

JOURNAL OF MAMMALOGY

Published Quarterly by the American Society of Mammalogists

VOL. 72

13 FEBRUARY 1991

No. 1

EVOLUTIONARY GENETICS AND ZOOGEOGRAPHY OF MIDDLE AMERICAN POCKET GOPHERS, GENUS *ORTHOGEOMYS*

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ABSTRACT.—Average levels of protein heterozygosity ($\bar{H} = 0.015$) and polymorphism ($P = 0.048$) in 13 populations of Middle American pocket gophers (*Orthogeomys*, subgenus *Macrogeomys*) are unusually low by mammalian standards. This low genetic variability is attributed to subdivision of populations into small, isolated demes. Locus-by-locus and parsimony analyses of the protein data generally support retention of the currently recognized species of *Macrogeomys*. Phylogenetic analysis reveals that gross morphological similarities among highland pocket gophers (large body size and long pelage) and among lowland species (small body size and short pelage) are the result of evolutionary convergence. Most speciation in *Macrogeomys* appears to have occurred during the past 4.5×10^6 years, presumably influenced by Quaternary sea-level fluctuations that resulted in repeated fragmentations of geographic ranges of the species.

Pocket gophers (Geomyidae) of Middle America and Mexico south of the central Mexican plateau are referred to the genus *Orthogeomys*. This genus, as revised by Russell (1968), includes three extant subgenera: *Orthogeomys* (two species), inhabiting western Mexico from Jalisco south into El Salvador and Honduras; *Heterogeomys* (two species), distributed throughout eastern Mexico from Tamaulipas south to northern Honduras; and *Macrogeomys* (six species), known from Nicaragua, Costa Rica, Panama, and Colombia.

Interspecific variation in body size and diversity of dorsal-pelage markings in the subgenus *Macrogeomys* far exceeds that seen in any other geomyid taxon (Hafner and Hafner, 1987). The three smaller species (*O. cherriei*, *O. matagalpae*, and *O. underwoodi*; 150–300 g body mass) are restricted to seasonally dry, low-elevation habitats. The three larger species (*O. cavator*, *O. dariensis*, and *O. heterodus*; 500–950 g) usually are found at higher elevations, but also are known from humid lowlands. The large species are unicolored dorsally and show a high degree of background (soil-color) matching characteristic of most other species of pocket gophers. The small species of the subgenus *Macrogeomys* are unique among geomyids by virtue of conspicuous dorsal-pelage markings: a white headspot in *O. cherriei* and *O. matagalpae*, and a white belt in *O. underwoodi* (Hafner and Hafner, 1987).

Hafner (1982) used electrophoretic and immunological evidence to demonstrate that the genus *Orthogeomys* is monophyletic, and that the three subgenera of *Orthogeomys* are genetically well differentiated from one another (average Rogers', 1972, genetic distance approximately 0.5). The electrophoretic evidence also indicated that the subgenera *Orthogeomys* and *Heterogeomys* are sister taxa within the genus *Orthogeomys* (Hafner, 1982).

Herein, protein-electrophoretic evidence is used to investigate evolutionary relationships among pocket gophers of the subgenus *Macrogeomys*. Results are interpreted in a zoogeographic framework of relevant geologic and paleoclimatic events that may have influenced phylogenesis in the group.

