NEW POPULATIONS AND BIOGEOGRAPHIC PATTERNS OF THE GEOMYID RODENTS *LIGNIMUS* AND *MOJAVEMYS* FROM THE BARSTOVIAN OF WESTERN MONTANA

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ABSTRACT—New dental specimens described here from the Barstovian CC South and Flint Creek localities of western Montana are determined to be of two geomyid rodent species, *Lignimus transversus* and *Mojavemys* sp. These species were known previously from sparse material and the new samples aid the clarification of their biogeography and evolution. The presence of *Lignimus transversus* at both localities extends the range of that species to the north. In *Mojavemys*, a cline of increasing tooth size from south to north is analogous to clines in extant geomyids that correlate with nutritional or climatic gradients. Comparisons of various dental morphologic features of the new material and of the previously described populations of both genera reveal that the examined traits as well as the populations themselves were not genetically linked, and suggest mosaic evolution operated in these species. The differences in dental morphology between the various depositional basins are consistent with the idea of a tectonic influence on mammalian evolution.

INTRODUCTION

Geomyid rodents in the northern Rocky Mountains declined in species diversity and density about 17 million years ago (Barnosky, 2001). That time closely followed the development of the Mid-Tertiary unconformity (Thompson et al., 1981; Fields et al., 1985; Burbank and Barnosky, 1990), which occurred as the region began to be configured into the basins and ranges that characterize it today, and was coincident with local and global warming, the Miocene Climatic Optimum (Zachos et al., 2001). As the gopher-like geomyids declined, the pocket-mice-like heteromyid rodents became more speciose and began to dominate in numbers of individuals.

With the goal of a greater understanding of the role of physical environmental changes in affecting these and other biotic changes, this is one of a series of papers intended to explore the population-level and species-level taxonomic affinities of the small mammals of Miocene intermontane basins of Wyoming, Montana, and Idaho (see also Hopkins, 2004; Kraatz and Barnosky, 2004). Additionally, this study sheds light on the evolutionary events that followed the reduction in geomyid species richness and density, which set the stage for development of features that characterize modern geomyids.

We describe new rodent populations of two genera, *Mojavemys* and *Lignimus*. By exploring taxonomic affinities, we are able to group these populations into appropriate species, thereby giving us a basis to make inter- and intra-species morphologic comparisons. Taking into consideration the respective geographic location of these species, the morphologic comparisons allow us to determine whether or not physical environmental changes had an influence on evolution in these taxa, and to infer some details about their presumed genetic relatedness through their geographic range in the Barstovian.

The specimens described in this paper were collected at the CC South (CM 1935) locality within the Hepburn's Mesa Formation and from the Flint Creek (KU-MT-29) locality from sediments equivalent to the Six Mile Creek Formation in southwestern Montana. The CC South and Flint Creek localities have been dated biostratigraphically to near the boundary between the early Barstovian and late Barstovian land mammal age (Fields et al., 1985; Barnosky and Labar, 1989; Burbank and Barnoksy, 1990; Tedford et al., 2004). These specimens are curated at the Carnegie Museum of Natural History (**CM**) and University of Kansas Natural History Museum (**KU**), and consist solely of isolated teeth and jaw fragments. No skull or postcranial material of these taxa has been found at these localities. Other specimens of *Mojavemys* and *Lignimus* have been reported from the localities indicated on Figure 1.

METHODS

The CC South locality occurs in the Hepburn's Mesa Formation in the Yellowstone Valley of southwestern Montana. The specimens from CC South were collected by screen washing in the claystone and clayey siltstone layers low in the CC South section (Burbank and Barnosky, 1990). Paleomagnetic and biostratigraphic analyses of the Hepburn's Mesa Formation suggest an early-late Barstovian age around 14.5 Ma for these specimens (Barnosky and Labar, 1989; Burbank and Barnosky, 1990; Tedford et al., 2004). The Flint Creek specimens were screen-washed from sediments equivalent to the Six Mile Creek Formation, and are assigned to the early Barstovian, falling in the interval between 15 and 16 Ma (Tedford et al., 2004).

Measurements follow those illustrated by Barnosky (1986). The specimens from CC South and Flint Creek were measured with a Wild Heerbrugg M3C dissecting microscope at 40×, as was comparative material from the University of California Museum of Paleontology for the species listed in Table 1. For other specimens we relied on measurements taken directly from previously published literature. Within the text, values in parentheses are means.

Abbreviations—**AP**, total anterior-posterior length of tooth; **CHEV**, total lingual chevron height; **OR**, observed range*;* **TA**, total width of anterior loph; **TP**, total width of posterior loph; **T**, greatest width of tooth, either TA or TP, whichever is larger.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowditch, 1821
Family GEOMYIDAE Bonaparte, 1845
Genus *LIGNIMUS* Storer, 1970
LIGNIMUS TRANSVERSUS Barnosky, 1986
(Figs. 2, 3)

Locality—CC South (CM 1935) and Flint Creek (KU-MT-29), both in southwest Montana (Fig. 1).

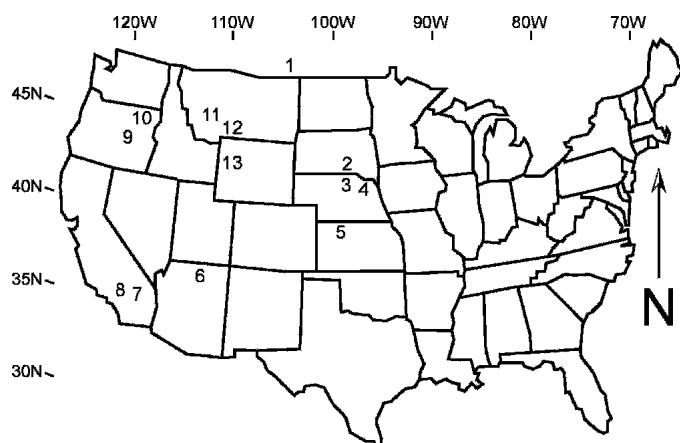FIGURE 1. Occurrence of species of *Lignimus. Mojavemys*, and *Phelosaccomys* in North America. 1. *Lignimus montis*, Wood Mountain Formation, southern Saskatchewan; 2. *L. austridakotensis*, Fort Randall Formation, Charles Mix Co., South Dakota; 3. *L.* cf. *L. montis*, Valentine Formation, Brown Co., Nebraska; 4. *Phelosaccomys annae*, Valentine Formation, Knox Co., Nebraska; 5. *P. hibbardi*, Ogallala Formation, Trego Co., Kansas; 6. *Mojavemys galushai*, Tesuque Formation, Rio Ariba Co., New Mexico; 7. *M. alexandrae* and *M. lophatus*, Barstow Formation, San Bernadino Co., California; 8. *M. wilsoni*, Caliente Formation, Ventura Co., California; 9. *M. mascallensis*, Mascall Formation, Grant Co., Oregon; 10. *M. mascallensis*, Shutler Formation, Umatilla Co., Oregon; 11. *L. transversus* and *M.* sp., Flint Creek locality, sediments equivalent to the Six Mile Creek Formation, Granite Co., Montana; 12. *L. transversus* and *M.* sp., Hepburn's Mesa Formation, Park Co., Montana; 13. *L. transversus* and *M. magnumarcus*, Colter Formation, Teton Co., Wyoming.

