**Geomys tyrioni**, a new species of early Pleistocene dwarf pocket gopher from the Meade Basin of southwestern Kansas

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A new early Pleistocene dwarf pocket gopher species is described from the Short Haul, Aries A, and Nash 72 assemblages in the Borchers Badlands of Meade County, Kansas. *Geomys tyrioni* is defined by its diminutive size and modern dental and mandibular masseter muscle configuration. *G. tyrioni*, currently known from the interval of about 2.0–1.70 millions of years ago (Ma), replaced the larger *G. floridanae* and *G. quinni* of the slightly earlier (2.11 Ma) Borchers assemblage. Mandibular and dental characters place *G. tyrioni* in the group of *Geomys* including the extant Great Plains *G. bursarius*. Within about 24,000 years after the Nash 72 assemblage, *G. tyrioni* was replaced by modern-sized *Geomys* cf. *G. bursarius* in the Rick Forester assemblage, the earliest record of the extant plains pocket gopher in the Meade Basin and North America. *G. tobinensis* Hibbard is synonymized with *G. bursarius*. An evolutionary scenario is provided for the Meade Basin geomyines based on current information, and it is suggested that ashfalls may have played a significant role in geomyine cladogenesis and turnover.

Key words: ashfall, *Geomys*, Kansas, Meade Basin, Pleistocene, Yellowstone Caldera


**MATERIALS AND METHODS**

The new fossil specimens reported here were recovered from approximately 1 ton of washed matrix from the Short Haul locality (Fig. 3). Localities in the Borchers Badlands and collecting and washing methods were described by Martin et al. (2003, 2008). With the exception of the Borchers assemblage, recovered by C. W. Hibbard from an unknown depth of sediment directly overlying the Huckleberry Ridge ash (Hibbard 1941), all of the material recovered here as part of the Meade Basin Rodent Project (MBRP) was excavated from quarries of no more than 1.0 m in vertical height. Matrix from the Short Haul locality was removed from ~0.2 m of vertical sediment. Consequently, the name of the rodent assemblage as used here is synonymous with the rodent locality (quarry) from which it was excavated. Quarries in the same outcrop at different vertical elevations were given either different names or letters (Borchers and Nash 72 in the Aries section; Short Haul, Aries A, and Aries B in the Aries section—Martin et al. 2008).

Measurements of *G. tyrioni* in Table 1 were made with a DinoXcope digital microscope. Remaining measurements in Table 1 are from Martin et al. (2011). Geomyid dental and mandibular terminology is presented in Fig. 4. Upper and lower molars are identified by upper and lower case letters (e.g., p4 = lower 4th premolar; I = incisor). Left and right are
indicated by L and R, respectively. FHSM = Fort Hays State University, Sternberg Museum.

Lower fourth premolar measurements from Paulson (1961) for the Cudahy *G. tobinesis*, a sample of which I remeasured for this study (Table 1), are inexplicably small. Schultz (2010) also remeasured a large sample of *G. tobinesis* from the Kansas Cudahy and Sunbrite localities, and his measurements are statistically indistinguishable from mine. A final check was made by A. Rountrey (Museum of Paleontology, University of Michigan, pers. comm., 8/15), and his measurements on 3 p4s from Cudahy were in the range of those in Table 1 and measurements from Schultz (2010).

Based almost exclusively on genetic comparisons, some investigators break gopher populations in western Kansas into 2 or 3 sibling species (or semispecies), including *G. bursarius* and either *G. lutescens* or *G. jugossicularis* (Sudman et al. 2006; Genoways et al. 2008; Chambers et al. 2009). Populations recognized by these investigators as *G. bursarius* are found mostly associated with dark, silty, loamy soils, and the latter 2 with sandier soils, such as the sand hills of Nebraska and the drier prairies of western *G. lutescens*.

