BIOSYSTEMATICS OF THE NATIVE RODENTS OF THE GALAPAGOS ARCHIPELAGO, ECUADOR

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The native rodent fauna of the Galapagos Archipelago consists of seven species belonging to the generalized Neotropical rice rat (oryzomyine) stock of the family Cricetidae. These species comprise three rather distinct assemblages, each of which is varyingly accorded generic or subgeneric rank: (1) *Oryzomys* (*sensu stricto*), including *O. galapagoensis* [known only from Isla San Cristóbal] and *O. bauri* [from Isla Santa Fe]; (2) *Nesoryzomys*, including *N. narboroughi* [from Isla Fernandina], *N. swarthi* [from Isla Santiago], *N. darwini* [from Isla Santa Cruz], and *N. indefessus* [from both Islas Santa Cruz and Baltra]; and (3) *Megalomys curioi* [from Isla Santa Cruz]. *Megalomys* is only known from subfossil material and will not be treated here. Four of the remaining six species are now probably extinct as only *O. bauri* and *N. narboroughi* are known currently from viable populations.

The time and pattern of radiation, and the phylogenetic relationships of *Oryzomys* and *Nesoryzomys* are assessed by karyological, biochemical, and anatomical investigations of the two extant species, and by multivariate morphometric analyses of existing museum specimens of all taxa. These data suggest the following: (a) *Nesoryzomys* is a very unique entity and should be recognized at the generic level; (b) there were at least two separate invasions of the islands with *Nesoryzomys* representing an early entrant followed considerably later by *Oryzomys* (*s.s.*); (c) both taxa of *Oryzomys* are quite recent immigrants and are probably derived from *O. xantheolus* of the coastal Peruvian river valleys, or a common ancestor; (d) the origin of *Nesoryzomys* is ambiguous at the moment; (e) the three large forms of *Nesoryzomys* (*narboroughi*, *swarthi*, and *indefessus*) are best considered races of a single species, which differ primarily in pelage color; and (f) similarly, *O. galapagoensis* and *O. bauri* should probably be considered conspecific.

The fauna of the Galapagos Islands has certainly represented more of a cornerstone to the field of systematic and evolutionary biology than that of any other comparable area in the world. Since the initial visit by Darwin in 1835, countless scientific investigations have detailed the uniqueness and importance of this evolutionary theater. It is somewhat surprising, therefore, to note that the native mammalian fauna has received only cursory attention, an attention which has been almost exclusively in the form of taxonomic treatments. The list of native mammals includes but 12 species (2 bats, 3 pinnipeds, and 7 rodents). Although this complement is somewhat unremarkable when compared to other faunal elements of the archipelago, the rodent complex is more diverse than that on any similar group of oceanic islands and does include two major endemic taxa.

The seven species of native rodents are members of the rice rat, or oryzomyine, complex of the Neotropical assemblage of the family Cricetidae. The Galapagos species have been varyingly placed into one (*Oryzomys* [*s.l.*]) to three genera (*Oryzomys* [*s.s.*], 2 species; *Nesoryzomys*, 4 species; and *Megalomys*, 1 species) within this larger group. Beyond the original description of each and a few brief notes on natural history (e.g. Brosset 1963; Rosero Posso 1975), our knowledge of

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this fauna is indeed poor. No comprehensive attempt has been made to assess the evolutionary relationships of these species, both among themselves and to their potential mainland relatives. The purpose of the present effort is to review these relationships and to develop an understanding of the course of evolution among the Galapagoan species.

History of Discovery of Galapagos Rodents

The first species from the Archipelago was collected by Charles Darwin in 1835 from Isla San Cristóbal (= Chatham) and was described as *Mus galapagoensis* by Waterhouse in 1839. J. A. Allen described a second species in 1892, *O. bauri* from Isla Santa Fe (= Barrington); this was followed in 1899 by Thomas' description of *O. indefessus* from Isla Santa Cruz (= Indefatigable). In 1904, Edmund Heller erected a new genus (*Nesoryzomys*) to include *O. indefessus* Thomas and another new species, from Isla Fernandina (= Narborough), which he named *N. narboroughi.* Two additional species of *Nesoryzomys* were added to the faunal list of the islands after Heller's report: *N. darwini* was described by Osgood in 1929 from Isla Santa Cruz; and *N. swarthi* from Isla Santiago (= James) was described by Orr in 1938. The only addition to the rodent fauna subsequently has been the discovery of subfossil remains of a giant cricetine from Isla Santa Cruz, described as *Megalomys curioi* by Niethammer in 1964. The distribution of these species is given in Fig. 1.

The genus *Oryzomys* is a widespread, highly diverse taxon ranging from the southern United States to Tierra del Fuego. It is most diverse in tropical habitats, and many workers consider it to represent the stem stock of all Neotropical cricetines in the Tribe Sigmodontini [e.g. Hershkovitz 1962]. *Nesoryzomys* is endemic to the Galapagos, but *Megalomys* has the curious distribution of both Galapagoan and Lesser Antillean members but with no known mainland representatives.

The status of the genus *Nesoryzomys* has been open to some debate since it was initially proposed. The characters distinguishing members of this group from other oryzomyines center on the elongate, narrow snout and hourglass-shaped interorbital region (when viewed dorsally) with rounded frontal edges. In contrast, the typical oryzomyine condition is one of a short, broad rostrum with a strongly directed, divergent interorbital region, the edges of which form a supraorbital bead or shelf (Fig. 2). While a cranial demarcation between Galapagoan species in these characters is quite strong (e.g. *galapagoensis* and *bauri* versus *indefessus, narboroughi, darwini* and *swarthi*), several authors (notably Goldman [1918]) have remarked that the alleged generic characters of *Nesoryzomys* are " . . . not widely different from some of the continental species of *Oryzomys*" (Goldman 1918:13). Hence, Ellerman (1941:340) and Hershkovitz (1962:84) list *Nesoryzomys* as a subgenus of *Oryzomys* while De Beaufort (1963) regards it as generally distinct. A thorough analysis of existing specimens relative to both the status of *Nesoryzomys* and its relationship with other oryzomyine genera or subgenera has never been attempted. Below we summarize the existing data base relative to these questions, a data base that is frustratingly incomplete because of the apparent extinction of four of the species in question. No attention will be given here to the subfossil *Megalomys curioi.* A detailed synopsis of the status and relationships of this form is being prepared by Dr. Clayton Ray, Division of Paleobiology, National Museum of Natural History, Washington, D. C.

MATERIALS AND METHODS

Specimens examined consisted primarily of conventional museum study skins and skulls supplemented by soft anatomical structures (e.g. glandes penes, male reproductive tracts, stomachs) where available. Details as to methodology and specifics as to number and kinds of specimens examined for those analyses other than standard morphometric approaches are given in their appropriate sections, below.

Twenty-eight cranial and external characters were quantified for each specimen: (1) total length [ToL]; (2) tail length [TaL]; (3) hind foot length [HF]; (4) ear height [E]; (5) occipitonasal length [ON]; (6) basilar length of Hensel [BaL]; (7) breadth of braincase [BB]; (8) least interorbital width [IOC]; (9) greatest zygomatic breadth [ZB]; (10) rostral width [RW]; (11) rostral length [RL]; (12) width across maxillary tooth rows [MTRW]; (13) diastema length [DL]; (14) maxillary tooth row length [MTRL]; (15) bullar length [BuL]; (16) rostral depth [RD]; (17) cranial depth [CD]; (18) mandibular tooth row length [mTRL]; (19) ramus height at M^1 [RH]; (20) mandibular height from angle to condyle [ACH]; (21) braincase length [BCL]; (22) zygomatic plate width [ZPW]; (23) incisive foramen length [IFL]; (24) mestopterygoid fossa width [MPFW]; (25) mesopterygoid fossa length [MPFL]; (26) M^1 length [1L]; (27) M^2 length [2L]; (28) M^3 length [3L].

Measurements (1) through (4) were taken from the specimen label; measurements (25) through (28) were taken with the aid of a binocular measuring microscope; all others were taken with dial calipers.

In addition to the 28 mensural characters listed above, 23 qualitative characters of the skin and skull were scored for each specimen. Two to four states were recognized for every character with each state given a serial numerical score. The characters, states within, and scores are as follows:

Ventral view of skull. (1) shape of incisive foramina: teardrop shaped with lateral margins expanded posteriorly [1], lateral margins evenly rounded [2], or lateral margins straight and parallel [3]; (2) position of incisive foramina relative to M^1: posterior margin ends well anterior to M^1 [1] or posterior margin extends to or beyond anterior margin of M^1 [2]; (3) ventral width of maxillary septum of incisive foramina: very narrow [1], moderately broad [2], or very broad [3]; (4) relative size of ethmoid portion of incisive foramina septum: less than 1/2 length [1] or greater than 1/2 length [2]; (5) condition of posterior palatine pits: large and deep [1], large and shallow [2], or small and shallow [3]; (6) position of mesopterygoid fossa relative to M^3: anterior margin extends to or beyond M^3 [1] or anterior margin does not extend to M^3 [2]; (7) condition of sphenopalatine vacuity: open [1], mostly closed [2], or completely closed [3]; (8) relative size of foramen ovale (FO) and medial lacerate foramen (MLF): FO larger than MLF [1], FO and MLF subequal in size [2], or FO smaller than MLF [3]; (9) condition of petrotympanic fissure: completely closed, no visible fissure [1], moderately open [2], or greatly enlarged [3].

Lateral view of skull. (10) posterior shape of cranium: lambdoidal crest square, occiput flat [1], lambdoidal crest square, occiput rounded [2], or lambdoidal crest and occiput evenly rounded [3]; (11) prominence of anterior zygomatic plate: very prominent [1], moderately prominent [2], or not prominent [3]; (12) anterior profile of anterior zygomatic plate: square [1], weakly rounded [2], or strongly rounded [3].

Dorsal view of skull. (13) shape of supraorbital region: margins rounded [1] or margins divergent posteriorly [2]; (14) condition of supraorbital ridges: sharply shelved [1], beaded [2], or rounded [3].

Hind foot. (15) nature of hair covering claws: not covering claws [1] or covering claws [2]; (16) general foot proportions: short and broad [1], long and narrow [2], or long and broad [3]; (17) relative length of hallux: not reaching base of digit 2 [1], reaching base of digit 2 [2], or extending beyond base of digit 2 [3], (18) hairiness of heel: naked [1] or clothed in hair [2]; (19) presence of digital webbing; present [1] or absent [2].

