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Source: Journal of Mammalogy, 90(2) : 270-305

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/07-MAMM-A-309.1

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Journal of Mammalogy, 90(2):270–305, 2009

GENERIC REVISION IN THE HOLARCTIC GROUND SQUIRREL GENUS *SPERMOPHILUS*

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The substantial body of research on Holarctic ground squirrels amassed over the past century documents considerable variability in morphological, cytogenetic, ecological, and behavioral attributes in the genus *Spermophilus* F. Cuvier, 1825. Recent molecular phylogenetic studies suggest that the traditionally recognized genera *Marmota* Blumenbach, 1779 (marmots), *Cynomys* Rafinesque, 1817 (prairie dogs), and *Ammospermophilus* Merriam, 1892 (antelope ground squirrels) render *Spermophilus* paraphyletic, potentially suggesting that multiple generic-level lineages should be credited within *Spermophilus*. Herein, we recognize 8 genera formerly subsumed in *Spermophilus*, each of which is morphologically diagnosable, craniometrically distinctive, and recovered as a monophyletic clade in phylogenetic analyses utilizing the mitochondrial gene cytochrome *b*. Generic-level names are available for each of these ground squirrel assemblages, most of which are exclusively or predominantly North American in distribution (*Notocitellus* A. H. Howell, 1938; *Otospermophilus* Brandt, 1844; *Callospermophilus* Merriam, 1897; *Ictidomys* J. A. Allen, 1877; *Poliocitellus* A. H. Howell, 1938; *Xerospermophilus* Merriam, 1892; and *Urocitellus* Obolenskij, 1927). Only *Spermophilus* sensu stricto is restricted to Eurasia. Generic subdivision of *Spermophilus* more aptly illuminates the taxonomic relationships, ecomorphological disparity, and biogeographic history of Holarctic ground squirrels.

Key words: biogeography, cytochrome *b*, genus, ground squirrels, morphology, morphometrics, phylogeny, *Spermophilus*, systematics, taxonomy

> Investigation has shown the necessity of subdividing older groups, as the older generic limits were too broad to permit grouping forms with sufficient precision. (Palmer 1904:7)

Historically, the classification of organisms was long reliant on comparisons involving anatomy only, often with considerable disagreement between experts over the relationships of particular phyla and taxa. Today's systematists, drawing especially from molecular comparisons and cladistic methodology, are able to evaluate taxonomic and phylogenetic hypotheses with higher expectations for accurate reconstruction of evolutionary histories. Modern reassessments usually require reconcilation of phylogenetic interpretations based on molecular evidence with previous frameworks based on more traditional character sets. Congruence is rarely perfect in such cases, and a common outcome is the recognition of more taxa than before, or the elevation of taxa to higher ranks than before, or both. In essence, molecular studies often provide finer tuning to established taxonomies, and ideally this new evidence meshes sufficiently with morphological information to yield a classification that more appropriately accommodates the evolutionary relationships of the group in question. Generic boundaries should effectively indicate evolutionary relationships not only for taxonomic consistency, but also because the genus is commonly employed as the level of analysis in phylogenetic, paleontological, macroevolutionary, and other comparisons. This is especially true for rodents, the most species-rich order of mammals (e.g., Amori and Gippoliti 2001; Grelle 2002; Helgen 2003; Jansa and Weksler 2004; McKenna and Bell 1997; Mercer and Roth 2005). The sciurid genus *Spermophilus* F. Cuvier, 1825, is an excellent example of a well-studied genus that is in need of modern, integrative revision, and this paper is an attempt to provide such an overview for this varied group of ground squirrels.

As currently recognized, the sciurid genus *Spermophilus* is Holarctic in distribution, occurring throughout temperate and

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arctic Eurasia from central Europe to China, Mongolia, and Siberia, and throughout western North America, from Alaska to Mexico, extending as far east as Ohio (Ellerman and Morrison-Scott 1966; Hall 1981; McKenna and Bell 1997; Thorington and Hoffmann 2005; Wilson and Ruff 1999). Species classified in *Spermophilus* inhabit a wide range of habitats, including tropical, subtropical, and temperate forests; hot and cold deserts; prairies and steppes; open woodlands; and tundra (Howell 1938; Ognev 1947; Wilson and Ruff 1999). As currently recognized (Thorington and Hoffmann 2005), *Spermophilus* is composed of 41 species allocated into 6 subgenera: *Callospermophilus* Merriam, 1897 (3 species), *Ictidomys* J. A. Allen, 1877 (4 species), *Otospermophilus* Brandt, 1844 (5 species), *Poliocitellus* A. H. Howell, 1938 (1 species), *Spermophilus* (26 species), and *Xerospermophilus* Merriam, 1892 (2 species). All 6 subgenera occur in North America, but only the subgenus *Spermophilus* is represented in Eurasia.

The most comprehensive taxonomic revision of Holarctic ground squirrels to date was the influential overview by Howell (1938). He united most larger ground squirrels of North America and Eurasia (with the exception of prairie dogs and marmots) under the single genus *Citellus* Oken, 1816, and recognized several distinctive subgenera (including *Ammospermophilus* Merriam, 1892, *Notocitellus* A. H. Howell, 1938, *Otospermophilus*, *Callospermophilus*, *Poliocitellus*, *Ictidomys*, and *Xerospermophilus*). Oken proposed the name *Citellus* for this group in 1816, and although much of the earlier literature uses this name, it was subsequently ruled unavailable (Hershkovitz 1949; International Commission on Zoological Nomenclature 1956). The basis of the ruling was that Oken's names were non-Linnaean, which renders them unavailable in scientific nomenclature. Before Howell's (1938) review, it also was common for many authors to regard some of these subgenera, especially *Otospermophilus* and *Callospermophilus*, as distinctive genera (e.g., Linsdale 1938; Miller 1924), but essentially all subsequent authors have followed Howell in including these groupings within *Spermophilus* (e.g., Black 1963; Miller and Kellogg 1955; Moore 1959, 1961). The most influential change to Howell's scheme was made by Bryant (1945), who raised one of Howell's subgenera, *Ammospermophilus*, to full generic rank; this has been followed in most subsequent taxonomic compendia and checklists (e.g., Hall 1981; Hall and Kelson 1959; Hoffmann et al. 1993; Thorington and Hoffmann 2005). Nevertheless, the species of *Ammospermophilus* are not more distinctive morphologically relative to the type species of *Spermophilus* than are the species of several of Howell's other subgenera, especially *Notocitellus*, *Otospermophilus*, and *Callospermophilus*, as we will show in this revision.

In Russia, various workers studied the Eurasian forms, recognizing the diversity in the group. Ognev (1947) further divided Howell's (1938) nominate subgenus *Citellus* into 3 component subgenera (*Colobotis* Brandt, 1844; *Urocitellus* Obolenskij, 1927; and *Citellus*) and Gromov et al. (1965) elevated several subgenera to generic rank, but these arrangements have not been widely followed, especially among North American workers.

In the latter part of the 20th century, chromosomal studies became increasingly influential in estimations of taxonomic relationships among ground squirrels (e.g., Nadler 1966a, 1966b; Nadler et al. 1973), but these had little impact on the definition of the genus *Spermophilus* overall. Most recently, molecular studies have been used to refine understanding of the phylogenetic relationships of ground squirrel species, subgenera, and genera (Harrison et al. 2003; Herron et al. 2004).

Apart from *Ammospermophilus*, 2 additional genera of ground squirrels—prairie dogs (*Cynomys* Rafinesque, 1817, western North America, 5 recognized species) and marmots (*Marmota* Blumenbach, 1779, North America and Eurasia, 14 recognized species)—are considered very closely related to *Spermophilus*, as indicated by their classification alongside *Spermophilus* and *Ammospermophilus* in the sciurid tribe Marmotini (Mercer and Roth 2005; Thorington and Hoffmann 2005). The chipmunks (*Tamias* Illiger, 1811, *Eutamias* Trouessart, 1880, and *Neotamias* A. H. Howell, 1929) and Asian rock-squirrels (*Sciurotamias* Miller, 1901) together are thought to constitute the sister lineage to *Spermophilus*, *Ammospermophilus*, *Cynomys*, and *Marmota* (Giboulet et al. 1997; Steppan et al. 2004). Although commonly classified in the tribe Marmotini (Thorington and Hoffmann 2005), chipmunks and Asian rock-squirrels are sometimes segregated into a distinct tribe, Tamiini (Black 1963; Giboulet et al. 1997). For convenience throughout this paper we use the tribal designator Marmotini to refer to *Spermophilus* (sensu lato), *Ammospermophilus*, *Cynomys*, and *Marmota* but not to tamiinin genera. The tribe Marmotini is 1 (along with Xerini and Protoxerini) of 3 tribes (4 if Tamiini is recognized) in the subfamily Xerinae (Thorington and Hoffmann 2005).

Recently, molecular analyses based on the mitochondrial gene cytochrome *b* (Harrison et al. 2003; Herron et al. 2004) have suggested that *Cynomys* is phylogenetically nested within the taxonomic bounds of the genus *Spermophilus* as currently recognized. Marmots, the largest of the ground squirrels, were traditionally considered to be an early phylogenetic offshoot in the tribe, but evidence from molecular studies also nested them within the phylogenetic scope of *Spermophilus* (Giboulet et al. 1997; Harrison et al. 2003; Herron et al. 2004; Steppan et al. 1999; Thomas and Martin 1993). As with *Cynomys* and *Marmota*, analyses of molecular data indicate that *Ammospermophilus* also is subsumed phylogenetically within the intrageneric radiation comprised by the current taxonomic bounds of *Spermophilus* (Harrison et al. 2003; Herron et al. 2004).

Both Harrison et al. (2003) and Herron et al. (2004) declined to tackle the question of appropriate generic boundaries and nomenclature in Marmotini in light of the paraphyly of *Spermophilus*. Delineation of revised generic boundaries in this case ideally requires not only a well-resolved phylogeny, but also an overview of available generic names and their type species, critical considerations of generic definitions and content, and revised morphological diagnoses of recognized genera. Herein, we provide this background in order to present

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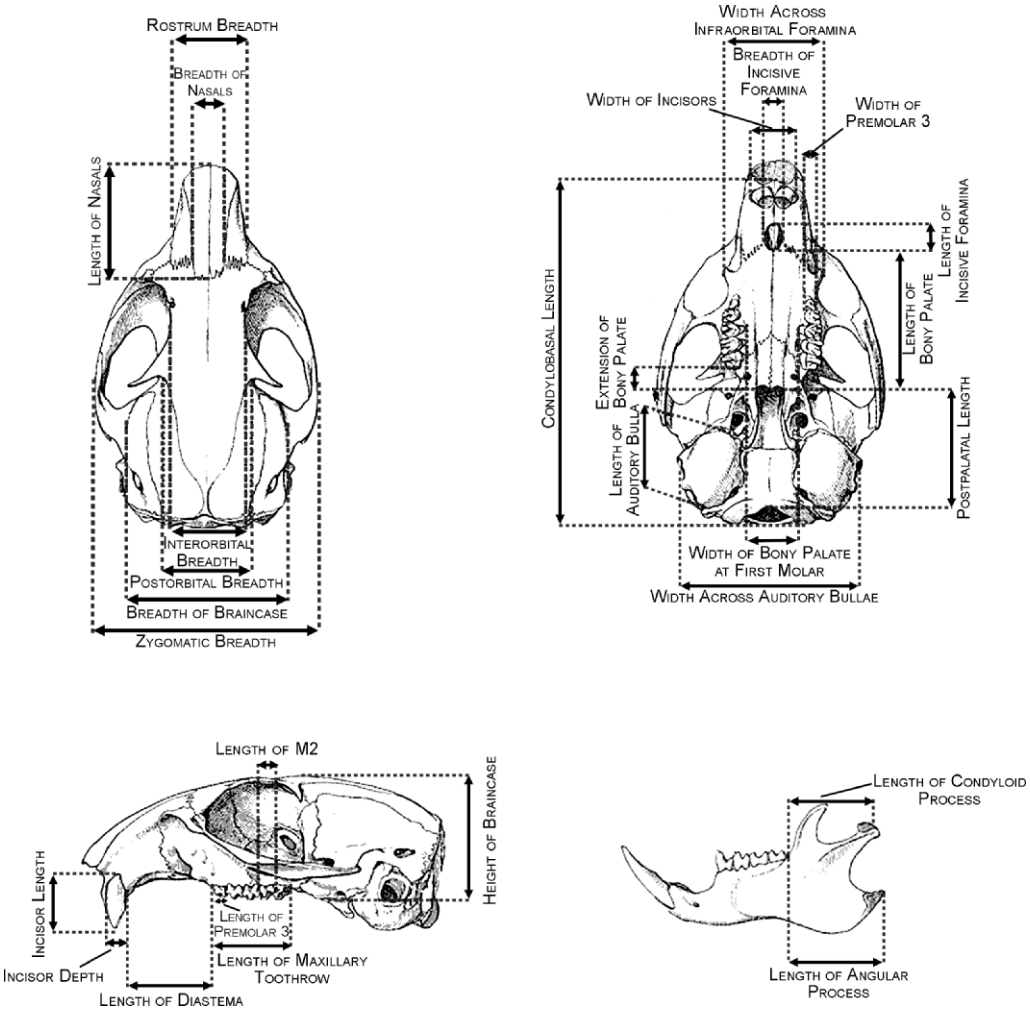


Fig. 1.—Limits of craniodental measurements employed in our study. Skull drawing of *Marmota monax* modified from Bezuidenhout and Evans (2005).

a fresh generic-level classification of squirrels in the tribe Marmotini.

Materials and Methods

Our study draws upon the unparalleled collections of North American ground squirrels in the United States Biological Surveys collection, stored at the United States National Museum of Natural History (USNM) at the Smithsonian Institution in Washington, D.C. We collected data on standard external dimensions from original specimen labels, and calculated selected external proportions based on these data. These external measurements are abbreviated here as total length (TL), head and body length (HBL), tail length (TV), and hind-foot length (HFL). Ear (pinna) length (EL) was not available for all specimens.

Craniodental variables were measured by the authors with handheld calipers to the nearest 0.01 mm while viewing the skull under a stereoscopic microscope as necessary. Single-tooth measurements are measured across dental crowns. All measurements of length are reported in millimeters.

For our craniometric comparisons, we measured 33 craniodental variables on 2 intact adult female skulls for every species of *Spermophilus* (sensu lato), *Ammospermophilus*, and *Cynomys* (i.e., following the taxonomy of Thorington and Hoffmann [2005]) available at USNM. All North American species in these genera are represented in our analyses, along with 6 of the 14 currently recognized Eurasian species. We chose fully adult females (with basioccipital–basisphenoid suture fused and teeth fully erupted and lightly but not excessively worn) to render comparisons consistent with respect to age and sex, and because females were better represented in the USNM collections for several rarer taxa. For widespread species we generally chose specimens of the nominate subspecies for inclusion (Appendix I). We measured the following craniodental variables (as defined and illustrated in Fig. 1): condylobasal length (CBL); zygomatic breadth (ZB); breadth of braincase (BBC); height of braincase, measured from the basioccipital plane to the crown of the braincase (HBC); rostral breadth (RB); length of nasals (LN); width of nasals (WN); interorbital breadth (IOB); postorbital breadth (POB); length of diastema (LD); length of incisive foramina

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(= anterior palatal foramina; LIF): width of incisive foramina (WIF); width across infraorbital foramen (WAIF); length of auditory bulla (LAB); width of auditory bulla (WAB); width of auditory bullae across external auditory meati (WAAM); width of palate at P3 (WPP3); width of palate at M1 (WPM1); width of palate at M3 (WPM3); length of bony palate (LBP); extension of bony palate (LEBP); postpalatal length (PPL); length of maxillary toothrow (LMTR); length of angular process (LAP); and length of condyloid process (LCP). Dental variables measured (all upper teeth) included width of incisors (WI), length of incisors (LI), depth of incisors (DI), width of P3 (WP3), length of P4 (LP4), width of 2nd molar (WM2), width of 3rd molar (WM3), and length of 3rd molar (LM3). USNM catalog numbers and localities for examined specimens are provided in Appendix I.

Qualitative comparisons of external and craniodental anatomy and variation within and among species and genera were made via direct comparisons of specimens and series at USNM (the whole collection was utilized). Our comparisons of Eurasian taxa were bolstered by additional information on external measurements, cranial measurements, and qualitative morphology extracted from literature. To clarify and bolster the generic boundaries we advocate here, our morphological and morphometric comparisons emphasize differences *between* genera, as well as similarities *among* species classified together in each genus. To this end, we test and explore craniometric distinctions between generic clades elucidated by molecular analyses of the cytochrome-*b* gene (Fig. 2) primarily with discriminant function analysis. These and all other statistical analyses were performed with the software package Statistica 6.0 (Statsoft Inc., Tulsa, Oklahoma).

Results

Molecular Analyses

Analyses by Herron et al. (2004) and Harrison et al. (2003), both based on the cytochrome-*b* gene, recovered 11 clades that we recognize here as genera based on our clarifying morphological and taxonomic investigations. We discuss and label them here by number and name (in no special order) with explicit reference to the results of Herron et al. (2004), whose analyses included more species and were published more recently than those of Harrison et al. (2003). Our numbering of these recovered clades is not linked to the numbering scheme used by Herron et al. (2004). We have refigured the phylogenetic topologies recovered in their paper (Fig. 2) both from maximum-parsimony analyses and Bayesian analyses. To indicate the robustness of resolution, we abbreviate maximum-parsimony bootstrap percentages as MP and Bayesian posterior probabilities as BPP (e.g., 100 MP, 100 BPP). Our purpose in reviewing these clades recovered by Herron et al. (2004) is to link generic names to each of these assemblages by identifying the type species of available generic-level names and the phylogenetic affiliations of those species. For convenience, species are referenced in the section immediately below only by specific epithet.

Clade 1 (Notocitellus).—In both trees (Fig. 2), a well-supported clade (99 MP, 100 BPP) consisting of *annulatus* (the type species of *Notocitellus* A. H. Howell, 1938) and *adocetus* was recovered as the sister group to *Ammospermophilus* (albeit with weak support). These 2 genera are highly divergent from all other genera in the tribe Marmotini. This clade corresponds to Howell's (1938) original taxonomic definition and concept of *Notocitellus*, except that Howell recognized this grouping at the subgeneric level.

Clade 2 (Ammospermophilus).—In both trees (Fig. 2), species traditionally classified in the genus *Ammospermophilus*, along with *Notocitellus*, were recovered as the most divergent lineage among ground squirrels formerly classified in *Spermophilus* (Howell 1938). The 4 sampled species, including *leucurus*, the type species of *Ammospermophilus*, were recovered as a monophyletic clade in both trees, albeit with weaker support than for any other genus that we recognize in this paper (85 MP, 90 BPP).

Clade 3 (Otospermophilus).—In both trees (Fig. 2), the species *variegatus* (the type species of *Otospermophilus* Brandt, 1844), *beecheyi*, and *atricapillus* form a well-supported monophyletic group (100 MP). These species are traditionally (and most often exclusively—as done by Howell 1938) classified together in the subgenus (or genus) *Otospermophilus*. A few authors have lumped the species of *Notocitellus* and *Otospermophilus* together under a single genus or subgenus (Bryant 1945; Hall 1981; Miller 1924)—an arrangement not supported by the cytochrome-*b* data.

Clade 4 (Callospermophilus).—In both trees (Fig. 2), the species *lateralis* (the type species of *Callospermophilus* Merriam, 1897), *saturatus*, and *madrensis* form a well-supported monophyletic group (100 MP). These species are traditionally and exclusively classified together in the subgenus (or genus) *Callospermophilus*. In both trees, this clade is recovered as the sister lineage to clade 3 (*Otospermophilus*) with relatively high support (88 MP, 100 BPP).

Clade 5 (Xerospermophilus).—In both trees (Fig. 2), the species *mohavensis* (the type species of *Xerospermophilus* Merriam, 1892), *tereticaudus*, *spilosoma*, and *perotensis* form a well-supported monophyletic group (87 MP, 100 BPP). Two of these species (*mohavensis* and *tereticaudus*) have been traditionally and exclusively classified together in the subgenus (or genus) *Xerospermophilus*; the 2 others (*spilosoma* and *perotensis*) are usually associated with the subgenus (or genus) *Ictidomys*, the type species of which falls in clade 8. In addition, *spilosoma* is paraphyletic in relation to *perotensis*. In both trees, *Cynomys* is recovered as the sister group to clade 5 (*Xerospermophilus*).

Clade 6 (Cynomys).—In both trees (Fig. 2), the 5 species of *Cynomys* Rafinesque, 1817, including *ludovicianus* (Ord, 1815), the type species of *Cynomys*, are recovered as a monophyletic group with high support (100 MP, 100 BPP). These species are traditionally and exclusively classified together in the genus *Cynomys*. As noted, in both trees *Cynomys* is recovered as sister group to clade 5 (*Xerospermophilus*).