<table>
<thead>
<tr>
<th>Epoch</th>
<th>MPTS</th>
<th>Ma</th>
<th>Geol. Markers</th>
<th>Local Faunas</th>
<th>RZ</th>
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<tr>
<td>Br</td>
<td>C1n</td>
<td>0.78</td>
<td>Lava Crk B ash (0.65)</td>
<td>Arkan, Cudahy (N); Couch 3,4</td>
<td>15</td>
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<tr>
<td>Jar</td>
<td>1n</td>
<td>0.99</td>
<td><strong>Cerro Tol B ash (1.23-1.47)</strong></td>
<td>Aries B (R)</td>
<td>14</td>
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<tr>
<td>Ma</td>
<td>2r</td>
<td>1.77</td>
<td><strong>Huckash (2.11)</strong></td>
<td>Nash 72 (N)</td>
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<tr>
<td>Old</td>
<td>C2n</td>
<td>1.95</td>
<td><strong>Segur Qu.</strong></td>
<td>Aries NE (N); Aries A (R); Short Haul (R)</td>
<td>12</td>
</tr>
<tr>
<td>Reun</td>
<td>C2r</td>
<td>2.14</td>
<td><strong>CGN2</strong></td>
<td>Borchers (R)</td>
<td>11</td>
</tr>
<tr>
<td>Kaena</td>
<td>C2an</td>
<td>2.15</td>
<td><strong>CGN1</strong></td>
<td>Margaret</td>
<td>11</td>
</tr>
<tr>
<td>Ga</td>
<td>1n</td>
<td>3.04</td>
<td>Wolf Gr.</td>
<td>Senders (N)</td>
<td>10</td>
</tr>
<tr>
<td>Mam</td>
<td>2n</td>
<td>3.11</td>
<td><strong>XReCreek</strong></td>
<td>Paloma</td>
<td>A</td>
</tr>
<tr>
<td>3n</td>
<td>3.22</td>
<td><strong>Ornamented</strong></td>
<td>Rexroad Loc. 2</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Coch</td>
<td>3.33</td>
<td><strong>Bishop Gr.</strong></td>
<td>Rexroad Loc. 2A (R)</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>Nun</td>
<td>4n</td>
<td>3.58</td>
<td><strong>XTeHuck R</strong></td>
<td>Deer Park, Rex 3D (R)</td>
<td>8</td>
</tr>
<tr>
<td>Gi</td>
<td>4n</td>
<td>4.18</td>
<td><strong>XtTeHuck R</strong></td>
<td>Rexroad Loc. 3A-C (N)</td>
<td>7</td>
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<tr>
<td>Sud</td>
<td>2n</td>
<td>4.29</td>
<td><strong>Bishop Gr.</strong></td>
<td>Bender 1B (N)</td>
<td>7</td>
</tr>
<tr>
<td>Thv</td>
<td>3n</td>
<td>4.48</td>
<td><strong>Keeler C, Rop 1C (R)</strong></td>
<td>Hornet (R)</td>
<td>7</td>
</tr>
<tr>
<td>4n</td>
<td>4.62</td>
<td><strong>Ripley R, XTeHuck R</strong></td>
<td>6</td>
<td></td>
<td></td>
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<tr>
<td>C3n</td>
<td>5.24</td>
<td><strong>Nebraska</strong></td>
<td>5</td>
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<tr>
<td>Thv</td>
<td>5.23</td>
<td><strong>Bishop Gr.</strong></td>
<td>Fallen Angel (?)R</td>
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<tr>
<td>3n</td>
<td>5.89</td>
<td><strong>Bishop Gr.</strong></td>
<td>Argonaut</td>
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<td>6.27</td>
<td><strong>Keeler C, Rop 1C (R)</strong></td>
<td>Saw Rock C. (?R)</td>
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<td></td>
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<tr>
<td>C3r</td>
<td>6.57</td>
<td><strong>Bishop Gr.</strong></td>
<td>4</td>
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</table>

Fig. 1.—Stratigraphic relationships of Meade Basin local faunas. MPTS = magnetic polarity time scale, Ma = millions of years ago, C = Chron, r = reversed, n = normal, Br = Brunhes, Ma = Matuyama, Ga = Gauss, Gi = Gilbert, Jar = Jaramillo, Old = Olduvai, Reun = Reunion, Mam = Mammoth, Coch = Cochiti, Nun = Nunivak, Sud = Sidufjall, Thv = Thvera, Crk = Creek, Tol = Toledo, Huck R = Huckleberry Ridge, Gr. = gravel, CC = calcium carbonate layer, (N) and (R) = normal and reversed polarity, Rex = Rexroad, Rap = Raptor, C. = Canyon, RZ = rodent zones of Martin (2003).
Kansas. Hybrids between *G. bursarius* and *G. lutescens/J. jugossicularis* are known (Heaney and Timm 1983, 1985; Genoways et al. 2008). Another related species group, represented on the Central Great Plains by *G. breviceps*, extends northward from the Gulf Coast to eastern Oklahoma. Currently, based on dental and mandibular material, the most common pocket gopher elements recovered in paleontological collections, it is impossible to separate these species. Thus, there is always the possibility that more than one of these entities is represented in our collections. It would be useful if dental or mandibular markers could be found to distinguish “*bursarius*” from “*lutescens/jugossicularis*” populations, as that would help with environmental reconstruction, perhaps indicating dominance of soil types, but until those characters are found, fossil materials inseparable from the 4 species mentioned above will be referred to *G. bursarius*.