Tail. (20) color pattern: bicolored [1] or unicolored [2]; (21) degree of hair covering: essentially naked [1], moderately haired with scales visible [2], or well haired with scales hidden [3]; (22) condition of scales: heavy and large [1] or light and small [2].

Pelage. (23) general quality of pelage: guard hairs not discernibly present [1], underfur soft and woolly with guard hairs present [2], underfur long and woolly with guard hairs present [3], or guard hairs thickly present, long, and somewhat bristle-like [4].

Samples of all Galapagoan species except *O. galapagoensis* (Waterhouse) were available for study. In addition, species representative of most other major oryzomyine genera and subgenera have been examined. Listed below are the 22 sampled taxa (operational taxonomic units, or OTU's) used in the morphometric analyses, along with general locality data and number of

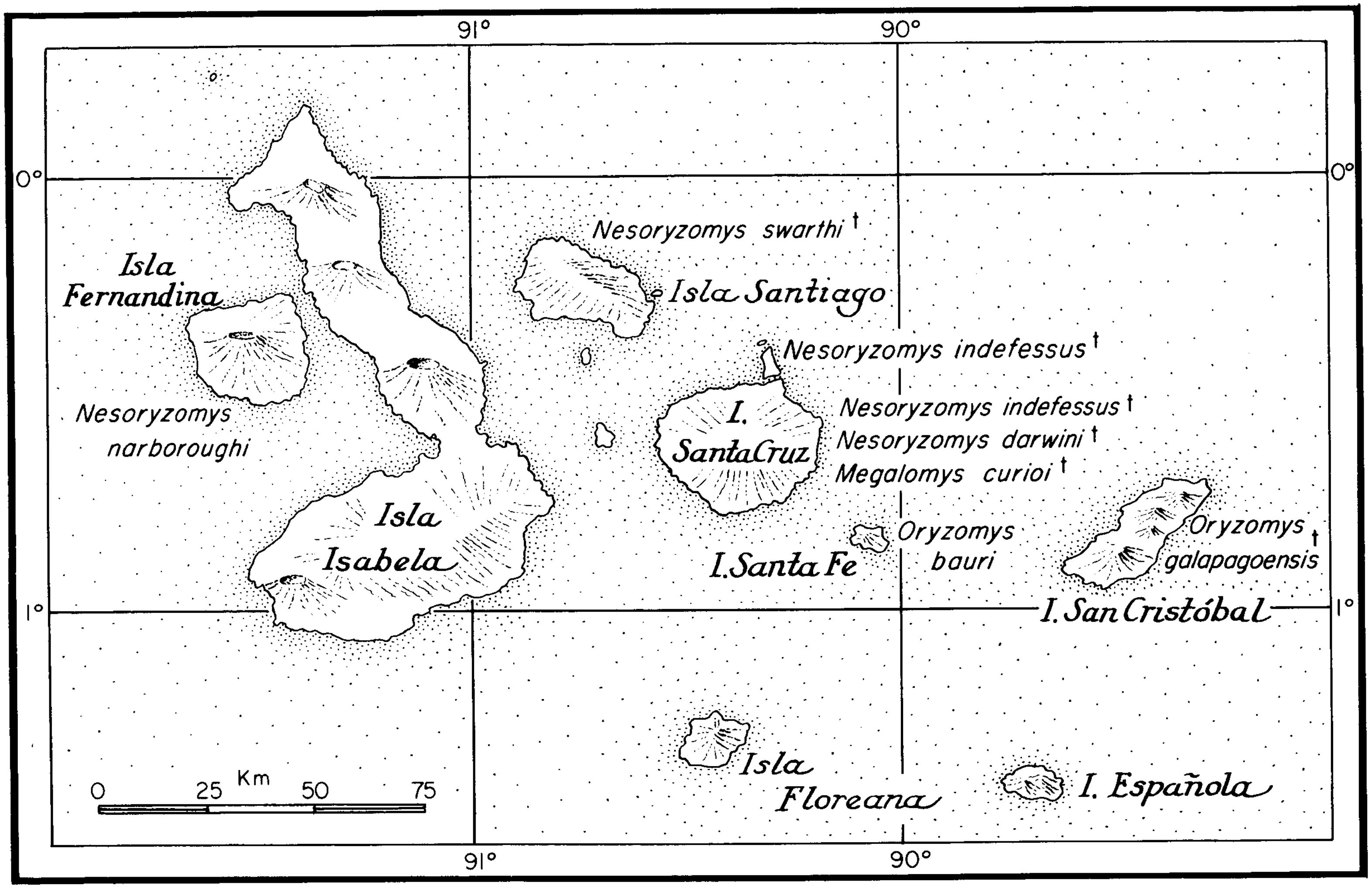


Fig. 1. Distribution of native rodents in the Galapagos Archipelago, Ecuador. A cross next to a name indicates an extinct taxon.

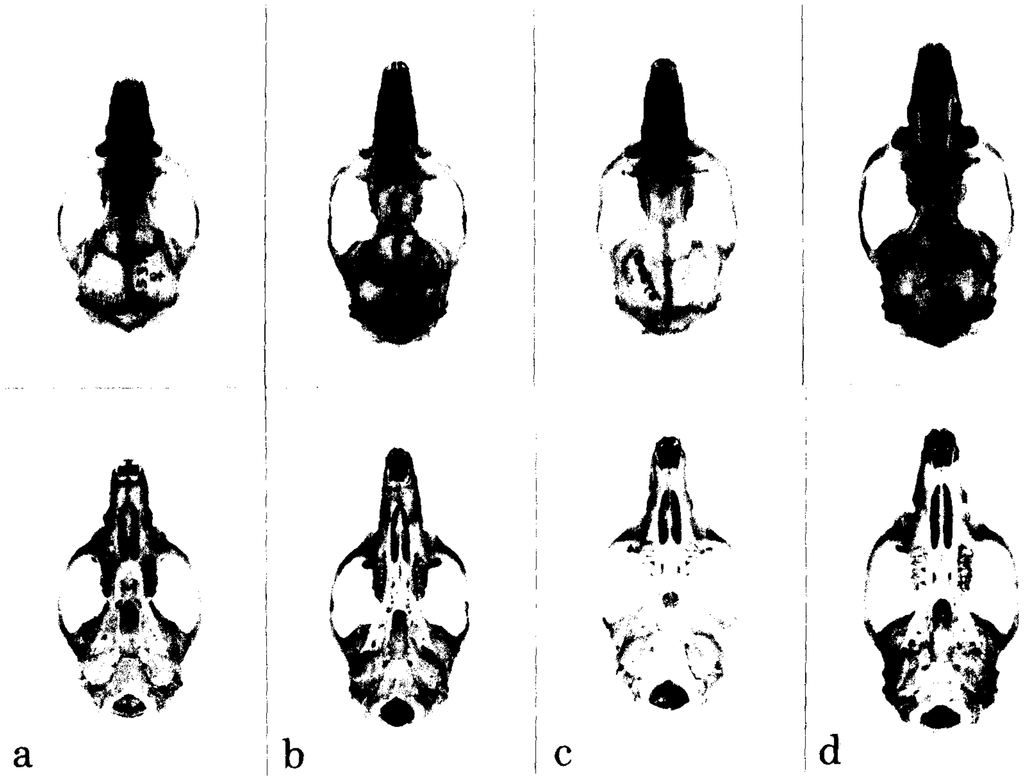


Fig. 2. Dorsal and ventral views of crania of four taxa of Galapagos rodents: (a) *Oryzomys bauri* J. A. Allen (♀, MVZ 145376); (b) *Nesoryzomys narboroughi* Heller (♀, MVZ 145386); (c) *Nesoryzomys indefessus* (Thomas) (♀, FMNH 30875); and (d) *Nesoryzomys swarthi* (♂, CAS 2561).

specimens available. All non-Galapagoan specimens are housed in the Museum of Vertebrate Zoology, University of California, Berkeley. More complete locality information with a list of all Galapagos specimens examined, catalogue numbers, and museum repositories is given in Appendix I.

Nesoryzomys
(1) *N. narboroughi* Heller: Isla Fernandina, Galapagos (57).
(2) *N. indefessus* (Thomas): Isla Santa Cruz (51) and Isla Baltra (25), Galapagos.
(3) *N. darwini* Osgood: Isla Santa Cruz, Galapagos (5).
(4) *N. swarthi* Orr: Isla Santiago, Galapagos (4).
Oryzomys (*Oryzomys*)
(5) *O. bauri* Allen: Isla Santa Fe, Galapagos (31).
(6) *O. xantheolus* Thomas: Depto. Arequipa, Peru (11).
(7) *O. keaysi* Allen: Depto. Puno, Peru (2).
(8) *O. albigularis* (Tomes): Deptos. Amazonas and Cajamarca, Peru (3).
(9) *O. palustris palustris* (Harlan): South Carolina, USA (3).
(10) *O. palustris peninsulae* Thomas: Baja California Sur, Mexico (3).
(11) *O. palustris regillus* Goldman: Michoacan, Mexico (3).
(12) *O. capito* (Olfers): Depto. Loreto, Peru (6).
(13) *O. yunganus* Thomas: Depto. Loreto, Peru (1).
(14) *O. nitidus* (Thomas): Depto. Loreto, Peru (5).
Oryzomys (*Melanomys*)
(15) *O. caliginosus* (Tomes): Cauca and Valle, Colombia (2).

Oryzomys (*Microryzomys*)
(16) *O. minutus* (Tomes): Depto. Ancash, Peru (3).
Oryzomys (*Oecomys*)
(17) *O. concolor* (Wagner): Depto. Loreto, Peru (1).
(18) *O. bicolor* (Tomes): Depto. Loreto, Peru (3).
Oryzomys (*Oligorozymys*)
(19) *O. longicaudatus longicaudatus* (Bennett): Santiago Prov., Chile (2).
(20) *O. longicaudatus destructor* (Tschudi): Depto. Loreto, Peru (10).
Neacomys
(21) *N. spinosus* (Thomas): Depto. Loreto, Peru (10).
Nectomys
(22) *N. squamipes* (Brants): Depto. Loreto, Peru (2).

