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Postilla Number 198
30 December 1986

Relationships of the Silver Rice Rat *Oryzomys argentatus* (Rodentia: Muridae)

Numi C. Goodyear and James D. Lazell, Jr.

(Received 2 September 1986)

Abstract

Nine skulls of the rare *Oryzomys argentatus* are compared to 109 skulls of the six races of *O. palustris*. Mahalanobis distance is greater between *O. argentatus* and all Floridian forms of *O. palustris* than the Floridian forms are from each other. In a canonical discriminant analysis, two models grouping *O. argentatus* with one or both of the insular races of *O. palustris* (*sanibeli* and *planirostris*) were shown by the Roy's Greatest Root statistic to fit the data less well than a model in which *O. argentatus* was regarded as distinct. A one-way ANOVA and Duncan's Multiple Range Test on the variation in nasal bone proportions show that there are two significantly different groups of these *Oryzomys* ($p < 0.05$): all *O. palustris* together and *O. argentatus* alone. We hypothesize *O. argentatus* originated on the Lower Keys in the late Sangamon and underwent selection for character divergence in sympatry with *O. palustris* during the Wurm.

ISSN No. 0-912532-00-9

Key Words

Oryzomys argentatus, Florida Keys, speciation, morphometrics, discriminant analysis, silver rice rat.

Introduction

Oryzomys argentatus, the silver rice rat, was originally described on the basis of two specimens (Spitzer and Lazell 1978). The work was criticized by Humphrey and Barbour (1979) and Barbour and Humphrey (1982) who felt that the use of ratios was not appropriate, and that the species was probably invalid. Because of a lack of data they did not substantiate these claims; they stated that the issue was moot because the taxon was probably extinct. Since, we have found that *O. argentatus* is extant on at least nine of the Lower Florida Keys (Goodyear, in press). Because the original sample size was too small for a statistically significant analysis of differences between *O. argentatus* and *O. palustris*, we present herein additional data corroborating our earlier results. We compare nine silver rice rat skulls with 109 skulls from the six races of *O. palustris*. The possibility of a close relationship between *O. argentatus* and the other insular forms, *O. p. sanibeli* and *O. p. planirostris* is especially considered. Two skulls are shown in Figure 1.

Fig. 1
Skulls of male rice rats in dorsal view. Right, *Oryzomys argentatus,* YPM 4667, Raccoon Key, Monroe Co., Florida. Left, *Orzyomys palustris sanibeli,* YPM 4670, Sanibel Island, Lee Co., Florida. Bar = 1 cm.

Specimens Examined and Related Abbreviations

Abbreviations for museums in which specimens are housed are as follows:

AMNH American Museum of Natural History, New York
ANSP Academy of Natural Sciences, Philadelphia
FSM Florida State Museum, Gainesville
NCSM North Carolina State Museum, Raleigh
MCZ Museum of Comparative Zoology, Harvard University
USNM US National Museum of Natural History, Smithsonian Institution
YPM Peabody Museum of Natural History, Yale University

Not all specimens could be used for all characters.

Oryzomys argentatus. YPM 4664-9; USNM 514994-5; AMNH 256405-6; FSM 16366.

O. p. palustris. YPM 4406-7; ANSP 11870, 11875; MCZ 1527-8, 2687, 2689-90, 56111-2, 5114, 5121, 5127, 5886, 6454, 6456; USNM 117384, 286831, 71368; AMNH 91146; NCSM 301-2, 472, 484-3, 491.
O. p. texensis. MCZ 2701-4, 2712-3, 2715-7, 2874; ANSP 14439; USNM 43299-300; AMNH 136499-500.
O. p. coloratus. MCZ 4454-59, 4461-2, 4465-9; USNM 71354-5, 73747-9, 228418, 228420-22, 228425, 228427.
O. p. natator. MCZ 3056-60, 7047, 7049, 7051, 7128, 7133-4, 7241-2; USNM 1090, 2250, 2253, 3872, 6172-4, 6176, 6183, 64061-7, 64069, 64071, 78705, 142693, 142697, 142748, 142811, 163993, 163995.
O. p. sanibeli. YPM 4670-2; USNM 301534.
O. p. planirostris. USNM 301533.