Clade 7 (Poliocitellus).—In both trees (Fig. 2), the species *franklinii* (type species of *Poliocitellus* A. H. Howell, 1938) is

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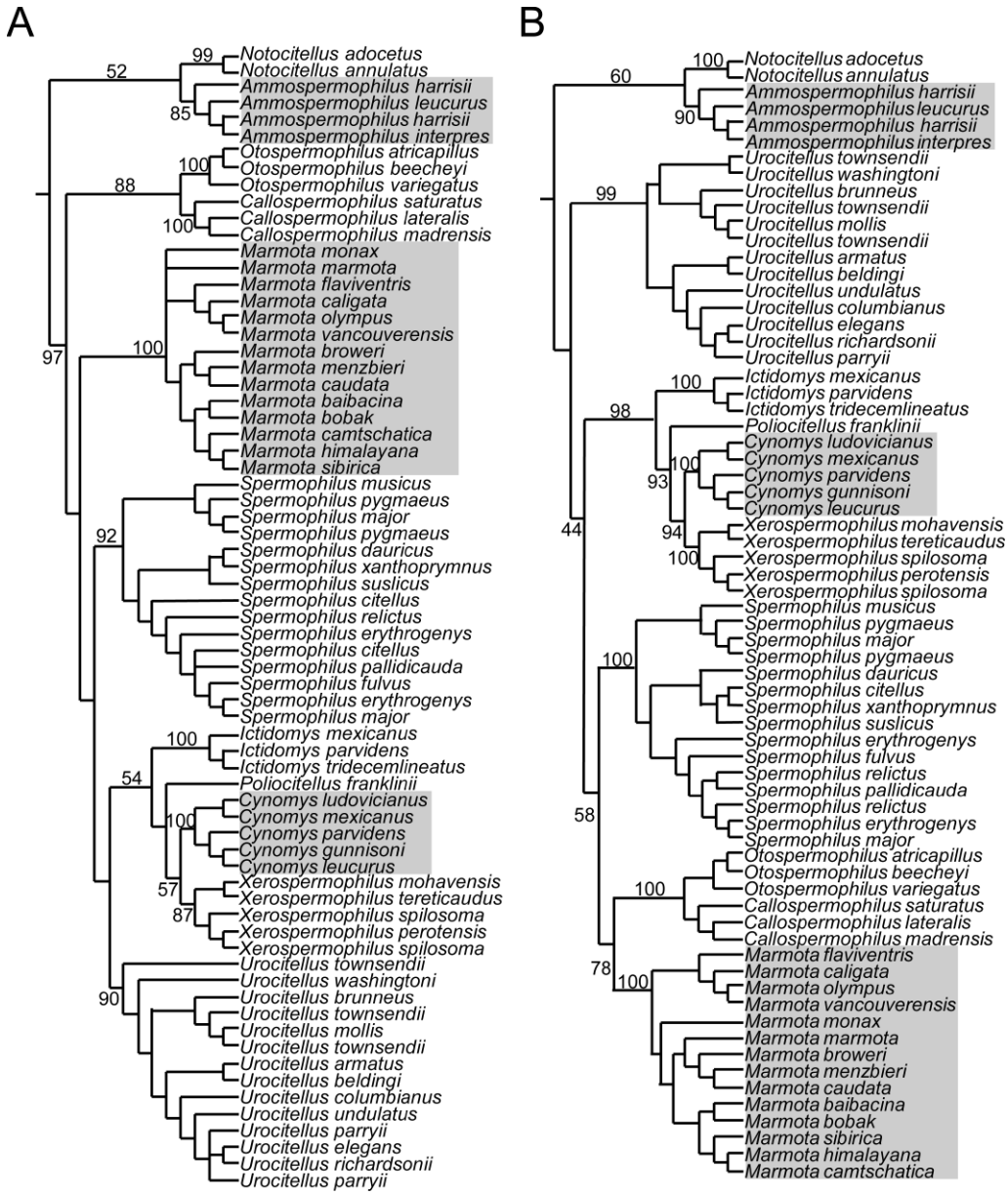


Fig. 2.—Phylogeny of Marmotini proposed by Herron et al. (2004) based on analyses of complete sequences of the cytochrome-*b* gene. Harrison et al. (2003) presented very similar results. Multiple terminal branches representing the same taxon have been collapsed for simplification in some cases, and some identifications have since been modified. The shaded taxa represent the 3 genera that have not been traditionally recognized in *Spermophilus*. A) Maximum parsimony: ''Strict consensus of all 208 equally optimal trees based on unweighted maximum parsimony search'' (Herron et al. 2004:1022). Bootstrap percentages for nodes of taxonomic interest (generic and supergeneric) are shown following Herron et al. (2004). B) Bayesian analysis: ''Majority rule consensus phylogram (with branch lengths averaged over all trees) resulting from Bayesian phylogenetic analysis using a GTR + G + I model of evolution'' (Herron et al. 2004:1024). Posterior probabilities ''estimated from a total of 4 million post-burn-in generations (from four independent runs)'' are provided for nodes of taxonomic interest (generic and supergeneric) following Herron et al. (2004:1024).

recovered in an isolated position. It is weakly supported (<50 MP, 93 BPP) as sister to a group that includes clades 5 and 6 (*Xerospermophilus* and *Cynomys*). This species is traditionally classified exclusively in the subgenus *Poliocitellus*.

Clade 8 (Ictidomys).—In both trees (Fig. 2), the species *tridecemlineatus* (the type species of *Ictidomys* J. A. Allen, 1877), *mexicanus* (the type species of the later name *Ictidomoides* Mearns, 1907), and *parvidens* (see generic account of *Ictidomys*, below) form a well-supported monophyletic group (100 MP, 100 BPP). These species are traditionally classified together in the subgenus (or genus) *Ictidomys*. In both trees, this clade is recovered as the sister lineage to a group that consists of clades 5–7, albeit with variable support (54 MP, 98 BPP). However, *Ictidomys* also has included *Xerospermophilus spilosoma* and *X. perotensis*, which appear in clade 5.

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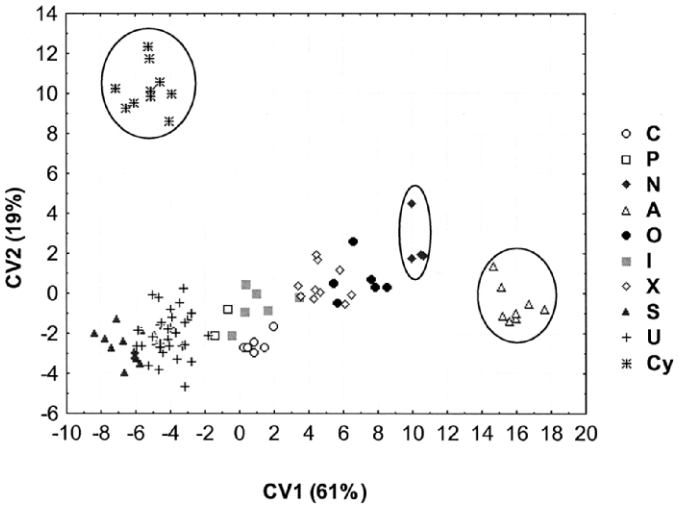


Fig. 3.—Discriminant function analysis illustrating craniometric differentiation in the smaller-bodied genera of the tribe Marmotini (i.e., excluding *Marmota*, markedly larger than all other lineages), including *Cynomys* (Cy) and *Ammospermophilus* (A), phenetically distinctive lineages traditionally separated generically from other North American ground squirrels, and generic lineages previously included within *Spermophilus* sensu lato—*Spermophilus* (S), *Urocitellus* (U), *Poliocitellus* (P), *Ictidomys* (I), *Callospermophilus* (C), *Xerospermophilus* (X), *Otospermophilus* (O), and *Notocitellus* (N) (Table 1). *Cynomys*, *Ammospermophilus*, and *Notocitellus* (denoted by circled clusters) separate widely from other lineages in concert along the 1st and 2nd roots, whereas the other lineages form a more-or-less linear continuum along the 1st axis (see Fig. 5).

Clade 9 (Marmota).—In both trees (Fig. 2), the 14 sampled species of *Marmota*, including *marmota* (Linnaeus, 1758), the type species of *Marmota* Blumenbach, 1779, are recovered as a monophyletic group with high support (100 MP, 100 BPP). These species are traditionally and exclusively classified together in the genus *Marmota*. The phylogenetic position of this clade differs markedly between the 2 trees, but in both trees it is nested within the taxonomic boundaries of *Spermophilus* as currently defined (Thorington and Hoffmann 2005).

Clade 10 (Urocitellus).—In both trees (Fig. 2), a group of 12 species including *undulatus* (the type species of *Urocitellus* Obolenskij, 1927), *armatus*, *beldingi*, *brunneus*, *canus*, *columbianus*, *elegans*, *mollis* (including the subspecies *idahoensis* [see Herron et al. 2004]), *parryii*, *richardsonii*, *townsendii*, and *washingtoni* are recovered as a monophyletic group with high support (90 MP, 99 BPP). These species are traditionally classified in the nominate subgenus *Spermophilus* along with a diverse group of Eurasian ground squirrels (but the type species of *Spermophilus* is *citellus*, which falls in clade 11). The phylogenetic position of this clade differs markedly between the 2 trees.

Clade 11 (Spermophilus sensu stricto).—In both trees (Fig. 2), a group of 11 sampled Eurasian species including *citellus* (the type species of *Spermophilus* F. Cuvier, 1825, and the unavailable generic name *Citellus* Oken, 1816), *fulvus* (the type species of the later name *Colobotis* Brandt, 1844), *dauricus*, *erythrogenys*, *major*, *pallidicauda*, *pygmaeus* (including *musicus*), *relictus* (and *ralli* [see Harrison et al. 2003]), *suslicus*, and *xanthoprymnus* are recovered as a monophyletic group with high support (92 MP, 100 BPP). These species are traditionally classified in the nominate subgenus *Spermophilus* along with a diverse group of primarily North American ground squirrels associated with clade 10, but these groupings are not recovered as each others' closest relatives. The phylogenetic position of *Spermophilus* (clade 11) differs markedly between the 2 trees.

Table 1.—Underlying statistics (variable coefficients and correlations, eigenvalues, and cumulative varance of canonical variates) of a discriminant function analysis (see Fig. 3) illustrating craniometric differentiation among genera within the tribe Marmotini (excluding *Marmota*). See "Materials and Methods" for variable names.

	Standardized coefficients			Correlations		
Variable	CV1	CV2	CV3	CV1	CV2	CV3
CBL	0.694	−1.420	−4.634	−0.049	0.222	0.021
ZB	−1.086	1.914	−1.102	−0.097	0.286	−0.027
BBC	−0.242	−2.151	2.013	−0.016	0.201	0.018
HBC	0.742	0.544	−0.352	−0.043	0.222	0.044
RB	−1.446	0.001	0.508	−0.047	0.171	0.066
LN	−1.409	−0.609	−0.273	−0.101	0.188	0.005
WN	−1.144	−0.053	0.120	−0.106	0.140	0.032
IOB	0.020	−0.102	−0.642	0.031	0.201	0.016
POB	1.171	0.500	−0.008	0.055	0.116	0.022
LD	1.612	−1.374	0.834	−0.028	0.125	0.082
LIF	0.250	0.341	−0.524	−0.059	0.163	−0.044
WIF	−0.324	−0.136	0.447	−0.029	0.138	0.098
WAIF	−0.787	−0.385	−0.185	−0.146	0.231	−0.023
LAB	0.632	0.315	−0.459	0.027	0.247	−0.048
WAB	0.289	−0.340	−0.350	−0.074	0.256	−0.158
WAAM	1.290	−0.220	−2.886	−0.088	0.273	−0.116
WPP3	−0.607	0.097	0.897	−0.057	0.227	0.050
WPM1	1.316	−0.147	−0.862	−0.043	0.081	0.006
WPM3	−0.003	0.133	0.275	0.005	−0.003	0.062
LBP	0.499	−0.155	2.119	−0.054	0.196	0.055
LEBP	−0.336	0.128	0.096	0.015	0.116	−0.010
PPL	0.505	0.520	1.498	−0.046	0.227	−0.002
LMTR	−0.387	−0.138	1.264	−0.119	0.271	−0.013
WI	−1.720	−0.943	0.455	−0.091	0.179	0.044
LI	0.348	0.404	0.252	−0.019	0.341	0.085
DI	1.964	1.692	0.005	0.040	0.362	0.055
WP3	−1.342	0.119	0.691	−0.255	0.320	−0.097
LP4	−0.437	−0.432	−0.130	−0.111	0.236	0.010
WM2	0.681	0.905	0.248	−0.122	0.386	0.000
WM3	−0.846	0.574	1.054	−0.154	0.343	−0.011
LM3	0.692	−0.020	−2.039	−0.169	0.303	−0.098
LAP	−0.578	0.114	0.307	−0.131	0.310	−0.062
LCP	−0.210	1.127	2.000	−0.067	0.256	0.086
Eigenvalue	49.953	15.615	5.901			
Cumulative variance	0.610	0.800	0.872			

Craniometric Analyses

In a preliminary discriminant function analysis comparing all small to medium-sized members of the tribe Marmotini (as delineated above), *Cynomys*, *Ammospermophilus*, and *Notocitellus* clearly diverge from remaining clades in combination along the 1st and 2nd canonical variates (CV1 and CV2), reflecting consistent differences amongst these groupings in craniodental shape, expressed especially in incisor, cheekteeth,

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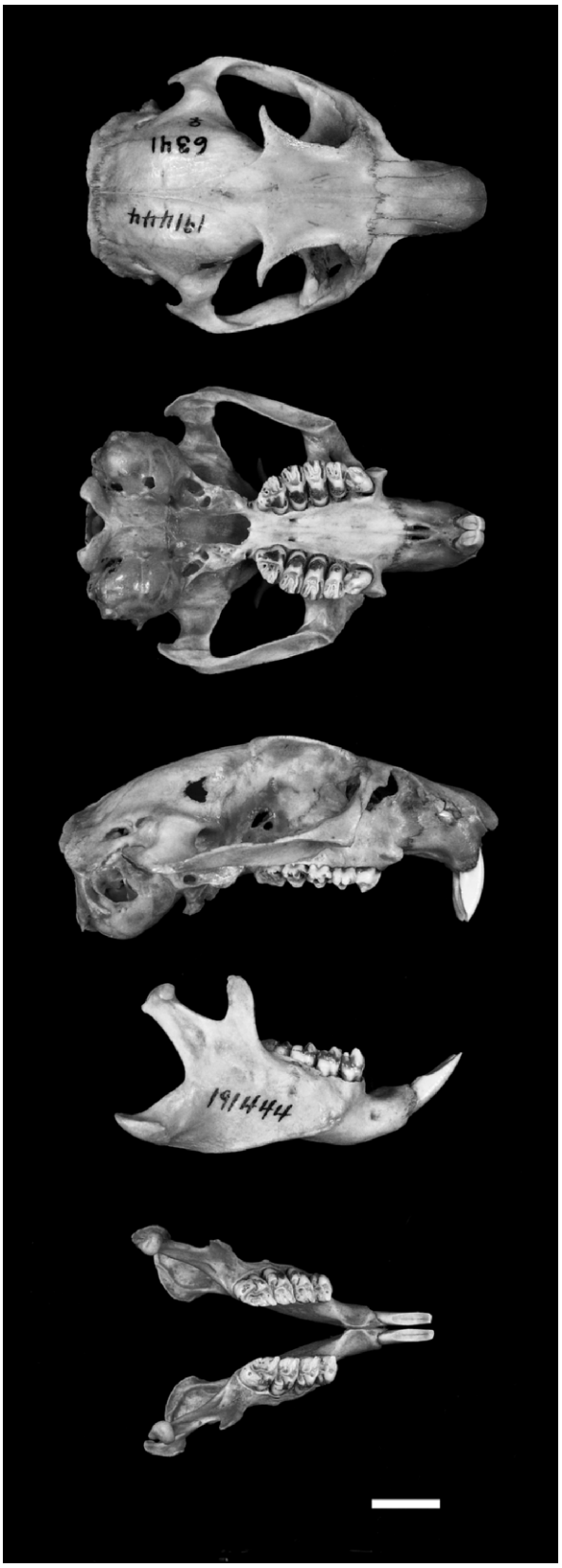


Fig. 4.—Skull of *Cynomys ludovicianus*, the type species of *Cynomys* (USNM 191444, adult female, Boulder County, Colorado, United States). From top to bottom: dorsal view of cranium, ventral view of cranium, lateral view of cranium, lateral view of mandible, and dorsal view of mandible. Scale bar = 10 mm.

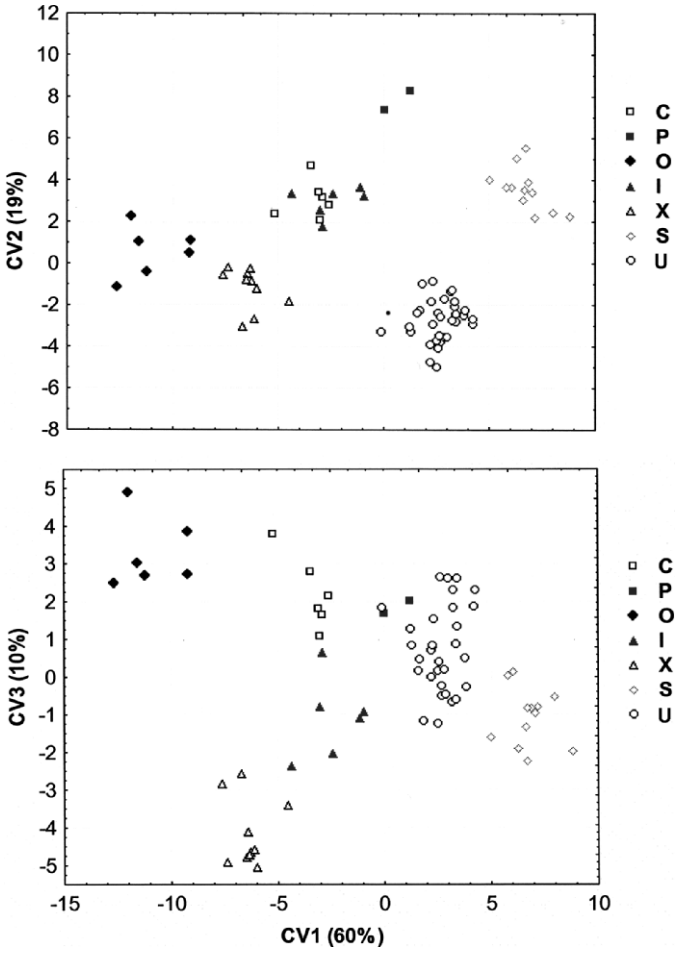


Fig. 5.—Discriminant function analysis highlighting craniometric distinctions between generic lineages within Marmotini, excluding the genera *Marmota*, *Cynomys*, *Ammospermophilus*, and *Notocitellus* (see Fig. 3). All lineages achieve discrimination along the first 2 canonical variate roots (CV1 is shown along the horizontal axis in both plots), reflecting consistent differences in craniodental shape, with the exception of *Callospermophilus* and *Ictidomys*, ecomorphologically similar but phylogenetically unrelated genera (Fig. 2) that segregate along the 3rd canonical variate primarily on the basis of slight differences in size and comparative robustness (Table 2).

bullae, nasal, zygomatic, and mandibular dimensions (Fig. 3; Table 1). We elected to exclude the species of *Marmota*—already very well known for their very large and diagnostically distinctive skulls and teeth—from our craniometric contrasts. *Cynomys* possesses the most distinctive skull features of the medium-sized ground squirrels and diverges from all other groupings along CV2 based especially on proportions of the incisors, premolars, molars, and auditory bullae; zygomatic width and the length of the angular process of the dentary; and relative divergence of the toothrows (Figs. 3 and 4; Table 1; cf. Howell 1938). *Ammospermophilus* and *Notocitellus*, which may be sister genera (Fig. 2), cluster together separately from other genera previously associated within *Spermophilus* along CV1 due in part to their proportionally small teeth (especially P3), shorter and narrower nasals, and shorter angular process of the dentary.

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TABLE 2.—Underlying statistics (variable coefficients and correlations, eigenvalues, and cumulative varance of canonical variates) of a discriminant function analysis (see Fig. 5) illustrating craniometric differentiation among genera within the tribe Marmotini (excluding *Marmota*, *Cynomys*, *Ammospermophilus*, and *Notocitellus*). See "Materials and Methods" for variable names.

	Standardized coefficients			Correlations		
Variable	CV1	CV2	CV3	CV1	CV2	CV3
CBL	−0.982	−4.832	3.750	−0.031	0.022	0.293
ZB	2.641	−2.605	−1.685	−0.004	−0.019	0.297
BBC	2.002	2.969	0.256	−0.045	0.026	0.283
HBC	−1.550	−0.628	−2.036	−0.044	0.048	0.227
RB	2.120	0.352	−0.360	−0.005	0.049	0.194
LN	−0.359	0.091	1.496	−0.009	0.023	0.311
WN	1.332	−0.325	0.303	0.015	0.026	0.233
IOB	−0.703	−0.589	0.380	−0.088	0.019	0.290
POB	−0.811	−0.215	−0.446	−0.070	0.022	0.009
LD	−0.441	2.577	−1.258	−0.022	0.077	0.314
LIF	−1.114	−0.598	0.206	−0.045	0.003	0.312
WIF	0.770	0.393	−0.192	−0.031	0.087	0.198
WAIF	1.586	0.163	−0.306	0.052	−0.027	0.288
LAB	−0.726	−0.375	−1.244	−0.087	−0.032	0.063
WAB	−0.458	−0.815	0.575	−0.016	−0.144	0.188
WAAM	−2.932	−2.056	1.194	0.000	−0.095	0.323
WPP3	−0.049	1.649	−1.328	−0.020	0.047	0.212
WPM1	−1.437	−0.907	1.525	−0.027	0.021	0.289
WPM3	−0.067	−0.148	−0.283	−0.060	0.075	0.340
LBP	−0.831	2.389	1.264	−0.005	0.037	0.236
LEBP	0.549	−0.200	−0.993	0.004	−0.037	−0.051
PPL	−0.927	1.072	−0.251	−0.036	0.005	0.290
LMTR	0.531	1.486	−1.210	0.012	−0.009	0.234
WI	1.802	0.607	0.677	0.005	0.051	0.300
LI	−0.525	0.536	−0.107	−0.085	0.084	0.258
DI	−2.041	0.188	−0.392	−0.139	0.063	0.215
WP3	1.777	0.571	−0.789	0.127	−0.102	0.224
LP4	−0.092	−0.047	−0.190	0.020	−0.004	0.226
WM2	−0.613	−0.487	0.323	0.009	−0.007	0.274
WM3	0.694	1.127	1.279	0.026	−0.012	0.315
LM3	0.127	−2.278	−0.931	0.056	−0.093	0.261
LAP	0.244	−0.321	−0.009	0.016	−0.054	0.223
LCP	0.609	1.490	0.314	0.008	0.055	0.290
Eigenvalue	29.953	9.550	4.649			
Cumulative variance	0.598	0.789	0.882			

In continuing comparisons excluding *Cynomys*, *Ammospermophilus*, and *Notocitellus*, most of the remaining clades recovered in the molecular analyses are clearly discriminated from one another in combination along CV1 and CV2, reflecting consistent and diagnostic distinctions in cranial shape (e.g., Fig. 5; Table 2).

Although *Otospermophilus* and *Callospermophilus* are apparently closely related (Fig. 2; Harrison et al. 2003; Herron et al. 2004), these lineages are highly divergent morphologically. Our analyses of both qualitative morphology and craniometrics (Fig. 5) indicate that these taxa form discrete groupings that should be regarded as distinct at the genus level.

Our craniometric results credit indications by Herron et al. (2004) that 2 species traditionally classified in the subgenus *Ictidomys* (*spilosoma* and *perotensis*) bear consistent craniodental resemblance to species traditionally classified in *Xerospermophilus* (*mohavensis* and *tereticaudus*). The previous classification of *perotensis* and *spilosoma* within *Ictidomys* represents convergent achievement of an external striping pattern rather than a close evolutionary relationship (see generic account of *Ictidomys*, below).

In our analyses, *Callospermophilus* and *Ictidomys* are recovered as strikingly similar in craniometrics. Although rather deeply distinct lineages phylogenetically (Fig. 2), they do not segregate along CV1 and CV2, but instead segregate only along the 3rd canonical variate (CV3) on the basis of minor but consistent differences in overall size and robustness (Fig. 5; Table 2). The remarkable craniometric similarity of these unrelated lineages of ground squirrels has gone previously unremarked in the literature but may betray similarities in ecomorphology and lifestyle.

Consistent craniometric distinctions documented between these clades of Marmotini complement differences in body size, external proportions, pelage coloration and ornamentation, and qualitative cranial distinctions that also diagnose these distinctive lineages (see generic accounts, below).

SYSTEMATICS

We propose that ground squirrels currently allocated to the genus *Spermophilus* (sensu Thorington and Hoffmann 2005) can be classified in 8 genera, as defined, diagnosed, and discussed in the following generic accounts. For completeness of reference, we provide the full citations for each of the original descriptions of these 8 generic-level names in the Literature Cited (Allen 1877; Brandt 1844; Cuvier 1825; Howell 1938; Merriam 1892, 1897; Obolenskij 1927).

Genus *Notocitellus* A. H. Howell

Tropical Ground Squirrels (Figs. 6 and 7)

Notocitellus A. H. Howell, 1938, N. Am. Fauna, 56:44. Type species *Spermophilus annulatus* Audubon and Bachman, 1842.

Content.—Two species of *Notocitellus* are recognized: *N. adocetus* Merriam, 1903, and *N. annulatus* Audubon and Bachman, 1842.

Notocitellus adocetus (Merriam, 1903). Proc. Biol. Soc. Wash., 16:79.

N. a. adocetus (Merriam, 1903:79). Type locality: La Salada, 40 miles [64 km] south of Uruapan, Michoacan, Mexico. [*arceliae* (Villa-R., 1942) is a synonym.]