Standard descriptive statistics (mean, standard deviation, standard error of the mean, range, and coefficient of variation) were derived for each of the 28 mensural and 23 qualitative variables for all taxa examined (Tables 1 and 2). Patterns of phenetic similarity among taxa were examined by the multivariate methods of factor analysis, discriminant function analysis, and cluster analysis. Taxa means served as the character states in all cases with quantitative and qualitative traits considered both separately and in unison. In the cluster analyses, both distance and correlation matrices were computed as measures of phenetic resemblance. Phenograms were derived from both matrices by the unweighted pair group method using arithmetic averages (UPGMA; Sneath and Sokal 1973), with the cophenetic correlation coefficient computed for each. The statistical programs of the Numerical Taxonomy Package written by W. W. Moss and the Statistical Package for the Social Sciences (SPSS), both adapted for the CDC 6400 computer, were used for all analyses.

DESCRIPTION AND ANALYSIS

Data from four sources representing three levels of biological organization (genic, gene packaging, and organismic) are available for the assessment of the phenetic and phylogenetic relationships of the Galapagos rats.The genic level was assayed by starch gel electrophoretic analysis; gene packaging by standard karyotypic analysis; and organismic by cranial and external morphometrics and by descriptive soft anatomical analysis.

Starch Gel Electrophoresis

Tissues for electrophoresis were available from 10 specimens each of *N. narboroughi* and *O. bauri* (kidney, liver, plasma, and hemolysate) and four *O. xantheolus* (kidney and liver only). Twenty-two enzymatic and non-enzymatic proteins representing 29 presumptive gene loci were scored for *N. narboroughi* and *O. bauri*. Since no blood was available from *O. xantheolus*, only 22 of these loci were scored for that species.

Loci scored for all three species include: lactate dehydrogenase (LDH-1 and 2), glutamic oxaloacetic transaminase (GOT-1 and 2), peptidase (Pept-1, 2, and 3), malate dehydrogenase (MDH-1 and 2), malic enzyme (ME), sorbitol dehydrogenase (SDH), isocitrate dehydrogenase (IDH-1 and 2), α-glycerophosphate dehydrogenase (αGPD), mucophosoisomerase (MPI), 6 phosphogluconate dehydrogenase (6PGD), xanthine dehydrogenase (SDH), indolphenol oxidase (IPO), alcohol dehydrogenase (ADH), phosphogluconate isomerase (PGI), and phosphoglucomutase (PGM-1 and 3). Systems scored from blood fractions included: hemoglobin (Hb), albumin (Alb), transferrin (Trf-1 and 2), and three general proteins (Pt-1, 2, and 3). In addition, six esterase loci were identifiable for each of the three species.

Based on the 22 loci for which all three species were compared, *N. narboroughi* shares a major or fixed allele at 13 loci with both *O. bauri* and *O. xantheolus* (overall genetic similarity = 59.1%). The latter two species share a major or fixed allele at all but three loci (86.4% similarity).

TABLE 1. MEAN CHARACTER STATES OF THE 23 QUALITATIVE CHARACTERS FOR EACH OF THE 22 OTU'S OF ORYZOMYINE RODENTS EXAMINED

CHARACTER	*Nectomys*	*Neacomys*	*O. keaysi*	*O. albigularis*	*O. yunganus*	*O. nitidus*	*O. capito*	*O. palustris peninsulae*	*O. palustris palustris*	*O. palustris regillus*	*O. xantheolus*	*O. bauri*	*O. (Melanomys) caliginosus*	*(Microryzomys) minutus*	*(Oligoryzomys) l. destructor*	*(Oligoryzomys) l. longi*	*(Oecomys) concolor*	*(Oecomys) bicolor*	*N. indefessus*	*N. narboroughi*	*N. darwini*	*N. swarthi*
1	1.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	2.5	1.0	1.0	1.0	1.0	1.0	1.0	1.5	1.0	1.0	1.0	1.0	1.0	1.0
2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.8	1.8	2.0	2.0	2.0	1.0	2.0	1.0	2.0	1.0	1.0	2.0	1.5	1.5	1.5
3	1.7	3.0	2.0	2.2	2.0	2.0	3.0	1.8	1.7	2.0	1.0	2.0	1.0	2.0	1.0	2.0	1.0	1.0	2.0	2.0	2.5	2.0
4	2.0	1.7	1.5	1.7	1.5	2.0	2.5	2.0	1.5	2.0	1.8	1.5	1.7	2.0	1.7	1.0	1.5	1.8	1.6	1.8	1.7	1.7
5	1.0	2.0	1.5	2.7	2.0	2.7	2.1	1.0	1.0	1.0	1.1	1.6	1.0	2.7	2.1	3.0	3.0	3.0	1.3	1.0	1.5	1.5
6	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.9	1.9	2.0	1.8	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
7	3.0	1.9	2.5	2.7	2.5	2.9	3.0	3.0	1.3	3.0	1.3	1.1	3.0	1.0	2.1	1.0	2.5	2.5	1.0	1.0	1.0	1.0
8	3.0	1.8	2.5	2.2	1.0	1.4	1.3	2.0	1.7	2.8	2.9	2.4	2.5	2.7	1.8	2.0	3.0	2.7	2.8	3.0	2.0	3.0
9	1.7	2.1	1.7	2.0	3.0	3.0	3.0	1.8	1.3	1.5	1.8	1.1	1.7	1.0	1.8	1.0	3.0	3.0	1.3	1.2	1.0	1.3
10	1.0	2.3	1.0	1.7	1.5	1.3	1.8	1.5	1.8	2.0	1.9	1.9	1.0	3.0	1.8	1.7	1.0	1.7	1.6	1.1	1.5	1.5
11	1.0	2.1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	3.0	1.2	1.0	2.0	1.7	1.0	1.0	1.0	1.0
12	1.5	2.1	1.7	1.7	1.0	1.1	1.4	2.0	1.2	1.4	1.6	1.8	1.0	3.0	2.0	1.5	1.0	1.7	1.4	1.7	1.5	1.5
13	1.0	1.0	1.5	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	2.0	2.0	2.0	2.0
14	1.0	2.0	2.0	3.0	2.0	1.4	1.9	1.8	1.2	1.2	1.2	1.0	1.5	2.5	2.0	2.0	1.0	1.0	2.3	2.6	3.0	2.5
15	2.0	1.0	1.0	1.0	1.0	1.0	1.0	2.0	2.0	2.0	1.5	1.0	2.0	1.5	1.5	1.5	1.0	1.5	1.0	1.0	1.0	1.0
16	3.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	3.0	3.0	3.0	1.0	2.0	2.0	2.0	1.0	1.0	3.0	3.0	3.0	3.0
17	1.0	1.0	3.0	3.0	1.0	2.0	1.0	2.0	1.0	1.0	3.0	3.0	3.0	1.0	2.0	1.0	3.0	3.0	3.0	3.0	3.0	3.0
18	1.0	1.5	1.0	1.0	1.0	2.0	1.0	1.0	1.0	1.0	1.0	1.5	1.0	1.5	1.0	1.0	2.0	2.0	1.5	1.5	1.5	1.5
19	1.0	2.0	2.0	2.0	2.0	2.0	2.0	1.5	1.5	1.5	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
20	2.0	2.0	1.5	1.0	1.5	1.5	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	1.0	2.0	2.0	2.0	2.0
21	2.0	1.0	1.0	1.0	1.0	2.0	1.0	2.0	2.0	2.0	2.5	2.0	2.0	2.0	1.0	2.0	1.5	1.0	3.0	3.0	3.0	3.0
22	1.0	1.0	2.0	2.0	2.0	2.0	2.0	1.0	1.0	1.0	1.0	1.0	2.0	2.0	1.5	1.0	2.0	2.0	1.0	1.0	1.0	1.0
23	1.0	4.0	1.0	1.0	1.0	1.0	1.0	2.0	3.0	3.0	3.0	3.0	1.0	3.0	1.0	2.0	1.0	1.0	2.5	3.0	2.5	3.0

TABLE 2. TWENTY-EIGHT QUANTITATIVE CHARACTERS FOR THE SIX TAXA OF ENDEMIC GALAPAGOS RODENTS[1]

	Oryzomys galapagoensis	*Oryzomys bauri*	*Nesoryzomys indefessus*		*Nesoryzomys narboroughi*	*Nesoryzomys darwini*	*Nesoryzomys swarthi*
			Santa Cruz	Baltra			
Character	[N=1]	[N=31]	[N=26]	[N=17]	[N=31]	[N=5]	[N=4]
ToL	- - -	290.9±2.90 260-335 5.52	256.0±3.90 222-297 7.97	245.7±2.90 220-264 4.86	280.8±2.50 243-303 4.87	193.0±8.00 177-202 9.28	307.5±14.3 267-334 9.32
TaL	- - -	145.2±1.50 129-165 5.94	107.3±1.70 91-121 7.86	99.4±1.60 88-114 6.70	121.9±1.60 101-136 7.14	85.8±1.90 79-90 5.04	132.0±3.90 124-140 5.84
HF	34	32.7±0.30 30-36 4.73	30.8±0.30 28-33 4.27	29.1±0.40 27-32 5.93	32.8±0.30 30-36 4.68	25.2±0.70 23-27 5.89	34.5±1.50 30-36 8.70
E	22	23.3±0.40 21-25 4.54	23.9±0.20 22-25 3.72	23.2±0.20 22-25 3.24	22.9±0.20 20-26 5.45	19.0±0.40 18-20 5.26	27.5±0.30 27-28 2.10
ON	32.9	34.03±0.21 31.4-36.8 3.38	36.77±0.26 34.5-39.1 3.60	35.92±0.16 34.8-36.9 1.79	38.39±0.23 34.4-41.5 3.35	29.58±0.29 28.6-30.1 2.22	38.98±1.36 34.9-40.4 6.97
BaL	27.1	26.68±0.22 24.3-29.3 4.64	27.35±0.25 25.1-29.6 4.64	26.79±0.14 25.7-27.9 2.14	28.92±0.23 25.1-31.3 4.42	21.36±0.30 20.2-21.8 3.12	29.37±1.32 25.8-31.4 8.85
MW	14.0	13.45±0.07 12.6-14.3 2.73	14.03±0.09 13.3-14.9 3.10	13.67±0.08 13.0-14.3 2.52	13.93±0.06 13.3-14.6 2.23	11.80±0.13 11.3-12.0 2.47	14.85±0.26 14.1-15.3 3.50
ZB	17.9	17.97±0.13 16.3-19.8 3.91	18.45±0.14 17.0-19.6 3.77	17.75±0.11 17.0-18.5 2.52	18.79±0.10 17.0-19.5 2.23	14.08±0.19 13.5-14.7 3.06	19.70±0.71 17.9-20.5 6.19
RL	- - -	13.83±0.12 12.3-14.9 4.90	15.99±0.17 14.8-17.7 5.48	15.43±0.11 14.7-16.2 2.86	16.63±0.13 14.5-18.3 4.28	12.62±0.25 12.0-13.3 4.46	16.50±0.80 14.1-17.5 9.75
DL	8.8	8.99±0.10 7.9-10.2 6.22	9.40±0.12 8.4-10.5 6.68	9.37±0.08 8.9-10.2 3.60	10.02±0.10 8.4-11.4 5.25	7.42±0.30 6.4-8.2 9.06	9.98±0.53 8.4-10.6 10.62
CD	- - -	11.97±0.08 11.1-13.0 3.89	12.85±0.10 11.6-13.7 3.61	12.85±0.08 12.3-13.5 2.64	13.47±0.08 12.5-14.5 3.31	10.66±0.12 10.2-10.9 2.54	14.10±0.41 12.9-14.8 5.88
RH	7.6	9.36±0.10 8.1-10.5 5.81	9.14±0.10 8.3-10.1 5.30	8.77±0.06 8.3-9.2 3.01	9.60±0.07 8.1-10.3 4.08	7.16±0.21 6.5-7.8 6.45	10.45±0.47 9.1-11.2 9.06
BCL	- - -	11.48±0.07 10.7-12.4 3.56	12.34±0.10 11.4-13.6 3.92	12.16±0.07 11.6-12.8 2.40	13.19±0.10 12.1-14.4 4.06	9.94±0.06 9.8-10.1 1.35	13.43±0.30 12.6-14.0 4.40

[1] Mean ± standard error of the mean; range; and coefficient of variation are given.