Methods

Nine *O. argentatus,* 16 *O. p. texensis,* 25 *O. p. palustris,* 24 *O. p. coloratus,* 39 *O. p. natator,* four *O. p. sanibeli,* and one *O. p. planirostris* skulls were used in the analysis. Variables used were condylobasal length, zygomatic breadth, nasal length, and nasal width. In the original description of the species the ratios of nasal length/nasal width and condylobasal length/zygomatic breadth were used to discriminate *O. argentatus* from all subspecies of *O. palustris.* Pelage color was not used as a variable because this character is so definitive that it would have unfairly weighted the data. In a canonical discriminant analysis—Statistical Analysis System (SAS) CANDISC procedure—we used only the metric data and no ratios to generate the models. In Model I we determined the Mahalanobis distance between all seven groups—the six races of *O. palustris* and *O. argentatus.* In Model II *O. argentatus* was lumped with the insular rice rat *O. p. sanibeli.* In Model III *O. p. sanibeli, O. p. planirostris* and *O. argentatus,* the three insular taxa, were lumped. Roy's Greatest Root, a summary statistic not affected by the number of classification groups, was used to determine which model best fit the data.

The skull measurements were also examined using the SAS DISCRIM procedure with and without the ratios. Last we performed a one-way ANOVA and a Duncan's Multiple Range test on the ratio of nasal length/nasal width between the seven taxonomic groups.

Results

The Roy's Greatest Root, for which larger values mean better fit, was largest for Model I (0.82872), smaller for Model II (0.814489), and smallest for Model III (0.749208). This indicated that it was better to view *O. argentatus* as a separate taxon, distinct from the other insular forms.

The Mahalanobis distances between *O. argentatus* and the races of *O. palustris* (from Model I) are shown in Table 1. The values show that the *O. argentatus* centroid is farther from all other groups than they are from each other with the exception of one pair, *O. p. sanibeli* and *O. p. texensis* which seem quite different from each other. However, the distance between *O. argentatus* and *O. p. texensis* is the greatest of all. Canonical variables 1 and 2 are plotted for Model I in Figure 2. Though the program attempted to maximally separate all seven groups, only the *O. argentatus* lie distant from the main mixed cloud of *O. palustris* subspecies. One individual *O. argentatus* lies within the *O. palustris* cloud. This was a captive female runt, which died at three months, weighing only 31 g (a normal female weighs 60 to 70 g). It had badly recurved teeth and did not grow at the rate of its litter mates. It died retaining the juvenile skull proportions which caused the misclassification. In the five discriminant analyses performed it was consistently grouped with *O. palustris.* No *O. palustris* was ever grouped with *O. argentatus.*

The case of overlap should be disregarded, as in Vogt and McCoy (1980), as the result of one teratogenic individual. However, cranial characters in combination with coloration do render every *O. argentatus* unequivocally distinct from every *O. palustris.*