I follow the International Commission on Stratigraphy 2015 International Chronostratigraphic Chart in recognizing the Pliocene-Pleistocene boundary at 2.58 Ma. Thus, the Borchers assemblage, often considered Pliocene in previous accounts, is here considered early Pleistocene in age.

**Systematic Paleontology**

Family Geomyidae Bonaparte, 1845
Subfamily Geomyinae Baird, 1858
Tribe Geomyini Russell, 1968
Genus Geomys Rafinesque, 1817
*Geomys tyrioni*, new species
(Figs. 5 and 6)
Table 1.—Measurements of the p4 for some Pliocene and Pleistocene Geomys species of the Meade Basin. Mean is followed by the observed range in parentheses; N = number of specimens, SD = standard deviation. Cud = Cudahy, RF = Rick Forester, N72 = Nash 72, ARA = Aries A, SH = Short Haul, Bor = Borchers, San = Sanders, 2RA = Redroad Loc. 2A, FC = Fox Canyon, MA = millions of years ago. L = length, W = width.

<table>
<thead>
<tr>
<th></th>
<th>Geomys bursarius</th>
<th></th>
<th>Geomys bursarius</th>
<th></th>
<th>Cerro Toledo B ash (~1.35 Ma)</th>
<th></th>
<th>Olduvai subchron (1.95–1.77 Ma)</th>
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<tbody>
<tr>
<td></td>
<td>Modern, Meade Co., KS</td>
<td></td>
<td>Cudahy</td>
<td></td>
<td>Aries A</td>
<td></td>
<td>Aries A</td>
<td></td>
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<tr>
<td>Lp4</td>
<td>2.81 (2.46–3.08), N = 11, SD = 0.07</td>
<td></td>
<td></td>
<td></td>
<td>2.19</td>
<td></td>
<td>2.19</td>
<td></td>
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<tr>
<td>Wp4</td>
<td>2.17 (1.85–2.46), N = 11, SD = 0.05</td>
<td></td>
<td></td>
<td></td>
<td>1.74</td>
<td></td>
<td>1.74</td>
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<tr>
<td>Lp4</td>
<td>2.68 (2.21–2.92), N = 15, SD = 0.05</td>
<td></td>
<td></td>
<td></td>
<td>2.01</td>
<td>1.95–2.06, N = 2, SD = 0.08</td>
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<tr>
<td>Wp4</td>
<td>2.13 (1.72–2.46), N = 15, SD = 0.05</td>
<td></td>
<td></td>
<td></td>
<td>1.75</td>
<td>1.66–1.84, N = 2, SD = 0.13</td>
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<tr>
<td>Lp4</td>
<td>2.11 (2.00–2.21), N = 4, SD = 0.11</td>
<td></td>
<td></td>
<td></td>
<td>1.63</td>
<td>1.37–1.85, N = 4, SD = 0.20</td>
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<tr>
<td>Wp4</td>
<td>2.82 (2.46–3.30), N = 10, SD = 0.38</td>
<td></td>
<td></td>
<td></td>
<td>2.82</td>
<td>1.99–2.88, N = 20, SD = 0.24</td>
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<tr>
<td>Lp4</td>
<td>1.97 (1.67–2.39), N = 20, SD = 0.16</td>
<td></td>
<td></td>
<td></td>
<td>1.97</td>
<td>1.67–2.39, N = 20, SD = 0.16</td>
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<tr>
<td>Wp4</td>
<td>2.41 (1.99–2.88), N = 20, SD = 0.24</td>
<td></td>
<td></td>
<td></td>
<td>2.41</td>
<td>1.99–2.88, N = 20, SD = 0.24</td>
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<tr>
<td>Lp4</td>
<td>2.82 (2.46–3.30), N = 10, SD = 0.26</td>
<td></td>
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<td></td>
<td>1.97</td>
<td>1.67–2.39, N = 20, SD = 0.16</td>
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<tr>
<td>Wp4</td>
<td>2.40 (2.10–2.67), N = 10, SD = 0.17</td>
<td></td>
<td></td>
<td></td>
<td>1.91</td>
<td>1.56–2.26, N = 10, SD = 0.20</td>
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<tr>
<td>Lp4</td>
<td>2.01 (1.95–2.06), N = 2, SD = 0.08</td>
<td></td>
<td></td>
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<td>2.01</td>
<td>1.95–2.06, N = 2, SD = 0.08</td>
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<tr>
<td>Wp4</td>
<td>1.75 (1.66–1.84), N = 2, SD = 0.13</td>
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<td>1.75</td>
<td>1.66–1.84, N = 2, SD = 0.13</td>
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<tr>
<td>Lp4</td>
<td>1.91 (1.56–2.26), N = 10, SD = 0.20</td>
<td></td>
<td></td>
<td></td>
<td>1.91</td>
<td>1.56–2.26, N = 10, SD = 0.20</td>
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<tr>
<td>Wp4</td>
<td>1.51 (1.30–1.70), N = 17, SD = 0.10</td>
<td></td>
<td></td>
<td></td>
<td>1.51</td>
<td>1.30–1.70, N = 17, SD = 0.10</td>
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<tr>
<td>Lp4</td>
<td>2.05 (2.09–2.72), N = 13, SD = 0.17</td>
<td></td>
<td></td>
<td></td>
<td>2.50</td>
<td>2.09–2.72, N = 13, SD = 0.17</td>
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<tr>
<td>Wp4</td>
<td>2.89 (1.54–2.13), N = 13, SD = 0.17</td>
<td></td>
<td></td>
<td></td>
<td>1.89</td>
<td>1.54–2.13, N = 13, SD = 0.17</td>
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<tr>
<td>Lp4</td>
<td>1.91 (1.56–2.26), N = 10, SD = 0.20</td>
<td></td>
<td></td>
<td></td>
<td>1.91</td>
<td>1.56–2.26, N = 10, SD = 0.20</td>
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<tr>
<td>Wp4</td>
<td>1.61 (1.48–1.75), N = 10, SD = 0.10</td>
<td></td>
<td></td>
<td></td>
<td>1.61</td>
<td>1.48–1.75, N = 10, SD = 0.10</td>
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</tbody>
</table>