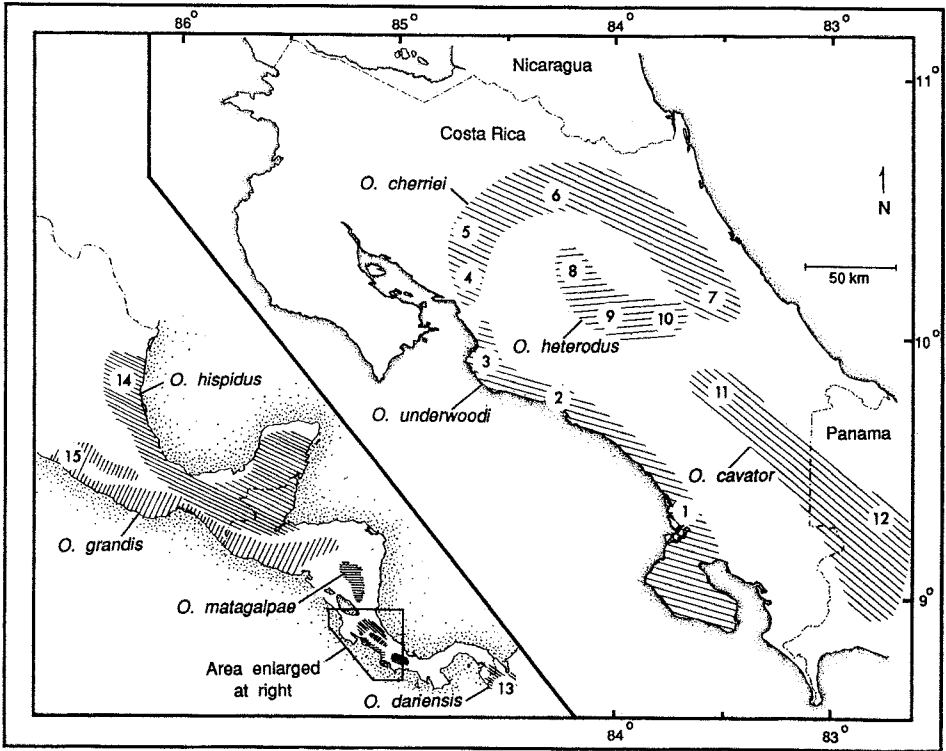


FIG. 1.—Collecting localities of pocket gophers (*Orthogeomys*) analyzed in the present study. Precise localities are described in the Appendix. Geographic ranges are indicated for all species in the subgenus *Macrogeomys*, *O. hispidus* (subgenus *Heterogeomys*), and *O. grandis* (subgenus *Orthogeomys*).

MATERIALS AND METHODS

Thirty-nine specimens representing five of the six species in the subgenus *Macrogeomys* (Appendix I; Fig. 1) were analyzed for electrophoretically detectable protein variation. Two specimens of the subgenus *Orthogeomys* and one of the subgenus *Heterogeomys* served as outgroups in the protein analysis.

Homogenates of kidney were prepared according to the methods of Selander et al. (1971). Procedures for horizontal starch-gel electrophoresis followed Selander et al. (1971) and Harris and Hopkinson (1976), as modified by Patton and Yang (1977). Thirty-five presumptive gene loci were examined: malate dehydrogenase (MDH-1, MDH-2, Enzyme Commission No. 1.1.1.37); glycerol-3-phosphate dehydrogenase (GPD, 1.1.1.8); lactate dehydrogenase (LDH-1, LDH-2, 1.1.1.27); isocitrate dehydrogenase (ICD-1, ICD-2, 1.1.1.42); alcohol (octanol) dehydrogenase (ADH, 1.1.1.1); sorbitol dehydrogenase (SORDH, 1.1.1.14); malic enzyme (ME, 1.1.1.40); 6-phosphogluconate dehydrogenase (6-PGD, 1.1.1.44); glutamate dehydrogenase (GDH, 1.4.1.2); glutamate-oxaloacetate transaminase (GOT-1, GOT-2, 2.6.1.1); mannose phosphate isomerase (MPI, 5.3.1.8); glucosephosphate isomerase (GPI, 5.3.1.9); superoxide dismutase (SOD-1, SOD-2, 1.15.1.1); peptidase (PEP-A, leucyl-alanine; PEP-B, leucyl-glycyl-glycine; PEP-C, leucyl-alanine; 3.4.11); leucine aminopeptidase (LAP, 3.4.11—Selander et al., 1971); adenylate kinase (AK, 2.7.4.3); creatine kinase (CK-1, CK-2, 2.7.3.2); hexokinase (HK, 2.7.1.1); glucose-6-phosphate dehydrogenase (G6PD, 1.1.1.49); glutamate-pyruvate transaminase (GPT, 2.6.1.2); fumarate hydratase (FUM, 4.2.1.2); aconitate hydratase (ACON-1, ACON-2, 4.2.1.3); phosphoglucomutase (PGM, 2.7.5.1); 4-methylumbelliferyl acetate esterase (EST-D, 3.1.1.1); hemoglobin (HB); albumin (ALB). Alleles at each locus were separated in at least two buffer systems following the protocol of Hafner (1982), and alleles were designated alphabetically. Rogers' (1972) coefficient of genetic similarity (*S*) and Nei's (1978) genetic distance measure (*D*) were calculated using the BIOSYS-1 program of Swofford and Selander (1981).