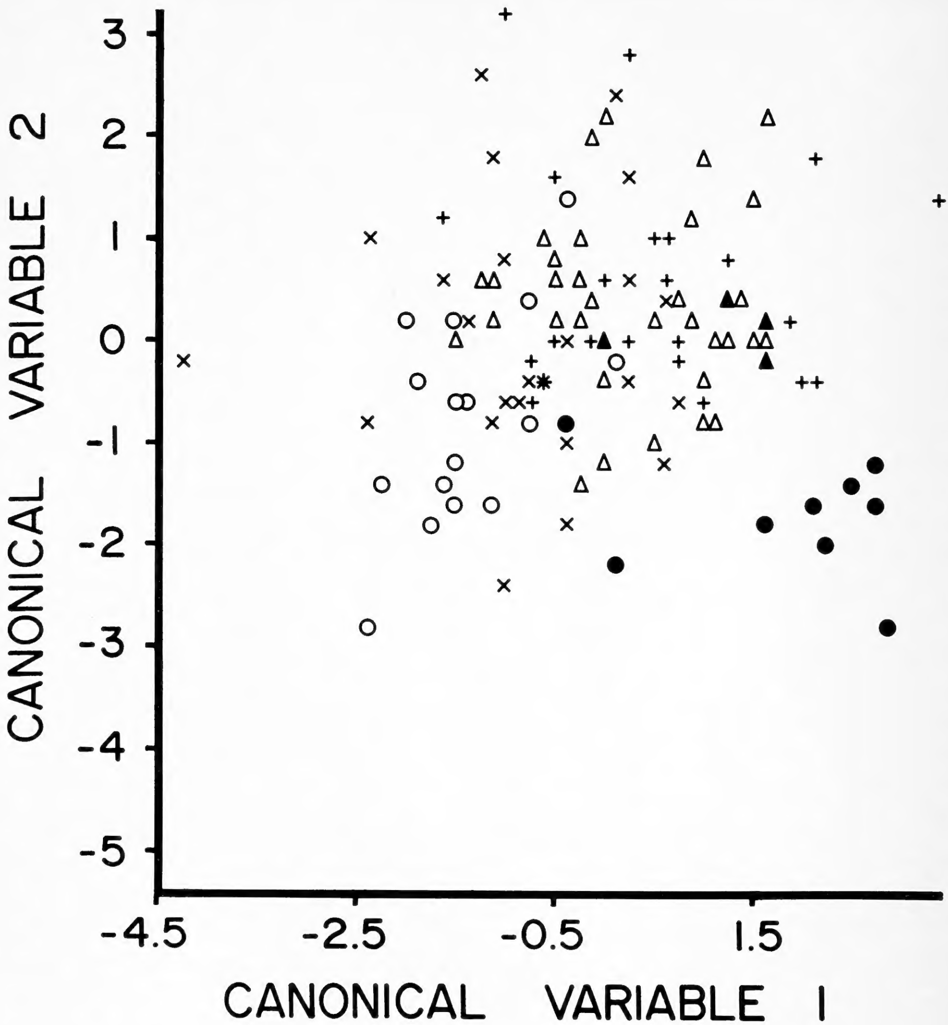

Fig. 2
Canonical variables one and two (Model I: see text) for seven North American rice rats (*Oryzomys*) using four cranial characters. Solid circles = *O. argentatus*; open circles = *O. palustris palustris*; X = *O. p. texensis*; + = *O. p. coloratus*; open triangles = *O. p. natator*; solid triangles = *O. p. sanibeli*; ★ = *O. p. planirostris*.

Using the DISCRIM procedure with no ratios, the program correctly classified individuals as follows: *O. argentatus*, 79%; *O. p. natator*, 77%; *O. p. texensis*, 63%; *O. p. palustris*, 40%; *O. p. coloratus*, 25%; *O. p. sanibeli* and *O. p. planirostris* 0%. Predictably, with the ratios used instead of the raw data, the program correctly classified more *O. argentatus*, 89% (i.e., all but the runt noted above); *O. p. natator*, 85%; *O. p. palustris*,

Table 1

Mahalanobis distance values between seven North American *Oryzomys*. The distance values are in the upper triangle, and probability values for greater distance are in the lower triangle. O.p.p. = *Oryzomys palustris palustris*, O.p.t. = *O. p. texensis*, O.p.c. = *O. p. coloratus*, O.p.n. = *O. p. natator*, O.p.s. = *O. p. sanibeli*, O.p.pl. = *O. p. planirostris*, O.a. = *O. argentatus*.

Species	O.p.p.	O.p.t.	O.p.c.	O.p.n.	O.p.s.	O.p.pl.	O.a.
O.p.p.	—	1.09	1.52	1.18	2.22	1.10	3.16
O.p.t.	4.37	—	2.28	2.09	2.85	1.51	3.37
O.p.c.	6.61	18.26	—	0.68	1.28	1.98	2.68
O.p.n.	8.03	29.24	2.69	—	1.47	1.46	2.55
O.p.s.	0.66	1.58	0.23	0.20	—	2.71	2.25
O.p.pl.	0.01	0.03	0.04	0.01	0.36	—	2.86
O.a.	5.80	8.92	4.28	2.68	7.68	16.15	—

32%; *O. p. coloratus*, 21%; *O. p. texensis*, *O. p. sanibeli* and *O. p. planirostris* 0%. The only *O. argentatus* misclassified was the female runt, YPM 4664.

In the one-way ANOVA on the ratio of nasal length divided by nasal width, there was a highy significant difference between *O. argentatus* and *O. palustris* ($p \ll 0.01$). A Duncan's Multiple Range test showed that there were two significantly different groups: one consisted of *O. argentatus* alone; the other contained all the subspecies of *O. palustris* ($p < 0.05$).