N. a. infernatus (Alvarez and Ramírez-P., 1968:183). Type locality: 14 km al norte de El Infiernillo, Michoacan [Mexico].

Notocitellus annulatus (Audubon and Bachman, 1842). J. Acad. Nat. Sci. Phila., 8:319.

N. a. annulatus (Audubon and Bachman, 1842:319). Type locality: western prairies. Restricted by A. H. Howell (1938:163) to Manzanillo, Colima, Mexico.

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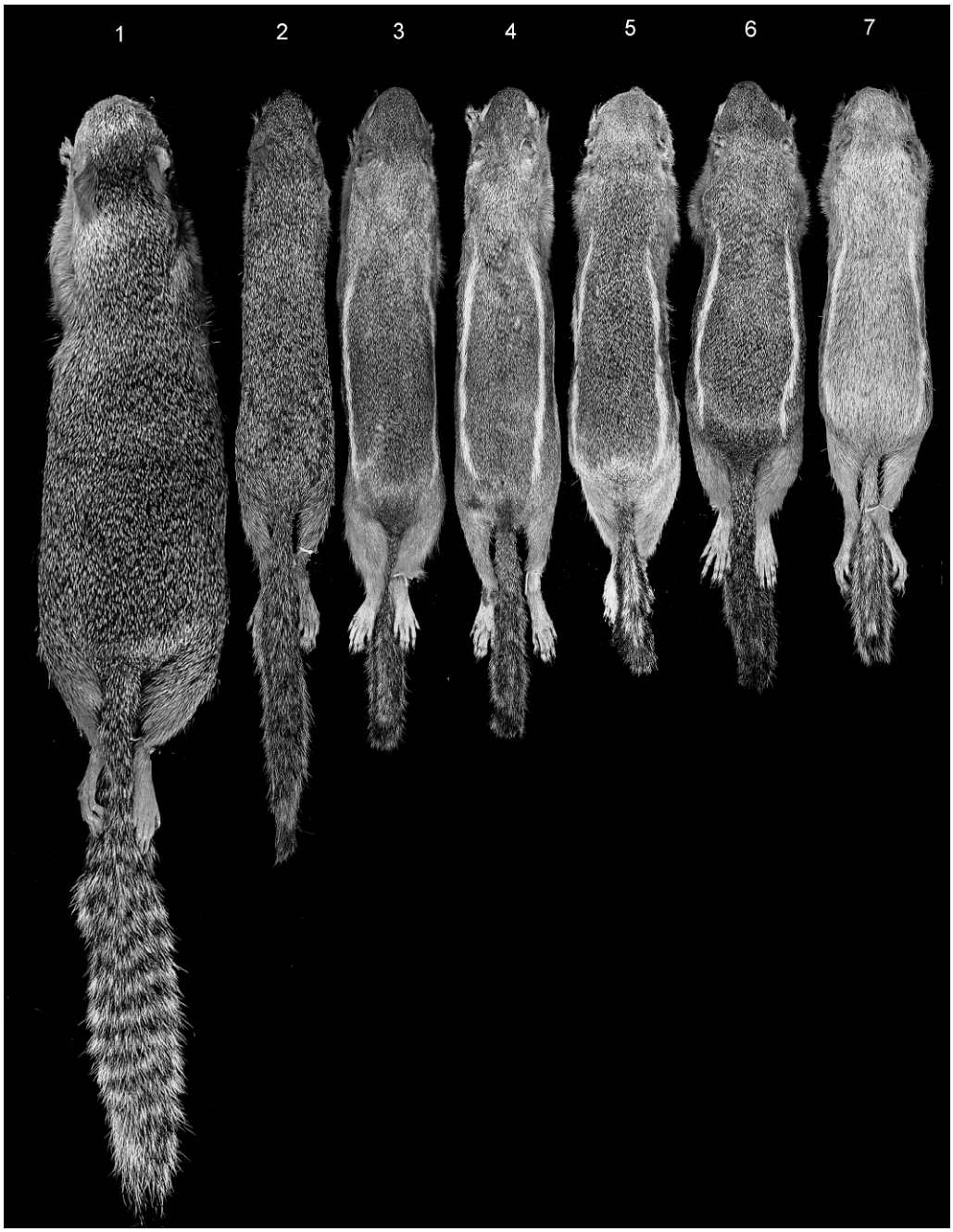


Fig. 6.—Representative skins (all adult females) of the species of *Notocitellus* (1, 2) and *Ammospermophilus* (3–7): 1) *N. annulatus*, USNM 32662, Manzanillo, Colima, Mexico; 2) *N. adocetus*, USNM 126123, La Salada, Michoacan, Mexico; 3) *A. interpres*, USNM 119910, San Andreas Mountains, New Mexico, United States; 4) *A. insularis*, USNM 146782, Espiritu Santo Island, Baja California Sur, Mexico; 5) *A. leucurus*, USNM 61157, San Diego County, California, United States; 6) *A. harrisii*, USNM 59861, Quitovaquito, Arizona, United States; 7) *A. nelsoni*, USNM 54655, Tipton, California, United States. We note that subsequent to our preparation of figures and analyses, Alvarez-Castañeda (2007) argued convincingly that *insularis* should be recognized as a subspecies of *A. leucurus*.

N. a. goldmani (Merriam, 1902:69). Type locality: Santiago, Tepic, Mexico.

Etymology.—The name *Notocitellus* is derived from the Greek *noto* meaning the back and the Latin *citellus* for ground squirrel (Jaeger 1955).

Diagnosis.—The species of *Notocitellus* differ conspicuously from all other ground squirrels both in external appearance and craniodental conformation. There are only 3 pairs of teats (1 axillary and 2 inguinal pairs, verified here for both species), a trait unique among the tribe Marmotini (Table 3)—all other genera have 4–6 pairs, usually 5 (Moore 1961). Both species of *Notocitellus* have a grizzled black and tan dorsum, borne of dark–pale banding in the hairs of the dorsal pelage (Fig. 6). The dorsal fur is coarse, rather than soft as in most other members of the tribe Marmotini. Externally, the species of *Notocitellus*

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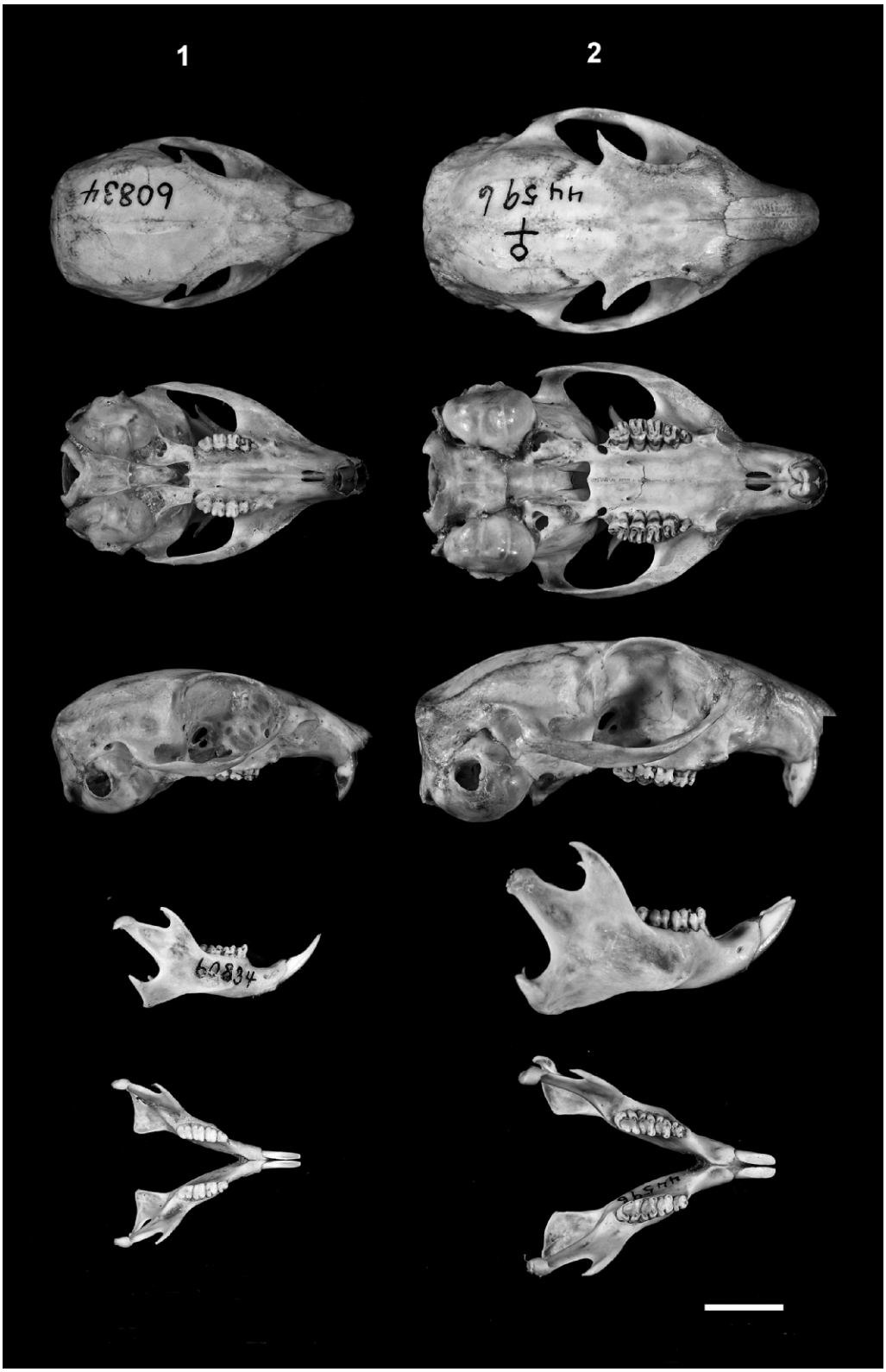


Fig. 7.—Representative skulls of the respective type species of *Ammospermophilus* (1) and *Notocitellus* (2): 1) *A. leucurus*, USNM 60834, adult female, San Diego County, California, United States; 2) *N. annulatus*, USNM 44596, adult female, Manzanillo, Colima, Mexico. From top to bottom: dorsal view of cranium, ventral view of cranium, lateral view of cranium, lateral view of mandible, and dorsal view of mandible. Scale bar = 10 mm.

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Table 3.—Selected characteristics of ground squirrel genera previously included within the genus *Spermophilus*.

	Notocitellus	*Otospermophilus*	*Callospermophilus*	*Spermophilus*	*Ictidomys*	*Poliocitellus*	*Xerospermophilus*	*Urocitellus*
No. species	2	3	3	14	3	1	4	12
Range	West-central Mexico	Western North America	Western North America	Central Eurasia	Central and western North America	Central North America	Central and western North America	Central and western North America, northeastern and central Asia
Habitat	Tropical deciduous forests	Rocky habitats in semiarid areas	Shrub steppe, woodlands, coniferous forests	Grasslands, deserts, tundra	Grasslands	Grasslands	Grasslands, deserts	Grasslands, shrub steppe, alpine and arctic tundra
Size								
Head–body length (mm)	287–476	374–578	206–312	172–350	265–313	345–400	210–320	193–475
Tail length (mm)	127–238	156–278	52–116	25–112	80–150	120–155	57–113	27–120
Tail : head and body (%)	>75	70–90	37–55	17–33	50–70	50	40–60	25–45
Hind-foot length (mm)	38–64	51–68	31–48	28–60	35–46	49–59	31–46	31–49
Ear length (mm)	14–18	16–35	15–25	5–12	6–12	15–18	5–10	4–19
Pelage pattern	Flecked	Flecked, shoulder stripes	Light and dark dorsal stripes	Unmarked, flecked, or spotted	Lined with spots, stripes	Flecked	Unmarked, flecked, or spotted	Unmarked or flecked
Tail characteristics	Long, distichous	Long, bushy	Short to medium, thin to bushy	Short, thin	Medium, bushy	Medium, bushy	Medium, thin	Short to medium, thin to bushy
No. pairs mammae	3	5 or 6	4 or 5	5	4–6	5 or 6	5	5 or 6

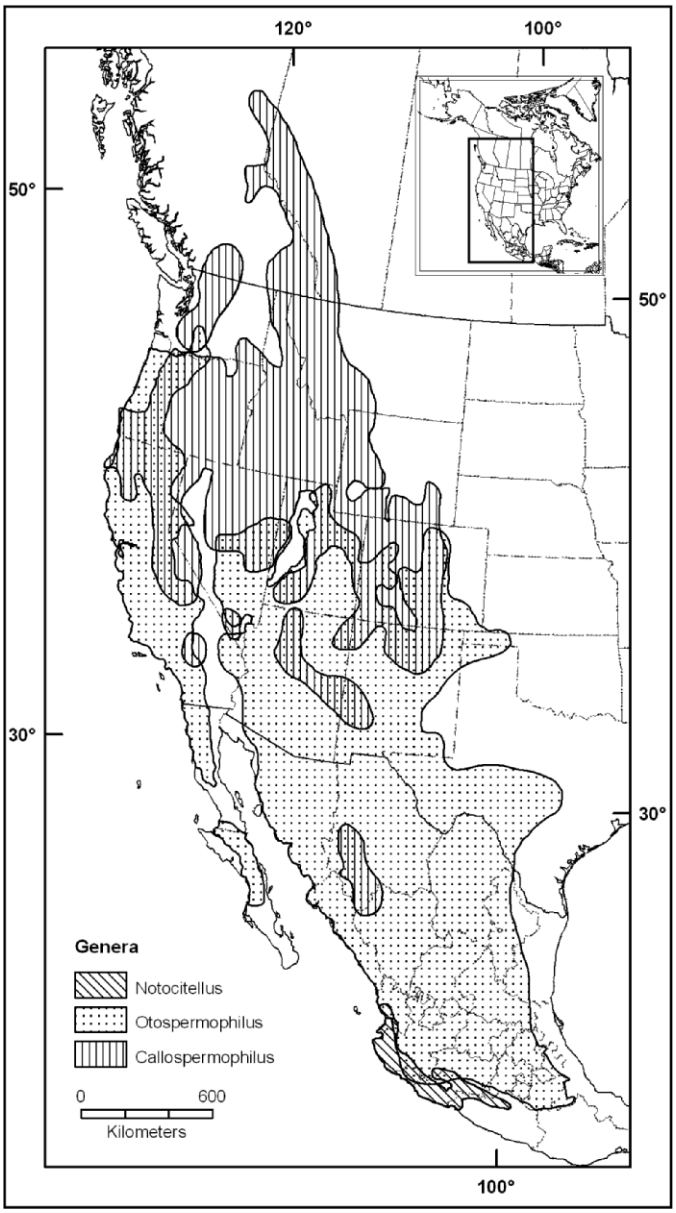


Fig. 8.—Geographic distributions of the tropical ground squirrels (*Notocitellus*), rock squirrels (*Otospermophilus*), and golden-mantled ground squirrels (*Callospermophilus*) (after Hall 1981).

are distinctive in having relatively long tails, measuring >75% of head–body length (78–113%, usually about 90%), which are distichous (as in tree squirrels) rather than being either bushy or thinly clad (as in other Marmotini); slender bodies; long and narrow feet; and ears that are large but distinctively short and broadly rounded (proportionally larger than, but resembling in shape, the pinnae of *Ammospermophilus*). Apart from its distinctively rounded ears, this apomorphous character suite (in the context of xerine ecomorphology) is convergent on the body plan of arboreal tree squirrels (i.e., the tribes Nannosciurini, Tamiasciurini, and Sciurini) and we suggest that it reflects the semiarboreal lifestyle of *Notocitellus*, unique among the tribe Marmotini (see below). The cranium of *Notocitellus* features a blunt rostrum with very short incisive foramina; opisthodont, anteroposteriorly deep incisors (usually with very deep-red enamel faces); weakly expanded, relatively gracile zygomata; large and broad auditory bullae; a rounded braincase; closed supraorbital foramina; and a relatively small P4 and a simple and smaller P3 (less than one-fourth of the size of P4), which is a unique combination of traits within the tribe Marmotini (Fig. 7). The molars are relatively brachyodont, with the parastyle ridge on M1 and M2 rising to join the protocone without abrupt change in direction (Howell 1938).

Of the ground squirrel genera previously classified within *Spermophilus* (sensu lato), only *Notocitellus* and *Otospermophilus* have relatively long tails (Table 3), and previous authors have hypothesized a phylogenetic alliance between these 2 lineages based on morphology (cf. Harrison et al. 2003; Howell 1938; Miller 1924), but this is not supported by molecular phylogenetic analyses (Fig. 2). The skulls of the 2 genera are superficially similar, but skulls of *Notocitellus* can be easily discerned from those of *Otospermophilus* in having a blunter rostrum, proportionally much wider interorbital region, much bigger bullae, proportionally smaller molars, very small P3, short incisive foramina, and heavier incisors. These and other distinctions are reflected in their multivariate morphometric separation in our discriminant function analysis (Fig. 3).

Distribution.—The genus *Notocitellus* is endemic to west-central Mexico (Fig. 8), where it is represented by 2 species that differ conspicuously in body size and have parapatric or marginally overlapping geographic distributions (Howell 1938). The distribution of *N. adocetus* extends from eastern Jalisco and Michoacan to northern Guerrero, including both humid lowland habitats and more arid areas on the Mexican Plateau, up to 3,000 m (Best 1995a). *N. annulatus* is restricted to lowlands (sea level to approximately 1,200 m) from southern Nayarit to northwestern Guerrero (Best 1995b). The distributions of these 2 species may overlap in northern Guerrero (Howell 1938).

Cytogenetics.—The karyotype of *N. adocetus* consists of 32 chromosomes, with a fundamental number (number of autosomal arms) of 60 (Birney and Genoways 1973). The karyotype of *N. annulatus* has not been studied (Best 1995b).

Ecology.—*Notocitellus* is endemic to Mexico, and both species occupy unique habitats relative to other species of Marmotini. *N. adocetus* lives in upland desert shrub communities such as mesquite woodlands with columnar cactus. It also occupies low tropical deciduous forest in some areas. Much of this habitat has recently been converted to low-level agriculture, and *N. adocetus* has become adapted to many of these habitats as well. This species is common in rocky areas along canyon sides, and also can be found along stone walls in agricultural areas (Best 1995a). *N. annulatus* occurs along the Pacific coast in tropical deciduous forest that is seasonally quite arid (Best 1995b). *N. annulatus* is equally at home in areas converted to a variety of agricultural uses. Both species are omnivorous, but feed mainly on a variety of fruits, seeds, and green vegetation. In some areas, they are considered a pest on crops. Both species are apparently more arboreal than other Marmotini, climbing in low trees and shrubs in search of food. They are diurnal, with most activity in the morning hours (Valdéz Alarcón and Téllez-Girón 2005).

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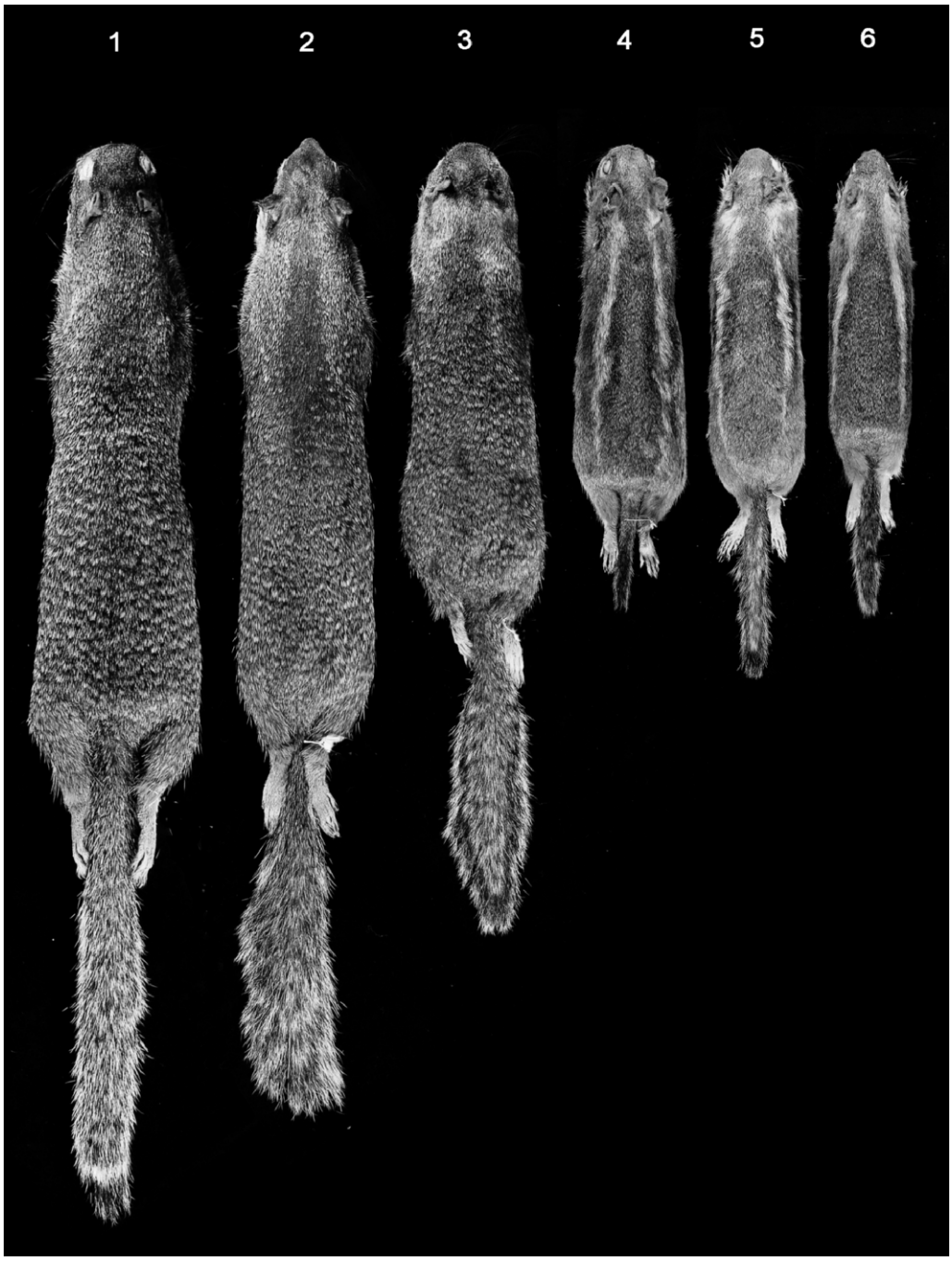


Fig. 9.—Representative skins (all adult females) of the species of *Otospermophilus* (1–3) and *Callospermophilus* (4–6): 1) *O. variegatus*, USNM 91718, Santa Rosa, Guanajuato, Mexico; 2) *O. atricapillus*, USNM 146185, Comondu, Baja California Sur, Mexico; 3) *O. beecheyi*, USNM 63960, Half Moon Bay, California, United States; 4) *C. madrensis*, USNM 95348, Sierra Madre, Chihuahua, Mexico; 5) *C. saturatus*, USNM 89001, Trout Lake, Washington, United States; 6) *C. lateralis*, USNM 158507, Beaver Mountains, Utah, United States.