* Estimate.

Holotype.—FHSN 18804, Lp4 from the Short Haul assemblage.

Paratypes.—FHSN 14068 (Rp4), 14060 (5 upper and lower molars), 18813 (8 upper and lower molars), 14113 (LP4, juvenile p4), FHSN 18800 (RP4), 18801 (RP4), 18802 (LP4), 18815 (1 broken P4), 18803 (LP4; juvenile), 18810 (LP4), 18811 (Rp4 fragment), 14095 (8 upper incisor fragments), 18808 (17 upper incisor fragments), 18812 (2 upper I fragments), 18806 (2 lower incisor pieces), 18807 (6 M3s), 18814 (1 M3), 18809 (anterior piece of left mandible).

Referred specimens.—Aries A: USGS 41009 (upper and lower molars), FHSN 14296 (Rp4), FHSN 14297 (2 upper incisor pieces); Aries NE: FHSN 14232 (3 upper and lower molars); Nash 72: FHSN 14295 (Rp4), 14452 (Rp4), 14453 (LP4), 14454 (Rp4).

Locality and horizon.—Short Haul, Aries A, Aries NE, and Nash 72 assemblages, Borchers Badlands, Meade Co., Kansas. Early Pleistocene, between top of Huckleberry Ridge ash (2.11 Ma) and Rick Forester level in Aries section of Martin et al. (2008); below Cerro Toledo B ash (~1.35 Ma).


Etymology.—Named for the smart, witty, compassionate dwarf character Tyrion Lannister, played by award-winning actor Peter Dinklage in Game of Thrones, the Homebox adaptation of George R. R. Martin’s Fire and Ice novel series.

Nomenclatural statement.—A life science identifier (LSID) number was obtained for the new species G. tyrioni: urn:lsid:zoobank.org:pub:39299FFF-1F12-4D70-8501-A4A307F92F8E.

Description and comparisons.—Table 1 presents comparative measurements for the p4. G. tyrioni is about the same size as late Blancan G. minor from Redroad Loc. 2A, representing the last appearance datum for G. minor in the Meade Basin, and the early Blancan G. adamsi, known only from the Fox Canyon locality.

The upper incisor of G. tyrioni has a double sulcus, confirming identification of G. tyrioni as a member of the subgenus Geomys. The p4 of G. tyrioni has a circular anterolophid and anteriorly-posteriorly compressed posterolophid. Reentrant folds on p4 are U-shaped and filled with cement, unlike the condition in G. adamsi in which the reentrants are V-shaped. A few p4s of G. floralindae display V-shaped reentrants, and this was considered by Martin et al. (2011) as predominantly due to sampling bias of younger specimens, as juvenile p4s tend to have V-shaped reentrants. However, it may be that larger samples would show this to be typical of adult G. floralindae, and thus provide another character for this species. The holotype p4 of G. tyrioni is compared with adult and juvenile p4s of extant G. bursarius from Meade County, Kansas, in Fig. 5.