TABLE 1. Number of comparative specimens for each tooth position of *Lignimus*, *Mojavemys*, *Parapliosaccomys*, and *Phelosaccomys* used in this study

Species	p4	m1 or m2	m3	P4	M1 or M2	M3
Lignimus austridakotensis	—	53	4	—	14	1
L. montis	5	37	5	3	24	6
Lignimus cf. *L. montis*	—	3	1	—	4	—
L. transversus	3	8	5	2	5	2
Phelosaccomys annae	11	2	1	11	6	2
Pehlosaccomys hibbardi	5	3	2	—	2	1
Parapliosaccomys oregonensis	18	44*	—	24	56*	—
Mojavemys alexandre	—	1	1	1	5	2
M. galushai	5	8	5	4	5	2
M. lophatus	2	9	—	3	8	1
M. mascallensis	2	4	2	2	4	1
M. magnumarcus	2	10	10	4	7	3
M. wilsoni	—	2	—	—	—	—

*Total number of molars, including third molars (Shotwell,1967).

Age—CC South is late Barstovian; Flint Creek is early Barstovian (Tedford et al., 2004)

Referred Specimens—CC South (CM 1935; Fig. 2), P4, CM 61218, 61223, 61228, 61233, 61251, 61256, 61257, 64025, 66758, 66778. M1 or M2, CM 61231, 61247, 61271, 61272, 61274, 63429, 63920, 63933, 64034, 66761, 66762, 66767, 66768, 66777, 66781. M3, CM 61237, 66773. Lower fourth premolar, CM 61268, 63889, 64028, 64031, 64551, 66766, 66769. Lower first or second molar, CM 61234, 61236, 61240, 61244, 61246, 61248, 61249, 61253, 61254, 61259, 61264, 61280, 61285, 63811, 63907, 63911, 63914, 63931, 63932, 64552, 66757, 66760, 66765, 66770, 66776, 66780. Lower third molar, CM 61210, 61242, 63215, 63887, 63909, 66772, 66775, 66779. Flint Creek (KU-MT-29; Fig. 3 A–C), P4, KU 103813, 103833, 103839, 103848, 103841. Lower fourth premolar, KU 103803, 103805, 103808, 103809, 103811, 103812. Lower first or second molar, KU 103790–103793, 103797, 103800, 103823, 103826–103828, 103831.

Measurements—See Table 2. Comparative measurements from Barnosky (1983, 1986), Korth (1979, 1987, 1996), Shotwell (1967), and Storer (1970, 1973).

Species Comparisons—*Lignimus austridakotensis*, *L. montis*, *L. transversus*. The referred specimens were further compared to *Phelosaccomys annae* and *Phelosaccomys hibbardi*, because those taxa are morphologically similar; in fact, *P. annae* and *P. hibbardi* at one time were included within *Lignimus* (Korth, 1987, 1994; Korth and Reynolds, 1994). We also compared the specimens qualitatively to *Parapliosaccomys oregonensis* due to the former inclusion of some *Lignimus* species in this genus.

Description—All teeth are relatively brachydont, more so at CC South, and lack dentine tracts at both localities, which distinguish this taxon from *P. oregonensis*. Lower fourth premolars have a slight notch between the protoconid-metaconid and protostylid. Mean AP/T of p4 specimens (AP/T = 1.07) from CC South equals that of *L. transversus* from the Colter Formation in

Jackson Hole and is similar to *L. montis* (AP/T = 1.08). The p4s from CC South are less narrow than the p4s of *P. hibbardi* (AP/T = 1.22), while the mean AP/T found at Flint Creek (AP/T = 1.16) is similar to *P. hibbardi*. Anterior-posterior p4 lengths are similar for all species.

The lower m1 or m2s are rooted. The occlusal surface of m1 or m2s displays anterior and posterior 'Vs' that point rostrally; the posterior 'V' is more flattened. An anterolabial cingulid is prominent. The mean AP/T ratios of m1 or m2s from CC South (AP/T = 0.83) and Flint Creek (AP/T = 0.82) are equal to those of *L. transversus* and *L. austridakotensis* (AP/T = 0.83), and are narrower than those of *P. hibbardi* (AP/T = 0.65) and *P. annae* (AP/T = 0.70), but not as narrow as those of *L. montis* (AP/T = 1.15). The mean AP measurement of m1 or m2s from CC South equals 1.40 mm, while mean AP from Flint Creek equals 1.61 mm. These mean values are similar to those of *L. montis* (AP = 1.53 mm), *L. transversus* (AP = 1.46 mm), and *P. hibbardi* (AP = 1.40 mm).

Lower m3s of CC South specimens have a mean AP/T of 0.89 and a range from 0.83 to 0.95. The measurements for the m3s of the CC South specimens are similar to those of *L. austridakotensis* (AP/T = 0.81), *L.* cf. *L. montis* (AP/T = 0.92), and *L. transversus* (AP/T = 0.93), all of which are wider than those of *L. montis* (AP/T = 1.15). *Lignimus* m3s are unknown from Flint Creek. Lower third molar AP lengths are similar for all species.

In many specimens, especially from Flint Creek, unworn P4s possess an accessory cuspule, which is always lateral rather than anterior as found in *Lignimus montis*. AP/T values for P4s of CC South and Flint Creek specimens average 0.95 (Table 2). This mean is similar to that of *L. transversus* (AP/T = 0.89), and is broader than that of *L. montis* (AP/T = 1.18). P4s from CC South and Flint Creek lack dentine tracts, a similarity to *L. transversus* and *L. montis*. These teeth are similar in AP length to the teeth of *L. transversus* and *P. annae*, but are smaller than teeth of *L. montis*.