TABLE 2 (Continued). TWENTY-EIGHT QUANTITITATIVE CHARACTERS FOR THE SIX TAXA OF ENDEMIC GALAPAGOS RODENTS

	Oryzomys galapagoensis	*Oryzomys bauri*	*Nesoryzomys indefessus*		*Nesoryzomys narboroughi*	*Nesoryzomys darwini*	*Nesoryzomys swarthi*
			Santa Cruz	Baltra			
Character	[N=1]	[N=31]	[N=26]	[N=17]	[N=31]	[N=5]	[N=4]
IOC	5.5	5.45±0.04 5.1-6.1 3.99	4.62±0.04 4.3-5.0 3.97	4.49±0.03 4.2-4.7 2.72	4.69±0.04 4.3-5.1 4.28	4.52±0.09 4.2-4.7 4.53	4.93±0.08 4.7-5.0 3.05
RW	6.1	6.24±0.06 5.6-7.0 5.37	6.25±0.08 5.6-6.9 6.17	6.26±0.05 6.06-6.6 3.05	6.42±0.06 5.6-7.2 4.93	5.32±0.20 4.8-5.9 8.34	7.33±0.31 6.4-7.7 8.52
MTRW	---	6.85±0.05 6.3-7.4 4.02	7.31±0.07 6.7-8.0 4.60	7.44±0.05 7.1-7.8 2.60	7.36±0.04 7.0-7.7 2.66	5.94±0.10 5.7-6.2 3.88	7.83±0.22 7.2-8.2 5.56
MTRL	5.5	5.67±0.04 5.3-6.4 3.52	5.58±0.03 5.3-5.9 3.10	5.33±0.05 5.0-5.7 3.56	5.51±0.03 5.2-6.0 3.41	4.94±0.07 4.7-5.1 3.07	6.15±0.12 5.8-6.3 3.87
BuL	---	5.87±0.04 5.4-6.3 3.67	6.71±0.05 5.8-7.1 4.11	6.35±0.05 6.0-6.7 2.95	6.57±0.04 6.0-7.1 3.61	5.40±0.10 5.1-5.7 4.14	6.95±0.12 6.6-7.4 4.92
RD	6.2	6.17±0.06 5.3-6.8 5.56	6.73±0.08 6.1-7.4 5.85	6.48±0.06 6.1-6.9 3.48	6.71±0.05 6.0-7.3 3.93	4.86±0.04 4.5-5.2 6.28	7.18±0.33 6.2-7.6 9.13
mTRL	5.6	5.77±0.03 5.4-6.0 2.61	5.56±0.04 5.2-5.9 3.64	5.35±0.04 5.1-5.8 3.31	5.36±0.03 5.0-6.0 3.00	4.88±0.04 4.8-5.0 1.71	6.20±0.11 6.0-6.5 3.48
ACH	---	6.40±0.08 5.6-7.5 6.65	6.52±0.10 5.5-7.3 7.43	6.29±0.08 5.8-7.1 5.21	6.45±0.06 5.4-7.1 5.50	4.68±0.07 4.5-4.9 3.17	7.28±0.40 6.2-8.1 11.08
ZPW	3.6	4.05±0.07 3.4-4.9 9.92	4.07±0.07 3.6-4.8 8.10	3.91±0.05 3.5-4.5 5.31	4.03±0.06 3.3-4.7 8.63	3.22±0.04 3.1-3.3 2.60	4.55±0.25 3.8-4.8 10.99
IFL	---	6.96±0.06 6.2-7.5 4.60	6.84±0.09 6.2-7.9 6.81	6.72±0.06 6.4-7.2 3.69	6.81±0.04 6.3-7.1 2.94	5.36±0.14 4.9-5.6 5.69	7.83±0.34 6.9-8.4 8.57
1L	---	2.56±0.03 2.3-2.8 5.95	2.56±0.02 2.3-2.8 4.43	2.51±0.03 2.3-2.7 4.20	2.47±0.02 2.2-2.7 4.81	2.16±0.07 2.0-2.3 7.02	2.73±0.05 2.6-2.8 3.51
2L	---	1.68±0.02 1.5-1.9 5.04	1.61±0.02 1.5-1.8 6.32	1.61±0.02 1.5-1.7 4.85	1.64±0.01 1.5-1.8 4.66	1.50±0.03 1.4-1.6 4.71	1.88±0.03 1.8-1.9 2.67
3L	---	1.27±0.02 1.1-1.5 7.09	1.20±0.01 1.1-1.3 4.41	1.22±0.02 1.1-1.3 5.22	1.20±0.01 1.1-1.4 6.09	1.08±0.04 1.0-1.2 7.75	1.50±0.03 1.4-1.6 5.44
MPFW	---	2.32±0.02 2.0-2.6 5.85	2.19±0.03 1.9-2.7 7.51	2.05±0.04 1.6-2.2 7.72	1.99±0.02 1.7-2.2 6.20	1.68±0.02 1.6-1.7 2.66	2.28±0.13 1.9-2.5 11.56
MPFL	---	5.57±0.06 4.7-6.1 5.81	4.91±0.06 4.4-5.4 5.94	4.87±0.04 4.4-5.2 3.76	4.75±0.04 4.0-5.1 5.18	3.84±0.08 3.6-4.0 4.73	5.48±0.20 4.9-5.8 7.21

The figure for *N. narboroughi* and *O. bauri* is considerably lower if the blood and esterase loci are included in the analysis. These represent an additional 13 loci for which the two species are fixed for different alleles at 10. Hence, a minimal estimate of overall genetic similarity for these species based on 35 loci is 45.7%.

There are 7 of the 22 loci which serve to differentiate *N. narboroughi* from both *O. bauri* and *O. xantheolus* (Fig. 3). *N. narboroughi* and *O. xantheolus* share an allele at one locus (XDH^a) which is not found in the sample of *O. bauri*, and *N. narboroughi* shares an allele at each of two loci with *O. bauri* (MDH-1^b and ME^a) not found in *O. xantheolus*.

These data argue strongly that the Galapagoan *O. bauri* (and probably *O. galapagoensis*) shares a closer genic-based relationship with the coastal Peruvian *O. xantheolus* than it does with *N. narboroughi*, and undoubtedly with other species of *Nesoryzomys* as well. The only way to account for these data is to postulate a much earlier introduction and radiation of *Nesoryzomys* in the archipelago with the origin of the taxon at that time, or a derivation of *Nesoryzomys* on the mainland before introduction. In either event, clearly *O. bauri* has a close genetic relative on the mainland today in *O. xantheolus* while *Nesoryzomys* is not closely related to either of these species. A much more expanded data base is required to establish genic relationships of *Nesoryzomys*.

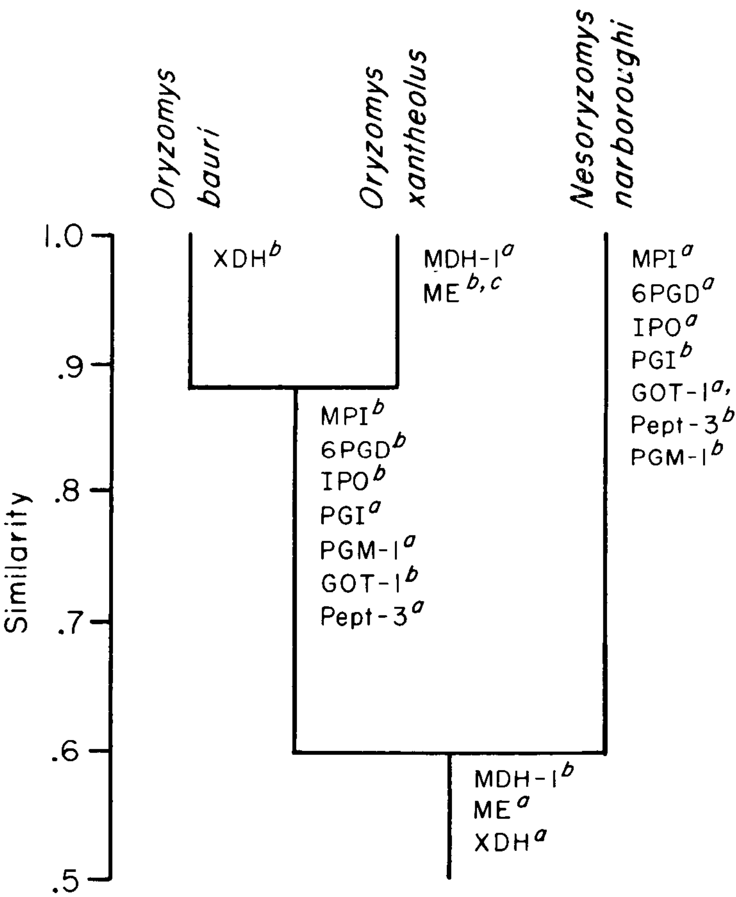


Fig. 3. Phenogram of relationships among the two extant Galapagos species (*O. bauri* and *N. narboroughi*) and the coastal Peruvian relative (*O. xantheolus*) based on electrophoretic analysis of 22 genetic loci (see text). Alleles at those loci which serve to differentiate each lineage are indicated.