Lower molars of G. tyrioni do not display the anterior sheath of enamel that may persist to the tooth base as in a small percentage of G. bursarius (G. tobinesis) from the Cudahy assemblage (Paulson 1961). The posterior face of 3 P4s of G. tyrioni also lacks enamel.

The mandibular fragment of G. tyrioni, FHSN 18809, preserves a bit of the anterior masseter scars, the mental foramen, and the diastema (Fig. 6). The mental foramen is developed anterior to the dorsal masseteric scar, distinguishing G. tyrioni...
from the subgenus *Nerterogeomys*, including *G. minor*, in which the mental foramen is located directly beneath the dorsal masseteric scar. In this regard, *G. tyrioni* is also advanced over *G. floralindae*, in which the mental foramen is only slightly anterior to the dorsal masseteric scar.

A ratio composed of the distance from the center of the mental foramen to the ventral border of the mandible divided by the distance from the same foramen to the anterior edge of the mandible, reflecting the length of the diastema as a function of mandible size, was similar in *G. tyrioni*, *G. bursarius*, and *G. breviceps* mandibles (*G. tyrioni*, FHSM 18809 = 0.42; *G. bursarius*, modern from Kansas, mean (observed range, number of specimens) = 0.38 (0.35–0.42, N = 3), *G. breviceps*, modern from Oklahoma, mean = 0.33 (0.28–0.38, N = 5). The oldest, largest individual *G. bursarius* and *G. breviceps* had the smallest ratios, suggesting that diastema length increased disproportionately to mandible depth as the mandible increased in size with age. Given the minimal difference in ratio values and the similarity in allometric response, neither the ratio nor the 2 measurements have much taxonomic utility, at least in the species compared. Additional ratios generated from measurements of p4 segments (e.g., anterolophid length/total length) also failed to discriminate *G. tyrioni*, *G. bursarius*, and *G. breviceps* and are not reported here.

**DISCUSSION**

**Taxonomic and Phylogenetic Considerations**

Based on morphology and proportions of the mandible and p4, *G. tyrioni* appears to be an isometric dwarf of the *G. bursarius* complex of extant pocket gophers. Without defining character other than size, there is always the possibility that *G. tyrioni* represents very small *G. bursarius*. However, there are 3 observations that suggest otherwise. First, today the *G. bursarius* complex demonstrates significant size change throughout its range (Connor 2011), with the smallest individuals, such as *G. bursarius ozarkensis* and *G. breviceps (= *G. b. dutcheri*), in the south (Arkansas, Louisiana, and Texas) and considerably larger...
individuals in the north, such as *G. b. illinoensis* in Illinois and *G. b. bursarius* from Wisconsin. However, latitude (temperature) does not fully explain size distributions in this group, as there is some overlap in size among populations of *G. bursarius* from the lower latitudes (see below). Nevertheless, based on the measurements in Table 1, early Pleistocene *G. tyrioni* in Kansas are considerably smaller than even the smallest, most southern populations of modern *G. bursarius* and *G. breviceps*. Second, no species of the *G. bursarius* complex are known in the fossil record prior to Short Haul. Third, according to field measurements made by J. Honey and P. Peláez-Campomanes (Martin et al. 2008), there is little vertical distance between Nash 72 (the highest quarry with *G. tyrioni*) and Rick Forester (with the earliest *Geomys* cf. *G. bursarius*; < ~ 0.2 m). This implies a rapid replacement of *G. tyrioni* by *G. cf. bursarius* or very rapid phyletic increase in size in the 1st *G. cf. bursarius* (~24,000 years). If size relationships in the extant *G. bursarius* complex represent adaptation to environmental conditions, we might expect the gophers from approximately 2.0–1.70 Ma to be larger rather than smaller, as this time period apparently represented a glacial interval in which sea level was considerably lower and seasonal temperatures were significantly depressed. Consequently, *G. tyrioni* is interpreted here as a dwarf species that evolved, possibly from *G. floridanae*, in response to the ecological challenges of the Huckleberry Ridge ash. Other isometric dwarf mammals are known; perhaps the most famous is the extinct California island gray fox, *Urocyon littoralis*, which apparently evolved rapidly during the Holocene from a larger mainland ancestor (Schauber and Falk 2008; Hofman et al. 2015).