M1 or M2s from CC South are similar to *L. montis* and *L. transversus* in occlusal pattern. At CC South, the teeth are 20–40% longer in mean length (AP = 1.77 mm; Table 2) than in *L. austridakotensis* (AP = 1.10 mm), *L. montis* (AP = 1.10 mm), *L. cf. L. montis* (AP = 1.20 mm), *L. transversus* (AP = 1.28 mm), *P. annae* (AP = 1.10 mm), and *P. hibbardi* (AP = 1.40 mm). The teeth are, however, similar in shape to teeth of *L. austridakotensis* (AP/T = 0.74), *L. montis* (AP/T = 0.77), *L.* cf. *L. montis* (AP/T = 0.80), *L. transversus* (AP/T = 0.72), and *P. hibbardi* (AP/T = 0.74), but are narrower than teeth of *P. annae* (AP/T = 0.66). CHEV/T for the Hepburn's Mesa *Lignimus* M1 or M2s is 0.17. *Lignimus* M1 or M2s are unknown from Flint Creek.
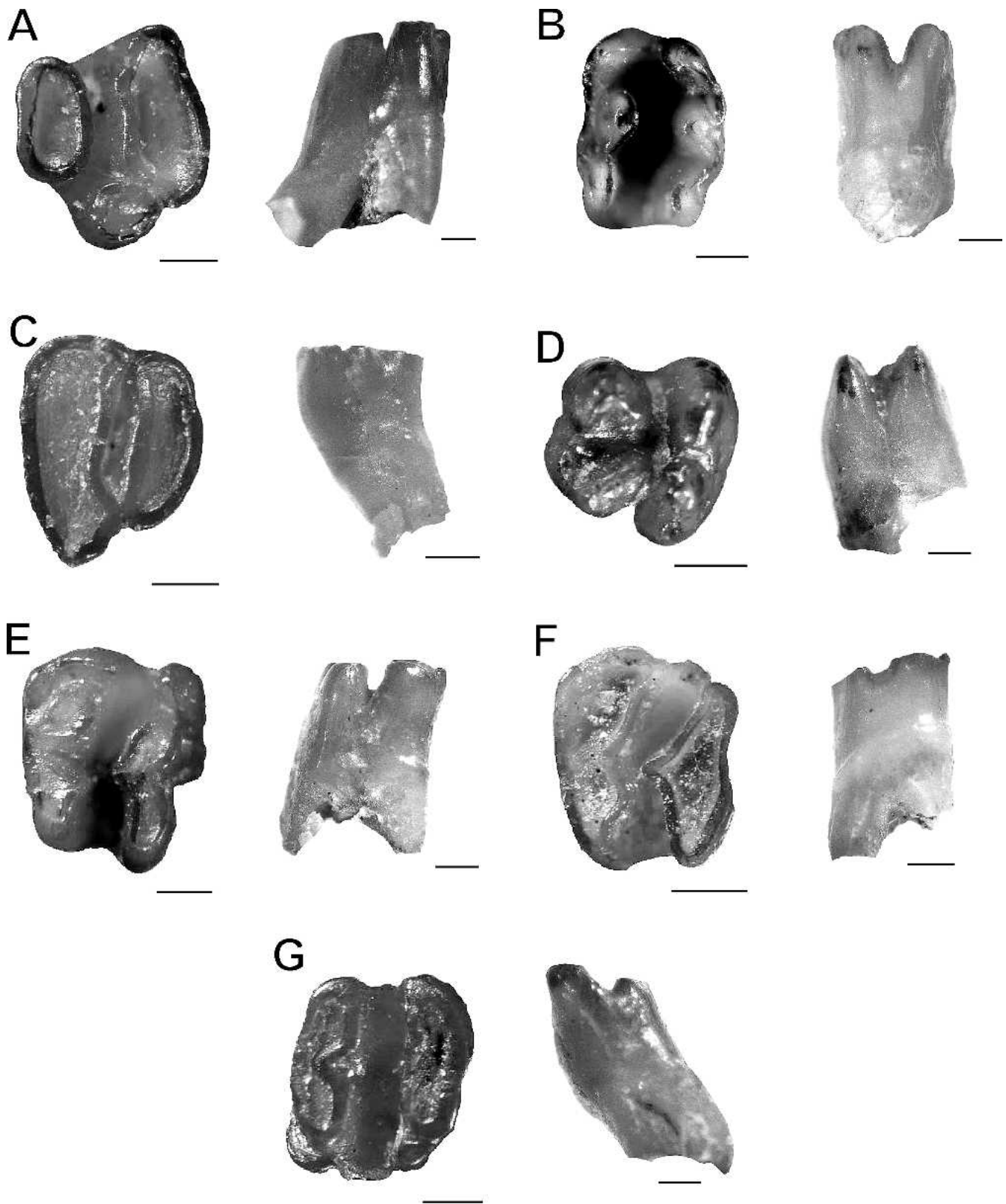
FIGURE 2.   Occlusal, lingual (upper teeth), and labial (lower teeth) views of teeth of *Lignimus transversus* from the CC South locality, Hepburn's Mesa Formation. Anterior to left for occlusal views. *Lignimus transversus*: **A**, CM 61233, Left P4; **B**, CM 66768, Right M1 or M2; **C**, CM 61210, Left M3; **D**, CM 61268, Left p4; **E**, CM 61280, Right m1; **F**, CM 63931, Right m2; **G**, CM 61237, Left m3. Scale bar equals 0.5 mm.

TABLE 2. Measurements for *Lignimus* teeth from CC South (CM 1935) and Flint Creek (KU-MT-29)

Tooth	Statistic	TA	TP	AP	AP/T	CHEV/T
		CC South (CM 1935); Hepburn's Mesa Formation				
p4	Mean	1.14	1.42	1.51	1.07	—
	SD	0.070	0.144	0.163	0.060	—
	OR	1.07–1.28	1.12–1.56	1.19–1.65	0.97–1.15	—
	N	7	7	7	7	—
m1 or m2	Mean	1.65	1.63	1.40	0.833	—
	SD	0.078	0.183	0.156	0.059	—
	OR	1.26–1.91	1.23–1.93	1.00–1.70	0.73–0.96	—
	N	26	26	26	26	—
m3	Mean	1.29	1.17	1.15	0.890	—
	SD	0.225	0.228	0.176	0.038	—
	OR	1.09–1.81	0.98–1.72	1.02–1.56	0.83–0.96	—
	N	8	8	8	8	—
P4	Mean	1.04	1.80	1.71	0.95	—
	SD	0.191	0.190	0.213	0.070	—
	OR	0.77–1.28	1.44–2.09	1.33–1.98	0.84–1.06	—
	N	10	10	10	10	—
M1 or M2	Mean	1.77	1.71	1.39	0.77	0.17
	SD	0.207	0.195	0.174	0.045	0.070
	OR	1.49–2.33	1.30–2.21	0.98–1.77	0.66–0.84	0.11–0.24
	N	15	15	15	15	9
M3	Mean	1.50	1.31	1.30	0.81	—
	SD	0.148	0.115	—	—	—
	OR	1.40–1.60	1.23–1.40	—	0.81	—
	N	2	2	1	1	—
		Flint Creek (KU-MT-29); Sediments equivalent to the Six Mile Creek Formation				
Tooth	Statistic	TA	TP	AP	AP/T	CHEV/T
p4	Mean	1.36	1.62	1.88	1.16	—
	SD	0.214	0.247	0.367	0.052	—
	OR	1.07–1.70	1.40–2.09	1.58–2.60	1.10–1.24	—
	N	6	6	6	6	—
m1 or m2	Mean	1.91	1.94	1.61	0.82	—
	SD	0.153	0.140	0.110	0.049	—
	OR	1.58–2.12	1.77–2.16	1.47–1.86	0.73–0.88	—
	N	11	11	11	11	—
P4	Mean	1.16	1.88	1.77	0.95	—
	SD	0.193	0.079	0.065	0.051	—
	OR	0.98–1.47	1.79–2.00	1.67–1.84	0.89–1.01	—
	N	5	5	5	5	—

Dimensions are illustrated in Barnosky (1986). **Abbreviations**: **AP**, total anterior-posterior length; **CHEV**, total lingual chevron height; **N**, number of specimens; **OR**, observed range; **SD**, standard deviation; **TA**, total width of anterior loph; **TP**, total width of posterior loph; **T**, greatest width, TA or TP, whichever is larger.

AP/T for the unbroken M3 from CC South is 0.81. This value is between the values for the other comparative species: *L. austridakotensis* (AP/T = 0.76), *L. montis* (AP/T = 0.78), *L. transversus* (AP/T = 0.88), *P. annae* (AP/T = 0.71), and *P. hibbardi* (AP/T = 0.71). Length measurements (AP = 1.30 mm) are similar to those of *L. transversus* (AP = 1.35 mm) but are 10–30% longer than in *L. austridakotensis* (AP = 0.94 mm), *L. montis* (AP = 0.97 mm), *P. annae* (AP = 1.02 mm), and *P. hibbardi* (AP = 1.2 mm). *Lignimus* M3s are unknown from Flint Creek.

Discussion—The lack of dentine tracts, presence of roots on the m1 or m2s, and the similarity in features and tooth measurements of the specimens from CC South and Flint Creek suggest that these specimens are from populations of *Lignimus transversus*.

Genus *MOJAVEMYS* Lindsay, 1972
MOJAVEMYS sp.
(Figs. 3, 4)

Localities—CC South (CM 1935) and Flint Creek (KU-MT-29).