Chromosomes

The pattern and extent of chromosomal variability among the oryzomyine complex of Neotropical cricetines has been summarized recently by Gardner and Patton (1976). This report presented karyotypes of *Nectomys, Neacomys*, and representatives of six subgenera of *Oryzomys*, including *Nesoryzomys*. These authors consider *N. narboroughi*, the only extant species of the group, to have the most strongly differentiated karyotype among the array of 34 oryzomyine taxa examined. It has the lowest combination of diploid and fundamental number of any oryzomyine with a karyotype composed primarily of biarmed chromosomes rather than the large number of acrocentrics characterizing nearly all other oryzomyines. The conclusion was reached that "*Nesoryzomys* is so aberrant chromosomally as to demand recognition as a full genus" (Gardner and Patton 1976:20). In a summary of hypothesized phylogenetic relationships among oryzomyines based on karyotypes, Gardner and Patton (1976) remarked that *Nesoryzomys* did not share a close or even obvious relationship with any examined taxon of the group. The karyotypic data at hand, therefore, only demonstrate significant differentiation for *Nesoryzomys* and do not really help in establishing phylogenetic affinities between it and other oryzomyine taxa.

Gross Stomach Morphology

The muroid rodent stomach has recently received attention from workers in mammalian systematics (e.g. Vorontsov 1957; Carleton 1973). Carleton has suggested relationships between 27 South American muroid genera based solely upon the type, location, and extent of stomach epithelial tissues. According to Carleton, 21 of the 27 genera (including several *Oryzomys* species) are fundamentally similar in gastric morphology and show the presumed ancestral unilocular-hemiglandular condition described below. Several other South American genera, representing more or less tight taxonomic units by other criteria, show various degrees of deviation from this basic condition, supporting the taxonomic usefulness of gross stomach morphology.

We surveyed the gross stomach morphology of *N. narboroughi* (4 specimens: MVZ 145382 - 145385), *O. bauri* (5 specimens: MVZ 125460, 145374, 145375, 145380, 145381) and two specimens of *O. palustris* (MVZ 98763 and 126831). The stomachs were excised from the specimens, longitudinally bisected, and preserved in 70% ethanol. Stomach contents were removed and saved. Anatomical observations using a Bausch and Lomb stereozoom microscope (10X-40X) focused on gross stomach shape and the type and extent of epithelial tissues. Although the general anatomical characteristics of the stomach were easily discerned regardless of the degree of stomach distention, only fully distended stomachs were used for illustrative purposes. Terminology follows Carleton (1973).

The gross stomach morphology of *O. bauri* (Fig. 4) is, in most respects, representative of the basic unilocular-hemiglandular condition characteristic of mainland *Oryzomys* species (e.g. *O. palustris*, Fig. 4). This basic type consists of a single large chamber with a cornified proximal portion (corpus) and a glandular distal portion (antrum). The incisura angularis roughly marks the division between the two epithelial zones. The stomach of *O. bauri* does show some noteworthy deviations from the basic and presumed ancestral (Carleton 1973) unilocular-hemiglandular condition of *O. palustris*. The antrum shows a considerably thicker glandular lining that is most apparent at the bordering fold. In all specimens, this hind-region of the gut contained numerous hairs and, in one specimen, sand and some unidentified chitinous material. Likewise, the cornified epithelium of the corpus appears to be somewhat thickened over the *O. palustris* condition. As in *O. palustris*, the antrum is maximally distensible to accommodate a volume of nearly one-half of the entire stomach volume.

The stomach of *N. narboroughi* (Fig. 4) is also of the unilocular-hemiglandular type. However, certain modifications of the basic *O. palustris* condition are noteworthy. First, the antrum is highly glandularized, even more so than in *O. bauri*. Second, the incisura angularis is deep and the

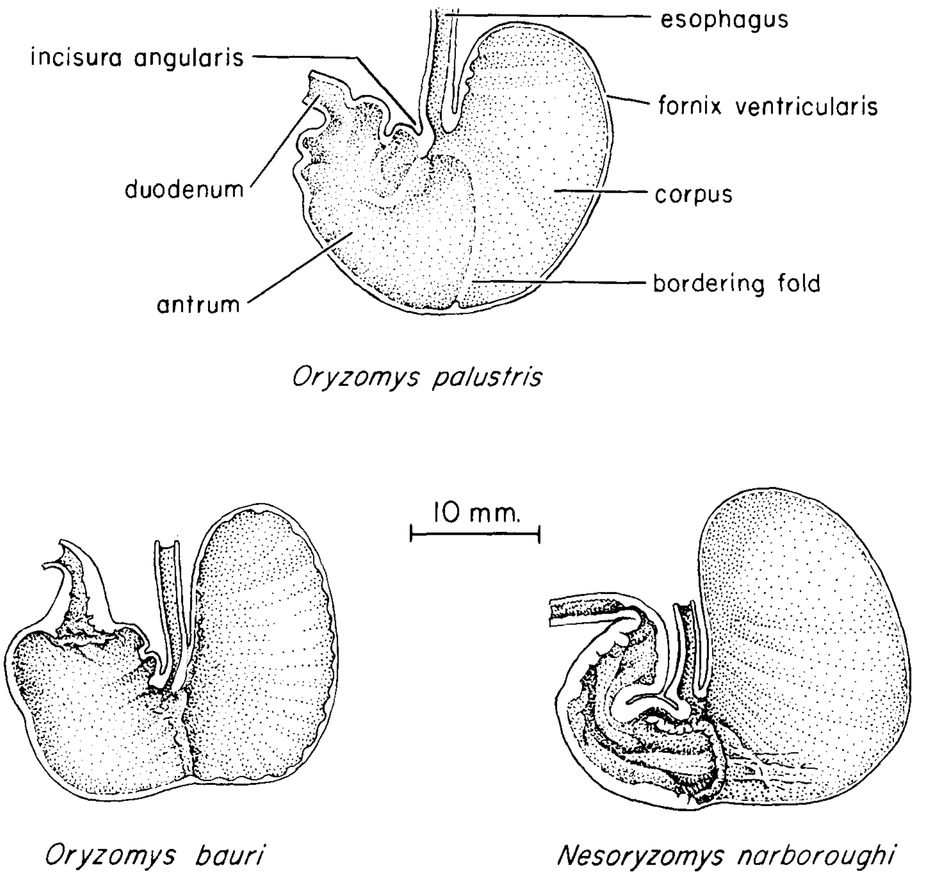


Fig. 4. Details of stomach morphology for two native Galapagos rats (*O. bauri*, MVZ 145374, and *N. narboroughi*, MVZ 145385) and the North American *O. palustris* (MVZ 98763).

bordering fold thus short, resulting in a narrow passageway between the corpus and antrum regions. Third, the antrum region is maximally distensible to accommodate considerably less than one-half of the entire stomach volume. The fornix ventricularis is high and broadly arched over the esophageal opening.

Judging from our specimens, it is evident that the stomachs of both species of native Galapagoan rats have undergone modification from the ancestral mainland type characterized by 21 of 27 genera examined by Carleton (1973). These changes are best interpreted as the result of dietary shifts concomitant with colonization of the islands. The apparent trend towards thickening of the glandular epithelium of the antrum may be related to the observed high incidence of abrasive material in the stomach contents.

As with the karyological survey, comparative gastric morphology does not aid in determining phylogenetic affinities between Galapagoan and mainland oryzomyine taxa. The derived gastric morphology of *Nesoryzomys* and the morphologically intermediate grade seen in *O. bauri* might, however, be interpreted as evidence of an earlier island invasion by *Nesoryzomys*. Considering the lack of knowledge of inter-island diet differences that could account for different rates of stomach modification, this interpretation as to the timing of the island invasions must be viewed in light of evidence from other sources. Certainly though, the stomach of *Nesoryzomys* is significantly differentiated from the basic oryzomyine condition.

Male Accessory Reproductive Glands

Arata (1964) reviewed the pattern and extent of variation in the male accessory reproductive glands of 23 genera of muroid rodents. We here use Arata's description of *Oryzomys palustris* to analyze, on a comparative basis, the degree of differentiation seen in the male reproductive system of the native Galapagos rats. Specimens available for examination were: *Nesoryzomys narboroughi* (3 specimens: MVZ 145382, 145384, 145385) and *Oryzomys bauri* (4 specimens: MVZ 145374, 145375, 145380, 145381). A single specimen of *O. palustris* (MVZ 126831) was used on occasion as a direct comparative reference. All specimens were adult with scrotal testes and enlarged tubules visible in the cauda epididymis. The entire reproductive tract was excised from each specimen and preserved in 70% ethanol. Anatomical observations were made using a Bausch and Lomb stereozoom microscope (10X-40X). Measurements of glands, when included, merely serve to indicate the approximate greatest length and width of the gland for comparative purposes. Determination of homologies within the prostate gland complement was particularly difficult. When in doubt as to whether a prostate element is bilobed or actually represents two separate glands, we have chosen to follow Arata's (1964) conservative approach and consider the element to constitute a single, bilobed gland.

Nesoryzomys narboroughi (Fig. 5). A single pair of preputial glands is present. The glands are smaller in size (10x2 mm) than those of *Oryzomys palustris* as examined by us and figured by Arata (1964). The main mass of each gland lies to the side of the glans penis. Each tapers distally and is drained by a single duct which enters the ventral edge of the preputial orifice.

The paired bulbo-urethral glands lie dorso-laterad to the urethral bulb. These glands are smaller in size than in the *Oryzomys* material examined (4x2 mm versus 8x4 mm in *Oryzomys*). Each gland is drained by a single, large duct that enters the urethra just caudad to the proximal penile urethra.

A single pair of ampullary glands is recognized, each gland intimately associated with its respective vas deferens. Numerous ducts drain each gland entering the lumen near the junction of the ampullary vestibule with the deferent duct. In *Nesoryzomys*, the ampullary glands are enlarged and entirely encircle the vasa deferentia.