Discussion

Since it was originally described (Spitzer and Lazell 1978) the validity of *O. argentatus* has been repeatedly challenged (Humphrey and Barbour 1979; Barbour and Humphrey 1982). Because the species is so rare (Goodyear, in press) collection of information has been slow. Research on aspects of the natural history and the results of this taxonomic re-evaluation show that the animal is indeed as distinctive as originally thought. Radiotelemetry of individuals (Spitzer 1983) showed that, unlike their closest geographic relative, *O. p. coloratus*, they are primarily salt marsh inhabitants that can have home ranges 10 to 100 times larger than one might expect for an animal of their size and guild. Their pelage is distinctive: always the silver-grey of the limey Florida Keys' mud regardless of condition of molt or diet. The coats of rice rats from temperate Florida tend to be grey-brown in juveniles (because of shorter guard hairs) and develop red hues when animals mature. Humphrey et al. (1986) raise the point that pelage is affected by "chemicals and light in the environment and by fumigants in museum cabinets." This may cause some of the variation they observed in specimens of the Sanibel and Pine Island rice rats. We find that silver rice rats raised in the laboratory on Purina Dog Chow are identical in all respects to those captured wild, and that our museum specimens appear unchanged.

The silver rice rat's distinctive features may be due to an early separation from the mainland stock of *Oryzomys* and a subsequent period of sympatry when character divergence occurred. *Oryzomys* is known to be a successful colonizer of oceanic islands: the only rodent to have naturally reached the Galapagos Archipelago over more than a thousand kilometers of ocean (Heller 1904). We suspect that *Oryzomys* arrived in the Florida Keys as waters of the Sangamon Interglacial receded and exposed the islands (Lazell 1984; Goodyear, in press). We calculate the probable earliest exposure of land in what are now the Keys to be about 75 000 years BP from the curves provided by Morris et al. (1977). This date is corroborated by the climatic curves of Brunner (1982). If they arrived over water, differentiation may have begun before the Wurm reconnected the islands with the mainland. During the transition from interglacial to glacial, and in the more recent reversal of that transition, Florida Bay was largely freshwater swamp, continuous with the Everglades; the oolitic Lower Keys were connected by mangrove swamp (Hoffmeister 1974). At these times, flanking the 65 000 year glacial maximum, the mainland and the Florida Keys rice rats may have been sympatric. This could explain the degree of character divergence seen in osteology, pelage, behavior, and habitat preferences that persist today after their re-isolation.

While the ecological significance of the elongate nasal bones of *O. argentatus* is not apparent to us at present, the other three characters seem the very sorts which selection for character divergence might produce. While *O. argentatus* and the distant forms of *O. palustris* utilize salt marsh (Spitzer 1973), the proximate form *O. p. coloratus* seems confined to freshwater areas. We have trapped extensively for *coloratus* in the Everglades and Upper Keys and have never taken it in brackish or salt habitats. The vast home ranges documented for *O. argentatus* indicate a very different foraging strategy for this species compared to any subspecies of *O. palustris* (Goodyear, in press).

Finally, pelage color is far more different between *O. argentatus* and its nearest neighbor *O. p. coloratus* than between *argentatus* and geographically remote forms like nominate *palustris* and *texensis*. The Everglades *O. p. coloratus* is richly patterned in russet and ochraceous tones; *O. argentatus* is overall chinchilla grey to ash white. The grey-brown nominate *palustris* and *texensis*, geographically remote from *O. argentatus*, most closely resemble it in color. The insular form *O. p. sanibeli* has a dark grey-brown dorsum shading to warm fawn-brown on the sides (Hamilton 1955; YPM specimens); the ventral hairs of *sanibeli* are cream-white tipped with plumbeus bases. The ventral hairs of *O. argentatus* are ashy to the bases.

Pelage color differences are often strong evidence of character divergence in small mammals. For example, two species of mice, *Peromyscus leucopus* and *P. gossypinus*, can scarcely be separated on any consistent characters where far removed from each other, but sharp color (and hind foot) distinctions are seen where their ranges overlap (Webster et al. 1985). A similar case is described by these authors involving the shrews *Blarina brevicauda* and *B. carolinensis*.

Character divergence between presently allopatric, isolated species resulting from past contact was discussed theoretically by Williams (1969). Lazell (1972, p. 103–104) provided further discussion and an Antillean example.

Acknowledgments

Our field work was supported in part by The Conservation Agency, Friends of the Everglades, U.S. Fish and Wildlife Service, Earthwatch, The Explorers Club, The Nature Conservancy, and State of Florida Department of Parks and Recreation. The University of Rhode Island provided computer time. George Garrett and numerous others assisted us in the field.

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The Authors

Numi C. Goodyear. Doctoral candidate, Department of Zoology, University of Rhode Island, Kingston, RI 02881.

James D. Lazell, Jr. Curatorial Affiliate for Recent Vertebrates, Peabody Museum of Natural History, Yale University, and President, The Conservation Agency, 6 Swinburne Street, Jamestown, RI 02835.