Age—CC South is late Barstovian; Flint Creek is early Barstovian (Tedford et al., 2004)

Referred Specimens—CC South (CM 1935; Fig. 4). P4, CM 61207, 61217, 61229, 61232, 61260, 61278, 61284. M1 or M2, CM 61206, 61230, 61238, 61241, 61250, 61267, 61286, 63397, 63923, 64029, 64074, 64094, 64440, 64545, 64546. M3, CM 61211, 61261, 61263, 63202, 63234, 63401, 63817, 63821, 63885, 63927, 63935, 66676–66678. Lower fourth premolar, CM 61269, 63588, 63823. Lower first or second molar, CM 61209, 61227, 61235, 61239, 61243, 61258, 61266, 61276, 61282, 61283, 63436, 63816, 63822, 63824, 63919, 64078, 64548, 64549, 66735. Lower third molar, CM 61289, 66713, 66733. Flint Creek (KU-MT-29; Fig. 3 D–G), P4, CM 103801, 103834–103836, 103847, 103851. M1 or M2, CM 103856, 103857, 103862. Lower first or second molar, CM 103824, 103863.

Measurements—See Table 3. Comparative measurements are from Barnosky (1983, 1986), Downs (1956), Lindsay (1972), and Korth and Chaney (1999).

Species comparisons—*Mojavemys alexandrae*, *M. galushai*, *M. lophatus*, *M. mascallensis*, *M. magnumarcus*, and *M. wilsoni*.

Description—The mean AP/T ratio for p4 specimens at CC South (AP/T = 1.11) is larger than the mean ratios for *M. lophatus* (AP/T = 1.07), *M. galushai* (AP/T = 0.96), and *M. mascallensis* (AP/T = 0.96), but smaller than that for *M. magnumarcus* (AP/T = 1.20). One p4 (CM 63588) is not single rooted and shows separate anterior and posterior roots as found in *M. magnumarcus* and *M. mascallensis*. *Mojavemys* p4s are unknown from Flint Creek. Lower fourth premolar anterior–posterior length measurements are similar for all species.
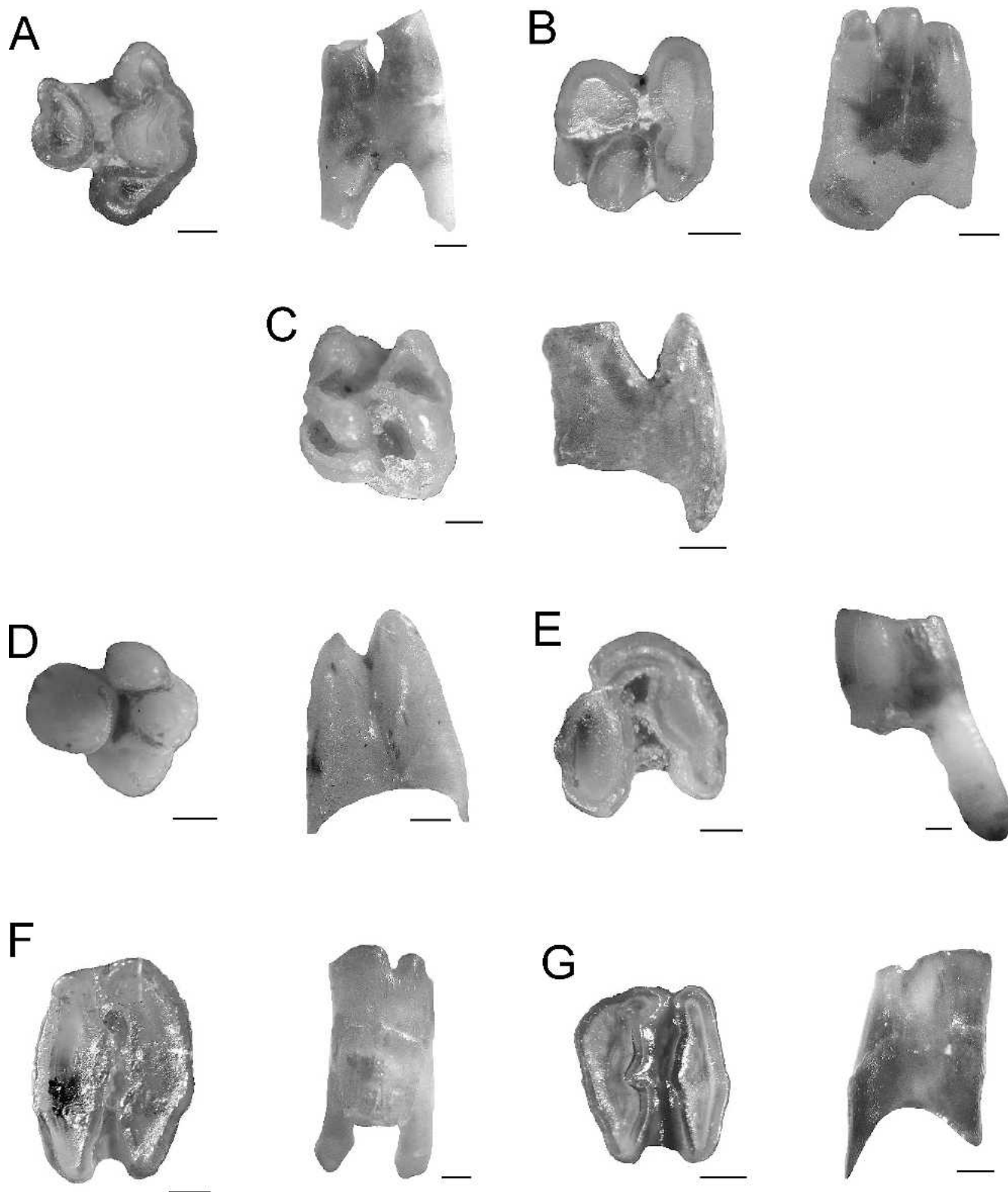
FIGURE 3.   Teeth of *Lignimus transversus* (**A–C**) and *Mojavemys* sp. (**D–G**) from the Flint Creek locality from sediments equivalent to the Six Mile Creek Formation. Anterior to left for occlusal views. Side views are lingual for upper teeth and labial for lower teeth. *Lignimus transversus*: **A**, KU 103841, Left P4; **B**, KU 103808, Left p4; **C**, KU 103797, Left m1 or m2. *Mojavemys* sp.: **D**, KU 103851, Right P4; **E**, KU 103834, Right P4; **F**, KU 103856, Left M1 or M2; **G**, KU 103824, Right m1 or m2. Scale bar equals 0.5 mm.
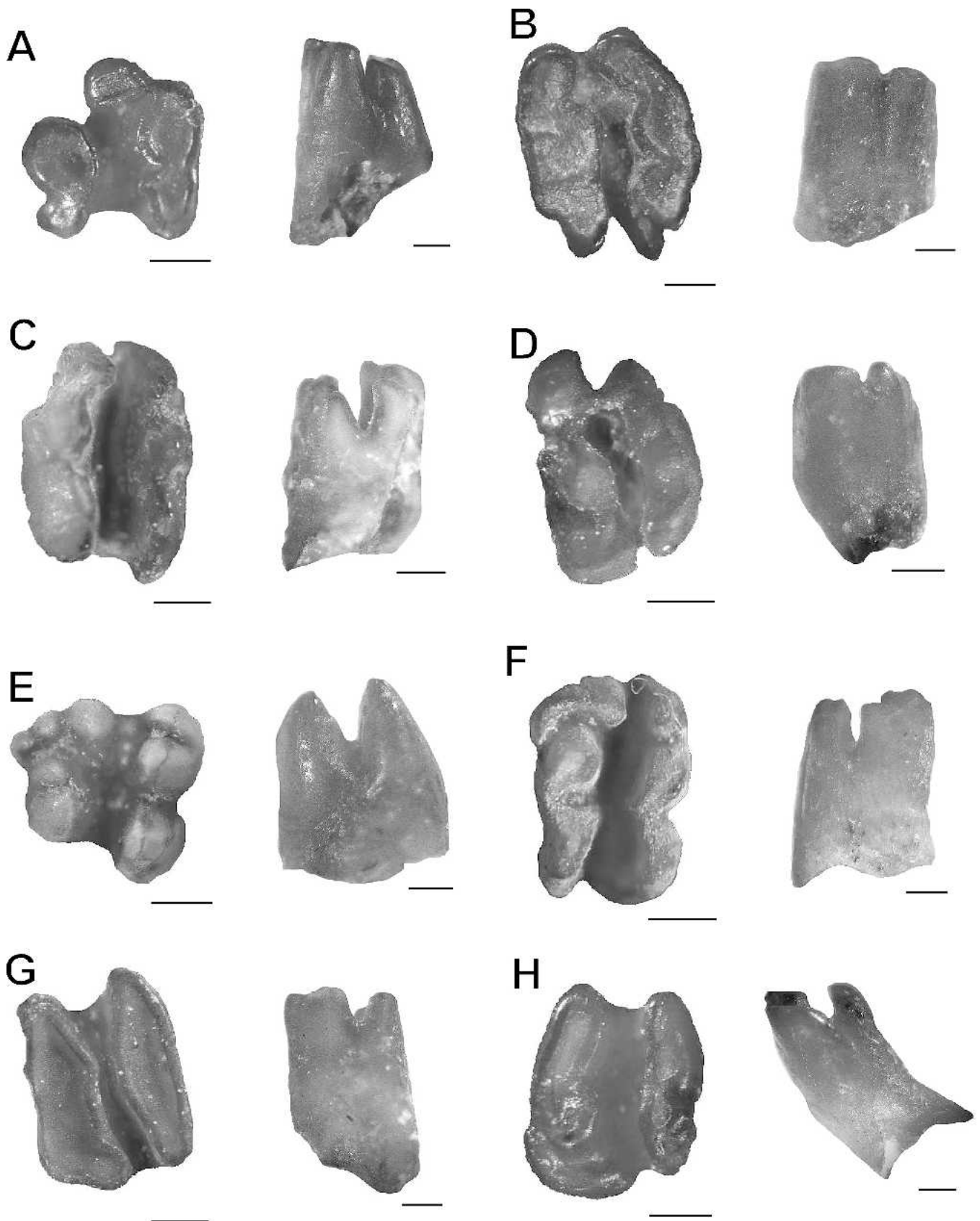
FIGURE 4. Occlusal, lingual (upper teeth), and labial (lower teeth) views of teeth of *Mojavemys* sp. from the CC South locality, Hepburn's Mesa Formation. **A**, CM 61207, Right P4; **B**, CM 61230, Right M1 or M2; **C**, CM 63923, Left M1 or M2; **D**, CM 63234, Right M3; **E**, CM 61269, Left p4; **F**, CM 63822, Right m1; **G**, CM 64078, Left m1 or m2; **H**, CM 66713, Left m3. Scale bar equals 0.5 mm.