Protein data were analyzed cladistically by use of the locus-by-locus approach (Baverstock et al., 1979; Honeycutt and Williams, 1982) as modified by Hafner et al. (1987). This method focuses on phylogenetically

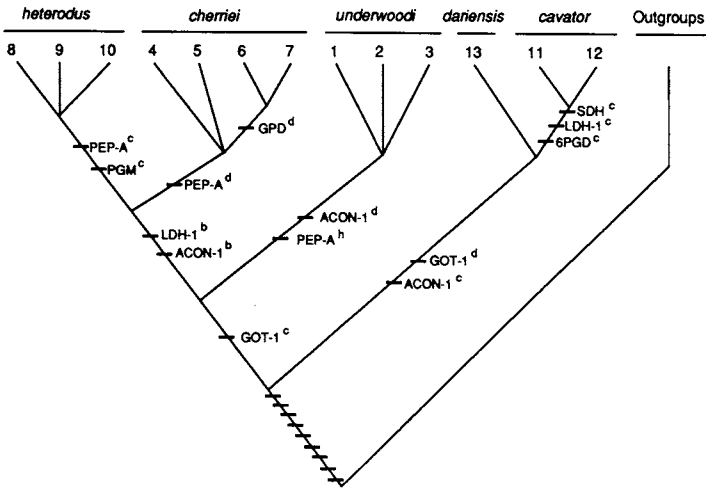


FIG. 2.—Relationships among 13 populations of pocket gophers of the subgenus *Macrogeomys* (genus *Orthogeomys*) based on a locus-by-locus analysis of allelic data. Members of the subgenera *Heterogeomys* and *Orthogeomys* were used as outgroups in the analysis. Alleles that define subgroups are unique to those groups and present in all members of the group, with the exception of ACON-1^b (absent in populations 5, 6, 8, and 9) and LDH-1^b (absent in population 7). Alleles that define the subgenus *Macrogeomys* (base of tree) are ICD-2^d, SOD-2^b, ALB^b, ACON-2^b, ME-2^d, CK-1^c, GDH^d, ADH^c, and GPT^b. Taxon numbers refer to collecting localities (Appendix I, Fig. 1).

informative portions of the data set by eliminating autapomorphic alleles (alleles unique to individual taxa) and symplesiomorphic alleles (ingroup alleles shared with outgroup taxa). Patterns of allele sharing in the resulting data set are used to cluster taxa, with conflicting components depicted as unresolved polychotomies. Data also were subjected to a parsimony analysis by use of the PAUP (Phylogenetic Analysis Using Parsimony) program of Swofford (1985), with specimens of the subgenera *Heterogeomys* and *Orthogeomys* designated as outgroups.