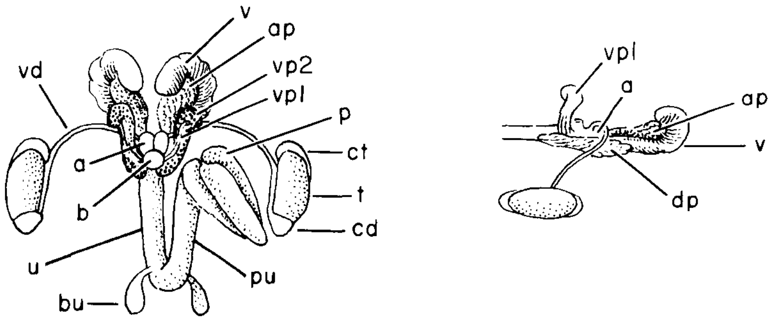
The paired vesicular glands of *Nesoryzomys* are considerably smaller than those of *Oryzomys* (7 mm length versus 17 mm in *O. bauri*). Each gland is approximately pear-shaped, tapering somewhat near its junction with the prostatic urethra just laterad to the vas deferens. While the surface of the vesicular is quite smooth, transparent portions reveal extreme folding of mucous membrane within.

The prostate gland compliment consists of a single pair of dorsal prostates lying along the dorso-lateral aspect of the prostatic urethra. In 70% ethanol, the prostates are white in color. These glands encroach anteriorly onto the vesicular glands for approximately three-quarters of the latter's length. The dorsal prostates are multi-lobed structures that drain into the anterior dorso-lateral wall of the prostatic urethra.

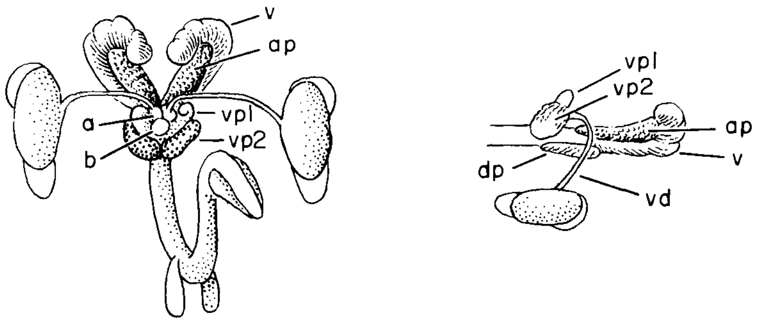
Oryzomys bauri (Fig. 5). The single pair of preputial glands are reduced in size as in the *Nesoryzomys* material examined. Each tapers distally and is drained by a single duct opening at the preputial orifice.

The bulbo-urethral glands of *O. bauri* are less spheroid and more elongate in shape than those of both *Nesoryzomys* and *O. palustris* (8x2 mm in *O. bauri* vs. 8x4 mm in *O. palustris*). In other aspects of general morphology the bulbo-urethral glands are quite similar in all oryzomyine specimens examined.

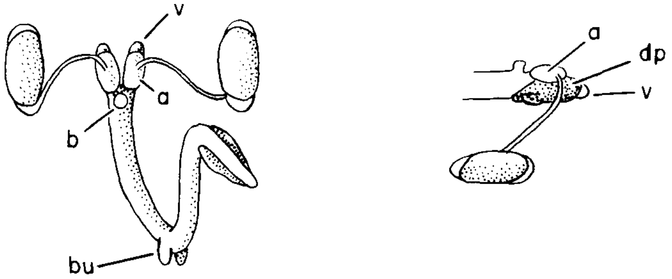
The paired ampullary glands are compact, tubular structures lying adjacent to the vasa deferentia. These glands are of the same approximate size as those of *O. palustris* and are considerably smaller than those of *Nesoryzomys*. The ampullary glands entirely encircle the vasa deferentia and lie compressed between the prostate (ventrad) and vesicular (dorsad) elements. Each gland is



Oryzomys palustris



Oryzomys bauri



Nesoryzomys narboroughi

Fig. 5. Male reproductive tracts of the native Galapagos rats, *O. bauri* (MVZ 145374) and *N. narboroughi* (MVZ 145385) compared to the North American species *O. palustris* (MVZ 126831). a = ampullary gland; ap = anterior prostate; b = urinary bladder; bu = bulbo-urethral gland; cd = cauda epididymis; ct = caput epididymis; dp = dorsal prostate; p = preputial gland; pu = penile urethra t = testis; u = urethra; v = vesicular gland; vd = vas deferens; vp = ventral prostate.

drained by numerous ducts entering the vestibule of the ampulla near its junction with the vas deferens.

The vesicular glands are large, paired structures extending craniad from the prostatic urethra. Each gland is recurved postero-ventrally (and somewhat medially) for approximately the distal one-third of its length. These glands are highly rugose, being lobate along both the lesser and greater margins of the curvature. A single duct drains each gland into the prostatic urethra just laterad to the deferent duct.

Four pairs of prostate glands are recognized. This series closely resembles that described for *O. palustris* by Arata (1964). A large pair of ventrolateral prostates lies caudad and laterad to a smaller pair of ventromedial prostates, each gland draining independently into the prostatic urethra via single ducts. In 70% ethanol, the ventrolateral prostates are red in color, the ventromedial prostates are white. A single pair of elongate dorsal prostates (white in color) lies along the dorsal prostatic urethra extending largely onto the posterior portion of the vesicular glands. The dorsal prostate ducts enter the urethra just caudad to the vesicular ducts. A single pair of anterior prostates (white in color) lies embraced in the lesser curvature of the vesicular glands and is contained within the same connective tissue. A set of two ducts drains each gland into the antero-lateral wall of the prostatic urethra.

The accessory gland complement of the male reproductive system, as with the karyologic and stomach analyses above, sheds little light on the phylogenetic affinities of the endemic island rats. While *O. bauri* exhibits the pattern seen in most oryzomyines, the extreme morphologic divergence in the form of reduction or loss of gland elements in *Nesoryzomys* provides further evidence as to the distinctiveness of this form. In light of current knowledge, it is impossible to attach any degree of functional or taxonomic significance to the differences in glandular complements, save to document these differences and emphasize the uniqueness of *Nesoryzomys narboroughi*.

Glans Penis Morphology

The glans penis and associated bacular apparatus of the Neotropical cricetine rodents have found wide application in both general anatomical and systematic works (e.g. Arata et al. 1965; Hooper 1962; Hooper and Musser 1964). Based upon Hooper and Musser's work, the male phallus of all Neotropical cricetine species is of the "complex" type, that is, generally barrel-shaped with a terminal crater containing an osseous baculum armed distally with a three-pronged cartilaginous tip (see Hooper and Hart 1962 for a more complete description). In efforts to compare the phalli of certain native Galapagos rats with those of mainland species we have examined the glans penis of *Nesoryzomys narboroughi* (4 specimens: MVZ 133122, 133125, 133126 and 145385), *Oryzomys bauri* (2 specimens: MVZ 145375 and 145378), *O. xantheolus* (7 specimens: MVZ 135658, 135660, 135661, 135664, 135665, 135792, and 137943), and *O. palustris* (3 specimens: MVZ 98765, 98768, and 126381). All specimens were adults as determined by reproductive criteria mentioned above. The excised phalli were either preserved directly in 70% ethanol or cleared in KOH and stained with alizarin red as per the methods of Hooper (1958) and Lidicker (1968). Specimens were examined and figured with the aid of a Wild M5 stereomicroscope with a camera lucida attachment. Descriptive terminology follows that of previous workers.

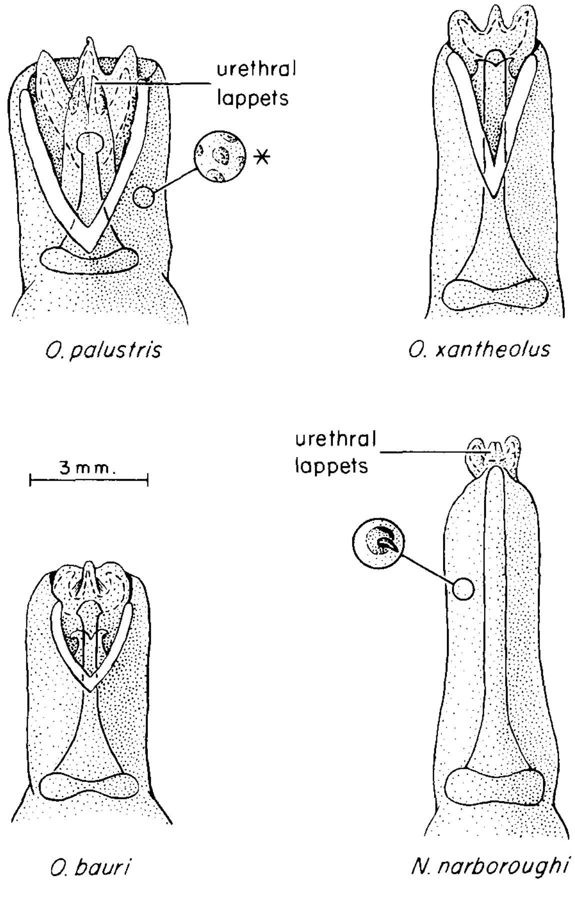
The glans penis of *Oryzomys palustris* (Fig. 6) is of the basic complex type described by Hooper and Musser (1964). The phallus is short and barrel-shaped (length/diameter ratio ~ 1.2) with three relatively long cartilaginous digits. The three digits are nearly equal in length, each measuring approximately 80% of the osseous bacular length. The urethral lappets are large and each has a subapical lobule. Epidermal spines are relatively small and dense.

The phallus of *Oryzomys xantheolus* (Fig. 6) is elongate relative to the *O. palustris* condition (length/diameter ratio ~ 2.3). The terminal crater is shallow and encompasses only the proximal portion of the cartilaginous bacular apparatus. The osseous baculum is long and slender (length/diameter ratio ~ 2.2) and is tipped with three relatively short cartilaginous digits. The medial cartilaginous digit is shorter and more slender than the lateral pair. The length of the entire cartilaginous element is approximately 20% of the os bacular length. The urethral lappets are large and single lobed. Epidermal spines appear much as in *O. palustris*.

The glans penis of *Oryzomys bauri* (Fig. 6) is much like that described for *O. xantheolus*. The phallus is somewhat elongate (length/diameter ratio ~ 1.8) having a terminal crater slightly deeper and enclosing more of the bacular apparatus than in *O. xantheolus*. The osseous baculum is likewise elongate (length/diameter ratio ~2.0) with a much reduced terminal cartilaginous element. Unlike *O. xantheolus*, the medial digit of the latter structure is elongate and slender relative to the lateral pair which is slightly recurved medially. The urethral lappets are small and single lobed. Epidermal spines are as in *O. palustris* and *O. xantheolus*.