TABLE 3. Measurements of *Mojavemys* from CC South (CM 1935) and Flint Creek (KU-MT-29)

Tooth	Statistic	TA	TP	AP	AP/T	CHEV/T
CC South (CM 1935); Hepburn's Mesa Formation						
p4	Mean	1.01	1.23	1.34	1.11	—
	SD	0.212	0.247	0.285	0.993	—
	OR	0.86–1.16	1.05–1.40	1.09–1.65	1.04–1.18	—
	N	2	2	3	2	—
m1 or m2	Mean	1.72	1.71	1.43	0.81	—
	SD	0.093	0.146	0.093	0.045	—
	OR	1.56–1.91	1.47–1.91	1.30–1.60	0.73–0.90	—
	N	19	17	17	17	—
m3	Mean	1.48	1.17	1.23	0.84	—
	SD	0.215	0.249	0.080	0.073	—
	OR	1.33–1.72	0.95–1.44	1.14–1.30	0.76–0.90	—
	N	3	3	3	3	—
P4	Mean	1.12	1.89	1.88	1.00	—
	SD	0.178	0.236	0.230	0.036	—
	OR	0.98–1.53	1.63–2.35	1.67–2.30	0.91–1.02	—
	N	9	8	8	8	—
M1 or M2	Mean	1.83	1.75	1.38	0.76	0.23
	SD	0.137	0.154	0.084	0.057	0.088
	OR	1.49–2.12	1.40–2.07	1.26–1.63	0.68–0.91	0.10–0.41
	N	15	15	15	15	13
M3	Mean	1.28	1.10	1.16	0.89	—
	SD	0.118	0.108	0.167	0.093	—
	OR	1.09–1.47	0.91–1.26	0.98–1.56	0.79–1.08	—
	N	13	13	14	13	—
Flint Creek (KU-MT-29); Sediments equivalent to the Six Mile Creek Formation						
Tooth	Statistic	TA	TP	AP	AP/T	CHEV/T
m1 or m2	Mean	1.90	1.79	1.60	0.841	—
	SD	0.050	0.071	0.050	0.041	—
	OR	1.86–1.93	1.74–1.84	1.56–1.63	0.84–0.85	—
	N	2	2	2	2	—
P4	Mean	1.21	1.89	1.86	0.98	—
	SD	0.168	0.197	0.230	0.032	—
	OR	1.02–1.51	1.77–2.26	1.65–2.30	0.93–1.02	—
	N	6	6	6	6	—
M1 or M2	Mean	2.33	2.29	1.52	0.66	0.14
	SD	0.362	0.387	0.234	0.071	0.103
	OR	1.95–2.67	1.88–2.65	1.37–1.79	0.58–0.72	0.07–0.26
	N	3	3	3	3	3

Dimensions are illustrated in Barnosky (1986). **Abbreviations**: **AP**, total anterior-posterior length; **CHEV**, total lingual chevron height; **N**, number of specimens; **OR**, observed range; **SD**, standard deviation; **TA**, total width of anterior loph; **TP**, total width of posterior loph; **T**, greatest width, TA or TP, whichever is larger.

One anterior and one posterior root, which join near the enamel base, are present in m1 or m2s from CC South and Flint Creek. This condition is similar to *M. magnumarcus* and *M. lophatus*, but differs from *M. mascallensis*, which has two separate anterior and two separate posterior roots. Lower first molars possess an anterolabial cingulid that extends only about one-third to one-half the length of the metalophid, similar to the condition in *M. lophatus* and *M. magnumarcus*. In the m2s from CC South and Flint Creek, the metaconid is transversely elongated and the prominent anterolabial cingulid extends to the protoconid, about one-half the length of the metalophid. This is similar to the condition found in *M. alexandrae* and *M. lophatus*. All AP/T measurements for *Mojavemys* m1 or m2s are similar among species. *Mojavemys mascallensis* has a mean AP/T that equals 0.96, and *M. galushai* and *M. wilsoni* have AP/T = 0.74 and 0.78, respectively. Each of the other species has an AP/T between 0.80–0.85. Mean AP length measurements of m1 or m2 specimens from CC South and Flint Creek (Table 3) are similar to each other as well as to those of *M. magnumarcus* (AP = 1.51 mm; OR 1.4–1.8 mm) and the one specimen of *M. alexandrae* (AP = 1.37 mm). These measurements are all slightly larger than measurements of the other species of *Mojavemys*.