RESULTS

Intrapopulation variability.—Levels of intrapopulation genetic variability in Central American *Orthogeomys* are lower than levels typically measured in mammalian populations (Nevo, 1978). Genetic polymorphism (P) in *Orthogeomys* populations with $n \geq 3$ ranged from zero to 16.1%, with an unweighted mean polymorphism of 4.8%. In contrast, Nevo (1978) reported an unweighted average P of 14.7% for 46 species of mammals. Genetic polymorphism in *Orthogeomys* also is lower than that typically measured in populations of other geomyid species. For example, Nevo et al. (1974) found 23.5% average polymorphism in 10 populations of *Thomomys talpoides*, Patton and Yang (1977) reported $P = 33.4\%$ for 23 populations of *Thomomys bottae*, and Penney and Zimmerman (1976) reported $P = 14.0\%$ for 12 populations of *Geomys bursarius*. Among geomyids, only species in the genera *Cratogeomys* (Honeycutt and Williams, 1982) and *Zygozemys* (Hafner and Barkley, 1984) show levels of genetic polymorphism as low as those reported herein for *Orthogeomys*.

Levels of mean individual heterozygosity in *Orthogeomys* populations also are low by typical mammalian standards; the unweighted mean heterozygosity is 1.5% for *Orthogeomys* compared to an average of 3.6% for 46 species of mammals (Nevo, 1978). Allele frequencies at all loci examined in *Orthogeomys* conformed to Hardy-Weinberg expectations (Table 1).

Interspecific genetic differentiation.—The cladistic (locus-by-locus) analysis of the allelic data (Fig. 2) clustered together all populations belonging to the same nominal species. Based on this analysis, *O. heterodus* of the central Costa Rican highlands is the sister species of *O. cherriei* of the Caribbean lowlands. The three species of *Orthogeomys* inhabiting northern and western

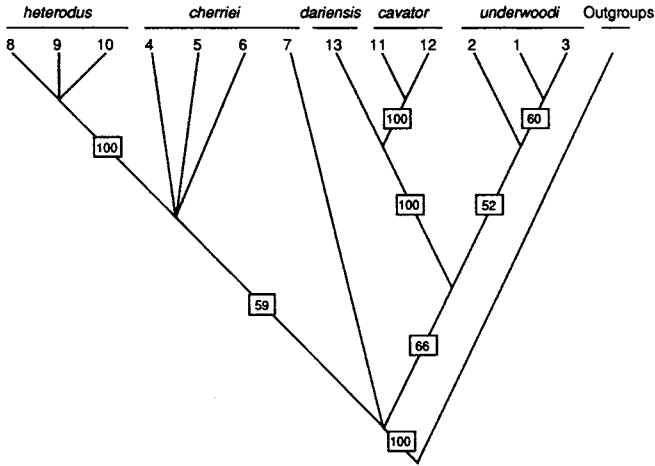


FIG. 3.—Relationships among Middle American pocket gophers (*Orthogeomys*) based on parsimony analysis of allele presence-absence data (Swofford, 1985). The 50% majority-rule tree is shown, with numbers on the branches indicating the percentage of the set of 118 shortest trees (all with 75 steps) that support the linkage. The consistency index is 0.61. Taxon numbers refer to collecting localities (Appendix I; Fig. 1).

Costa Rica (*O. cherriei*, *O. heterodus*, and *O. underwoodi*) form an assemblage distinct from the clade composed of *O. cavator* (found in southeastern Costa Rica and western Panama) and *O. dariensis* (known only from extreme eastern Panama and adjacent Colombia).

In general, the parsimony analysis based on presence-absence of alleles (Fig. 3) grouped populations in the same manner as the locus-by-locus analysis (Fig. 2). Noteworthy differences include placement of *O. cherriei* population 7 (which shares a synapomorphic allele with *O. cherriei* population 6 in the cladistic analysis), and the union of *O. underwoodi* with the *O. cavator*-*O. dariensis* group (Fig. 3) rather than the *O. heterodus*-*O. cherriei* group (Fig. 2).

DISCUSSION

Intrapopulational variability.—Pocket gophers of the genus *Orthogeomys* are poorly represented in museum collections because they live in small, isolated populations and are more difficult to capture than are other geomyids (Hafner and Barkley, 1984). Thus, samples available for this study average fewer than four individuals per locality. However, Gorman and Renzi (1979) demonstrated empirically that samples of only two individuals per population usually will yield an estimate of heterozygosity within 2.5% of the H value calculated from larger samples. Therefore, in this study estimates of genetic variability were calculated only for those populations with three or more individuals sampled.