Comments.—Phylogenetic analyses of cytochrome-*b* ally *Notocitellus* as the sister lineage to *Ammospermophilus* (Fig. 2; Harrison et al. 2003; Herron et al. 2004)—an alliance complemented by shape-related morphometric similarity (Figs. 3 and 7) and similarities in the shape of the ears, despite the otherwise extremely different external appearance of the 2 genera (Fig. 6). However, the craniometric resemblance between *Notocitellus* and *Ammospermophilus* might be credited largely to characteristics possibly primitive for the tribe Marmotini, including a narrow infraorbital foramen, inflated bullae, stout incisors, and a small P3.

Genus *Otospermophilus* Brandt

Rock Squirrels (Figs. 9 and 10)

Otospermophilus Brandt, 1844, Bull. Cl. Phys.-Math. Acad. Imp. Sci. St. Pétersbourg, 2:379. Type species: *Sciurus grammurus* Say, 1823 [= *S. variegatus* Erxleben, 1777].

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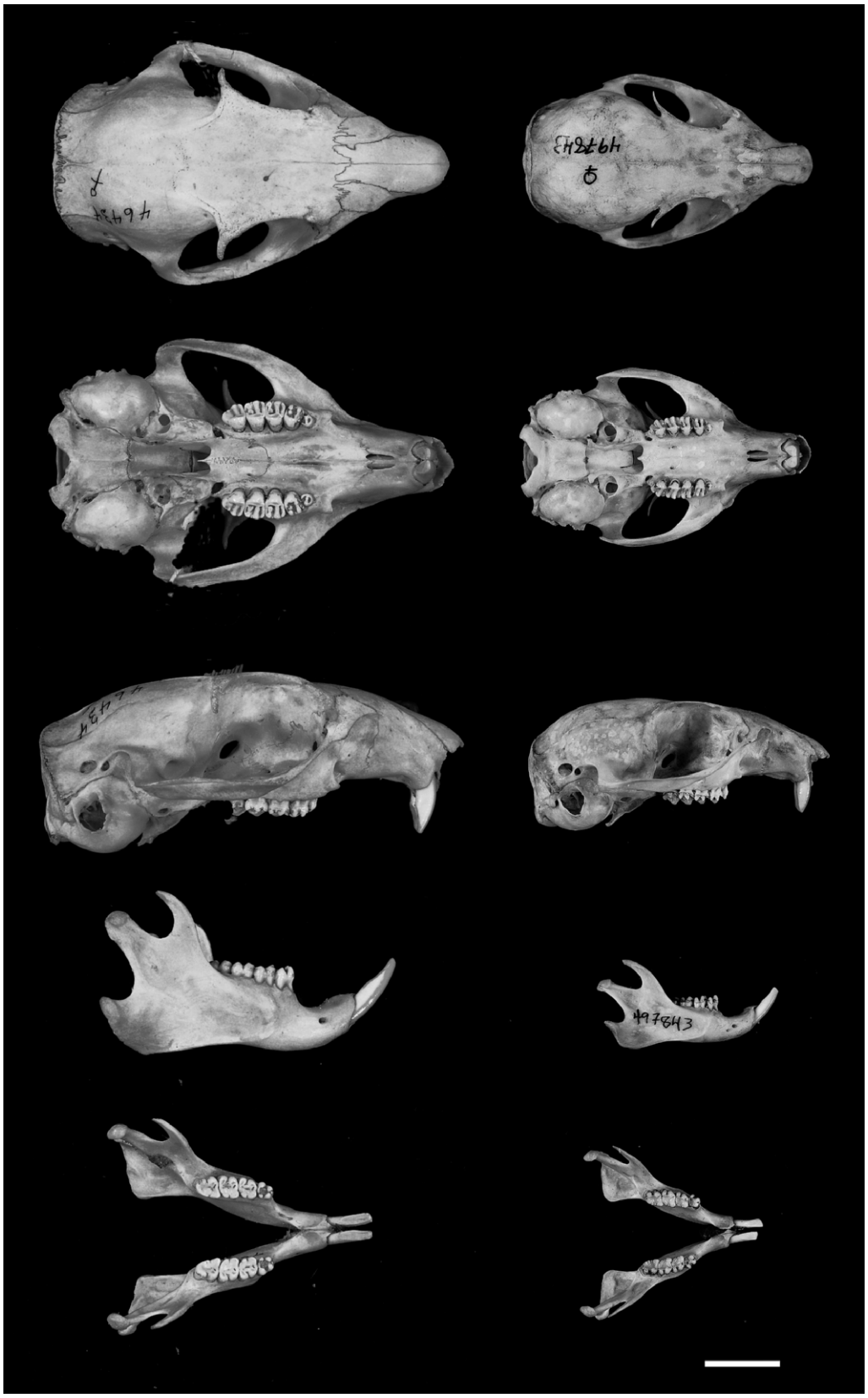


Fig. 10.—Representative skulls of the respective type species of *Otospermophilus* (left) and *Callospermophilus* (right): left) *O. variegatus*, USNM 46434, adult female, Atemajac, Jalisco, Mexico; right) *C. lateralis*, USNM 497843, adult female, Gunnison County, Colorado, United States. From top to bottom: dorsal view of cranium, ventral view of cranium, lateral view of cranium, lateral view of mandible, and dorsal view of mandible. Scale bar = 10 mm.

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Content.—Three allopatric species are recognized, with synonyms as delineated by Thorington and Hoffmann (2005): *O. atricapillus* (W. Bryant, 1889), *O. beecheyi* (Richardson, 1929), and *O. variegatus* (Erxleben, 1777). Type localities as given below are cited largely based on the authority of Thorington and Hoffmann (2005) and Howell (1938). Distinctions between *O. beecheyi* and *O. atricapillus*, which are morphologically very similar, deserve renewed study.

Otospermophilus atricapillus (W. Bryant, 1889). Proc. Calif. Acad. Sci., Ser. 2, 2:26. Type locality: Comondu, Lower California [Baja California Sur, Mexico].

Otospermophilus beecheyi (Richardson, 1829). Fauna Boreali-Amer.,1:170.

O. b. beecheyi (Richardson, 1829:170). Type locality: ''neighborhood of San Francisco and Monterey, in California.'' Restricted by Grinnell (1933) to Monterey, Monterey Co., California, USA.

O. b. douglasii (Richardson, 1829:170). Type locality: bank of the Columbia River, Oregon.

O. b. fisheri (Merriam, 1893:133). Type locality: S. Fork Kern River, 3 mi. above Onyx, California.

O. b. nesioticus (Elliot, 1904:263). Type locality: Santa Catalina Island, California.

O. b. nudipes (Huey, 1931:18). Type locality: Hanson Laguna, Sierra Juarez, 5,200 ft., Baja California, Mexico.

O. b. parvulus (A. H. Howell, 1931:160). Type locality: Shepherd Canyon, Argus Mts., California.

O. b. rupinarum (Huey, 1931:17). Type locality: Catavina, Baja California, Mexico.

O. b. sierrae (A. H. Howell, 1938:153). Type locality: Emerald Bay, Lake Tahoe, El Dorado Co., California.

Otospermophilus variegatus (Erxleben, 1777). Syst. Regn. Anim., 1:421.

O. v. buckleyi (Slack, 1861:314). Type locality: Packsaddle Mountain, Llano Co., Texas.

O. v. couchii (Baird, 1855:332). Type locality: Santa Catarina, few mi. W Monterey, Nuevo León, Mexico.

O. v. grammurus (Say, 1823:72). Type locality: Purgatory River, near the mouth of Chacuaco Creek, Las Animas Co., Colorado. [*juglans* (V. Bailey, 1913) and *tiburonensis* (Jones and Manning, 1989) are synonyms.]

O. v. robustus (Durrant and Hansen, 1954:264). Type locality: Pass Creek, Deep Creek Mountains, 8,000 ft., Juab Co., Utah.

O. v. rupestris (J. A. Allen, 1903:595). Type locality: Río Sestín, northwestern Durango.

O. v. tularosae (Benson, 1932:336). Type locality: French's Ranch, 5,400 ft., 12 mi. NW Carrizozo, Lincoln Co., New Mexico.

O. v. utah (Merriam, 1903:77). Type locality: foot of the Wasatch Mts., near Ogden, Weber Co., Utah.

O. v. variegatus (Erxleben, 1777:421). Type locality: not designated; restricted by Nelson (1898:898) to ''Valley of Mexico near the City of Mexico'' [Distrito Federal, Mexico]. [*buccatus* (Lichtenstein, 1830) and *macrourus* (Bennett, 1833) are synonyms.]

Etymology.—The name *Otospermophilus* is derived from the Greek *otos* meaning ear, *spermatos* for seed, and *phileo* for love (Jaeger 1955).

Diagnosis.—The species of *Otospermophilus* are easily recognized; they are relatively large squirrels, with long and bushy tails, pale crescent markings on the sides of the neck and shoulders, and relatively very large ears (Fig. 9). The fur is short and sleek, with the dorsal hairs banded dark brown and buff, generating an impression of grizzling or flecking in the pelage. There is usually middorsal darkening in the pelage, extending from the nose or crown to the midback. There are 5 or 6 pairs of mammae. The skull is relatively large but not particularly wide, and features relatively large molars, a small P3, orthodont or slightly opisthodont incisors, long incisive foramina, very large auditory bullae, a rounded braincase, and open supraorbital foramina—a combination of traits distinctive among the tribe Marmotini (Fig. 10). The molars are relatively brachyodont, with the parastyle ridge on M1 and M2 rising to join the protocone without an abrupt change in direction (cf. Howell 1938). As in *Notocitellus*, P3 is simple and very small, generally less than 25% the size of P4. The skull superficially resembles that of *N. annulatus* and *Poliocitellus* (to which *Otospermophilus* bears little external resemblance), but differs from the latter in its less elongate rostrum and incisive foramina, more expansive braincase, smaller P3, heavier molars, and proportionally larger auditory bullae.

Distribution.—The 3 species of *Otospermophilus* are disjunctly distributed across the western United States and Mexico (Fig. 8). *O. atricapillus* is endemic to the Baja California Peninsula. *O. beecheyi* occurs in the far western United States, from south-central Washington and western Oregon in the north, throughout much of California and southwestern Nevada, to northwestern Baja California in the south. *O. variegatus* is found in Idaho, Utah, southern Nevada, and western Texas, extending south to central Mexico (Botello et al. 2007; Groves et al. 1988; Howell 1938).

Cytogenetics.—The karyotypes of *O. variegatus* and *O. beecheyi* have a diploid number of 38 and a fundamental number of 72 (Nadler 1966b; Oaks et al. 1987). The karyotype of *O. atricapillus* has not been studied (Alvarez-Castañeda et al. 1996).

Ecology.—*Otospermophilus* is a genus of southwestern arid habitats, extending up into mountainous regions as high as 3,000 m. The 3 species are large ground squirrels that form colonies in suitable habitats. *O. atricapillus*, the Baja California rock squirrel, occupies montane oases in soils of volcanic origin (Alvarez-Castañeda et al. 1996; Castro Arellano and Ceballos 2005). The California ground squirrel, *O. beecheyi*, also uses rocky habitats, but also has adapted to agricultural habitats in the rich soils of the coastal mountain valleys (Cole and North 1999; Linsdale 1946; Losa Salas 2005). Rock squirrels, *O. variegatus*, are the most widespread, and use rocky habitats over a wide range of general habitat types from the lower slopes of the Rocky Mountains down through much of central Mexico (Valdéz

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Alarcón and Ceballos 2005b; Schmidt 1999). Although typically terrestrial, *Otospermophilus* will occasional climb trees and shrubs in search of food. All are colonial—perhaps a natural adaptation to their spotty local distributions dictated by surrounding terrain. All have benefited from anthropogenic modifications to their habitats that involve raising crops, which can augment their natural food supplies of fruit and seeds.

Comments.—Phylogenetic analyses of cytochrome-*b* conclusively ally *Otospermophilus* and *Callospermophilus* as sister lineages (Harrison et al. 2003; Herron et al. 2004), a result that echoes some previous hypotheses based on morphological and chromosomal comparisons (cf. Black 1963; Bryant 1945; Gerber and Birney 1968; Gromov et al. 1965; Nadler 1966a). Although these lineages are clearly very closely related, their respective monophyly (Harrison et al. 2003; Herron et al. 2004) and profound morphological divergence (Figs. 9 and 10) argue for their recognition as separate genera, rather than congeneric subgenera (Gromov et al. 1965; Harrison et al. 2003; Herron et al. 2004). Externally, both *Otospermophilus* and *Callospermophilus* share proportionally very large ears and paired crescent markings over the shoulders (Fig. 9), which we regard as likely synapomorphic in light of the molecular evidence for their close relationship. Qualitative cranial features are similar in the 2 genera (Howell 1938), but the skulls show little immediate resemblance in overall shape, at least as compared to other Marmotini (Figs. 3, 5, and 10). Skulls of *Otospermophilus* are much larger than those of *Callospermophilus*, and feature proportionally longer rostra, larger bullae, and heavier teeth, among other distinctions (Howell 1938).

Genus *Callospermophilus* Merriam

Golden-Mantled Ground Squirrels (Figs. 9 and 10)

Callospermophilus Merriam, 1897, Proc. Biol. Soc. Wash., 11:189. Type species: *Sciurus lateralis* Say, 1823.

Content.—Three species are recognized, with synonyms as delineated by Thorington and Hoffmann (2005): *C. lateralis* (Say, 1823), *C. madrensis* (Merriam, 1901), and *C. saturatus* (Rhoads, 1895). Type localities as given below are cited largely based on the authority of Thorington and Hoffmann (2005) and Howell (1938).

Callospermophilus lateralis (Say, 1823). In Long, Account Exped. Pittsburgh to Rocky Mtns., 2:46.

C. l. arizonensis (V. Bailey, 1913:130). Type locality: Little Spring, 8,250 ft., San Francisco Mtn., Arizona.

C. l. bernardinus (Merriam, 1898:134). Type locality: San Bernardino Peak, San Bernardino Co., California. [*brevicauda* (Merriam, 1893; not Brandt, 1843) is a synonym.]

C. l. castanurus (Merriam, 1890:19). Type locality: Park City, Wasatch Mts., Summit Co., Utah. [*caryi* (A. H. Howell, 1917) is a synonym.]

C. l. certus (Goldman, 1921:232). Type locality: north base of Charleston Peak, Clark Co., Nevada.

C. l. chrysodeirus (Merriam, 1890:19). Type locality: Fort Klamath, Klamath Co., Oregon.

C. l. cinerascens (Merriam, 1890:20). Type locality: Helena, 4,500 ft., Lewis and Clark Co., Montana.

C. l. connectens (A. H. Howell, 1931:161). Type locality: Homestead, Oregon.

C. l. lateralis (Say, 1823:46). Type locality: near Cañon City. Restricted by Merriam (1905:163) to Arkansas River, about 26 mi. [42 km] below Canyon City, Fremont Co., Colorado (USA).

C. l. mitratus (A. H. Howell, 1931:161). Type locality: South Yolla Bolly Mtn., California.

C. l. tescorum (Hollister, 1911:2). Type locality: head of Moose Pass, branch Smoky River, 7,000 ft., Alberta [Canada].

C. l. trepidus (Taylor, 1910:283). Type locality: head Big Creek, 8,000 ft., Pine Forest Mts., Humboldt Co., Nevada.

C. l. trinitatus (Merriam, 1901:126). Type locality: E. of Hoopa Valley, 5,700 ft., Trinity Mts., California.

C. l. wortmani (J. A. Allen, 1895:335). Type locality: Kinney Ranch, Bitter Creek, Sweetwater Co., Wyoming.

Callospermophilus madrensis (Merriam, 1901). Proc. Wash. Acad. Sci., 3:563. Type locality: Sierra Madre, near Guadalupe y Calvo, Chihuahua, Mexico (7,000 feet [2,134 m] altitude).

Callospermophilus saturatus (Rhoads, 1895). Proc. Acad. Nat. Sci. Phila., 47:43. Type locality: Lake Kichelos [= Keechelus], Kittitas Co., Wash[ington]n, (elevation 8,000 feet [2,438 m]).

Etymology.—*Callospermophilus* is derived from the Greek *kallos* for beauty, *spermatos* for seed, and *phileo* for love (Jaeger 1955).

Diagnosis.—The species of *Callospermophilus* are extremely distinctive externally relative to other Marmotini, a fact captured in part in their common name—the golden-mantled ground squirrels. Overall dorsal coloration is pale brown to reddish brown, and in all 3 species, 2 paired, cream-colored longitudinal lines extend along the back from the base of each ear to the rump. These lines are highlighted on either side throughout their length by thinner lines of dark brown or blackish fur, creating a striking pattern that contrasts with the duller brown fur-tipping of the middorsum and the buff to gray coloration of the sides of the body (Fig. 9). The head and forequarters are usually set apart from the rest of the body by their bolder orange-brown or golden-brown hue. Overall coloration and patterning of *Callospermophilus* resemble those of *Ammospermophilus* (Fig. 6), but differ in that blackish lines fringe the pale longitudinal lines (lacking in *Ammospermophilus*), the pale longitudinal lines extend anteriorly to the base of the ear (extending anteriorly to base of shoulders in *Ammospermophilus*), and the head and forequarters are markedly redder than the rest of the body (generally not so in *Ammospermophilus*). Externally, these genera also are easily discriminated by body size (larger in *Callospermophilus*) and in the size of the pinna (comparatively much larger in *Callospermophilus*). Species of *Callospermophilus* are small to medium-sized (Howell 1938; Table 3), and have a somewhat hefty or plump, rather than slender, appearance, and longer and less glossy pelage than most other Marmotini. The tail

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is usually quite short, averaging less than half the head–body length, and the ears are proportionally large (Table 3). Females have 4 or 5 pairs of mammae (Moore 1961). The rather generalized skull features orthodont to slightly opisthodont incisors; relatively long and narrow incisive foramina; a rostrum of moderate length; and incisors, cheek teeth, and auditory bullae of moderate size, as reflected in part by the intermediate position of *Callospermophilus* along both CV1 and CV2 (Fig. 5) in discriminant function comparisons of the genera of Marmotini contrasted in this paper (Fig. 5). P3 is relatively small. Compared to other Marmotini, the postorbital processes are relatively long and comparatively very slender. The molars are relatively brachyodont with no abrupt change of direction in the parastyle ridge on M1 and M2, and the upper incisors are relatively slender, but comparatively broad, and not distinctly recurved (cf. Howell 1938).

Distribution.—The 3 species of *Callospermophilus* are distributed allopatrically in western North America, from southern Canada to northern Mexico (Fig. 8). *C. madrensis* is restricted to the states of Chihuahua and Durango in northwestern Mexico (Best and Thomas 1991; Servin et al. 1996). *C. saturatus* occurs in the Cascade Mountains of western Washington in the United States and southwestern British Columbia in Canada (Leung and Cheng 1997). *C. lateralis* is widely distributed in montane regions of western North America from central British Columbia to southern New Mexico and the Columbia River south to southern California and Nevada (Howell 1938).

Cytogenetics.—*Callospermophilus lateralis* has a diploid number of 42 and a fundamental number of 78 (Nadler 1966b). The karyotypes of *C. madrensis* and *C. saturatus* have not been determined.

Ecology.—*Callospermophilus* comprises 3 closely related allopatric species that occupy mountain meadows and surrounding habitats in western North America. They are all inhabitants of midelevation habitats from about 1,000 m to 4,000 m. *C. lateralis* occupies sagebrush, open woodlands, scrubby forest edge habitats, disturbed areas such as logged or burned sites, mountain meadows, and rocky slopes in the mountainous parts of its range, which includes much of the Rocky Mountains and Sierra Nevada (Armstrong 1999; Bartels and Thompson 1993). *C. saturatus* inhabits krumholtz and talus in alpine habitats, forests, meadows, and sagebrush habitats within its range (Trombulak 1988, 1999). *C. madrensis* is found in pine forests at elevations above 3,000 m, on slopes with vegetative cover consisting of *Juniperus*, *Populus*, *Pseudotsuga*, and *Pinus* (Valdéz Alarcón 2005; Best and Thomas 1991). *Callospermophilus* species are omnivorous, feeding on seeds, fruits, leaves, fungi, flowers, stems, insects (including eggs, larvae, pupae, and adults), small mammals, carrion, eggs, and nestling birds. They tend to be solitary, but will aggregate at food sources. They hibernate during the winter months, and are active throughout the daylight hours in the summer.

Comments.—The close phylogenetic relationship between the morphologically divergent genera *Callospermophilus* and *Otospermophilus* (Fig. 2) was illustrated by the molecular phylogenetic studies of Harrison et al. (2003) and Herron et al. (2004). The discriminant function analyses ally *Ictidomys* and *Callospermophilus* as craniometrically similar (Figs. 3 and 5), although they are not closely related among Marmotini. This result suggests an overall ecomorphological similarity in these 2 boldly patterned genera of Marmotini, which are parapatrically distributed across their geographic ranges (Figs. 8 and 11). The parapatric distributions of these genera are no doubt influenced by their distinct (but abutting) habitat associations. Despite their association in our craniometric analyses, *Ictidomys* and *Callospermophilus* can be immediately discriminated on the basis of qualitative craniodental characters (Bryant 1945; Howell 1938) and external traits, including pelage patterning, pinna size, and tail length (Table 3).

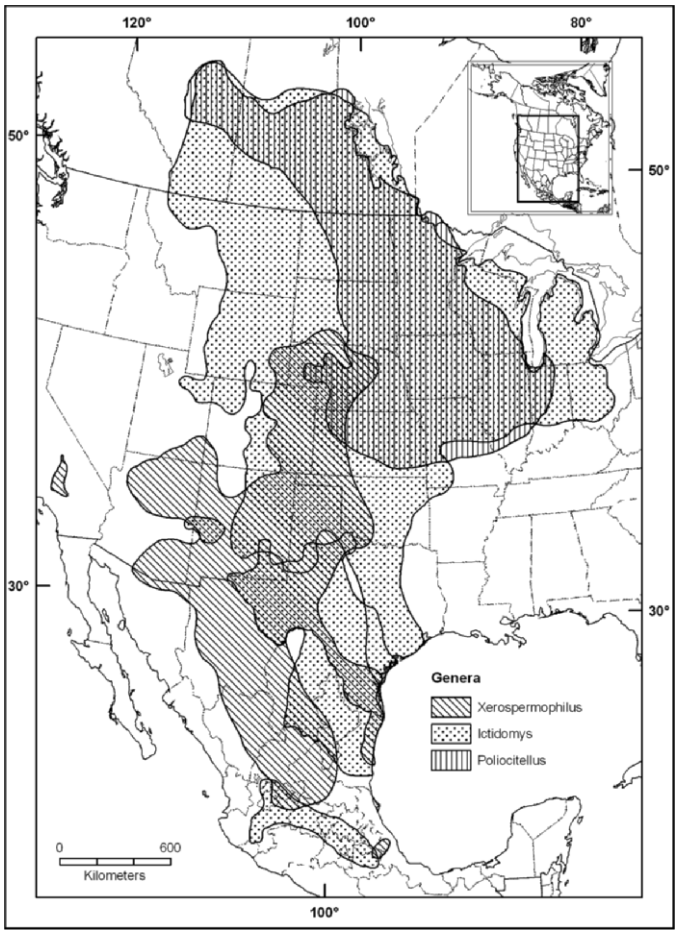


Fig. 11.—Geographic distributions of pygmy ground squirrels (*Xerospermophilus*), lined ground squirrels (*Ictidomys*), and Franklin's ground squirrel (*Poliocitellus*—after Hall 1981).

Genus *Spermophilus* F. Cuvier

Old World Ground Squirrels (Fig. 12)

Citellus Oken, 1816:842. Unavailable name; see International Commission on Zoological Nomenclature 1956.