Measurements for m3s from CC South and Flint Creek are similar to those for the other species of *Mojavemys*. Mean AP/T

equals 0.84 for specimens from CC South, a similarity to *M. magnumarcus* (AP/T = 0.88) and *M. alexandrae* (AP/T = 0.86), but broader than that of *M. mascallensis* (AP/T = 0.96) and narrower than that of *M. galushai* (AP/T = 0.70). *Mojavemys* m3s are unknown from Flint Creek. Mean AP measurements are similar for all species except for *M. galushai*, which is about 25% smaller.

P4 measurements from all species of *Mojavemys* are similar (AP/T = 0.95 at both CC South and Flint Creek). Mean AP length measurements are shorter in *M. mascallensis* compared with the other species of *Mojavemys*.

M1 or M2s from CC South (AP = 1.38 mm) and Flint Creek (AP = 1.52) are similar in size to those of *M. alexandrae* (AP = 1.39 mm) and *M. magnumarcus* (AP = 1.43 mm), but are larger than for *M. galushai* (AP = 1.12 mm), *M. lophatus* (AP = 1.05 mm), and *M. mascallensis* (AP = 0.97 mm). The lingual chevrons from CC South and Flint Creek (CHEV/T = 0.14 and 0.23, respectively) are lower than those found in *M. magnumarcus* (CHEV/T = 0.44) and similar to the chevron height found in other *Mojavemys* species.

M3s from CC South possess a central basin, which is surrounded by both the protoloph and the metaloph. This condition is found in *M. alexandrae*, *M. lophatus*, and *M. magnumarcus*. TA, TP, and AP are similar for CC South specimens, *M. alexandrae*, and *M. magnumarcus*; they are slightly larger than those

for *M. galushai* and larger than for *M. lophatus* and *M. mascallensis*. *Mojavemys* M3s are unknown from Flint Creek.

Discussion—Qualitative and quantitative characteristics of the teeth in specimens from CC South and Flint Creek are most similar to features of *M. alexandrae*, *M. lophatus*, and *M. magnumarcus*. The m1 or m2s at CC South and Flint Creek are larger than those of *M. alexandrae* and *M. lophatus*, but the differences are not statistically significant. The mean total lingual chevron heights of M1 or M2s from both localities are smaller than those of *M. magnumarcus*. *Mojavemys magnumarcus* has a CHEV/T greater than 0.3, a diagnostic feature of that species (Barnosky, 1986). None of the specimens from Flint Creek have CHEV/T greater than 0.3, while the specimens from Hepburn's Mesa range above and below this value. Based on the CHEV/T measure, the specimens from Flint Creek are most likely either *M. alexandrae* or *M. lophatus*. However, the specimens at Hepburn's Mesa defy placement in a defined species because of the wide range in CHEV/T values, which span ranges previously considered diagnostic for *M. alexandrae*, *M. lophatus*, and *M. magnumarcus*. It may be that two or possibly all three of these species occur at this locality, or the material may represent a new species that combines traits previously considered definitive of the other three taxa. Such variance is not unusual for this locality, from which the heteromyid rodent *Cupidinimus* was reported to show wide variation and unique combinations of characters relative to other species in that genus (Carrasco, 1998).

MORPHOLOGIC LANDSCAPES

Morphologic landscapes have been used to study evolutionary processes in Quaternary mammals (Barnosky, 1990, 1993) and are also applicable to identifying the spatial and temporal distribution of morphological change during earlier times. They are constructed by measuring a given morphologic trait in a sample of fossils from several geographic areas, then plotting the mean measurements at the appropriate map coordinates.

In an effort to assess whether the traits that identify the various geomyid species we studied vary independently or are linked, and whether any spatiotemporal patterns suggestive of genetic connectedness between populations are apparent, we constructed morphologic landscapes to depict AP/T and APT for P4, M1 or M2, M3, p4, m1 or m2, and m3 for the populations of *Lignimus* and *Mojavemys* (Figs. 5–8). The AP/T ratio is a simplified measure of tooth shape, a character that might be expected to respond to selective pressures related to food use (changing vegetation) or increased grit on food (dust correlated with environments of variable aridity or proximity to volcanic soils, for example). The tooth area, APT, is another measure that reflects tooth shape, but is also influenced by body mass with larger tooth area generally correlated with larger body mass (Damuth and MacFadden, 1990). We analyzed these traits on multiple teeth in order to understand whether or not the evolution of various features of the dental row were linked, an approach stimulated by the documentation of mosaic evolution in dental traits of Quaternary rodents (Barnosky, 1993).

We considered as a population each sample of teeth that came from a restricted lens of sediment. We predicted that if traits vary independently, the shapes of the morphological landscape (that is, the relative position of mean values) should be different for each trait. We also predicted that if there was genetic connectedness among populations, those populations should plot at similar places on the morphologic landscape, although of course there could be other reasons that populations share similar morphospace. We assumed that the mean dental morphologic values reasonably represented the mean for the original populations, even though sample sizes do vary among the different populations.

For *Lignimus*, the northern Great Plains *L. montis* stands out as having a considerably larger P4 area and AP length, indicating larger body size than the populations from Jackson Hole (*L. transversus*), Hepburn's Mesa, and Flint Creek, all of which are in the Rocky Mountains (Fig. 5). This difference is also evident, though less pronounced, for the area of p4. Thus, the northern Great Plains population (*L. montis*) may have been of larger body size than the Rocky Mountain populations. The more southerly Great Plains species, *L. austridakotensis*, *L.* cf. *L. montis*, *P. annae*, and *P. hibbardi*, have a similar M1 or M2 area as the Rocky Mountain species (Fig. 5), suggesting the lack of a size gradient between species from the Rocky Mountains and the Great Plains. *Phelosaccomys annae* and *P. hibbardi*, related Great Plains taxa that occur south of *L. austridakotensis*, are plotted on Figure 5 for comparison. Both are similar in tooth area and body size to the *Lignimus* species.

The P4 of *L. montis* is considerably longer than wide in comparison to the Rocky Mountain populations (Fig. 6). In this trait, the geographic separation mirrors the morphologic distance, suggesting less genetic connectedness between populations of the Rocky Mountains and northern Great Plains than among those within the Rocky Mountains. Similarity of AP/T measurements also prevails for all of the Rocky Mountain populations for the upper and lower molars. However, in AP/T of p4, the Flint Creek population provides anomalously large measurements (Fig. 6). These patterns imply that traits on p4 vary independently with respect to P4 and m1 or m2, and that the Flint Creek population was isolated in space and/or time from the other two Rocky Mountain populations. The populations referred to *P. annae* and *P. hibbardi* consistently plot at the lowest part of the morphologic landscape compared to *Lignimus*, supporting their referral to a different genus than *Lignimus* (Korth, 1987, 1994; Korth and Reynolds, 1994).

Populations of *Mojavemys*, except for *M. mascallensis*, demonstrate a cline of increasing size from south to north based on area of the P4 and m1 or m2 (Fig. 7). Additionally, we analyzed AP length of lower m1 or m2s since length of molars is commonly correlated with body size in a wide variety of mammals. The m1 or m2 AP lengths provided similar results to those found for the P4 and m1 or m2 areas. This is similar to clines found in extant geomyids that generally accord with Bergmann's rule, and which have been interpreted to result from differences in nutritional quality of vegetation as well as climatic gradients (Smith and Patton, 1980; Patton and Brylski, 1987; Hadly, 1997). In general, Bergmann's rule has only been tentatively corroborated in rodents (Baumgardner and Kennedy, 1993; Sullivan and Best, 1997; Koontz et al., 2001). The differences in tooth area of *M. mascallensis* for its latitude suggest isolation within an environment that differs markedly from that of the other populations and/or greater genetic distance.