The low levels of genetic variability observed in *Orthogeomys* (average $P = 0.048$; $\bar{H} = 0.015$) are consistent with patterns observed in other geomyids with similar densities and distributions (*Zygozomys trichopus*—Hafner and Barkley, 1984; *Thomomys talpoides*—Nevo et al., 1974; *Geomys tropicalis*—Selander et al., 1975). Low genetic variability is characteristic of species subdivided into small, isolated demes (Wright, 1969), consistent with observations of the size and distribution of *Orthogeomys* populations (Hafner and Hafner, 1987).

Interspecific genetic differentiation.—Archie et al. (1989) cautioned that small samples may decrease the stability of dendrograms calculated from allele-frequency data; however, they emphasized that certain data sets (those with low heterozygosities, allele frequencies generally near zero or one, and patterns of fixed or nearly fixed alleles unique to certain groups) were less prone to this potential source of error. Because the *Orthogeomys* data set (Table 1) shows all of these characteristics, a dendrogram generated from these data likely would resemble a dendrogram generated from a larger data set.

Although most populations of *Orthogeomys* presumed to be conspecific were grouped together in both the locus-by-locus and parsimony analyses of the protein data (Figs. 2 and 3), the parsimony analysis indicates that *O. cherriei* may not be a monophyletic unit (Fig. 3). It should be emphasized, however, that the protein data are equivocal with regard to the placement of *O. cherriei* population 7; although one unique allele at the LDH-1 locus (Table 1) links populations 4–6 with 8–10 (Fig. 3), this conflicts with the unique allele at the PEP-A locus that defines the *O. cherriei* clade (populations 4–7; Fig. 2). The morphological homogeneity of *O. cherriei* (including presence of the unique headspot in all populations) and its gross morphological distinctness from *O. heterodus* argue for retention of *O. cherriei* as presently defined.

Both the locus-by-locus and parsimony analyses linked *O. cherriei*, a small, lowland pocket gopher, with *O. heterodus*, a large, highland form. This relationship is supported by unique alleles at the LDH-1 and ACON-1 loci (Fig. 2). It also is supported, albeit indirectly, by a genetic survey of the chewing lice (Trichodectidae: *Geomydoecus*) that parasitize these pocket gophers (Hafner and Nadler, 1988); the louse survey revealed that lice from *O. cherriei* and *O. heterodus* are sister species, as are their hosts. Thus, the present analysis indicates that body-size similarities shared by the large, highland pocket gophers (*O. heterodus* and *O. cavator*) and by the small, lowland species (*O. cherriei* and *O. underwoodi*) are the result of evolutionary convergence. Patton and Brylski (1987) and Smith and Patton (1988) showed that body size in geomyids can be related directly to environmental variables; elevational differences in abundance and quality of food resources probably caused the observed body-size patterns in Middle American *Orthogeomys*.

There is strong support for the clade composed of *O. dariensis* and *O. cavator* (Figs. 2 and 3). These are the southernmost species in the genus, and although their geographic ranges presently are separated by approximately 600 km (Fig. 1), they are similar morphologically and ecologically, and both species are parasitized by a species of chewing louse (*Geomydoecus panamensis*) found on no other member of the genus (Price et al., 1985).

No unique allele supports the union of *O. underwoodi* with the *O. cavator*–*O. dariensis* group (Fig. 3), but a unique allele at the GOT-1 locus supports placement of *O. underwoodi* with the *O. heterodus*–*O. cherriei* lineage (Fig. 2). Because the protein data are equivocal on the placement of *O. underwoodi*, and only one unique allele defines the clade composed of *O. underwoodi*, *O. heterodus*, and *O. cherriei*, it is perhaps best to consider the systematic placement of *O. underwoodi* unresolved. Study of the systematic relationships among the chewing lice that parasitize these species (Hafner and Nadler, 1988) provides indirect evidence supporting the union of *O. underwoodi* with the *O. cavator*–*O. dariensis* clade. Chewing lice hosted by *O. underwoodi* are related more closely to those from *O. cavator* than to lice from *O. cherriei* or *O. heterodus* (Hafner and Nadler, 1988).

