens*, Deer Park sample	83.7%	*B. gidleyi*	88.6%
S. daamsi	98.3%	*B. lindsayi*	88.7%
		B. meadensis	~89%
		B. stirtoni	89.1%
		B. yazhi	78.1%

actually off the lower limits of the graphs. Furthermore, the majority of the specimens of *S. daamsi* plotted by Martin et al. (2000a) appear to have heights from about 0.63-0.70 mm (six of the ten plotted), whereas two specimens were plotted at about 0.65-0.67 mm, one plotted at 0.78 mm, and one plotted at 0.52 mm. This is a fairly large observed range and one would suspect that it included various wear stages. The wear stage of the specimen that plotted at 0.52 mm was unreported, but if it is significantly more worn than the others, then the mean height (0.63 mm) of the sample would be skewed lower. It would have been better to compare the crown heights of the species of *Symmetrodontomys* using teeth that are unworn or in a very early wear stage and then adjust for the difference in size between the two species. However, this information was not provided. In spite of this fact, the molars of the Smith Valley form are absolutely and relatively more brachydont than those of *S. simplicidens* and *S. daamsi*, more similar to those of species of *Bensonomys*. Furthermore, even in the well-worn m1s of the Smith Valley form, the lowest recorded m1 crown height is 0.41 mm, so that the overall observed range is 0.41-0.52 mm (well-worn to unworn), a much narrower observed range than that for *S. daamsi*. This would also indicate that the molars of *S. daamsi* are more hypsodont than those of the Smith Valley form, with a relatively higher crown height at the beginning of wear that can be worn down to a greater degree resulting in a greater observed range in crown height. This greater observed range in crown height is common in all mammalian lineages in which there is a phylogenetic progression towards hypsodonty in the cheek teeth. Thus, the Smith Valley form appears more similar in crown height morphology to *Bensonomys* than to *Symmetrodontomys*.

The M1 anterocone of the Smith Valley form does exhibit some similarity to those of *Symmetrodontomys* by being relatively large (transversely expanded) with bulbous cusps. However, only a small number of upper molars of *Bensonomys* have been documented, so the interspecific and intraspecific variation of this morphology cannot be properly evaluated at this time. However, M1s (i.e., IGCU 1169 and 1174, holotype) of *Bensonomys elachys* from Yepómera do exhibit similarly transversely widened anterocones with only slightly less bulbous cusps than those of the Smith Valley form. The greatest transverse width of the M1 anterocone in *B. elachys* is 70-71% of the greatest transverse width of the trigonid and that of the Smith Valley form is 71-72%. A similar morphology is exhibited by *Bensonomys baskini* from Yepómera, wherein the M1 anterocone width is 70% of the trigonid width and the anterocone cusps are somewhat bulbous. In both species from Yepómera, the M1 anterocone is also slightly pinched off, especially along the lingual border (Lindsay and Jacobs, 1985: fig. 8c, plate 2n; personal observation). A somewhat bulbous M1 anterocone is also present in *B. arizonae* from the Blancan Verde

Formation, Arizona (Czaplewski, 1987: fig. 1). What is significant also, is that the skull of the Smith Valley form was associated with a partial dentary in occlusion. When the partial dentary was separated from the skull, it was slightly damaged and was not as complete as others in the sample. This is why it and the skull were not designated as the holotype. However, the lower molars of this dentary are indistinguishable from those in the rest of the sample from Smith Valley, including a comparable reduction in m3 size (m3 A-P = 69.1% of m1 A-P, m3 A-P = 89.2% of m2 A-P). In addition, the alternations of the cusps on m1-2 of this specimen are distinct (Figure 2E), more like those of *Bensonomys* than of those of *Symmetrodontomys* (see Hibbard, 1941: fig. 12; Martin et al., 2000a: fig. 3, 2000b: fig. 7). As shown in Figure 2A and E, the M1 cusps in the skull alternate slightly less than the opposing m1 cusps in the associated dentary. It should be also noted that in the holotype M1 (IGCU 1174, crown height = 0.59 mm, early wear) of *B. elachys* from Yepómera, the major cusps appear to alternate moderately, but by moderate wear, as represented by another M1 (IGCU 1169, crown height = 0.56 mm) from Yepómera, the major cusps appear to alternate only slightly (more opposing). The M1 crown height of an unworn specimen from Smith Valley is 0.57 mm, whereas that of the more worn M1 in the skull is 0.52 mm. The m1 crown height of the dentary associated with the skull is 0.47 mm. Therefore in this specimen, the crown height of the M1 is slightly greater than that of the opposing m1.