The phallus of *Nesoryzomys narboroughi* (Fig. 6) is of the elongate type (length/diameter ratio ~ 3.5) having a very shallow terminal crater. The entire cartilaginous bacular apparatus and the distal tip of the os baculum extend beyond the main body of the phallus. The osseous baculum is long and very slender (length/diameter ratio ~ 3.6) and is tipped with a very small cartilaginous apparatus. The latter element is three-pronged with a much reduced medial digit. The length of the lateral digits approximates only 10% that of the osseous baculum. The urethral lappets are small and narrow and extend beyond the tip of the small medial bacular digit. Epidermal spines are larger and more widely spaced in the *Nesoryzomys* specimens than in other taxa examined.

Based on phallic morphology, Hooper and Musser (1964) divided members of the genus *Oryzomys* into two subgroups: (1) the "*albigularis*" subgroup characterized by a robust phallus



O. palustris *O. xantheolus*

O. bauri *N. narboroughi*

Fig. 6. Ventral views of male phalli of *O. palustris* (MVZ 98765), *O. xantheolus* (MVZ 137592), *O. bauri* (composite of MVZ 145375 and 145378), and *N. narboroughi* (MVZ 133122). A portion of each glans has been excised to reveal details of internal anatomy. Structure and position of the bacular apparatus is indicated by solid line (osseous baculum) and dashed line (cartilaginous baculum). The epidermal spines (*) of *O. xantheolus* and *O. bauri* are similar in structure and density to those figured for *O. palustris*.

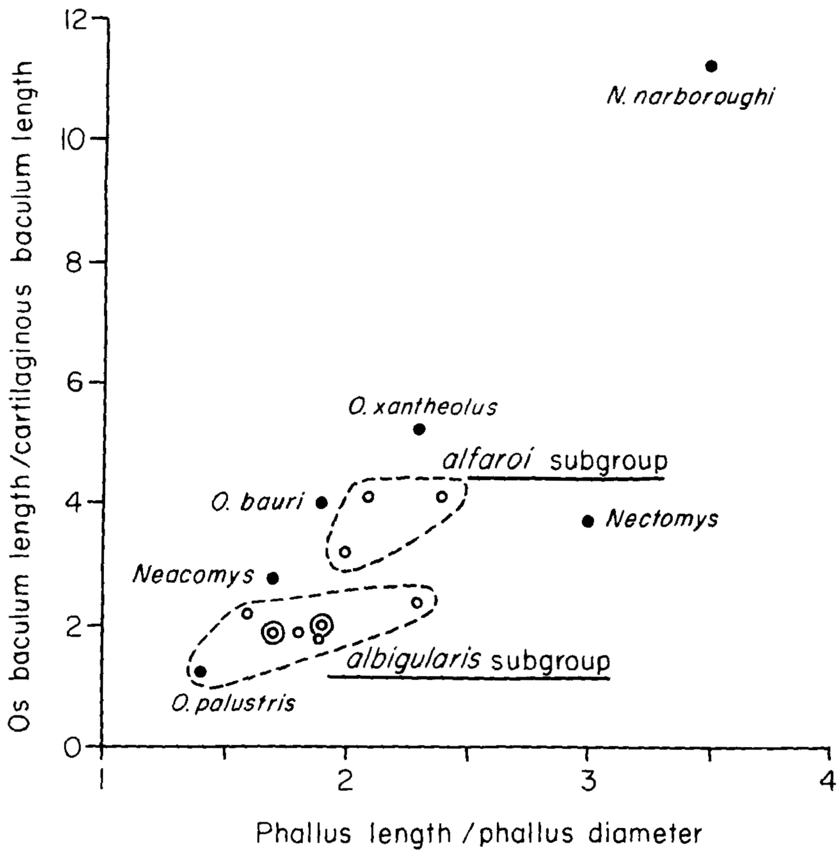


Fig. 7. Plot of bacular and phallus ratios for selected oryzomyine taxa based on data from Hooper and Musser (1964) except for *O. palustris*, *O. bauri*, *O. xantheolus*, and *N. narboroughi*. Species included within the "*alfaroi*" subgroup of Hooper and Musser (1964) are: *O. caliginosus*, *O. alfaroi*, and *O. melanotis*; those included within the "*albigularis*" subgroup are: *O. albigularis*, *O. devius*, *O. capito*, *O. concolor*, *O. flavescens*, *O. fulvescens*, *O. nigripes*, and *O. longicaudatus*.

with the cartilaginous bacular element long relative to the osseous baculum, and (2) the "*alfaroi*" subgroup characterized by a long, slender phallus with a much reduced cartilaginous bacular element. Figure 7 presents a bivariate plot comparing phallic robustness with the relative length of the cartilaginous baculum for the 14 oryzomyine taxa examined by Hooper and Musser (1964) and the three described here. Several aspects of this relationship among the included taxa are noteworthy. First, *Nesoryzomys* (as represented by *N. narboroughi*) is an extreme outlier in comparison to all other oryzomyines, including the genera *Neacomys* (as represented by *N. guianae*) and *Nectomys* (*N. alfaroi*). Second, of the other oryzomyine taxa only *O. xantheolus* shows tendencies of *Nesoryzomys* in terms of type and degree of phallic modification. This tendency is very slight indeed, as *O. xantheolus* is only slightly different from the "*alfaroi*" subgroup. Third, *O. bauri* is quite similar to "*alfaroi*" subgroup taxa but has a slightly stouter phallus than other members.

It is quite clear that *Nesoryzomys* is strongly differentiated and shows little resemblance in phallic structure to any other oryzomyine. While it is more similar to *O. xantheolus* than other taxa, the similarity is minimal and any phylogenetic connection must be remote. It is likely, however, that the basal stock leading to *Nesoryzomys* had a phallus of the type represented by the "*alfaroi*" subgroup. Slight modifications from this condition would lead to both *O. bauri* and *O.*

xantheolus, with change being in somewhat opposite directions: i.e. to a more slender condition in *O. xantheolus* and to a more robust condition in *O. bauri.*

Morphometric Analyses

The varied statistical approaches utilized to examine phenetic similarity among oryzomyine rodents describe two patterns of relationship. Both the cluster analyses based either on distance or correlation matrices and factor analysis show an obvious closeness among the four species of *Nesoryzomys*. However, the different approaches are not unanimous in the placement of *Nesoryzomys* relative to other oryzomyine taxa.

The cluster analyses actually depict three patterns of OTU placement, depending upon the method and character states used. Distance matrices based on both the 28 quantitative characters and the combination of quantitative-qualitative characters give nearly identical phenograms, with four groupings indicated (Fig. 8). There is, however, no association of the four species of *Nesoryzomys* nor other members of currently unified taxa (e.g. *O. palustris* or members of the subgenus *Oecomys*). This phenogram apparently reflects a strong size bias in the taxa examined as the four groups delineated correspond to rats with large, medium, or small body sizes rather than to potential phylogenetic units.

The second pattern, that based on correlation matrices of either all characters combined or quantitative characters only, indicates a marked association of the four *Nesoryzomys* taxa relative to all others (Fig. 9). *Nesoryzomys* as a unit is placed quite apart from other oryzomyines, but is phenetically closer to *Melanomys* than to any other OTU. *Oryzomys bauri* shows closest phenetic similarity to *O. xantheolus*, a species of the subgenus *Oryzomys* inhabiting the dry western

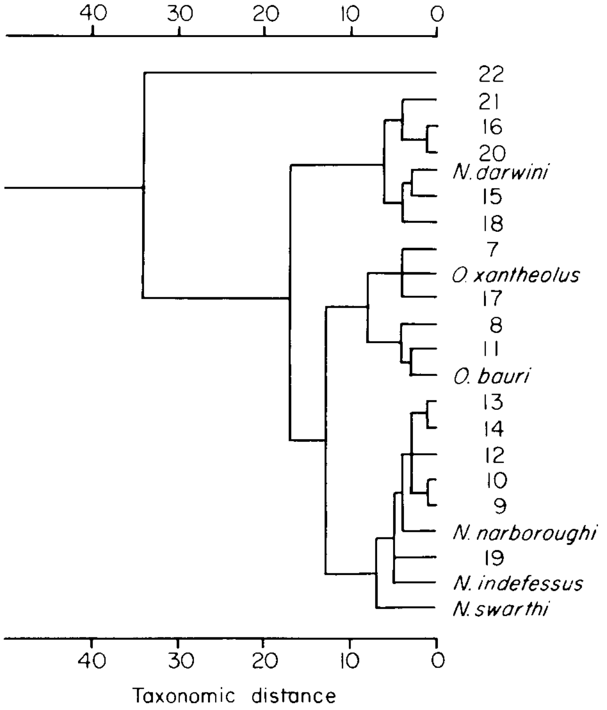


Fig. 8. Distance phenogram of 23 oryzomyine OTU's based on 28 quantitative characters. Numbers refer to OTU's as identified in Materials and Methods section of text. Cophenetic correlation coefficient = .701.

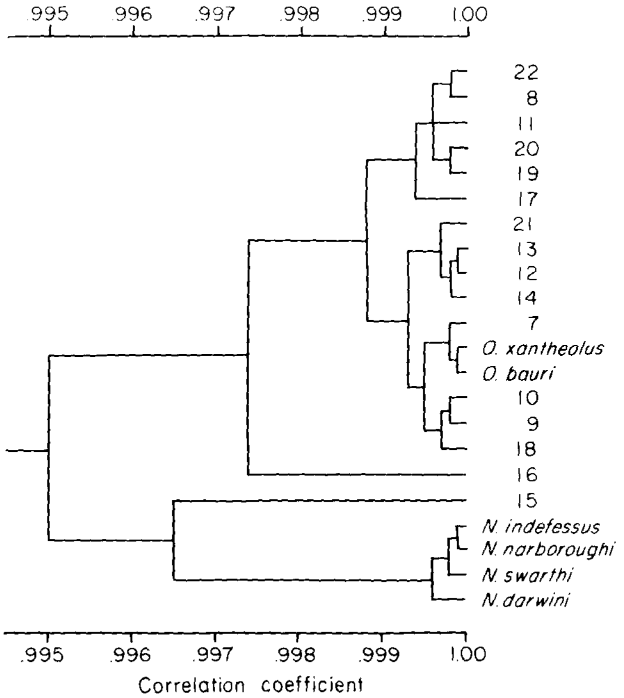


Fig. 9. Correlation phenogram of 23 oryzomyine OTU's based on 28 quantitative characters. Numbers refer to OTU's as identified in Materials and Methods section of text. Cophenetic correlation coefficient = .729.

coast of Peru. Both of these species are included within a larger gorup composed mostly of other medium-sized members of the subgenus *Oryzomys*.