Historical zoogeography.—The geological history of the Middle American landmass is extremely complex, and any attempt at zoogeographic reconstruction for the region is hampered by fragmentary data on timing and extent of changes in sealevel and periods of orogenesis. Nevertheless, North and South America are considered to have been linked by an unbroken dry-land connection since approximately 3×10^6 years ago (Marshall et al., 1979). Also, during the glacial maxima of the Quaternary, montane glaciers occurred in the Cordillera de Talamanca (approximately 9°N latitude), and eustatic changes in sea level during glacial and interglacial stages resulted in alternating exposure and inundation of lowlands. The maximum elevation and depression relative to current sea level was approximately 100 m (Bartlett and Barghoorn, 1973).

Because the family Geomyidae is of North American origin (Lindsay, 1972), geomyids could have invaded the Middle American landmass before completion of the isthmian landbridge to South America (before 3×10^6 years ago). If a value of $D = 1.0$ (Nei, 1978) is considered equivalent to roughly 16×10^6 years of divergence, as suggested by the multiple-species study by Murphy (1983), then all phyletic diversification within the subgenus *Macrogeomys* ($D \leq 0.28$) occurred within the last 4.5×10^6 years. Although there is no fossil evidence documenting the presence of pocket gophers in Middle America at that time, the estimate is roughly contem-

poraneous with the most recent uplift of the Middle American landmass in Late Pliocene (Marshall et al., 1979), and pocket gophers may have inhabited the area. If we postulate that pocket gophers invaded the region as soon as dry-land connections permitted, then it follows that subsequent geologic events in the region could have triggered phyletic diversification in the subgenus.

If pocket gophers were in Middle America by late Pliocene, their geographic distribution would have been fragmented repeatedly by glacial and interglacial events of the Quaternary. Although lowland dispersal corridors were available during glacial maxima, elevated sea levels during interglacial periods undoubtedly forced populations into higher elevations, where they remained as disjunct isolates until the next glacial period.

Orthogeomys dariensis and *O. cavator* likely represent relictual isolates within the subgenus *Macrogeomys*. The large genetic distance between these species and the *O. heterodus*-*O. cherriei* lineage (average $D = 0.28$) suggests that the initial isolation of the *O. dariensis*-*O. cavator* lineage from other *Macrogeomys* species dates to, at least, the earliest interglacial period of the Quaternary. These species presently occur in mountainous regions (eastern and western Panama, respectively) that would have been islands remote from the mainland during interglacial periods. Meanwhile, in early Quaternary the common ancestor of *O. cherriei* and *O. heterodus* (and, perhaps, *O. underwoodi*) may have occupied the much larger island that includes the higher elevations of present-day Costa Rica.

Geographic isolation of *O. underwoodi* from its sister lineage (either the common ancestor of *O. cherriei* and *O. heterodus* as in Fig. 2, or the common ancestor of *O. cavator* and *O. dariensis* as in Fig. 3) may have been associated with climatic shifts during glacial maxima that effectively elevated the continental divide, blocking dispersal corridors joining east and west versants; at present, *O. underwoodi* is exclusively a western species, *O. cherriei* is primarily eastern, and *O. cavator* is southern. Alternatively, *O. underwoodi* may have been separated from the ancestral *O. cherriei* lineage by the broad valley of the Rio Grande de Tarcoles in northwestern Costa Rica. The present ranges of *O. underwoodi* and *O. cherriei* come into close proximity at the mouth of the Rio Grande de Tarcoles (Hafner and Hafner, 1987), and this river valley is known to be a major climatic (Escoto, 1964), edaphic (West, 1964), and vegetational (Wagner, 1964) transition zone characterized by major shifts in the species composition of both bird (Carriger, 1910) and reptile (Savage, 1966) communities.