In the shape variable of AP/T, the morphologic landscapes for each of the *Mojavemys* tooth positions differ from one another (Fig. 8). For example, the landscape for P4 is relatively flat. The landscape for m1 or m2 shows a clustering of northern versus southern populations, and the landscape for p4 shows *M. magnumarcus* and the Hepburn's Mesa *Mojavemys* as differing greatly from all other populations. As was the case for *Lignimus*, the lack of congruence for morphologic landscapes among the shape variables for *Mojavemys* argues for decoupling of the genes that control morphology in the respective teeth. However, the clustering of *M. mascallensis*, the Flint Creek and Hepburn's Mesa *Mojavemys* sp., and *M. magnumarcus* for m1 or m2 and m3 correlates roughly with geographic proximity, which would be consistent with less genetic distance among those populations than between them and the southern group composed of *M. wilsoni*, *M. lophatus*, *M. alexandrae*, and *M. galushai*.
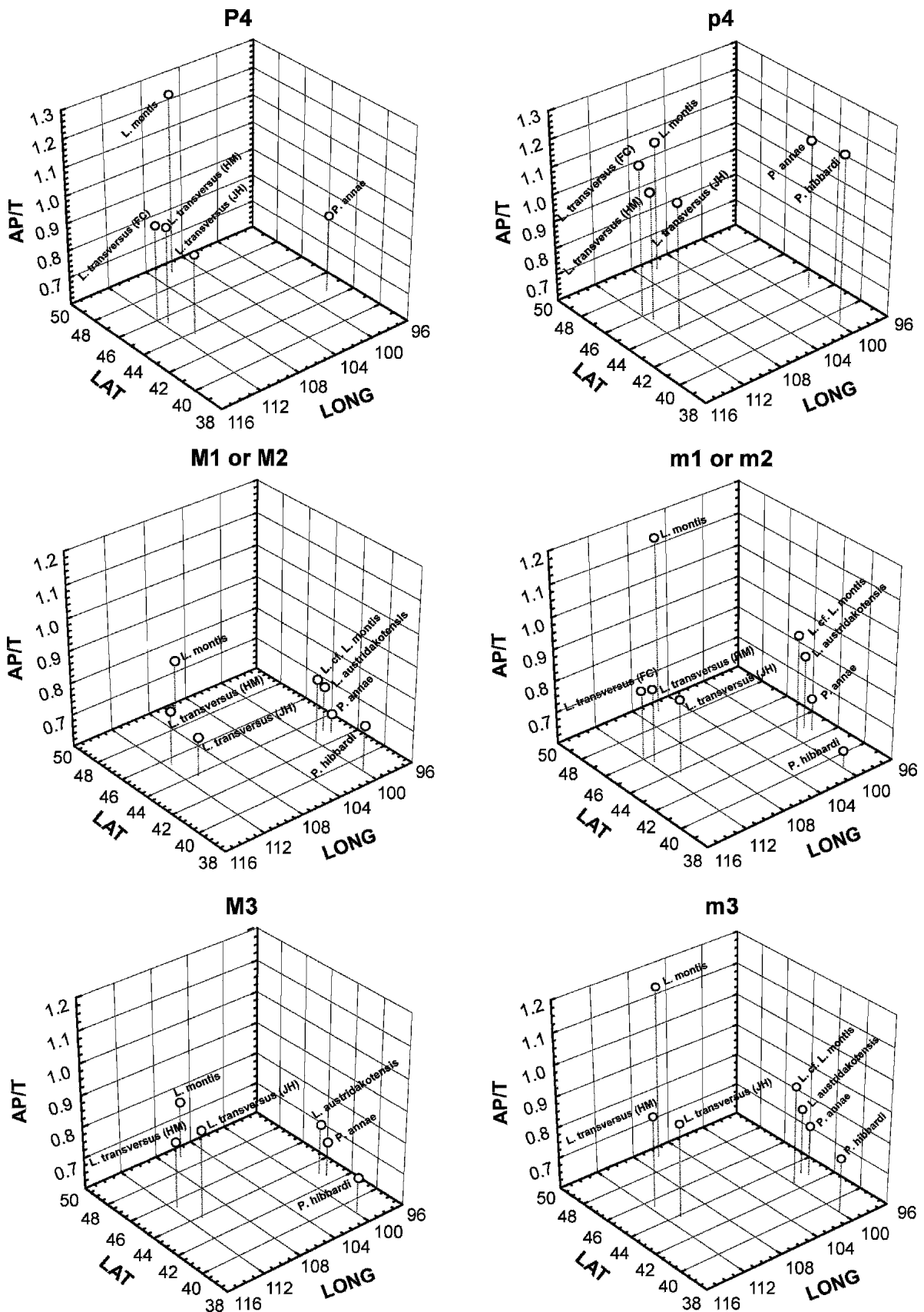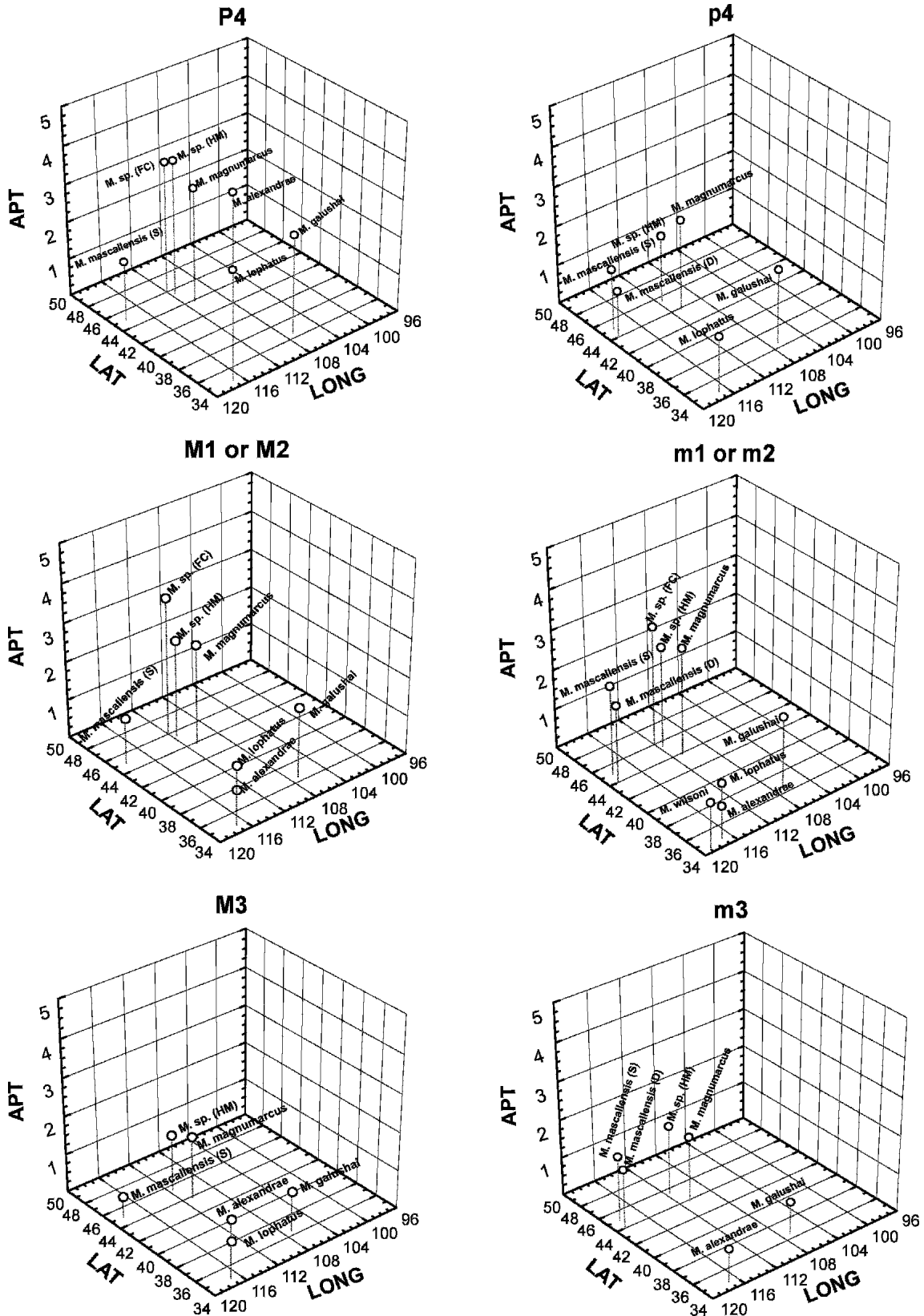
FIGURE 5.   Tooth area morphospaces for *Lignimus*. Area of tooth in mm². **LAT**, latitude; **LONG**, longitude.