Spermophilus F. Cuvier, 1825. Dents des Mammiferes, p. 255. Type species: *Mus citellus* Linnaeus, 1766:80.

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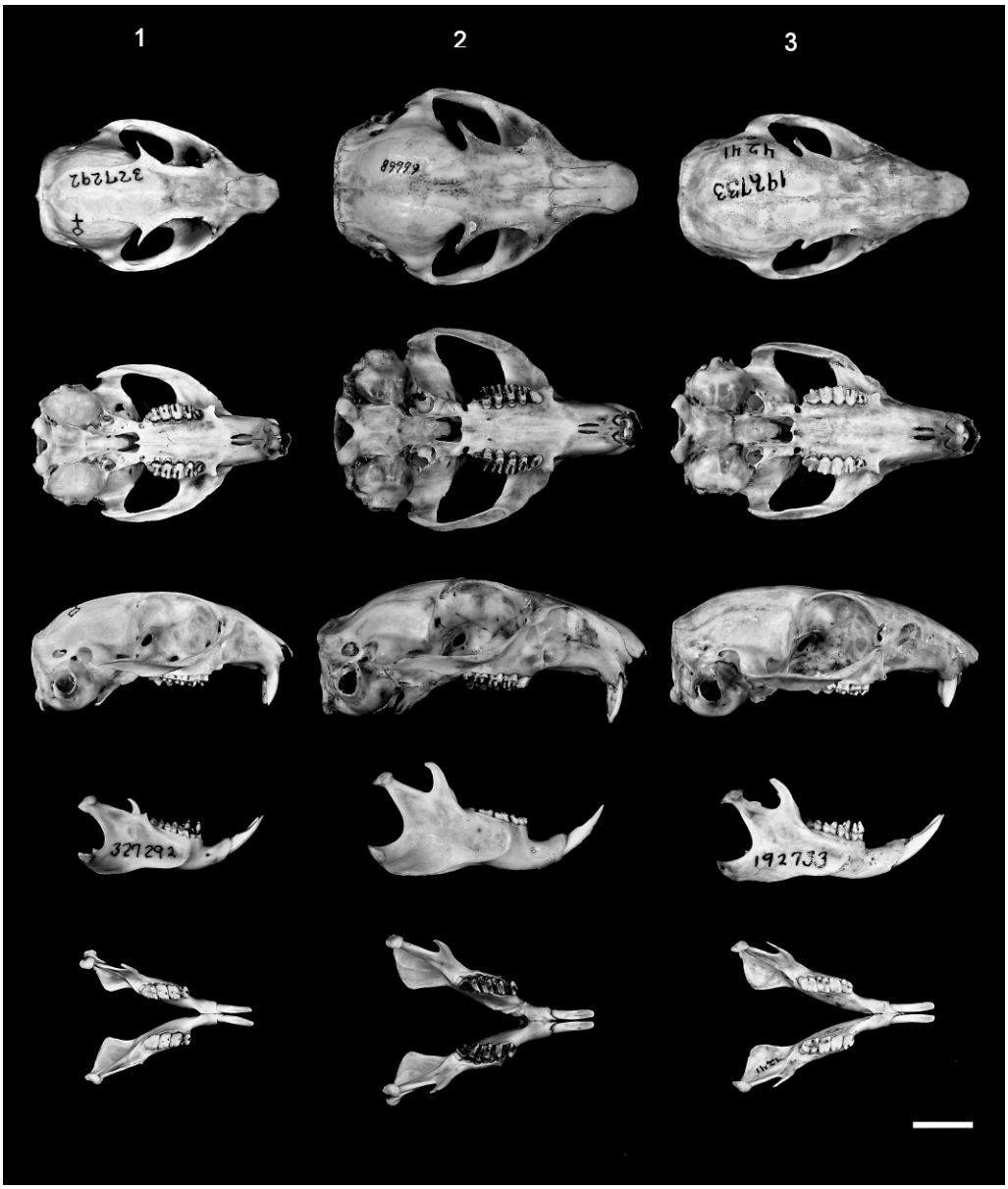


Fig. 12.—Representative skulls of the type species of *Spermophilus* (1), a North American species of *Urocitellus* (2), and the type species of *Poliocitellus* (3): 1) *S. citellus*, USNM 327292, adult female, Kagithane Dere, Istanbul, Turkey; 2) *U. columbianus*, USNM 66668, adult female, Nelson, British Columbia, Canada; 3) *P. franklinii*, USNM 192733, adult female, Brown's Valley, Minnesota, United States. From top to bottom: dorsal view of cranium, ventral view of cranium, lateral view of cranium, lateral view of mandible, and dorsal view of mandible. Scale bar = 10 mm.

Citillus Lichtenstein, 1830:plate 31. Incorrect subsequent spelling of *Citellus* Oken, 1816.

Spermatophilus Wagler, 1830:22. Incorrect subsequent spelling of *Spermophilus* F. Cuvier, 1825.

Colobotis Brandt, 1844:366. Bull. Cl. Phys.-Math. Acad. Imp. Sci. St. Pétersbourg, 2. Type species: *Arctomys fulvus* Lichtenstein, 1823:119.

Otocolobus Brandt, 1844:382. Apparent lapsus for *Colobotis* Brandt, 1844. Not *Otocolobus* Brandt, 1842 (a felid).

Colobates Milne-Edwards, 1874:157. Incorrect subsequent spelling of *Colobotis* Brandt, 1844.

Mamspermophilus Herrera, 1899:5. Unavailable name because it is based on zoological formulae (Palmer 1904).

Content.—The delineation of this genus embraces the Eurasian members of the genus *Spermophilus* as traditionally recognized (e.g., Corbet 1978; Ellerman and Morrison-Scott 1966; Gromov et al. 1965; Hoffmann et al. 1993; Ognev 1947; Thorington and Hoffmann 2005), with the exception of 2 species here classified in *Urocitellus*—*Urocitellus undulatus*, a species endemic to eastern Eurasia, and *U. parryii*, a mostly North American species that extends westward from Alaska into Siberia (the genus *Urocitellus* is otherwise restricted to North America). We follow Thorington and Hoffmann (2005), as supported and updated by Gündüz et al (2007a, 2007b), Ozkurt et al. (2007), Tsvirka et al. (2006b), Ermakov et al. (2006), and Nikol'skii et al. (2007), in recognizing 14 species

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of *Spermophilus*: *S. alashanicus* Büchner, 1888; *S. brevicauda* Brandt, 1843; *S. citellus* (Linnaeus, 1766); *S. dauricus* Brandt, 1843; *S. erythrogenys* Brandt, 1841; *S. fulvus* (Lichtenstein, 1823); *S. major* (Pallas, 1778); *S. pallidicauda* (Satunin, 1903); *S. pygmaeus* (Pallas, 1778) (now including *S. musicus* Ménétries, 1832, as a subspecies [see Ermakov et al. 2006; Nikol'skii et al. 2007]); *S. ralli* (Kuznetsov, 1948); *S. relictus* (Kashkarov, 1923); *S. suslicus* (Güldenstaedt, 1770); *S. taurensis* Gündüz, Jaarola, Tez, Yeniyurt, Polly, and Searle, 2007 (cf. Ozkurt et al. 2007; Gündüz et al. 2007b); and *S. xanthoprymnus* (Bennett, 1835). Thorington and Hoffmann (2005) provided lists of subspecies and synonyms, which we largely follow here. Type localities are cited largely based on the authority of Thorington and Hoffmann (2005), Ellerman and Morrison-Scott (1966), and Ognev (1947). Interspecific cytogenetic variability (see "*Cytogenetics*," below), apparent species-level paraphyly (e.g., Fig. 2), and the capacity for interspecific hybridization recorded across several species (Denisov 1961; Denisov and Smirnova 1976; Spiridonova et al. 2005; Tsvirka et al. 2006a) all indicate the need for continuing studies of alpha-level taxonomy in the genus.

Spermophilus alashanicus Büchner, 1888. Wiss. Res. Przewalski Cent. Asien Zool. I:(Säugeth.):11. Type locality: southern Ala Shan [China]. [*dilutus* (Formozov, 1929); *obscurus* Büchner, 1888; and *siccus* (G. M. Allen, 1925) are synonyms.]

Spermophilus brevicauda Brandt, 1843. Bull. Acad. Sci., St. Pétersbourg, p. 364. Type locality: habitat, ut videtur, in provincis Altaicis australiorbis versus lacum Balchasch [Zaisan Basin, Kazakhstan; see Ellerman and Morrison-Scott (1966)]. [*carruthersi* (Thomas, 1912); *intermedius* (Brandt, 1844); *ilensis* (Belyaev, 1945); *saryarka* (Selevin, 1937); and *selevini* (Argyropolu, 1941) are synonyms.]

Spermophilus citellus (Linnaeus, 1766). Syst. Nat., 12th ed., 1:80.

S. c. citellus (Linnaeus, 1766:80). Type locality: Austria; restricted by Martino and Martino (1940) to Wagram, Niederosterreich. [*citillus* (Pallas, 1779) is an incorrect subsequent spelling.]

S. c. gradojevici (Martino, 1929:76). Type locality: Djerdjelija [= Djevdjelija], Macedonia. [*karamani* (Martino, 1940) and *macedonicus* Fraguedakis-Tsolis and Ondrias, 1977, are synonyms.]

S. c. istricus (Calinescu, 1934:106). Type locality: Munteni, eastern Romania. [*laskarevi* (Martino, 1940) is a synonym.]

S. c. martinoi (Peshchev, 1955:290), Type locality: Rhodopen Mts., Bulgaria. [*balcanicus* (Markov, 1957) and *thracius* (Mursaloglu, 1964) are synonyms.]

Spermophilus dauricus Brandt, 1843:379. Type locality: circa Torei lacum exiccatum Dauuriae et ad Onon Bursa rivum (Torei-Nor (Lake), Chitinsk. Obl., Russia). [*mongolicus* (Milne-Edwards, 1867); *ramosus* (Thomas, 1909); *umbratus* (Thomas, 1908); and *yamashinae* (Kuroda, 1939) are synonyms.]

Spermophilus erythrogenys Brandt, 1841:43. Type locality: vicinity of Barnaul (Altaisk Krai, Russia). [*brunnescens* (Belyaev, 1943); *heptneri* (Vasil'eva, 1964); and *ungae* (Martino, 1923) are synonyms.]

Spermophilus fulvus (Lichtenstein, 1823). Naturh. Abh. Eversmann's Reise, p. 119.

S. f. fulvus (Lichtenstein, 1823:119). Type locality: near the Kuvandzhur River, east of Mugodzhary Mountains, north of Aral Sea [Kazakhstan]. [*concolor* (Fischer, 1829); *concolor* I. Geoffroy, 1831; *giganteus* (Fischer, 1829); *maximus* (Pallas, 1778); and *nanus* (Fischer, 1829) are synonyms.]

S. f. hypoleucos (Satunin, 1909:1). Type locality: Kutschan, northern Persia [Iran]. [*parthianus* (Thomas, 1915) is a synonym.]

S. f. oxianus (Thomas, 1915:422). Type locality: 50 mi. SW Bokhara, Russian Turkestan [Turkmenistan–Uzbekistan border]. [*nigrimontanus* (Antipin, 1942) is a synonym.]

Spermophilus major (Pallas, 1778:125). Type locality: steppe near Samara (Kuibyshev, Kuibyshevsk. Obl., Russia). [*argyropuloi* (Bazhanov, 1947); *rufescens* (Keyserling and Blasius, 1840); and *selevini* (Argyropulo, 1941) are synonyms.]

Spermophilus pallidicauda (Satunin, 1903). Ezheg. Zool. Muz., Akad. Nauk, St. Petersburg, 7:5–6. Type locality: vicinity of Lake Khulu-Nur, Ullyn Bulyk, Baidarak river, Mongolian Atlai [Mongolia, Gobi-Altai].

Spermophilus pygmaeus (Pallas, 1778). Nova Spec. Quad. Glir. Ord., p. 122.

S. p. brauneri (Martino, 1917:3). Type locality: Igren District, Ecaterinoslav Govt., Crimea [Ukraine]. [*kalabuchovi* (Ognev, 1937) is a synonym.]

S. p. herbicolus (Martino, 1916:278). Type locality: Aktyabinsk [= Aktyubinsk] steppes, northern Kirghizia, Russian Asia [Kazakhstan]. [*atricapilla* (Orlov, 1927) [not W. Bryant, 1889]; *herbidus* (Martino, 1915) [nomen nudum]; and *septentrionalis* (Obolenskij, 1927) are synonyms.]

S. p. mugosaricus (Lichtenstein, 1823:119). Type locality: Mugodshary Mountains [Kazakhstan]. [*kazakstanicus* (Goodwin, 1935) and *nikolskii* (Heptner, 1934) are synonyms.]

S. p. musicus Ménétries, 1832:21. Type locality: il habite le Caucase sur les montagnes le plus élevées et pas loin des nieges éternalles. Restricted to Ush-Kulan [Georgia] (see Ognev 1947). [*boehmii* (Krassovskii, 1932); *magisteri* (Heptner, 1948); *saturatus* (Ognev, 1947) [not Rhoads, 1895]; and *typicus* (Satunin, 1908) are synonyms.]

S. p. pygmaeus (Pallas, 1778:122). Type locality: "Maximos et paene dixerim monstrosos Citillós passim ad inferiorum laikum in campis squalidis." Restricted by Ognev (1947) to "lower reaches of the Ural River," Indersk [Kazakhstan]. [*arenicola* (Rall, 1935) [infrasubspecific, unavailable; not *arenicola* (A. H. Howell, 1938)]; *binominatus* (Ellerman, 1940); *ellermani* (Harris, 1944); *flavescens* (Pallas, 1779); *orlovi* (Ellerman, 1940); *pallidus* (Orlov and Fenyuk, 1927) [not J. A. Allen, 1874]; *planicola* (Satunin, 1909); *ralli*

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(Heptner, 1948) [replacement name for *arenicola* Rall, but apparently preoccupied by *ralli* Kuznetsov, 1948 (see discussion by Thorington and Hoffmann [2005])]; *satunini* (Sveridenko, 1922); and *saturatus* (Ognev, 1947) [not Rhoads, 1895] are synonyms.]

Spermophilus ralli (Kuznetsov, 1948). Zveri Kirgizii [Animals of Kirgiziya, Moscow Soc. of Naturalists], p. 39. Type locality: Tip iz kotlovinny Oz. Issyk-Kul' [basin of Lake Issyk-Kul, Kyrgyzstan]. The correct name for this species is in some doubt (Thorington and Hoffmann 2005:810).

Spermophilus relictus (Kashkarov, 1923). Trans. Turk. Sci. Soc., 1:185. Type locality: Kara-Bura Gorge and Kumysh-Tagh Gorge in the Talus Ala Tau [Talassk. Obl., Kyrgyzstan].

Spermophilus suslicus (Güldenstaedt, 1770). Nova Comm. Acad. Sci. Petropoli, 14:389.

S. s. boristhenicus (Pusanov, 1958:206). Type locality: between the rivers Dnestr and Bug, Ukraine.

S. s. guttatus (Pallas, 1770:566). Type locality: rivers Pyana and Sura, Russia. [*guttulatus* Schinz, 1845, and *leucopictus* (Dondorff, 1792) are synonyms.]

S. s. suslicus (Güldenstaedt, 1770:389). Type locality: in campis vastissimus tanaicensibus precipue urbes et Tambov [Voronezh area, Voronezhsk. Obl., Russia]. [*averini* (Migulin, 1927); *meridioccidentalis* (Migulin, 1927); *odessana* Nordmann, 1842; *ognevi* (Reshetnik, 1946); and *volhynensis* (Reshetnik, 1946) are synonyms.]

Spermophilus taurensis Gündüz, Jaarola, Tez, Yeniyurt, Polly, and Searle, 2007. Mol. Phylogenet. Evol., 43:929. Type locality: Akseki, Yarpuz (37°08′N, 31°53′E), 111 km E of the city of Antalya, Turkey. [*torosensis* Ozkurt et al., 2007, is a synonym.]

Spermophilus xanthoprymnus (Bennett, 1835). Proc. Zool. Soc. Lond., 1835:90. Type locality: Erzurum (Turkey). [*schmidti* (Satunin, 1908) is a synonym.]

Etymology.—*Spermophilus* is derived from the Greek *spermatos* for seed, and *phileo* for love (Jaeger 1955).

Diagnosis.—Species of *Spermophilus* lack the diagnostic pelage patterning or immediately discernible head–body to tail proportions that characterize members of the genera *Ammospermophilus*, *Notocitellus*, *Callospermophilus*, *Otospermophilus*, and *Ictidomys*, and differ from each of these genera in other ways described in our revision. Species of *Spermophilus* are cranially smaller than species of *Cynomys* and *Marmota*, and differ consistently from those phenetically distinctive genera in cranial shape and fur color patterning (Howell 1938). The pelage is usually longer and less sleek than in most other Marmotini. Most species of *Spermophilus* are larger than the species of *Xerospermophilus*, and have proportionally smaller bullae, longer and more parallel-sided rostra, and longer postorbital processes compared to members of that genus. Species of *Spermophilus* can be distinguished from *Poliocitellus* in having a proportionally wider braincase and zygomata, narrower interorbital region, heavier postorbital processes, shorter and narrower incisive foramina, less reduced P3, shorter and more parallel-sided rostra, more gracile and less opisthodont incisors, and a more elongate meatal portion of the auditory bulla (Fig. 12). Species of *Spermophilus* (sensu stricto) are morphologically most similar to species of *Urocitellus*, which they resemble especially in external morphology—a resemblance attested by their traditional classification together in the subgenus *Spermophilus* (sensu lato) (e.g., Hall 1981; Howell 1938; Thorington and Hoffmann 2005). Nevertheless, species of the subgenus *Spermophilus* (sensu stricto) can be firmly diagnosed against species of *Urocitellus* by a suite of consistent craniometric and qualitative cranial distinctions. In *Spermophilus*, the interorbital region is narrowed relative to the postorbital width, the braincase is somewhat higher-domed, the palate is proportionally wider between M1 and M1 but narrower between M3 and M3, the incisive foramina are wider, the maxillary diastema is proportionally longer, the mesopterygoid fossa is distinctively narrowed, the occipital condyles are less laterally expansive, the larger cheek teeth (molars and P4) are proportionally more massive but P3 is proportionally slightly smaller, the inflated portion of the auditory bulla is proportionally larger but the meatal portion is distinctly smaller, the mesopterygoid fossa is distinctively narrowed, and the upper incisor enamel is whitish to very pale yellow (more distinctly orange in *Urocitellus*). Many of these key differences are reflected in the clear multivariate discrimination between *Spermophilus* and *Urocitellus* in our craniometric analysis (Fig. 5; Table 2).

Distribution.—The geographic scope of the genus *Spermophilus*, as newly delineated here, is restricted to Eurasia. The distributional range of the genus (Fig. 13) is based on Ognev (1947), Thorington and Hoffmann (2005), Hoffmann and Smith (2008), and Zhang et al. (1997). *S. alashanicus* is endemic to north-central China (Ningxia, Gansu, Qinghai, and Nei Mongol). *S. brevicauda* occupies appropriate habitat south and westward along the Tien Shan Mountains to the vicinity of Almaty on both sides of the Kazakhstan–Chinese (Xinjiang) border. *S. pallidicauda* occurs in Mongolia and the adjacent Nei Mongol Autonomous Region and Xinjiang in China. *S. dauricus* ranges over Russian Transbaikalia, Mongolia, and northeastern China. *S. ralli* occupies the eastern Tien Shan Mountains and adjacent valleys of Xinjiang (China), Kyrgyzstan, and Kazakhstan, from the Terskii-Alatau in the southeast to the Ketmen in the northeast. *S. relictus* is found in the western Tien Shan Mountains of Kyrgyzstan and southeastern Kazakhstan. *S. erythrogenys* occurs in eastern Kazakhstan and southwestern Siberia. *S. fulvus* is broadly distributed from northern Kazakhstan south through Uzbekistan, western Tajikistan, and Turkmenistan to northern Iran, west to northern Afghanistan, and east into western Xinjiang in China (according to Thorington and Hoffmann [2005], although Hoffmann and Smith [2008] did not include *fulvus* in the Chinese fauna). *S. major* occurs in steppe habitats between the Volga and Irtysh rivers in Russia and northern Kazakhstan. *S. citellus* ranges from southeastern Germany, the Czech Republic, and southwestern Poland through southeastern Europe to European Turkey, Moldova, and western Ukraine. *S. pygmaeus* occurs from southwestern Ukraine to Georgia, northwestern Uzbeki-

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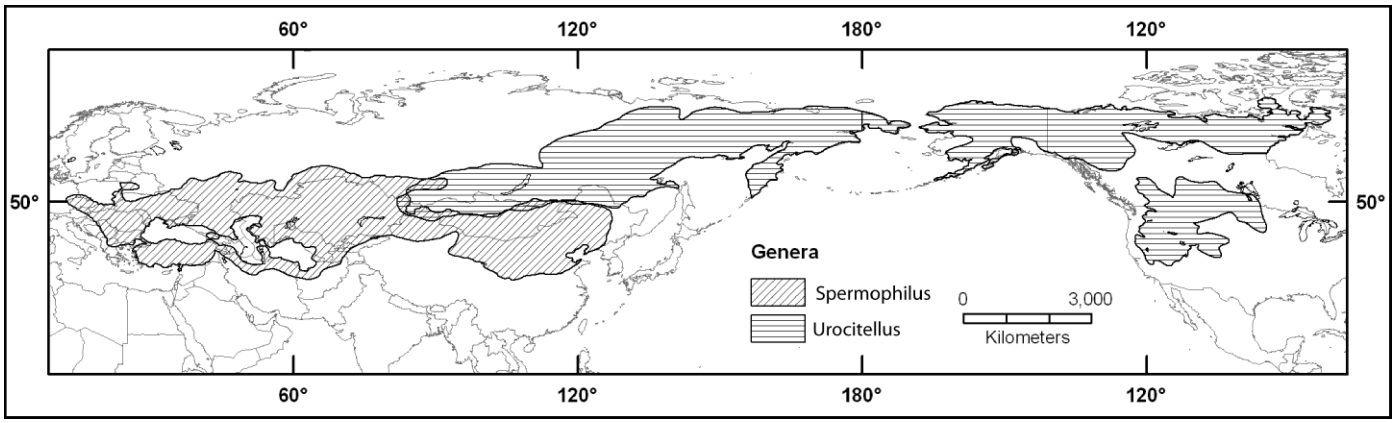


Fig. 13.—Geographic distributions of the Old World ground squirrels (*Spermophilus*) and Holarctic ground squirrels (*Urocitellus*—after Hall 1981; Hoffmann and Smith 2008; Ognev 1947).

stan, and Kazakhstan. *S. suslicus* ranges over the steppes of eastern and southern Europe, including Poland, eastern Romania, and the Ukraine north to the Oka River and east to the Volga River in Russia. *S. xanthoprymnus* occupies appropriate habitats in Transcaucasia, Turkey, Syria, and Israel. A newly described species, *S. taurensis*, occurs in the Taurus Mountains in southwestern Anatolia (Gündüz et al. 2007a; the newly described *S. torosensis* Ozkurt et al., 2007, is a synonym [Gündüz et al. 2007b]).