Genetic evidence indicates that *O. heterodus* is a relatively recent derivative of the *O. cherriei* lineage (Figs. 2 and 3) and, like the other high-elevation forms, it may represent an interglacial isolate. The common ancestor of *O. heterodus* and *O. cherriei* probably gained access to the central highlands through the valley of the Rio Reventazon, which links the central Costa Rican highlands with the Caribbean lowlands; the present range of *O. heterodus* encompasses the higher reaches of this valley and abuts the range of *O. cherriei* at approximately 500 m elevation (Fig. 1, populations 7 and 10).

Orthogeomys matagalpae, the northernmost species in the subgenus *Macrogeomys*, was not included in this analysis. Greater sampling efforts in northern Costa Rica may reveal that the range of this species is confluent with that of *O. cherriei* to the south. Exomorphologically, *O. matagalpae* and *O. cherriei* are difficult to distinguish, and the two forms may prove to be conspecific. Final determination of the systematic position of *O. matagalpae* based on genetic evidence must await the opportunity to collect tissue samples of this species in Nicaragua or Honduras.

ACKNOWLEDGMENTS

I thank D. J. Hafner and L. J. Barkley for assistance in the field and laboratory. J. W. Demastes helped with the computer analyses, and S. A. Nadler and D. J. Hafner provided helpful criticisms of this manuscript. This work was supported by National Science Foundation grants BSR-8607223 and BSR-8817329.

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Submitted 25 September 1989. Accepted 16 April 1990.

APPENDIX I

Specimens Examined

Locality numbers (in parentheses) refer to the map (Fig. 1), and sample sizes are indicated following each locality. All specimens are preserved as standard museum vouchers (skin plus skeleton) and are deposited in the mammal collection of Louisiana State University Museum of Natural Science.

Orthogeomys underwoodi.—(1) COSTA RICA: Puntarenas Province, 5 km N, 13 km W Palmar Norte, 10 m ($n = 2$); (2) COSTA RICA: San Jose Province, 14 km (by road) S La Gloria, 200 m ($n = 3$); (3) COSTA RICA: Puntarenas Province, 1.5 km NE Tarcoles, 16 km S, 9 km W Orotina, 25 m ($n = 3$).

Orthogeomys cherriei costaricensis.—(4) COSTA RICA: Puntarenas Province, 5 km S, 6 km W Esparza, 50 m ($n = 2$); (5) COSTA RICA: Guanacaste Province, 2 km N, 8 km W Juntas, 90 m ($n = 1$); (6) COSTA RICA: Alajuela Province, 7 km (by road) NE Quesada, 700 m ($n = 1$); (7) COSTA RICA: Limon Province, 1.5 km N, 1 km E Pacuarito, 80 m ($n = 3$).

Orthogeomys heterodus dolichocephalus.—(8) COSTA RICA: Alajuela Province, La Palmita, 1,700 m ($n = 5$).

Orthogeomys heterodus heterodus.—(9) COSTA RICA: San Jose Province, 1 km (by road) SW Poas, 1,500 m ($n = 3$).

Orthogeomys heterodus cartagoensis.—(10) COSTA RICA: Cartago Province, 2 km W Santa Rosa, 2,300 m ($n = 9$).

Orthogeomys cavator nigrescens.—(11) COSTA RICA: San Jose Province, Division, 2,300 m ($n = 1$).

Orthogeomys cavator cavator.—(12) PANAMA: Chiriqui Province, Santa Clarita, 32.5 km (by road) W. Volcan, 3,000 ft. ($n = 3$).

Orthogeomys dariensis.—(13) PANAMA: Darien Province, 6 km SW Cana, 1,200 m ($n = 3$).

Orthogeomys hispidus.—(14) MEXICO: Tamaulipas, 13 km S, 1 km W Llera, 450 m ($n = 1$).

Orthogeomys grandis.—(15) MEXICO: Michoacan, 3.6 km (by road) N Arteaga ($n = 2$).