In most regards except size, *G. tyrioni* also resembles *G. tobinensis*, the holotype mandible of which was described by Hibbard (1944) from the Tobin assemblage of Russell County, Kansas. Hibbard (1944) also referred a number of premolars and molars from the Cudahy and Sunbrite Mines from Meade County, Kansas, to *G. tobinensis*. Hibbard (1944) and Paulson (1961) noted that about 5% of the lower molars and P4s of *G. tobinensis* maintain enamel on their anterior and posterior faces, respectively. This seemed consistent with the holotype p4, KU 6652, in which the enamel perimeter was complete. Although Hibbard (1944, 736) recognized that the p4 in the holotype mandible of *G. tobinensis* was from an “...immature specimen,” he apparently did not realize that a complete enamel border on p4 associated with V-shaped reentrant folds and enamel on the anterior face of lower molars and posterior face of the P4 are conditions often found in very young modern *Geomys* (Martin et al. 2003). In his discussion of teeth recovered from the Sunbrite and Cudahy Mines in which the enamel periphery is incomplete, as in adult *G. bursarius*, Hibbard’s conclusion (1944, 723) was that “…two distinct forms of gophers were present.” It is the author’s conclusion that the premolars and molars with extra enamel on various faces are from juveniles, and those with incomplete enamel borders are from adults. This conclusion gains support from the description of *Geomys* material referred to *G. tobinensis* from fossil assemblages recovered from sediments directly beneath the Lava Creek B ash in Texas. Schultz (2010) found no anterior enamel plates on p4s and only 3 P4s, all likely juveniles, expressed a posterior plate. In no case did the posterior enamel plates on P4 extend more than 1.0 mm beneath the occlusal surface, and Schultz (2010) concluded they would have been eliminated with slightly more wear. Because neither the adult dentition nor mandible of *G. tobinensis* from Kansas is separable from *G. bursarius* on size or morphology, *G. tobinensis* material from Tobin, Cudahy, and Sunbrite is here referred to *G. bursarius*. The slightly smaller Texas *G. tobinensis* material reported by Schultz (2010) should also eventually be referred to one of the modern *Geomys* from that region.

**Diversity and Dispersal Patterns of Meade Basin Gophers**

The replacement pattern for Meade Basin gophers that emerges when all taxa are included is striking in its species diversity. Including occasional temporary residency of *Thomomys*, 3 genera and 10 species of geomyids have been recovered from 5 million years of Meade Basin deposits (Fig. 7). A total of 2 genera and 5 species are present in Pleistocene levels. Only the vole genus *Microtus* approaches this level of abundance, with 6 or 7 species, depending on whether *Microtus illanensis* is considered distinct or an archaic form of *M. ochrogaster*. With the exception of “*Geomys* adamsi” which, if originating from *Pliogeomys russelli* from the Hemphillian of Nebraska
(Korth 1995), probably belongs in a genus separate from *Geomys*, there is not enough information from the fossil record to speculate on the origins of early Blancan geomyines such as *G. minor* and *G. jacobi*. That is, they may or may not have originated from *P. louderbachi* or separate *Pliogeomys* ancestors. Both are considered to have been widely distributed throughout the southern and central Great Plains (“elsewhere” in Fig. 8).

In the Meade Basin, *G. minor* expresses a dwarfing chronoclone until its demise in the late middle Blancan (Martin et al. 2012). *G. quinni* certainly originated from *G. jacobi* (whether by a speciation event or phyletic change we cannot at this time be certain) and *G. floralindae* likely originated from medium-sized *G. minor* “elsewhere” than the Meade Basin. For a brief time during the early Pleistocene (Borchers), large *G. quinni* and medium-sized *G. floralindae* coexisted in the Meade Basin. At 2.11 Ma, the Great Plains were covered by a blanket of volcanic ash thrown from the Yellowstone Caldera (Ellis et al. 2012). One meter of sediments above the Borchers quarry (about 120,000 years later) at the Short Haul locality, *G. floralindae* and *G. quinni* are gone from the fossil record and the diminutive *G. tyrioni*, with essentially modern dental and mandibular morphology, appears. *G. tyrioni* persisted in the area for about 360,000 years (Short Haul through Nash 72 levels, about 3 m). Just slightly higher than Nash 72 in the Borchers Badlands sections, *G. tyrioni* is replaced by *G. cf. G. bursarius* at Rick Forester (Figs. 1 and 8). Like *G. tyrioni*, ancestors of
other members of the modern *G. bursarius* complex possibly also arose from various populations of *G. floralindae* in environments that better supported modern-sized individuals, partly around the time of the Huckleberry Ridge ashfall. *G. tyrioni* was replaced by one of these ancestral populations at Rick Forester as the harsh environmental conditions of the aftermath of the Huckleberry Ridge ash gave way to the modern prairie ecosystems of the Central Great Plains.