Cytogenetics.—Karyotypes for most species are recorded in the literature: *S. pallidicauda* (diploid number [2N] = 34), *S. suslicus* (2N = 34–36; fundamental number [FN] = 64–68), *S. brevicauda* (2N = 36; FN = 68), *S. dauricus* (2N = 36; FN = 68), *S. erythrogenys* (2N = 36; FN = 68), *S. fulvus* (2N = 36; FN = 68), *S. pygmaeus* (2N = 36; FN = 68), *S. ralli* (2N = 36; FN = 68), *S. relictus* (2N = 36; FN = 68), *S. alashanicus* (2N = 38; FN = 60), *S. citellus* (2N = 40; FN = 66–74), *S. xanthoprymnus* (2N = 40–42; FN = 64–78), and *S. taurensis* (2N = 40—Arslan 2005; Gündüz et al. 2007a; Liapunova and Vorontsov 1970; Robinson and Hoffmann 1975; Tsvirka et al. 2006a). Sporadic hybridization may occur where *S. major* occurs sympatrically with *S. fulvus*, *S. pygmaeus*, *S. erythrogenys*, or *S. brevicauda*, or where *S. pygmaeus* overlaps with *S. erythrogenys* or *S. suslicus* (Denisov 1961; Denisov and Smirnova 1976; Spiridonova et al. 2005; Thorington and Hoffmann 2005). A stable zone of hybridization apparently exists between *S. major* and *S. erythrogenys* in the Tobol–Ishim interfluvial area in Russia (Spiridonova et al. 2005). Tsvirka et al. (2006a) reported hybridization between *S. pallidicauda* and *S. alashanicus* at several localities in Mongolia.

Ecology.—The species of *Spermophilus* are primarily restricted to open plains, steppes, and tundra regions of the Palearctic. In forested regions, they are restricted to edge habitats. In the southern parts of the range, some species inhabit semidesert regions. Many of the species are strongly colonial, occupying suitable habitat over large areas (Hoffmann and Smith 2008; Ognev 1947). All are diurnal, and most are active in the morning once the sun warms the area slightly, then retreat to underground dens during the heat of the day, to reemerge late in the day for another feeding bout. Preferred food items include seeds, shoots, stems, leaves, tubers, and fruits of a wide variety of plains and grassland species (Hoffmann and Smith 2008; Ognev 1947). All of the northern species are hibernators, and in some areas the active season may be relatively short. In some areas they cause some depredation to agricultural crops. Several species of *Spermophilus* also are reservoirs for bubonic plague (Ognev 1947).

Comments.—The name *Citellus* Oken, 1816, was often used for this genus in the past. Hershkovitz (1949) argued successfully that *Citellus* Oken is not an available generic name and that *Spermophilus* F. Cuvier, 1825, is the appropriate name for the genus (International Commission on Zoological Nomenclature 1956). Gromov et al. (1965) retained *Colobotis* as a distinct Eurasian subgenus, containing *S. brevicauda*, *S. erythrogenys*, *S. fulvus*, and *S. major*. This subgeneric classification is not supported by phylogenetic analyses of cytochrome-*b* sequence data (Fig. 2; Harrison et al. 2003; Herron et al. 2004) and in the absence of more detailed studies, we do not advocate recognition of subgenera within *Spermophilus* (sensu stricto).

Genus *Ictidomys* J. A. Allen

Lined Ground Squirrels (Figs. 14 and 15)

Ictidomys J. A. Allen, 1877, in Coues and Allen, Monogr. N. Am. Rodentia, p. 821. Type species: *Sciurus tridecemlineatus* Mitchill, 1821.

Ictidomoides Mearns, 1907, Bull. U. S. Nat. Mus., 56:328. Type species: *Sciurus mexicanus* Erxleben, 1777.

Content.—We recognize 3 species in *Ictidomys*: *I. tridecemlineatus* (Mitchill, 1821), *I. parvidens* (Mearns, 1896), and *I. mexicanus* (Erxleben, 1777). Two other ground squirrel species, *Xerospermophilus spilosoma* (Bennett, 1833) and *Xerospermophilus perotensis* (Merriam, 1893), have traditionally been allied with *tridecemlineatus* and *mexicanus* in the subgenus *Ictidomys* (e.g., Cothran et al. 1977; Hall 1981; Howell 1938), but are not immediately related to those species (Harrison et al. 2003; Herron et al. 2004), and are here classified in *Xerospermophilus*. We suggest that the taxon

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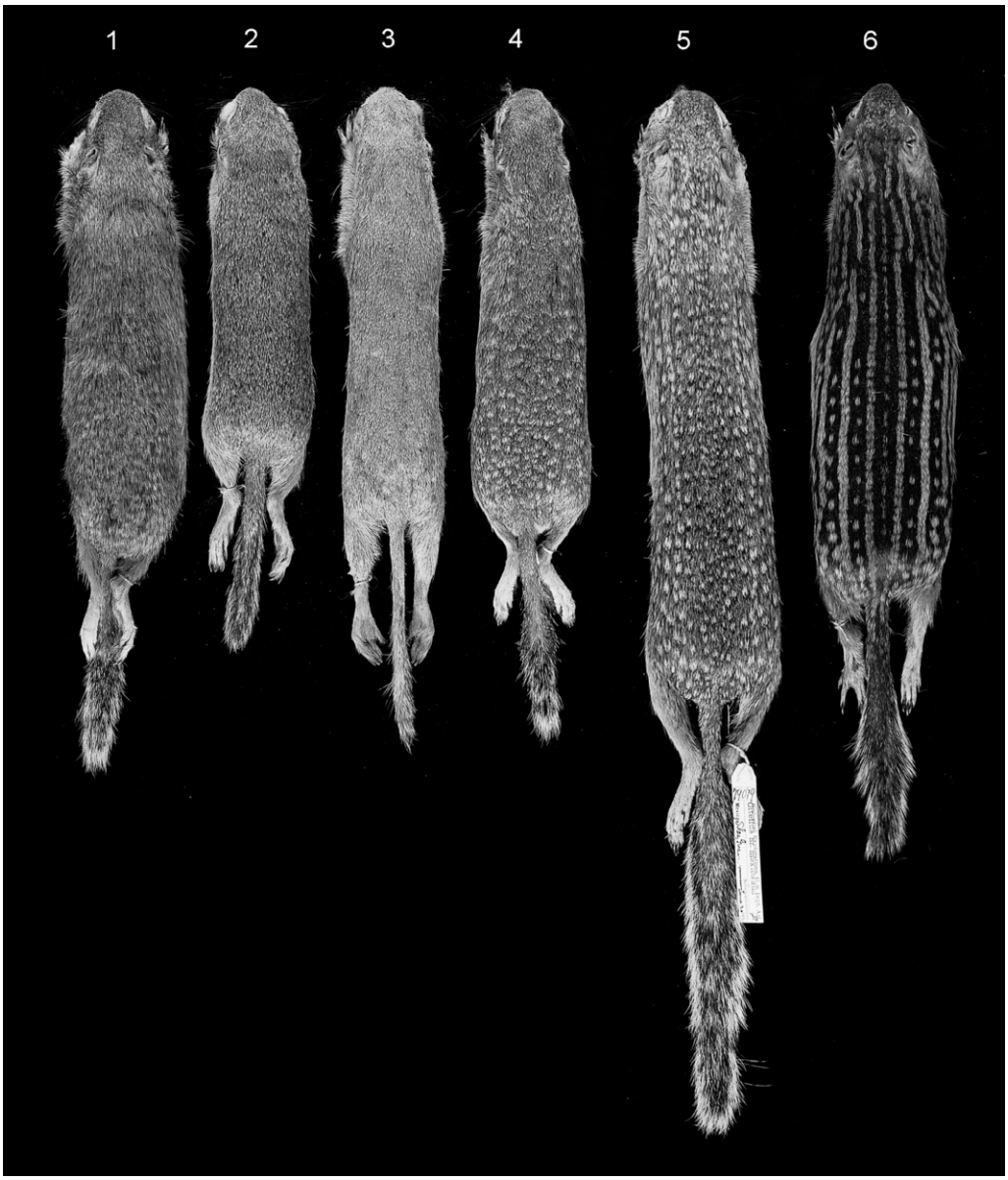


Fig. 14.—Representative skins (all adult females) of the species of *Xerospermophilus* (1–4) and *Ictidomys* (5, 6): 1) *X. perotensis*, USNM 54273, Perote, Veracruz, Mexico; 2) *X. mohavensis*, USNM 28743, Salt Wells Valley, California, United States; 3) *X. tereticaudus*, USNM 117343, Needles, California, United States; 4) *X. spilosoma*, USNM 78998, Chicalote, Aguascalientes, Mexico; 5) *I. mexicanus*, USNM 79019, Silas, Guanajuato, Mexico; 6) *I. tridecemlineatus*, USNM 250129, White County, Indiana, United States.

I. parvidens (Mearns, 1896), usually recognized as a subspecies of *I. mexicanus* (but markedly smaller than and disjunctly distributed relative to that taxon), deserves species-level recognition within *Ictidomys* (and see Fig. 2; Harrison et al. 2003; Herron et al. 2004). Subspecies and synonyms are as delineated by Thorington and Hoffmann (2005); and type localities, as given below, are cited largely based on the authority of Thorington and Hoffmann (2005) and Howell (1938).

Ictidomys mexicanus (Erxleben, 1777). Syst. Regn. Anim., 1:428. Type locality: ''In nova Hispania?'' Restricted by Mearns (1896:443) to Toluca, Mexico.

Ictidomys parvidens (Mearns, 1896). Proc. U. S. Nat. Mus., XVIII:443. Type locality: Fort Clark, Kinney Co., Texas.

Ictidomys tridecemlineatus (Mitchill, 1821). Med. Repos. (N.Y.), (n.s.), 6(21):248.

I. t. alleni (Merriam, 1898:71). Type locality: near head of Canyon Creek, 8000 ft., west slope Bighorn Mts., Wyoming.

I. t. arenicola (A. H. Howell, 1928:213). Type locality: Pendennis, Kansas.

I. t. blanca (Armstrong, 1971:533). Type locality: 5 mi. W Antonito, Conejos Co., Colorado.

I. t. hollisteri (V. Bailey, 1913:131). Type locality: Elk Valley, 8,000 ft., Mescalero Indian Reservation, Sacramento Mts., New Mexico.

I. t. monticola (A. H. Howell, 1928:214). Type locality: Marsh Lake, 9,000 ft., White Mts., Arizona.

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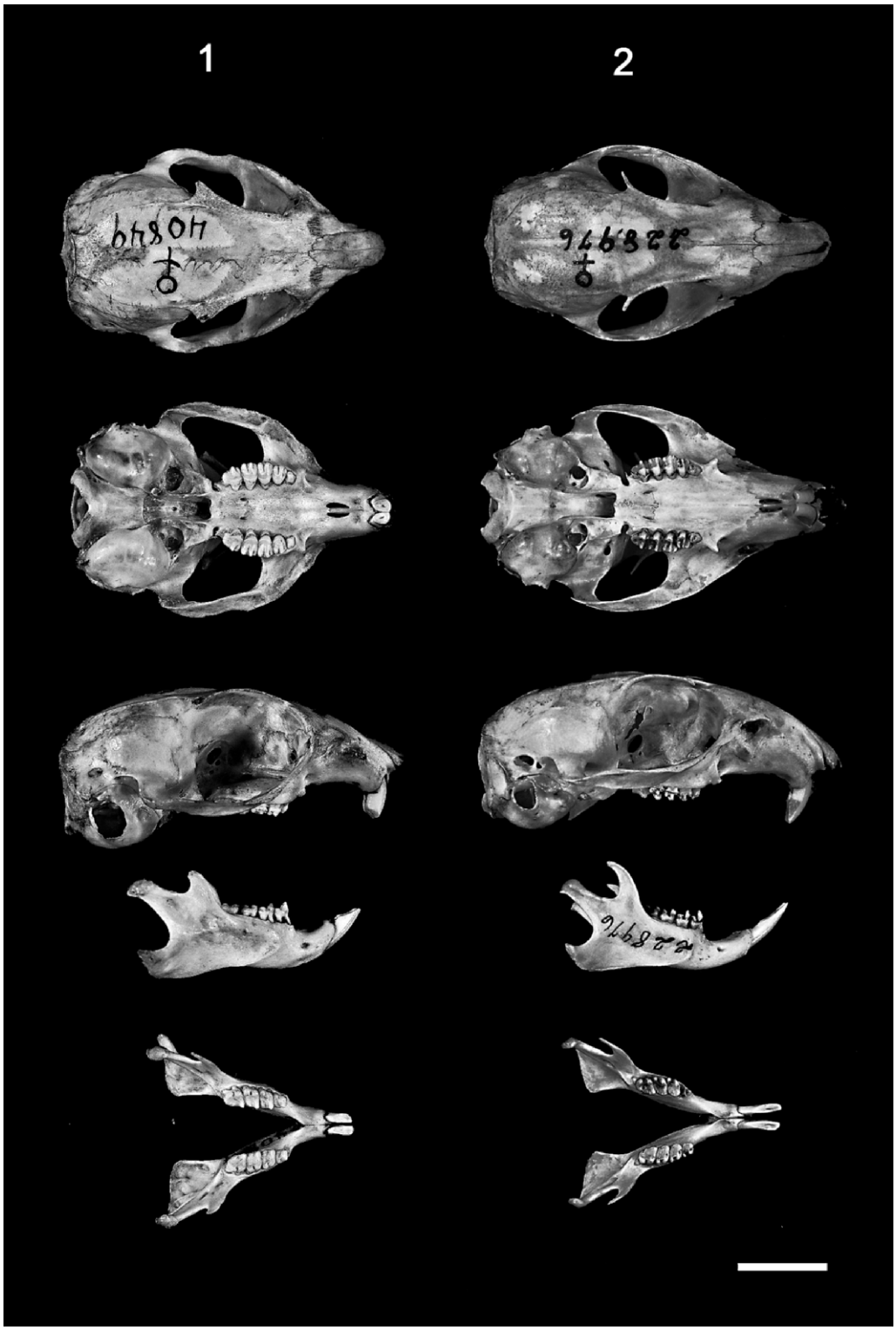


Fig. 15.—Representative skulls of the respective type species of *Xerospermophilus* (1) and *Ictidomys* (2): 1) *X. mohavensis*, USNM 40849, adult female, Salt Wells Valley, California, United States; 2) *I. tridecemlineatus*, USNM 228976, adult female, Rib Hill, Wisconsin, United States. From top to bottom: dorsal view of cranium, ventral view of cranium, lateral view of cranium, lateral view of mandible, and dorsal view of mandible. Scale bar = 10 mm.

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I. t. olivaceus (J. A. Allen, 1895:337). Type locality: Custer, Custer Co., Black Hills, South Dakota [misspelled as *olivaceous* by Hoffmann et al. (1993) and Thorington and Hoffmann (2005)].

I. t. pallidus (J. A. Allen, 1874:291). Type locality: plains of lower Yellowstone River, Montana.

I. t. parvus (J. A. Allen, 1895:337). Type locality: Uncompahgre Indian Reservation, 20 mi. northeast of Ouray, Uintah Co., Utah.

I. t. texensis (Merriam, 1898:71). Type locality: Gainesville, Cooke Co., Texas. [*badius* (Bangs, 1899) is a synonym.]

I. t. tridecemlineatus (Mitchill, 1821:248). Type locality: ''region bordering the sources of the river Mississippi''; restricted to ''Central Minnesota'' by Allen (1895:338). [*hoodii* (Sabine, 1822) is a synonym.]

Etymology.—The name *Ictidomys* is derived from the Greek words for weasel and mouse, referring to the slender, musteline body-form of these species.

Diagnosis.—Species of *Ictidomys* are easily identified on the basis of their dorsal pelage patterning. Dorsal spotting is more pronounced in the species of *Ictidomys* than in any other genus of Marmotini, such that well-defined linear rows of spots or stripes or both run anteroposteriorly along the length of the body, from the crown of the head to the proximal base of the tail. This pattern is fundamentally different from patterning in other Marmotini, including the golden-mantled ground squirrels (*Callospermophilus*), the other boldly marked genus formerly lumped within *Spermophilus*, and some populations of *X. perotensis* and *X. spilosoma*, in which pale dorsal spotting is much less pronounced and not clearly arranged in linear rows (Fig. 14). In *I. tridecemlineatus*, this patterning is boldly marked and the rows include continuous lines as well as rows of spots, whereas in *I. mexicanus* and *I. parvidens*, the dorsal spots are less distinct and form broken lines. The pelage is usually short and sleek. The external ears are relatively small and the tail is fringed terminally with pale hairs. The tail is more than half as long as the head–body (usually shorter in other smaller-bodied genera of Marmotini; Table 3; Fig. 14). The skull is distinctively narrowed and features stout and markedly opisthodont upper incisors, an elongate and distinctively downward-sloping rostrum, small cheek teeth separated from the incisors by a proportionally expansive diastema, delicate postorbital processes, a strikingly narrowed braincase, and relatively small and laterally compressed auditory bullae (Fig. 15). The metaloph of P4 is not continuous. The small molars are less hypsodont than in *Spermophilus* and *Urocitellus*, and the parastyle ridge on M1 and M2 joins the protocone with an abrupt change in direction (cf. Howell 1938). The species of *Ictidomys* also share similarities in bacular morphology (Bryant 1945).

Distribution.—*Ictidomys* occurs throughout the prairies, grasslands, and arid country of central North America (Fig. 11). *I. tridecemlineatus* is widely distributed across the Great Plains from central Texas and eastern New Mexico north to northeastern Utah, south-central Canada, and central Ohio. *I. parvidens* is found in the southern Great Plains from southeastern New Mexico through western Texas south into northeastern Mexico. *I. mexicanus* occurs in central Mexico (Hall 1981; Howell 1938; Streubel and Fitzgerald 1978b; Thorington and Hoffmann 2005; Young and Jones 1982). Zimmerman and Cothran (1976) used chromosomal and electrophoretic analyses to show that natural hybrids occur between *I. parvidens* and *I. tridecemlineatus* in areas where their ranges overlap in western Texas and southeastern New Mexico, although Cothran (1983) indicated that hybridization is localized and infrequent.

Cytogenetics.—Nadler (1962) reported cytogenetic characteristics of *I. tridecemlineatus* and *I. parvidens* and found both species to have the same diploid number (2N = 34). The fundamental number is 64 for *I. parvidens* and 62–64 for *I. tridecemlineatus* (Cothran and Honeycutt 1984).

Ecology.—*Ictidomys* comprises 3 ecologically similar species that are basically separated into northern and southern species. *I. mexicanus* and *I. parvidens* occur in grassland or arid habitats often in association with shrub species (Valdés Alarcón [sic] 2005), and prefer sandy or gravelly soils at elevations between 200 and 3,000 m (Young and Jones 1982). They are omnivorous, feeding on larval and adult insects, green plants, forbs, and grasses (Zimmerman 1999). The original habitat for *I. tridecemlineatus* was likely shortgrass prairie, especially open, sandy areas with patches of low grass (Whitaker 1999). However, all 3 species have adapted to live in disturbed habitats and can be found along roadsides, cemeteries, lawns, and golf courses throughout their range. In fact, *Ictidomys* has possibly extended its range with land clearance for agriculture (Streubel and Fitzgerald 1978b).

Comments.—As noted above, *X. perotensis* and *X. spilosoma* were previously included by most authors in *Ictidomys*, as influentially arranged by Howell (1938). Harrison et al. (2003) and Herron et al. (2004) demonstrated that these species are not closely related to the type species of *Ictidomys*, *I. tridecemlineatus* (and its close relatives *mexicanus* and *parvidens*) and instead demonstrated their close phylogenetic relationship with *X. mohavensis*, the type species of *Xerospermophilus*, and its immediate relative, *X. tereticaudus*. We suggest that this phylogenetic alliance is reflected also in craniometric and other morphological distinctions indicating an alliance between *perotensis/spilosoma* and *Xerospermophilus*, rather than *Ictidomys* (Figs. 5, 14, and 15). Some earlier studies also explored and queried the immediate association between *spilosoma/perotensis* and *tridecemlineatus/mexicanus/parvidens*, and their classification within a single subgenus (e.g., Bryant 1945; Nadler 1962; Nadler and Hughes 1966).

Genus *Poliocitellus* A. H. Howell

Franklin's Ground Squirrel (Fig. 12)

Poliocitellus A. H. Howell, 1938, N. Am. Fauna, 56:42. Type species: *Arctomys franklinii* Sabine, 1822:587.

Content.—*Poliocitellus* is monotypic, comprising only *P. franklinii* (Sabine, 1822).

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Poliocitellus franklinii (Sabine, 1822). Trans. Linn. Soc. Lond., 13:587. Type locality: none specified. Restricted by Preble (1908:165) to Carlton House, Saskatchewan, Canada.

Etymology.—The name *Poliocitellus* is derived from the Greek *polios*, meaning hoary or gray, and the Latin genus name for ground squirrels, *citellus* (Jaeger 1955).

Diagnosis.—*Poliocitellus franklinii* is a medium-sized member of the tribe Marmotini, larger than the species of *Xerospermophilus*, *Callospermophilus*, *Ictidomys*, and most *Spermophilus*, matching in size many species of *Urocitellus* as well as *Notocitellus annulatus*, but smaller than the species of *Otospermophilus*, *Cynomys*, and *Marmota*. The tail is bushy and subequal in length to the head–body, and the ears are short and rounded (Table 3). The dorsum is conspicuously infused with orange-brown tones, contrasting with the paler gray-buff head, rump, tail, and underside, and black banding throughout the dorsal pelages generates a grizzled overall appearance. Females have 5 or 6 pairs of teats (Moore 1961). The pelage is short and sleek. The skull of *Poliocitellus* differs from that of *Urocitellus* and *Spermophilus* in having a proportionally narrower braincase and zygomata, wider interorbital region, weaker postorbital processes, longer incisive foramina, a smaller P3, a longer and more tapering (rather than parallel-sided) rostrum, heavier and more opisthodont incisors, and a less laterally elongate meatal portion of the auditory bulla (Fig. 12). It differs further from *Spermophilus* in having more richly pigmented orange incisor enamel (much paler in *Spermophilus*). The skull of *Poliocitellus* closely resembles that of *Otospermophilus* in size and some qualitative features (Howell 1938), but differs especially from that genus in having broader nasals, longer incisive foramina, proportionally smaller bullae, and a larger, bicuspidate P3. The molars are relatively brachyodont, with the parastyle ridge on M1 and M2 rising to join the protocone without abrupt change in direction (cf. Howell 1938).

Distribution.—*Poliocitellus franklinii* is distributed widely over the northern Great Plains, extending from Alberta, Saskatchewan, and Manitoba in Canada south to Kansas and east to Illinois and Indiana in the United States (Hall 1981; Ostroff and Finck 2003; Thorington and Hoffmann 2005; Fig. 11).

Cytogenetics.—*Poliocitellus franklinii* has a diploid chromosome number of 42 and a fundamental number of 66 (Ostroff and Finck 2003).

Ecology.—*Poliocitellus* inhabits tall grasslands and tends to avoid shorter grass habitats. *P. franklinii* is often found along forest–grassland borders, marsh edges, and unmowed grass areas along highways and railroad tracks (Ostroff and Finck 2003). It also occurs in a narrow band of aspen parkland from the Canadian tallgrass prairie to central Alberta. This species tends to form small colonies that are occasionally larger in suitable habitat adjacent to wetter areas such as marshland. These ground squirrels hibernate for 7–8 months of the year, emerging around the 1st of May. This species is among the most carnivorous of the ground squirrels. These ground squirrels eat small mammals and birds, toads, and a variety of insects in addition to the more usual green plants, fruits, and seeds (Murie 1999).