Based on the rather consistent lower molar morphology, the unequivocal association of the upper and lower dentition, the degree of crown height development, the low coefficients of variation observed in the lower molar statistics, and the fact that all specimens came from a single locality, indicates that the Smith Valley sample represents a single taxon. Furthermore, because the Smith Valley form exhibits more characters diagnostic of *Bensonomys* than of *Symmetrodontomys*, it is referable to the former genus. *Bensonomys lindsayi* can be easily distinguished from all other species of *Bensonomys* and *Symmetrodontomys* by the differentiating characters presented in the diagnosis above.

The systematics of *Bensonomys* has a complicated history. Gidley (1922) assigned material from the Benson Fauna (Blancan) of the Saint David Formation, Arizona, to *Eligmodontia arizonae*. Hibbard (1938) described *Peromyscus eliasi* from Rexroad 2 (Blancan), Meade County, Kansas. Gazin (1942) erected the genus *Bensonomys* and made *E. ari*zonae the type species. Hibbard (1956) referred *P. eliasi* to *Bensonomys* and recognized a new species, *Bensonomys meadensis*, from the Big Springs Ranch Locality (Blancan), Meade County, Kansas. Hibbard (1953) described *Cimarronomys stirtoni* from the Saw Rock Canyon Fauna (Blancan), Rexroad Formation, Kansas. Noting morphological similarities of North American *Bensonomys* with the extant South American sigmodontine genus *Calomys*, Baskin (1978) reduced *Bensonomys* to a subgenus of *Calomys*. He also referred *Cimarronomys stirtoni* to *Calomys (Bensonomys)* and named two new species, *C. (B.) yazhi* and *C. (B.) gidleyi* from the White Cone Fauna (Hemphillian), Bidahochi Formation, Arizona. Dalquest (1983) described *C. (B.) coffeyi* from the Coffee Ranch local fauna (Hemphillian), Hemphill County, Texas. Lindsay and Jacobs (1985) recognized two new species, *C. (B.) elachys* and *C. (B.) baskini* from the Yepómera (latest Hemphillian) and Concha (earliest Blancan) Faunas, Chihuahua, Mexico (Lindsay et al., 2006). Carranza-Castañeda and Walton (1992) described *C. (B.) winklerorum* from the latest Hemphillian or earliest Blancan El Ocote Fauna of Guanajuato, Mexico (Flynn et al., 2005). Other records of the genus with no specific identifications include the following: 1) a M1 from the Blanco Fauna (Blancan) of Texas (Dalquest, 1975); 2) a partial dentary with m1-3 from the Guanajuato locality GTO 5 (Blancan), Mexico (Carranza-Castañeda and Walton, 1992); and 3) inclusion in faunal lists from the Palm Spring Group (late Blancan), Anza-Borrego, California (Downs and White, 1968; Cassiliano, 1999) and the White Narrows Formation (Blancan) of southeastern Nevada (Reynolds and Lindsay, 1999; Mead and Bell, 2001). Martin (2000) suggested that *Bensonomys* may be a distinct genus separate from *Calomys* based on the number of M1/m1 roots present in each taxon and because the M2/m2 major cusps of *Bensonomys* are less opposed (alternate more) than those of *Calomys*. Most recently, Martin et al. (2002a, 2002b) formally resurrected *Bensonomys* to generic status and described a new species, *B. hershkovitzi*, from the Pipe Creek Sinkhole (early Blancan) of Grant County, Indiana. In summary, with the addition of the new species described herein, twelve species of *Bensonomys* are now recognized (Table 4).

The sample of *Bensonomys* from Smith Valley is one of the most complete known, including a skull, which represents the most complete cranial record for the genus and demonstrates that the genus exhibits a myomorphous zygomasseteric structure, similar to those of other sigmodontine rodents where known. *Bensonomys* was widely distributed in the late Cenozoic (Hemphillian through Blancan) of North America. Prior to this report, *Bensonomys* was recorded during the Hemphillian from Arizona, Texas, and Mexico. The occurrence of *Bensonomys lindsayi* in the Smith Valley Fauna represents the first record of the genus from west central Nevada.

TABLE 4. Species of *Bensonomys*. NALMA, North American Land Mammal age.

NALMA	Species
Blancan	*B. arizonae* *B. eliasi* *B. hershkovitzi* *B. meadensis* *B. stirtoni*
Earliest Blancan and/or Latest Hemphillian	*B. elachys* *B. baskini* *B. winklerorum*
Hemphillian	*B. coffeyi* *B. gidleyi* *B. lindsayi* *B. yazhi*

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