Understanding the forcing mechanisms for Great Plains pocket gopher phylogeny and distribution is made difficult because of the many influences that tend to isolate fosssorial gophers, contributing to their genetic and morphological diversity (Downhower and Hall 1966; Patton and Smith 1990; Genoways et al. 2008; Chambers et al. 2009; Marcy et al. 2013; Henke et al. 2014). Montane western *Thomomys* of the subgenus *Megascapheus* (*T. townsendii* and *T. bottae*) are large tooth-diggers as well as claw-diggers, and are able to take advantage of indurated soils, whereas species in the subgenus *Thomomys* (*T. talpoides*, *T. mazama*, and *T. monticola*) are smaller (averaging about half the body mass of *Megascapheus* species) and restricted to softer soils. Blois et al. (2010) described replacement of *T. mazama* by *T. bottae* at the Pleistocene-Holocene transition in Samwell Cave Popcorn Dome excavations in northern California, near Mt. Shasta. Marcy et al. (2013) interpreted this diversity and distributional change as a result of increased aridification and accompanying soil hardness that favored the tooth-digging adaptation of *T. (M.) bottae* in the area at the close of the Pleistocene. Today, the subgenus *Thomomys* dominates ecosystems with cool, damp continental summers and, presumably, with higher soil moisture content. Should the climate change to a colder regime, suggest Marcy et al. (2013), the distribution could reverse.

Studies and reviews by Downhower and Hall (1966), Foster and Stubbendieck (1980), Hirsch et al. (1984), Kerley et al. (2004), Genoways et al. (2008), and Connor (2011) generally demonstrate the relationship between plains pocket gopher distributions and soil types and also, as noted earlier, identify a general tendency of plains pocket gopher size increase from south to north. However, as detailed morphological analysis of *Geomys* along an east–west transect in Kansas demonstrated by Hendrickson (1972), the smallest gophers in the region (now considered as *G. lutescens* and *G. jugossicularis*) are found in sandy soils of western Kansas and eastern Colorado, while the largest gophers (*G. b. majusculus*) are found in more loamy soils to the east. This is in contrast to the largest *G. personatus* found in sandy soils of Mustang and Padre Island off the coast of southern Texas (Williams 1982), with smaller *G. personatus* in less sandy, indurated soils inland (Kennerly 1954). Apparently, while species of *Geomys* may indeed segregate according to soil type, body size in *Geomys* is not purely a result of temperature (latitude) or soil type, but some combination, perhaps in concert with other factors, such as precipitation, vegetation, and predation. Correlation of the appearance of the diminutive *G. tyrioni* with the Huckleberry Ridge eruption suggests that this ashfall may have been another contributing influence (Fig. 9).

We tend to focus on the Mount St. Helens eruption because it occurred so recently and is so well studied. In that case, pocket gophers (*T. talpoides*) facilitated biotic recovery by enhancing plant succession as they brought soil and fungal spores to the surface through the ash (Andersen and Macmahon 1985). However, many gophers died after the Mount St. Helens eruption, apparently because of reduced plant resources. Volcanic eruptions on a larger scale, such as Krakatoa in 1883, are known to have affected global climate. According to Gleckler
et al. (2006), volcanically induced cooling of the ocean surface from Krakatoa significantly reduced ocean warming and sea level rise in the 20th century. The Mount St. Helens eruption (0.2–0.4 km³ DRE, dense rock equivalent—Mastin et al. 2014), and even Krakatoa (18–21 km³ DRE—Self and Rampino 1981), was trivial compared with eruptions of the Yellowstone complex, in which > 1,000 km³ of ash (>400 km³ DRE) was ejected into the atmosphere (Mastin et al. 2014). Observation of ash accumulations at many sites resulting from the Huckleberry Ridge (2.11 Ma) and Lava Creek B (0.65 Ma) Yellowstone events shows that significant deposits of ash can be found hundreds of km from the Yellowstone Caldera. However, as noted by Izett and Wilcox (1982) and Mastin et al. (2014), most of these accumulations have been “remobilized” since their initial deposition, and determination of primary airfall thickness is difficult to attain. In the Nash section of outcrops that preserves the Borchers quarry in the Meade Basin, primary ash-fall has been estimated at about 0.4–0.5 m (Martin et al. 2008, figure 2). Fluvial processes would have magnified the accumulations in depressions and lacustrine environments, leading to thicknesses in excess of 3 m of mostly reworked ash seen in many ash mines. A nuclear winter scenario would likely have occurred for a few years, with global temperatures significantly depressed. Age of the Short Haul assemblage, at about 2.0 Ma, also represents Marine Isotope Stage (MIS) 73, a period of glacial advance that lowered sea level and brought the Holarctic immigrant Microtus into North America (Shackleton 1995; Martin et al. 2008). The Huckleberry Ridge eruption would have briefly magnified the effects of colder climate during MIS 73. Based on stable carbon isotope composition of pedogenic carbonates, Fox et al. (2012) documented an increase of C₄ plant biomass from beneath the Huckleberry Ridge ash to the base of the Cerro Toledo B ash in the Borchers Badlands. The modern grassland ecosystem in the Meade Basin first appeared at about 1.3 Ma, just beneath the Cerro Toledo B ashfall layer, about 3 m above the Short Haul quarry.