Comments.—*Poliocitellus franklinii* was included in the subgenus *Ictidomys* by Allen (1877), and later isolated in a monotypic subgenus, *Poliocitellus*, erected by Howell (1938). Bryant (1945) considered *Poliocitellus* to be most closely related to *Callospermophilus* and *Otospermophilus*, but mitochondrial DNA (mtDNA) comparisons indicate that *Poliocitellus* is instead probably a member of a suprageneric clade that also includes *Ictidomys*, *Cynomys*, and *Xerospermophilus* (Harrison et al. 2003; Herron et al. 2004).

Genus *Xerospermophilus* Merriam

Pygmy Ground Squirrels (Figs. 14 and 15)

Xerospermophilus Merriam, 1892, Proc. Biol. Soc. Wash., 7:27. Type species: *Spermophilus mohavensis* Merriam, 1889:15.

Content.—Our definition of *Xerospermophilus* incorporates the 2 species previously classified in the subgenus *Xerospermophilus* (*tereticaudus* and *mohavensis*) as well as 2 species previously classified under the subgenus *Ictidomys* (*spilosoma* and *perotensis*). Four species of *Xerospermophilus* are thus recognized: *X. mohavensis* Merriam, 1889, *X. perotensis* Merriam, 1893, *X. spilosoma* Bennett, 1833, and *X. tereticaudus* Baird, 1858, with synonyms as delineated by Thorington and Hoffmann (2005). Type localities, as provided below, are cited largely based on the authority of Thorington and Hoffmann (2005) and Howell (1938). It is well established that *X. mohavensis* and *X. tereticaudus* form a species pair, as do *X. spilosoma* and *X. perotensis* (Ernest and Mares 1987; Hafner and Yates 1983; Herron et al. 2004; Howell 1938). Further research into species-level boundaries within the *spilosoma–perotensis* complex is warranted; *X. perotensis* may prove to be best classified as the southernmost subpopulation of *X. spilosoma* (Harrison et al. 2003; Herron et al. 2004; Howell 1938).

Xerospermophilus mohavensis (Merriam, 1889). N. Am. Fauna, 2:15. Type locality: Mohave River, California [USA]. Restricted by Grinnell and Dixon (1918) to near Rabbit Springs, about 15 mi. (24 km) E Hesperia, San Bernardino Co.

Xerospermophilus perotensis (Merriam, 1893). Proc. Biol. Soc. Wash., 8:131. Type locality: Perote, Veracruz, Mexico.

Xerospermophilus spilosoma (Bennett, 1833). Proc. Zool. Soc. Lond., 1833:40.

X. s. altiplanensis (Anderson, 1972:275). Type locality: 3 mi. ESE La Junta, Chihuahua, 6900 ft. [Mexico].

X. s. ammophilus (Hoffmeister, 1959:37). Type locality: 5½ mi. N Samalayuca, Chihuahua [Mexico].

X. s. annectens (Merriam, 1893:132). Type locality: The Tanks, 12 miles from Point Isabel, Padre Island, Texas.

X. s. bavicorensis (Anderson, 1972:276). Type locality: 2 mi. SW S. J. Babícora, Chihuahua, 7450 ft. [Mexico].

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X. s. cabrerai (Dalquest, 1951:106). Type locality: 10 km NNW Nuñez, San Luis Potosí, Mexico.
X. s. canescens (Merriam, 1890:38). Type locality: Willcox, Cochise Co., Arizona. [*arens* (V. Bailey, 1902); *macrospilotus* (Merriam, 1890); and *microspilotus* (Elliot, 1901) are synonyms.]
X. s. cryptospilotus (Merriam, 1890:57). Type locality: Tenebito [= Dinnebito] Wash, Painted Desert, Coconino Co, Arizona.
X. s. marginatus (V. Bailey, 1902:118). Type locality: Alpine, Texas. [*major* (Merriam, 1890) (preoccupied, not Pallas, 1778) is a synonym.]
X. s. obsoletus (Kennicott, 1863:157). Type locality: 50 miles west of Fort Kearney, Nebraska.
X. s. oricolus (Alvarez, 1962:123). Type locality: 1 mi. E La Pesca, Tamaulipas [Mexico].
X. s. pallescens (A. H. Howell, 1928:212). Type locality: La Ventura, Coahuila [Mexico].
X. s. pratensis (Merriam, 1890:55). Type locality: pine plateau at N foot San Francisco Mtn., Coconino Co., Arizona. [*obsidianus* (Merriam, 1890) is a synonym.]
X. s. spilosoma (Bennett, 1833:40). Type locality: Durango, México.

Xerospermophilus tereticaudus (Baird, 1858). Mammalia, in Repts. U. S. Expl. Surv., 8(1):315.

X. t. apricus (Huey, 1927:85). Type locality: Valle de la Trinidad, Baja California, Mexico (lat. 31°20′ north; long. 115°40′ west).
X. t. chlorus (Elliot, 1904:242). Type locality: Palm Springs, Riverside Co., California.
X. t. neglectus (Merriam, 1889:17). Type locality: Dolan Spring, 12 miles northwest of Chloride, Mohave Co., Arizona. [*arizonae* (Grinnell, 1918) and *sonoriensis* (Ward, 1891) are synonyms.]
X. t. tereticaudus (Baird, 1858:315). Type locality: [Old] Fort Yuma [Imperial Co., California]. [*eremonomus* (Elliot, 1904) and *vociferans* (Huey, 1926) are synonyms.]

Etymology.—*Xerospermophilus* is derived from the Greek *xeros*, meaning dry, *spermatos* for seed, and *phileo* for love (Jaeger 1955).

Diagnosis.—As a group, the species of *Xerospermophilus* are all relatively small-bodied (Fig. 14) and pale in coloration (buff to tan as the predominating color of the body). The pelage of 2 species (*X. mohavensis* and *X. tereticaudus*) is unmarked, but in some geographic populations of the other 2 species (*X. spilosoma* and *X. perotensis*) the dorsum is marked with distinctive pale flecking or spotting. It is primarily for this reason that these latter 2 species have in the past been allied subgenerically with the lined ground squirrels (*Ictidomys*—e.g., Howell 1938). However, unlike the species of *Ictidomys*, in *X. spilosoma* and *X. perotensis* the flecks or spots do not form clear anteroposteriorly directed linear rows or coalesce into stripes. The pelage is short and sleek, and the ears and tail are relatively short. Skulls of *Xerospermophilus* are rather delicately built, with opisthodont incisors, short incisive foramina, blunt or moderately long rostra, relatively narrow braincases, short postorbital processes, and proportionally large auditory bullae (Fig. 15). All species of *Xerospermophilus* depart from *Ictidomys* in having less precipitously downward-sloping rostra (when viewed in lateral profile), proportionally much larger bullae, relatively shorter tails, and hairier hind-foot soles (Figs. 14 and 15). The upper incisors are more gracile overall, and usually less markedly opisthodont in orientation, when compared to *Ictidomys* (Fig. 15). The molars are relatively brachyodont, with the parastyle ridge on M1 and M2 rising to join the protocone without an abrupt change in direction (cf. Howell 1938).

Distribution.—The distribution of *Xerospermophilus* embraces the deserts and grasslands of southern California and the southwestern United States, extending southward to northern and central Mexico (Hafner and Yates 1983; Howell 1938; Thorington and Hoffmann 2005; Fig. 11). *X. mohavensis* occupies a limited geographic range in the northwestern Mojave Desert of California. *X. tereticaudus* is found in deserts from southern Nevada through southeastern California and western Arizona, to northeastern Baja California and Sonora, Mexico (Ernest and Mares 1987). Hybridization between *X. mohavensis* and *X. tereticaudus* has been detected along the Mojave River, but the hybrid zone is apparently narrow and stable (Hafner 1992). *X. perotensis* occurs in Veracruz and Puebla in east-central Mexico (Best and Ceballos 1995; Valdéz and Ceballos 1997). *X. spilosoma* occurs in desert scrubland and grasslands from central Mexico north to southern and western Texas, throughout New Mexico to eastern and northwestern Arizona, and north from Texas to southwestern South Dakota (Streubel and Fitzgerald 1978a).

Cytogenetics.—All species in the genus have been karyotyped: *X. perotensis* and *X. spilosoma* (2N = 32; FN = 58); *X. tereticaudus* (2N = 36; FN = 68); and *X. mohavensis* (2N = 38; FN = 70) (Best and Ceballos 1995; Hafner and Yates 1983; Uribe-Alcocer et al. 1979).

Ecology.—*Xerospermophilus*, as the name implies, occupies arid, desert, or semidesert habitats. *X. mohavensis* (the Mohave ground squirrel) has a patchy distribution throughout its range in the Mojave Desert, where it occurs within a wide variety of arid habitats (Hafner 1999). Although omnivorous, Mohave ground squirrels tend to be short-term specialists on whatever appropriate food type is in abundance, be it seeds, leaves, or insect larvae (Best 1995c). *X. tereticaudus* (the round-tailed ground squirrel) lives in the Sonoran and Mojave deserts of the southwestern United States and typically occupies sandy, flat desert, sand dunes, and wash edges, but avoids rocky hills (Ernest 1999). Round-tailed ground squirrels feed primarily on green vegetation, augmented by seeds and insects seasonally (Ernest and Mares 1987). They occupy habitats that experience extremes of temperature from below freezing on winter nights to exceptionally hot summer days (Castillo 2005). *X. spilosoma* (the spotted ground squirrel) ranges throughout much of the arid and semiarid regions of the southwestern United States and Mexico (Young 1999). Spotted ground squirrels favor habitats with deep, sandy soils and scattered desert scrub vegetation (Streubel and Fitzgerald 1978a). They feed extensively on

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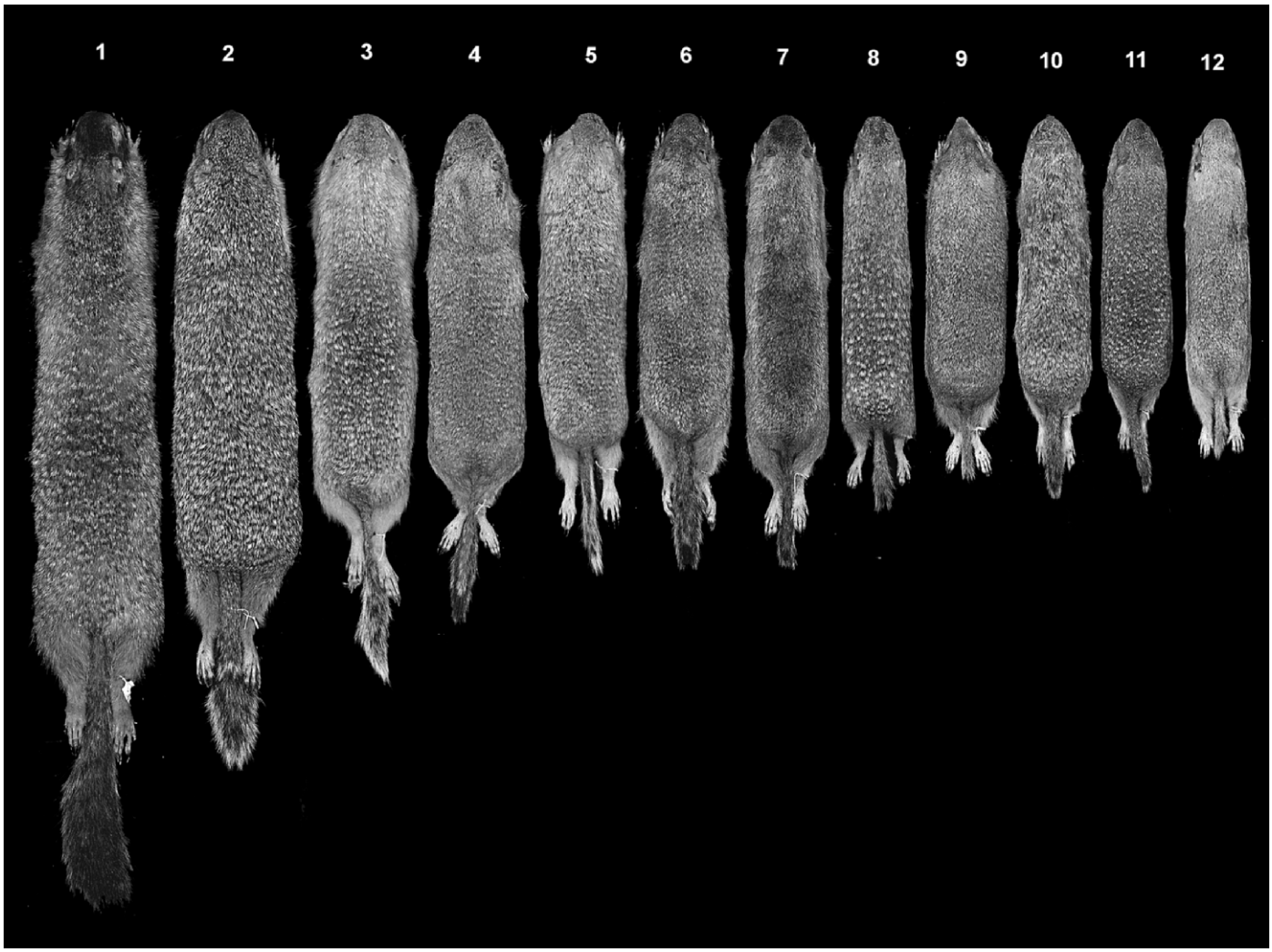


Fig. 16.—Representative skins (all adult females) of the species of *Urocitellus*, including the ''big-eared ground squirrels'' (1–7) and the ''small-eared ground squirrels'' (8–12): 1) *U. parryii*, USNM 128620, Yukon River, Alaska, United States; 2) *U. columbianus*, USNM 236182, Gifford, Washington, United States; 3) *U. undulatus*, USNM 175312, Altai Mountains, Siberia, Russia; 4) *U. elegans*, USNM 179821, Evanston, Wyoming, United States; 5) *U. richardsonii*, USNM 225873, Livingston, Montana, United States; 6) *U. armatus*, USNM 18830, Fort Bridger, Wyoming, United States; 7) *U. beldingi*, USNM 88285, McKinney, California, United States; 8) *U. washingtoni*, USNM 78578, Pendleton, Oregon, United States; 9) *U. townsendii*, USNM 235742, Ellensburg, Washington, United States; 10) *U. mollis*, USNM 201605, Payette, Idaho, United States; 11) *U. brunneus*, USNM 202410, Van Wyck, Idaho, United States; 12) *U. canus*, USNM 204835, Bend, Oregon, United States.

green vegetation, seeds, and a variety of insects, including ants (Aragón 2005). *X. perotensis* occupies sandy, semidesert habitat in the states of Veracruz and Puebla, Mexico (Valdéz Alarcón and Ceballos 2005a). This species also is found associated with agricultural areas within its range (Best and Ceballos 1995).

Comments.—Merriam (1892) established *Xerospermophilus* as a subgenus of *Spermophilus* with *X. mohavensis* as the type species. In his revision of the genus, Howell (1938) also included *X. tereticaudus* in this subgenus. Building on the molecular phylogenetic framework developed by Harrison et al. (2003) and Herron et al. (2004), here we transfer *X. spilosoma* and *X. perotensis* to *Xerospermophilus* for the 1st time, on the basis of their phylogenetic alliance with *X. mohavensis* and *X. tereticaudus*. This is an arrangement that appears to us to be solid on morphological grounds, because all species that we recognize in *Xerospermophilus* share similarities in body size, coloration, and qualitative and craniometric skull features to the exclusion of other Marmotini.

Molecular phylogenetic comparisons based on mtDNA (Harrison et al. 2003; Herron et al. 2004) identify *Xerospermophilus* as the sister genus to the prairie dogs (*Cynomys*), albeit with poor support. Species of *Xerospermophilus* depart from *Cynomys* markedly in body size and cranial anatomy, but resemble prairie dogs in their simple tan and buff coloration patterns. At least 1 species (*X. tereticaudus*) is semicolonial, maintaining individual burrows but also sharing others (Ernest and Mares 1987).

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Genus *Urocitellus* Obolenskij

Holarctic Ground Squirrels (Figs. 12 and 16)

Anisonyx Rafinesque, 1817, Am. Month. Mag., 2:45. Type species: *Anisonyx brachiura* Rafinesque [= *Arctomys columbianus* Ord] (preoccupied by a generic-level name in the insect order Coleoptera [*Anisonyx* Latreille, 1807]).

Urocitellus Obolenskij, 1927, C. R. Acad. Leningrad:188. Type species: *Spermophilus eversmanni* Brandt, 1841 [= *Urocitellus undulatus* (Pallas, 1778)].

Content.—The delineation of this genus corresponds to the North American and northeastern Eurasian members of the subgenus *Spermophilus* as traditionally recognized (e.g., Hall 1981; Howell 1938; Thorington and Hoffmann 2005). We recognize 12 species within *Urocitellus*: *U. armatus* Kennicott, 1863; *U. beldingi*, Merriam, 1888; *U. brunneus* (A. H. Howell, 1928); *U. canus* Merriam, 1898; *U. columbianus* (Ord, 1815); *U. elegans* Kennicott, 1863; *U. mollis* Kennicott, 1863; *U. parryii* (Richardson, 1825); *U. richardsonii* (Sabine, 1822); *U. townsendii* Bachman, 1839; *U. undulatus* (Pallas, 1778); and *U. washingtoni* (A. H. Howell, 1938), with synonyms and subspecies as delineated by Thorington and Hoffmann (2005). Type localities, as given below, are cited largely based on the authority of Thorington and Hoffmann (2005), Hall (1981), Ognev (1947), and Howell (1938).

Urocitellus armatus (Kennicott, 1863). Proc. Acad. Nat. Sci. Phila., 15:158. Type locality: in the foothills of the Uinta Mountains, near Fort Bridger, [Uinta Co.] Wyo[ming].

Urocitellus beldingi (Merriam, 1888). Ann. N. Y. Acad. Sci., 4:317.

U. b. beldingi (Merriam, 1888:317). Type locality: Donner, Placer Co., California.

U. b. creber (Hall, 1940:59). Type locality: Reese River Valley, 7 mi. N Austin, Lander Co., Nevada.

U. b. oregonus (Merriam, 1898:69). Type locality: Swan Lake Valley, Klamath Basin, Oregon.

Urocitellus brunneus (A. H. Howell, 1928). Proc. Biol. Soc. Wash., 41:211.

U. b. brunneus (A. H. Howell, 1928:211). Type locality: New Meadows, Adams Co., Idaho.

U. b. endemicus (Yensen, 1991:596). Type locality: Sand Hollow, 1 km E (up canyon from) OX Ranch headquarters; T9N, R4W, Sec. 7, NE ¼; 5.6 km N, 5.0 km E Payette, elev. 750 m, Payette Co., Idaho.

Urocitellus canus (Merriam, 1898). Proc. Biol. Soc. Wash., 12:70. Type locality: Antelope, Wasco County, Oregon. [*vigilis* (Merriam, 1913) is a synonym.]

Urocitellus columbianus (Ord, 1815). In Guthrie, New Geogr., Hist., Coml. Grammar, Phila., 2nd ed., 2:292.

U. c. columbianus (Ord, 1815:292). Type locality: between the forks of the Clearwater and Kooskooskie rivers (Idaho Co., Idaho, USA). [*albertae* (J. A. Allen, 1903); *brachiura* (Rafinesque, 1817); and *erythrogluteia* (Richardson, 1829) are synonyms.]

U. c. ruficaudus (A. H. Howell, 1928:212). Type locality: Wallowa Lake, Wallowa Co., Oregon.

Urocitellus elegans (Kennicott, 1863). Proc. Acad. Nat. Sci. Phila., 15:158.

U. e. aureus (Davis, 1939:177). Type locality: Double Springs, 16 mi. NE Dickey, Custer Co, Idaho.

U. e. elegans (Kennicott, 1863:158). Type locality: Fort Bridger, [Uinta Co., Wyoming, USA].

U. e. nevadensis (A. H. Howell, 1928:211). Type locality: Paradise, Humboldt Co., Nevada.

Urocitellus mollis (Kennicott, 1863). Proc. Acad. Nat. Sci. Phila., 15:157.

U. m. artemesiae (Merriam, 1913:137). Type locality: Birch Creek, about 10 mi. S Nicholia, Idaho. [*pessimus* (Merriam, 1913) is a synonym.]

U. m. idahoensis (Merriam, 1913:135). Type locality: Payette, Idaho.

U. m. mollis (Kennicott, 1863:157). Type locality: Camp Floyd [= Fairfield], Utah Co., Utah. [*leurodon* (Merriam, 1913); *stephensi* (Merriam, 1898); and *washoensis* (Merriam, 1913) are synonyms.]

Urocitellus parryii (Richardson, 1825). In Parry, Voy. Discovery Northwest Passage, Vol. 6, app. second voy., p. 316.

U. p. ablusus (Osgood, 1903:25). Type locality: Nushagak, Alaska. [*stonei* (J. A. Allen, 1903) is a synonym.]

U. p. kennicottii (Ross, 1861:434). Type locality; Fort Good Hope, Mackenzie [Northwest Territories, Canada]. [*barrowensis* (Merriam, 1900) and *beringensis* (Merriam, 1900) are synonyms.]

U. p. kodiacensis (J. A. Allen, 1874:292). Type locality: Kodiak Island, Alaska.

U. p. leucostictus (Brandt, 1844:379). Type locality: Okhotsk River, northeastern Siberia [Russia]. [*buxtoni* (J. A. Allen, 1903) and *tschuktschorum* (Chernyavskii, 1972) are synonyms.]

U. p. lyratus (Hall and Gilmore, 1932:396). Type locality: Iviktook Lagoon, about 35 mi. NW Northeast Cape (Howell 1938:101), St. Lawrence Island, Bering Sea, Alaska.

U. p. nebulicola (Osgood, 1903:26). Type locality: Nagai Island, Shumagin Islands, Alaska.

U. p. osgoodi (Merriam, 1900:18). Type locality; Fort Yukon, Alaska.

U. p. parryi (Richardson, 1825:316). Type locality: Five Hawser Bay, Lyon Inlet, Melville Peninsula [Hudson Bay, Nunavut Territories], Canada. [*phaeognatha* (Richardson, 1829) is a synonym.]

U. p. plesius (Osgood, 1900:29). Type locality: Bennett City, head of Lake Bennett, British Columbia [Canada].

U. p. stejnegeri (J. A. Allen, 1903:142). Type locality: near Petropavlovsk, Kamchatka [Russia]. [*brunniceps* (Kittlitz, 1858) [nomen nudum]; *coriakorum* (Portenko, 1963); and *janensis* (Ognev, 1937) are synonyms.]

Urocitellus richardsonii (Sabine, 1822). Trans. Linn. Soc. Lond., 13:589. Type locality: Carlton-House [Saskatchewan, Canada].

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Urocitellus townsendii (Bachman, 1839). J. Acad. Nat. Sci. Phila., 8:61.

U. t. nancyae (Nadler, 1968). Type locality: 5 mi. N Richland, Benton Co., Washington.

U. t. townsendii (Bachman, 1839:61). Type locality: On the Columbia River, about 300 miles [483 km] above its mouth. Restricted by A. H. Howell (1938:60, 62) to west bank of Walla Walla River near confluence with Columbia River [near Wallula, Walla Walla Co., Washington, USA]. [*yakimensis* (Merriam, 1898) is a synonym.]