FIGURE 6. Tooth shape morphospaces for *Lignimus*. AP/T is a measure of tooth shape. **LAT**, latitude; **LONG**, longitude.

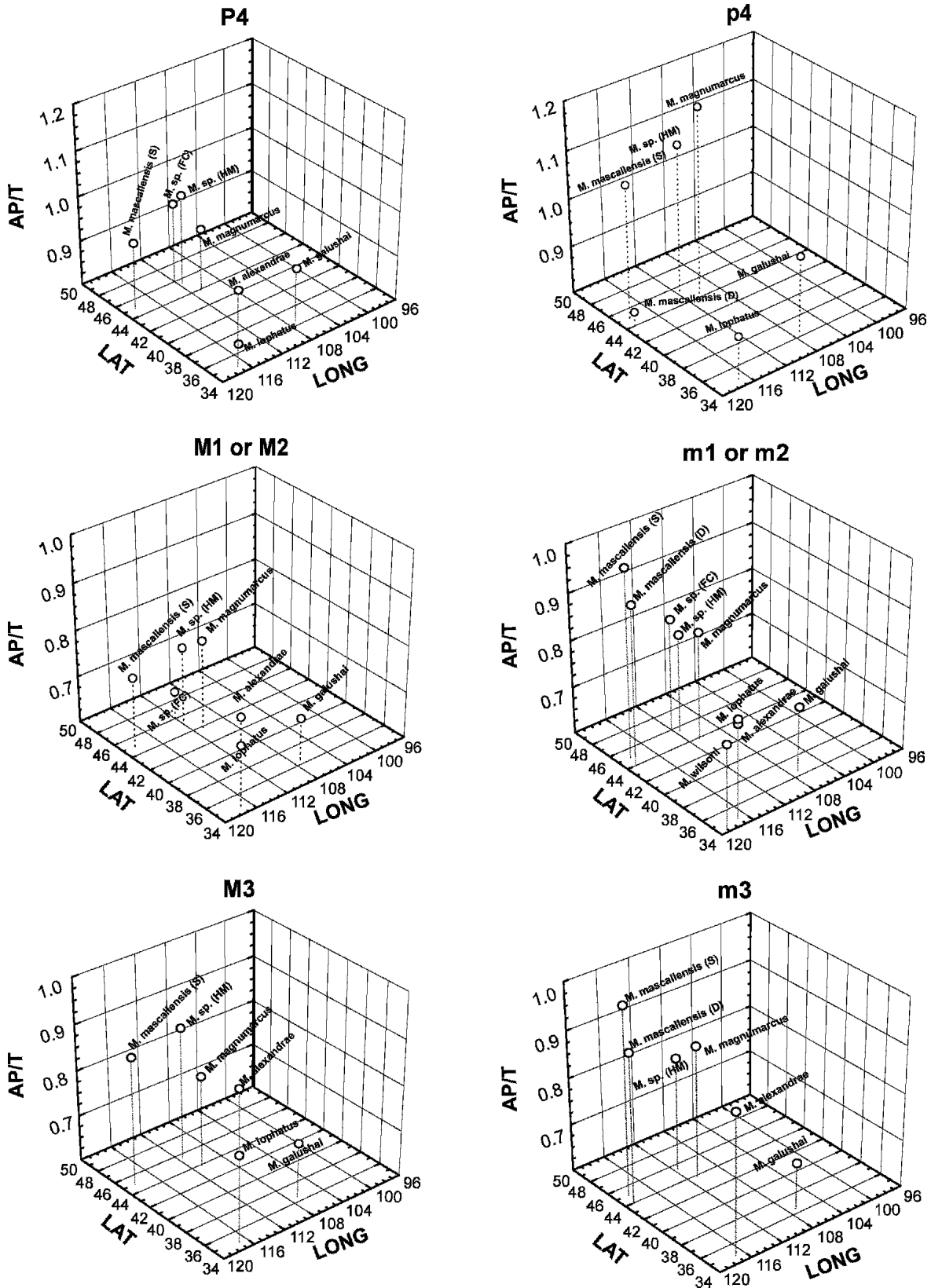FIGURE 7.   Tooth area morphospaces for *Mojavemys*. Area of tooth in mm^2. **LAT**, latitude; **LONG**, longitude.

FIGURE 8. Tooth shape morphospaces for *Mojavemys*. AP/T is a measure of tooth shape. **LAT**, latitude; **LONG**, longitude.

DISCUSSION AND CONCLUSIONS

The gopher-like geomyid species are represented by far fewer specimens than are pocket-mice-like heteromyid species at Hepburn's Mesa. This follows the trend seen in the geomyid rodents above the Mid-Tertiary unconformity throughout the Rocky Mountains (Barnosky, 2001; Barnosky et al., 2003). The lingering presence of at least two gopher-like geomyid rodent species implies that relatively moist habitats still existed, but the low population densities suggest that such habitats were less widespread than arid habitats preferred by heteromyids.

Comparison of morphologic landscapes among the different species within each of the two genera suggests that, as in modern geomyids and heteromyids, size clines existed for at least *Mojavemys* during the Barstovian. The patterns demonstrated by the morphologic landscapes, while suffering from lack of multiple fossil localities for each species, nevertheless show that morphologic (and by inference, genetic) distances were greater between northern and southern populations of *Mojavemys* than within each of those groups. For *Lignimus*, the morphologic landscapes support the separation of *P. hibbardi* and *P. annae* into different genera. For both *Mojavemys* and *Lignimus*, the morphologic landscapes show that populations from different basins in the Rocky Mountains maintained some degree of isolation, although with these data it still is not possible to say whether the isolation was through temporal or spatial separation. Even so, the differences in tooth morphology between basins are consistent with the idea of a tectonic influence on evolution of these small mammals.

The presence of *L. transversus* at these localities extends the northern range of this species. *Lignimus transversus* was formerly only found within the Jackson Hole region of Wyoming (Barnosky, 1983, 1986). The *Mojavemys* teeth from Flint Creek could be referable to *M. alexandrae* or *M. lophatus* because of the lack of high lingual chevrons. This would extend the range of either of these species significantly to the north; however, it is equally likely that the high lingual chevrons simply represent a convergent evolutionary grade in view of the clustering of the Flint Creek population with the other Rocky Mountain populations in tooth shape (AP/T). The wide range of lingual chevron height at Hepburn's Mesa prohibits us from confidently placing this population within a defined species. Multiple species may be present at this locality, or a new species that has a combination of characteristics similar to all three species may be present. More complete specimens would aid this determination.

ACKNOWLEDGMENTS

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