So what can we conclude from these observations? Body size in Geomys does not follow a simple pattern as it does for western montane Thomomys. Since there are no extant species of Geomys as small as G. tyrioni, G. adamsi, or small G. minor, we do not have in living Geomys any similar-sized avatars for comparison. Competitive scenarios only seem to make sense if we assume the competition was climatically induced, with 1 species favored because its environment (climate and habitat) was favored. Martin et al. (2012) examined the possibility that Meade Basin G. minor evolved small size in the presence of a larger congener, G. jacobi, a classic case of character displacement, but that scenario seems unlikely, as the dwarfing trend in G. minor began shortly before G. jacobi entered the basin. The allopatric distribution of western montane Thomomys seems, according to the description by Blois et al. (2010) and Marcy et al. (2013), to be more a function of environmental segregation than competition, though once environmental factors are included the distinction between direct and indirect competition blurs. In any case, environmental change seems to be the likely blanket selective mechanism involved in Meade Basin gopher turnover about 2.0 Ma, with the Huckleberry Ridge ashfall contributing to, and possibly magnifying, the process. Following

Fig. 9.—Geographic distribution of Geomys species (from Chambers et al. 2009) and approximate distribution of the Lava Creek B (LCB; pattern) and Huckleberry Ridge (HR) ashes in North America. Source area (star) for both ashes is the Yellowstone Caldera (YC; from U. S. Geological Survey Fact Sheet 2005–3024). MB = Meade Basin. Scale refers to Geomys figure.
the logic presented by Martin and Peláez-Campomanes (2014), it seems likely that the “perfect storm” of a catastrophic ashfall, environmental change, and the introduction of new competitors such as *M. pliocaeicus*, led to a rapid change in the Meade Basin rodent community (40% turnover) represented by the Short Haul assemblage just 1.0 m above Borchers. The larger *G. quinni* and *G. florinaldae* did not survive the post-Huckleberry Ridge environment, except in the sense that *G. tyrioni* originated from *G. florinaldae* under those harsh conditions.

One observation that could challenge this scenario to some extent is the presence of the rich Borchers assemblage with *G. quinni* and *G. florinaldae* developed in and on the Huckleberry Ridge ash (Martin et al. 2003, 2011). If the ash had a deleterious effect on gopher populations, then why are *G. quinni* and *G. florinaldae* not restricted to assemblages beneath the ash, and why is *G. tyrioni*, therefore, not found directly above the ash? At the Borchers level, we have found fossils in the ash itself as well as in silts developed from the ashfall. The concentration of small mammals at Borchers is extraordinary (thousands of cotton rat specimens alone have been collected) and it is conceivable that the site represents an accumulation of those animals that were living when the ash fell and immediately thereafter. The Borchers deposit appears to be a shallow pond or slough and associated wetland. Because of local erosion it is difficult to estimate its former size, but based on nearby sediments that lack this lithology it was probably not much more than 100 m in diameter. The disproportionately large representation of animal remains suggests that the site represented a small oasis, or energy sink, after the ashfall. Rather than indicating a lush ecosystem as one might initially suppose from the number of specimens recovered, the Borchers assemblage might instead represent the accumulation of a dying mammalian community in a relatively barren environment. The last of the warm-adapted Pliocene species such as *Sigmodon minor* and a number of other species that could not survive the post-Huckleberry Ridge ashfall environment disappeared, and *G. tyrioni* “arose from the ashes,” although its reign in the Meade Basin would turn out to be temporary.

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References


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