Urocitellus undulatus (Pallas, 1778). Nova Spec. Quad. Glir. Ord., p. 122.

U. u. eversmanni (Brandt, 1841). Type locality: ''In montibus Altaicus'' [Altai Mountains, Russia–Kazakhstan–China–Mongolia border region]. [*altaicus* (Eversmann, 1841) is a synonym.]

U. u. jacutensis (Brandt, 1844). Type locality: Yakutsk District, eastern Siberia [Russia].

U. u. menzbieri (Ognev, 1937). Type locality: twenty-three kilometers from Blagoveschensk (near Ignatijevka), Upper Amur, eastern Siberia [Russia].

U. u. stramineus (Obolenskij, 1927). Type locality: Near Leman Gegen, northwestern Mongolia.

U. u. transbaikalicus (Obolenskij, 1927). Type locality: Lake Ivan, Transbaikalia [Russia]. [*intercedens* (Ognev, 1937) is a synonym.]

U. u. undulatus (Pallas, 1778:122). Type locality: Selenga River valley (Buryat ASSR, Russia). [*undulatum* (Pallas, 1779) is a synonym.]

Urocitellus washingtoni (A. H. Howell, 1938). N. Am. Fauna, 56:69. Type locality: Touchet, Walla Walla Co., Wash[ington]. (USA). [*loringi* (A. H. Howell, 1938) is a synonym.]

Etymology.—The name *Urocitellus* is derived from the Latin *uro* for tail and *citellus* for ground squirrel (Jaeger 1955).

Diagnosis.—Species of *Urocitellus* lack the diagnostic pelage patterning or immediately discernible head–body to tail proportions that characterize members of the genera *Ammospermophilus*, *Notocitellus*, *Callospermophilus*, *Otospermophilus*, and *Ictidomys*, and differ from each of these genera in other ways described above. Species of *Urocitellus* are cranially smaller than species of *Cynomys* and *Marmota*, and differ consistently from those distinctive genera in cranial shape and color patterning (Howell 1938). The pelage is usually longer and less sleek than in most other ground squirrels. Most species of *Urocitellus* are much larger than species of *Xerospermophilus*, and have proportionally much smaller auditory bullae, longer and more parallel-sided rostra, longer postorbital processes, and more gracile incisors compared to members of that genus (Figs. 12 and 15). Species of *Urocitellus* can be distinguished from species of *Poliocitellus* in having a proportionally broader braincase and zygomata, better-developed postorbital processes, shorter incisive foramina, a less reduced P3, shorter and more parallel-sided rostra, more gracile incisors, and a more laterally elongate meatal portion of the auditory bulla (Fig. 12). Species of *Urocitellus* are morphologically most similar to species of *Spermophilus* (sensu stricto), which they resemble especially in external morphology—a resemblance attested by their traditional classification within the same subgenus (e.g., Hall 1981; Howell 1938; Thorington and Hoffmann 2005). Nevertheless, species of *Urocitellus* can be reliably diagnosed against species of *Spermophilus* by a suite of craniometric and qualitative cranial distinctions: in *Urocitellus* (compared to *Spermophilus*), the interorbital width is proportionally wider, the larger cheek teeth (i.e., molars and P4) are proportionally less massive but P3 is proportionally heavier, the inflated portion of the auditory bulla is proportionally smaller but the meatal portion is more expansive laterally (i.e., forming a more elongate tube), the mesopterygoid fossa is not distinctively narrowed, and the upper incisor enamel is more distinctly orange (whitish to very pale yellow in *Spermophilus*; Fig. 12), among other distinctions (see ''*Diagnosis*'' of *Spermophilus*, above; Fig. 12). Many of these key differences are reflected in the clear multivariate discrimination between *Urocitellus* and *Spermophilus* in our craniometric analyses (Fig. 5).

Distribution.—*Urocitellus* is disjunctly distributed in central and northeastern Asia, in far northern North America, and in southern Canada and the western contiguous United States (Fig. 13).

The distribution of the ''*columbianus* species-group'' (see below) encompasses much of western North America west of the Mississippi and north of Mexico, as well as Canada, Alaska, and eastern Eurasia at higher latitudes (Fig. 13). *U. undulatus* is the only member of this genus that is exclusively Eurasian in distribution, ranging through eastern Kazakhstan, southern Siberia, Transbaikalia (Russia), and northern Mongolia to the provinces of Heilungjiang and Xinjiang in China. *U. parryii* is Holarctic in distribution, extending from northeastern Russia through northwestern Alaska to northwestern Canada. The distribution of *U. columbianus* extends from southeastern British Columbia and western Alberta in Canada south to northeastern Oregon, central Idaho, and central Montana in the United States. *U. richardsonii* occurs in the northern Great Plains in southern Alberta, Saskatchewan, and Manitoba in Canada south into Montana, North Dakota, northeastern South Dakota, western Minnesota, and northwestern Iowa in the United States. *U. elegans* extends from southeastern Oregon, southern Idaho, southwestern Montana, and northeastern Nevada, south to central Colorado and western Nebraska. *U. armatus* ranges from south-central Utah to southern Montana and southeastern Idaho to western Wyoming. *U. beldingi* occurs from eastern Oregon and southwestern Idaho south to northeastern California, and east to northern Nevada and northwestern Utah.

The distribution of the ''*townsendii* species-group'' (see below) is centered in the intermountain west, including the Great Basin, Snake River Plain, and the Columbia Plateau and Basin. It encompasses primarily the states of Washington, Oregon, Idaho, Nevada, and Utah, extending marginally into eastern California (Hall 1981; Thorington and Hoffmann 2005; Yensen 1991). *U. townsendii* occurs in southeastern Washington. *U. washingtoni* is found in southeastern Washington and northeastern Oregon. *U. mollis* occurs in in southeastern

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TABLE 4.—Recognized species within the 8 genera of ground squirrels previously included within the genus *Spermophilus* (sensu lato).

Scientific name	Common name
Genus *Notocitellus*	Tropical ground squirrels
N. adocetus	Tropical ground squirrel
N. annulatus	Ring-tailed ground squirrel
Genus *Otospermophilus*	Rock squirrels
O. atricapillus	Baja California rock squirrel
O. beecheyi	California ground squirrel
O. variegatus	Rock squirrel
Genus *Callospermophilus*	Golden-mantled ground squirrels
C. lateralis	Golden-mantled ground squirrel
C. madrensis	Sierra Madre ground squirrel
C. saturatus	Cascade golden-mantled ground squirrel
Genus *Spermophilus*	Old World ground squirrels
S. alashanicus	Alashan ground squirrel
S. brevicauda	Brandt's ground squirrel
S. citellus	European ground squirrel
S. dauricus	Daurian ground squirrel
S. erythrogenys	Red-cheeked ground squirrel
S. fulvus	Yellow ground squirrel
S. major	Russet ground squirrel
S. pallidicauda	Pallid ground squirrel
S. pygmaeus	Little ground squirrel
S. ralli	Tien Shan ground squirrel
S. relictus	Relict ground squirrel
S. suslicus	Speckled ground squirrel
S. taurensis	Taurus ground squirrel
S. xanthoprymnus	Asia Minor ground squirrel
Genus *Ictidomys*	Lined ground squirrels
I. mexicanus	Mexican ground squirrel
I. parvidens	Rio Grande ground squirrel
I. tridemcemlineatus	Thirteen-lined ground squirrel
Genus *Poliocitellus*	Franklin's ground squirrels
P. franklinii	Franklin's ground squirrel
Genus *Xerospermophilus*	Pygmy ground squirrels
X. mohavensis	Mohave ground squirrel
X. perotensis	Perote ground squirrel
X. spilosoma	Spotted ground squirrel
X. tereticaudus	Round-tailed ground squirrel
Genus *Urocitellus*	Holarctic ground squirrels
U. armatus	Uinta ground squirrel
U. beldingi	Belding's ground squirrel
U. brunneus	Idaho ground squirrel
U. canus	Merriam's ground squirrel
U. columbianus	Columbian ground squirrel
U. elegans	Wyoming ground squirrel
U. mollis	Piute ground squirrel
U. parryii	Arctic ground squirrel
U. richardsonii	Richardson's ground squirrel
U. townsendii	Townsend's ground squirre
U. undulatus	Long-tailed ground squirrel
U. washingtoni	Washington ground squirrel

Oregon and western Idaho, extending southward through most of Nevada, east-central California, and western Utah. *U. canus* ranges from central Oregon to extreme west-central Idaho and northwestern Nevada. *U. brunneus* has the smallest range of any ground squirrel, comprising multiple populations isolated by habitat fragmentation in west-central Idaho.

Cytogenetics.—Karyotypes have been reported for all species in the genus (Liapunova and Vorontsov 1970; Nadler 1966a; Nadler et al. 1973, 1984; Yensen and Sherman 1997): *U. beldingi* (2N = 30; FN = 56), *U. columbianus* (2N = 32; FN = 60), *U. elegans* (2N = 34; FN = 64), *U. armatus* (2N = 34; FN = 64), *U. undulatus* (2N = 34; FN = 64), *U. parryii* (2N = 34; FN = 68), *U. richardsonii* (2N = 36; FN = 64), *U. washingtoni* (2N = 36; FN = 66), *U. townsendii* (2N = 36; FN = 68), *U. brunneus* (2N = 38; FN = 66), *U. mollis* (2N = 38; FN = 66), and *U. canus* (2N = 46; FN = 66).

Ecology.—*Urocitellus* occupies a variety of montane and steppe habitats in northern North America, with 1 Holarctic species (*U. parryii*) and 1 restricted to Eurasia (*U. undulatus*). *U. undulatus* occurs in thinly wooded savannahs and grassy steppes bordering the Gobi Desert, and northward from there it occupies bushy terrain among oak and beech groves, alpine meadows, and riparian areas (Ognev 1947). *U. parryii* inhabits arctic montane and tundra habitats farther north than any other ground squirrel (Iwen 1999). *U. beldingi* is a colonial species and is generally considered to be a high-elevation species common in the central Sierra Mountains (Bachman 1999; Jenkins and Eshelman 1984). *U. columbianus* also is colonial and lives in a variety of habitats including alpine meadows, mountain slopes, and agricultural lands (Elliott and Flinders 1991). Colonies inhabit alpine meadows and can be observed along roadsides and cultivated land where soil conditions are appropriate (Elliott 1999). *U. brunneus* is patchily distributed in mountain meadows and habitats dominated by sagebrush and bunch grasses (Yensen and Sherman 1997, 1999). *U. richardsonii* inhabits shortgrass prairies in south-central Canada and the adjacent north-central United States (Durrant and Hansen 1954; Michener 1999; Michener and Koeppl 1985). *U. elegans* is a colonial species limited by *U. armatus* to sagebrush and grass-covered valleys and foothills where the ranges of these 2 species overlap in Montana and Idaho (Zegers 1984). *U. elegans* is also found living in brushy and grass-covered areas of northern Nevada (Smith 1999). *U. armatus* inhabits sagebrush and grassy mountain meadows in Montana, Wyoming, Utah, and Idaho (Davis 1939; Eshelman and Sonnemann 2000; Yensen 1999b). *U. washingtoni* lives in perennial grassland habitats at low elevation in the Columbia River basin in southeastern Washington and northeastern Oregon (Rickart and Yensen 1991; Yensen 1999a). *U. townsendii* is typically found in sagebrush and agricultural habitats within its range (Rickart 1987, 1999c). *U. canus* occurs in sagebrush, juniper, and greasewood habitats, in grasslands and pastures, and in agricultural lands (Rickart 1999a). *U. mollis* is widely distributed throughout the Great Basin and along the Snake River in Idaho in desert and sagebrush habitats (Rickart 1999b).

Comments.—Morphological considerations (Bryant 1945; Davis 1939; Howell 1938), chromosomal complements (Liapunova and Vorontsov 1970; Nadler 1966a; Yensen and Sherman 1997), and some molecular analyses (Fig. 2; Harrison et al. 2003; Herron et al. 2004) suggest that there are 2

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distinctive species-groups within *Urocitellus*: the larger (HBL = 217–495 mm), long-footed (HF = 40–68 mm), proportionally longer-tailed species (32–46% of HBL) of the ''*columbianus* species-group'' (2N = 30–36), including *U. parryii*, *U. columbianus*, *U. undulatus*, *U. elegans*, *U. richardsonii*, *U. armatus*, and *U. beldingi* (Fig. 16: 1–7); and the smaller (HBL = 167–271 mm), short-footed (HF = 27–39 mm), proportionally shorter-tailed (23–32% of HBL) members of the ''*townsendii* species-group'' (2N = 36–46), incorporating *U. washingtoni*, *U. townsendii*, *U. mollis*, *U. brunneus*, and *U. canus* (Fig. 16: 8–12). These groups are sometimes referred to as the ''big-eared ground squirrels'' and ''small-eared ground squirrels,'' respectively (Davis 1939; Nadler 1966a; Robinson and Hoffmann 1975). Should additional molecular comparisons confirm their trenchant divergence and respective monophyly, in the future it may be worthwhile to classify these species-groups in distinct subgenera (there is currently no available generic-level name for the ''*townsendii* species-group'').

Discussion

The revision of generic boundaries for Holarctic ground squirrels (Table 4) better illustrates evolutionary relationships above the species level, and should set the scene for new avenues of research in ground squirrel comparative biology. The various North American and Eurasian ground squirrel genera differ in their geographic distributions, habitat associations, and in salient morphological aspects such as body size, skull conformation, limb and tail proportions, and mammary number, all of which pose standing questions about their differential biology. This new classificatory framework encourages fresh reviews to portray ground squirrel comparative biology in the light of these revised boundaries, including aspects of fossil history and nomenclature, and dating of divergence events (Black 1963, 1972; Goodwin and Hayes 1994; Harrison et al. 2003); anatomy and physiology (Bryant 1945, Hudson and Deavers 1973, 1976; Iwaniuk 2001; Miller et al. 1989; Russell et al. 2001); reproductive biology (Hayssen 2008a, 2008b; Mandier and Gouat 1996; Millesi et al. 1998, 1999; Moore 1961); behavioral and evolutionary ecology (Armitage 1981; Blumstein and Armitage 1998; Hare and Murie 2007; Livoreil and Baudoin 1996; Murie and Michener 1984; Yahyaoui et al. 1995); and conservation biology and management (Van Horne 2007)—tasks well beyond the scope of our cursory overview.

Our efforts in this paper have been focused on delineating a generic-level taxonomy of ground squirrels in the tribe Marmotini consistent with the evolutionary history of the group and establishing an appropriate nomenclature applicable to generic-level clades. We note that a great deal of systematic revisionary work on the tribe Marmotini is still needed. Higher-level relationships among genera remain to be conclusively established with solid resolution (Fig. 2), a goal probably best approached with studies of nuclear DNA sequence data. Species boundaries in some genera (especially *Spermophilus* and *Urocitellus*) require further detailed consideration, ideally combining morphological, cytogenetic, and mitochondrial and nuclear sequence data to demonstrate or reject reproductive isolation between nominal taxa that are closely related or difficult to distinguish.

Finally, renewed attention should be focused on the applicability of ground squirrel subspecies categorizations. Although subspecies are commonly and formally employed to characterize geographic variation in most genera (e.g., Ellerman and Morrison-Scott 1966; Hall 1981; Howell 1938; Ognev 1947; Thorington and Hoffmann 2005), detailed morphological and genetic studies are needed to evaluate whether currently recognized trinomial distinctions profitably characterize salient and consistent patterns of geographic variation among ground squirrels. We hope that our revision will set the stage for tackling these and other problems with renewed vigor.

Acknowledgments

This paper is dedicated to our friend and colleague Robert S. Hoffmann. We gratefully acknowledge the logistical support, collection access, and advice provided by staff and researchers in the Division of Mammals at USNM, including R. Hoffmann, R. Thorington, S. Peurach, R. Fisher, L. Gordon, C. Ludwig, H. Kafka, J. Whatton, J. Jacobs, D. Schmidt, A. Gardner, M. Carleton, L. Emmons, J. Mead, and C. Potter. We also thank M. Herron and an anonymous reviewer for helpful reviews of our manuscript, J. Matson for helpful discussion, and B. Gunnell, E. Robinson, M. Wells, and J. van Veldhuizen for assistance in recurating the USNM ground squirrel collection. This project was supported by a Postdoctoral Fellowship from the Smithsonian Institution to KMH and funding from Colby College and the Oak Foundation provided to FRC during a sabbatical leave.

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Submitted 24 September 2007. Accepted 22 July 2008.

Associate Editor was Burton K. Lim.

APPENDIX I

Specimens measured for craniometric analyses (all adult females) are listed by scientific name, specimen (skull) number, and locality. All specimens are at USNM.

Ammospermophilus.—193304, *A. harrisii*, United States, Arizona: Dolan's Spring; 193305, *A. harrisii*, United States, Arizona: Dolan's Spring; 146786, *A. insularis*, Mexico, Baja California Sur: Isla Espiritu Santo; 120449, *A. interpres*, United States, New Mexico: San Andreas Mts. opposite Bear Canyon; 131835, *A. interpres*, United States, New Mexico: Manzano Mts.; 135831, *A. leucurus*, United States, California: Mojave; 135839, *A. leucurus*, United States, California: Mojave; 140310, *A. nelsoni*, United States, California: Coalinga; 137939, *A. nelsoni*, United States, California: Coalinga. (NB: Subsequent to the completion of our analyses, Alvarez-Castañeda [2007] has argued convincingly that *insularis* should be recognized as a subspecies of *A. leucurus*.)

Notocitellus.—126139, *N. adocetus*, Mexico, Michoacán: La Salada; 126114, *N. adocetus*, Mexico, Michoacán: La Salada; 44585, *N. annulatus*, Mexico, Colima: Manzanillo; 44582, *N. annulatus*, Mexico, Colima: Manzanillo.

Otospermophilus.—139748, *O. atricapillus*, Mexico, Baja California Sur: San Ignacio; 139744, *O. atricapillus*, Mexico, Baja California Sur: San Ignacio; 57567, *O. beecheyi*, United States, California: Wilson's Peak; 57566, *O. beecheyi*, United States, California: Wilson's Peak; 45577, *O. variegatus*, Mexico, Jalisco: Zapotlan; 45575, *O. variegatus*, Mexico, Jalisco: Zapotlan.

Callospermophilus.—159752, *C. lateralis*, United States, Wyoming: Laramie Mountains; 25604, *C. lateralis*, United States, Wyoming: Bridger Pass; 95348, *C. madrensis*, Mexico, Chihuahua: Sierra Madre Mountains, 7,000 feet; 95368, *C. madrensis*, Mexico, Chihuahua: Sierra Madre Mountains, 7,000 feet; 233148, *C. saturatus*, United States, Washington: Mt. Rainier; 233147, *C. saturatus*, United States, Washington: Mt. Rainier.

Spermophilus.—248096, *S. citellus*, Hungary: Szegedin; 248103, *S. citellus*, Hungary: Szegedin; 155202, *S. dauricus*, China: ''Kansu''; 155201, *S. dauricus*, China: ''Kansu''; 251638, *S. erythrogenys*, Russia: Siberian Federal District, Altai Krai, Zmeinogorski, Novenkoie; 254949, *S. erythrogenys*, Russia: Siberian Federal District, Tomsk, Kuznetsk, Kuznetsk Steppe; 251637, *S. pygmaeus*, Ukraine: Ekaterinoslav (= Dnipropetrovsk), Tgren; 251636, *S. pygmaeus*, Ukraine: Ekaterinoslav (= Dnipropetrovsk), Tgren; 251634, *S. suslicus*, Belarus: Minsk; 251635, *S. suslicus*, Belarus: Minsk; 327282, *S. xanthoprymnus*, Turkey: Talas, Kayseri; 327281, *S. xanthoprymnus*, Turkey: Talas, Kayseri.

Ictidomys.—46200, *I. mexicanus*, Mexico, Jalisco: Atemajac; 46199, *I. mexicanus*, Mexico, Jalisco: Atemajac; 30816, *I. parvidens*, United States, Texas: Altuda; 40345, *I. parvidens*, United States, Texas: Carrizo; 314658, *I. tridecemlineatus*, United States, Indiana: Amboy; 314657, *I. tridecemlineatus*, United States, Indiana: Middletown.

Poliocitellus.—192733, *P. franklinii*, United States, Minnesota: Brown's Valley; 192734, *P. franklinii*, United States, Minnesota: Brown's Valley.

Cynomys.—47205, *C. gunnisoni*, United States, Colorado: Fort Garland; 47204, *C. gunnisoni*, United States, Colorado: Fort Garland; 54118, *C. leucurus*, United States, Colorado: Grand Junction; 54107, *C. leucurus*, United States, Colorado: Grand Junction; 246659, *C. ludovicianus*, United States, Colorado: Conifer, 7,300 feet; 191444, *C. ludovicianus*, United States, Colorado: Boulder County; 433834, *C. mexicanus*, Mexico, Coahuila, La Ventura, 5,600 feet; 433837, *C. mexicanus*, Mexico, Coahuila, La Ventura, 5,600 feet; 158060, *C. parvidens*, United States, Utah: Buckskin Valley; 158986, *C. parvidens*, United States, Utah: Buckskin Valley.

Xerospermophilus.—192756, *X. mohavensis*, United States, California: Mojave River; 192754, *X. mohavensis*, United States, California: Mojave River; 54272, *X. perotensis*, Mexico, Veracruz: Perote; 54273, *X. perotensis*, Mexico, Veracruz: Perote; 79006, *X. spilosoma*, Mexico, Aguascalientes: Chicalote; 79005, *X. spilosoma*, Mexico, Aguascalientes: Chicalote; 117343, *X. tereticaudus*, United States, California: Needles, 500 feet; 117344, *X. tereticaudus*, United States, California: Needles, 500 feet.

Urocitellus.—25565, *U. armatus*, United States, Wyoming: Fort Bridger; 25583, *U. armatus*, United States, Wyoming: Fort Bridger; 192683, *U. beldingi*, United States, California: Donner; 192688, *U. beldingi*, United States, California: Donner; 202410, *U. brunneus*, United States, Idaho: Van Wyck; 265912, *U. brunneus*, United States, Idaho: Round Valley; 227286, *U. canus*, United States, Oregon: Narrows; 227287, *U. canus*, United States, Oregon: Narrows; 66674, *U. columbianus*, Canada, British Columbia: Nelson; 66668, *U. columbianus*, Canada, British Columbia: Nelson; 179379, *U. elegans*, United States, Idaho: Dickey; 179378, *U. elegans*, United States, Idaho: Dickey; 181159, *U. mollis*, United States, Idaho: Nampa; 181160, *U. mollis*, United States, Idaho: Nampa; 180895, *U. parryii*, Canada, Northwest Territories: Mackenzie District, Artillery Lake; 180893, *U. parryii*, Canada, Northwest Territories: Mackenzie District, Kasba Lake; 398315, *U. richardsonii*, United States, Minnesota: 5 miles south and 6 miles east of Louisburg; 398240, *U. richardsonii*, United States, Minnesota: 5 miles south and 6 miles east of Louisburg; 235736, *U. townsendii*, United States, Washington: Yakima; 235737, *U. townsendii*, United States, Washington: Yakima; 175272, *U. undulatus*, Russia, Altai: Tchegan–Burgazi Pass; 175284, *U. undulatus*, Russia, Altai: Tchegan–Burgazi Pass; 398330, *U. washingtoni*, United States, Washington: 0.5 miles south and 0.5 miles east of Lind; 398318, *U. washingtoni*, United States, Washington: 0.5 miles south and 0.5 miles east of Lind.

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