The third pattern is based on both distance and correlation matrices of the 23 qualitative characters. The resultant phenogram (Fig. 10) again clusters all *Nesoryzomys* taxa as a tight-knit unit, but one linked to *O. bauri* and *O. xantheolus*. These taxa form a definite unit relative to other oryzomyines, not joining any of the latter until fairly far out on the dendrogram. The relative placement of OTUs on this phenogram is a very close approximation of most current views on their taxonomy. Such cannot be said for the other phenograms presented.

The factor analysis presents a picture of strong separation of *Nesoryzomys* from the other oryzomyines (Fig. 11). It is thus concordant with the correlation based phenogram for mensural characters. In general, all taxa of oryzomyines fall along a diagonal axis in the three-dimensional plot except for *Nesoryzomys* which is separated by a definite hiatus from this trend. It is apparent in Fig. 11 that members of the subgenus *Oryzomys* group in the center of the plot; species belonging to other subgenera of *Oryzomys* or to *Neacomys* are scattered close to that group; *Nectomys* is well differentiated but in the same directional trend; and *Nesoryzomys* is both separated and off the general trend. *Nesoryzomys darwini*, however, tends to bridge the gap between the main oryzomyine group and other *Nesoryzomys*.

A general size factor is indicated by the dispersion of OTUs along Factor I, which accounts for 76.8% of the total variance. Larger taxa are positioned on the positive side, smaller ones on the negative side (Fig. 11). All mensural characters except TaL and IOC contribute heavily and nearly equally to Factor I (Table 3). On the other hand, Factor II, accounting for 8.6% of the total variance, is most strongly influenced by TaL, IOC, BuL, and RL. The former two characters influence placement along Factor II in a direction opposite that of the latter two characters. Hence, Factor II largely separates out those OTUs with long tails and broad interorbital regions but with

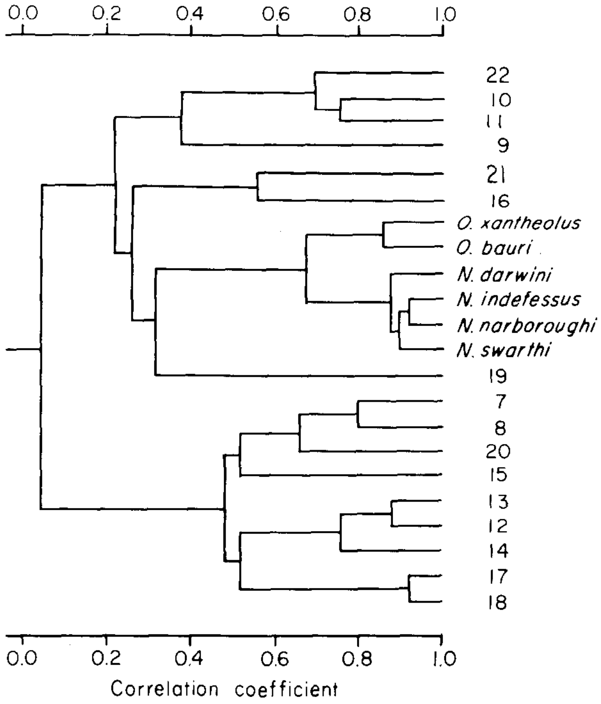


Fig. 10. Correlation phenogram of 22 oryzomyine OTU's based on 23 qualitative characters. Numbers refer to OTU's as identified in Materials and Methods section of text. Cophenetic correlation coefficient = .809.

short bullae and short rostra from those with the reverse combination of characters. *Nesoryzomys*, which is diagnosed by this particular combination of characters, is thus effectively separated along Factor II from all other oryzomyine OTU's examined.

The factor analysis permits us to evaluate the suggestion of Goldman (1918; quoted above)

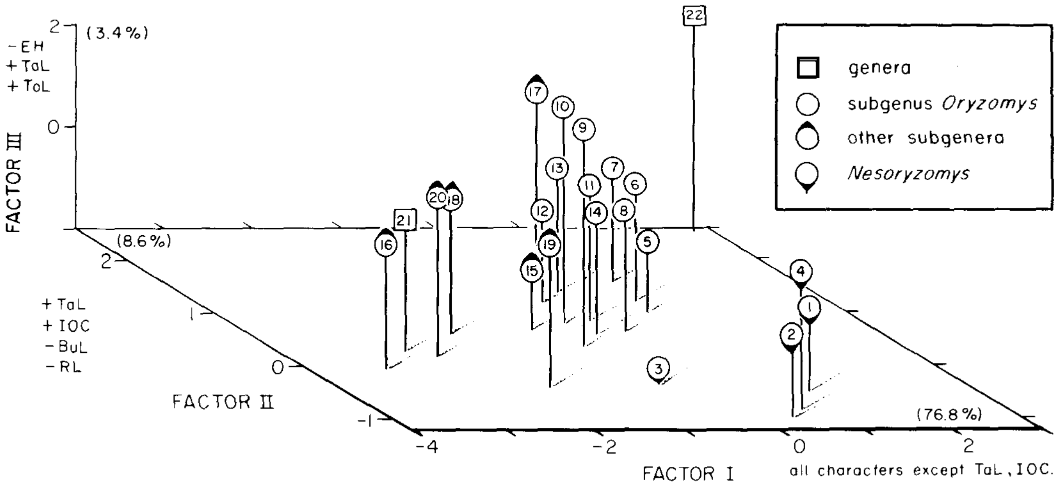


Fig. 11. Plot of the first three Factor axes for the 22 oryzomyine OTU's examined, numbered as in text. The percentage of total variance explained by each axis is given as are the characters which contribute to each axis.

TABLE 3. FACTOR ANALYSIS USING 28 MORPHOMETRIC VARIABLES FOR ALL 22 ORYZOMYINE OTU'S (SEE FIG. 11)

CHARACTER	I	II	III
ToL	.8191	.3942	.2990
TaL	.4882	.7328	.3302
HF	.8172	.3076	.2121
E	.7683	-.2080	-.3385
ON	.9413	-.2707	.1208
BaL	.9693	-.1035	.1517
BB	.9592	-.1621	.0365
ZB	.9730	-.0484	.1366
RL	.8745	-.4197	.0619
DL	.9286	-.2125	.1723
CD	.7947	-.3324	.1604
ACH	.9721	.0228	.1014
BCL	.8651	-.2690	.2368
IOC	.5683	.7254	-.0422
RW	.8958	.1330	.2457
MTRW	.9289	-.2580	-.0743
MTRL	.9489	.0489	-.2050
BuL	.7938	-.5224	-.0713
RD	.9198	-.1688	.2240
mTRL	.9375	.1685	-.2295
RH	.9567	-.0189	.1001
ZPW	.9176	-.0591	-.0377
IFL	.8320	-.1764	.0088
1L	.9291	.0556	-.1749
2L	.8992	.0889	-.1999
3L	.9083	.1894	-.1285
MFPW	.7522	.3586	-.2299
MFPL	.8449	.3721	-.1060
% total variance	76.8	8.6	3.4
Eigenvalue	23.82	2.66	1.07

and others that the diagnostic characters of *Nesoryzomys* are in reality shared by other oryzomyines, hence invalidating the generic status of these endemic Galapagos rats. Several oryzomyines were included in the present analysis which do indeed have features suggestive of *Nesoryzomys* (for example, *Melanomys caliginosus* and *O. xantheolus* have rather short tails and *O. keaysi* has a rounded, hourglass-shaped interorbital region). These taxa, however, fail either to cluster with *Nesoryzomys* in the phenograms or to be positioned with that form in the factor plot. None of the taxa of oryzomyines examined here encompasses the totality of cranial and external configuration characterizing *Nesoryzomys*. Indeed, the endemic rice rats of the Galapagos are the most strongly divergent in general body plan among all those oryzomyines examined, including OTU's currently given generic status.

DISCUSSION

Origin and Timing of Galapagos Endemic Radiation

The distinctiveness of *Nesoryzomys* as a morphologic and phylogenetic unit should no longer be questioned. In consideration of available data for the oryzomyine complex, *Nesoryzomys* is unique and quite divergent in a number of functionally unrelated morphological bases, including karyotype, male accessory reproductive structures, stomach, and glans penis. Indeed, even the nominal diagnostic features of the skin and skull segregate *Nesoryzomys* from other oryzomyines examined herein. While some of these features are seemingly shared with other taxa of oryzomyines, no single species or group of species combines the totality of features that separate *Nesoryzomys* as the most distinctive oryzomyine examined. The summation of data available, therefore, does support the proposal of Heller (1904) of generic status for *Nesoryzomys*.

This conclusion, however, does not aid one in an understanding of the phylogenetic relationships of *Nesoryzomys*. While on an overall phenetic basis *Nesoryzomys* is further from other genera of oryzomyines than the latter are among themselves, this does not mean that it necessarily shares a more distant common ancestor than that, for example of *Oryzomys, Neacomys*, and *Nectomys*. Indeed, an overview of the morphological data given above leaves the question of the relationships and origin of *Nesoryzomys* quite ambiguous. The uniqueness of the male reproductive tract, stomach, and karyotype provide little help to this problem, and the available biochemical data are too incomplete as yet. However, both the structure of the glans penis and certain of the exomorphological analyses provide suggestions as to affinities. A relationship between *Nesoryzomys* (as represented by *N. narboroughi*) and *O. xantheolus* is suggested by similar patterns in glans penis morphology, a pattern which is quite divergent relative to the oryzomyine complex as a whole (Hooper and Musser 1964). This alliance is also seen in the clustering pattern based on the qualitative skin and skull characters which link *Nesoryzomys* with *O. xantheolus* and *O. bauri*. We thus advance the hypothesis that *Nesoryzomys* owes its origin to a "*xantheolus*-like" ancestral stock inhabiting the xeric coastal regions of Peru and Chile. Significantly, this same pattern of origin is seen for *O. bauri* and *O. galapagoensis*, the other Galapagos endemics belonging to *Oryzomys* (*s.s.*). There is no evidence to date which suggests that any of the endemic Galapagos rats have had their origins among tropical representatives of the oryzomyine complex, as suggested by Orr (1966).

While we believe that both *Nesoryzomys* and the two forms of *Oryzomys* from the islands share a similar mode and place of origin, the timing of island invasion must have been considerably different. Several lines of evidence suggest that *Nesoryzomys* is an old immigrant to the archipelago while the *Oryzomys* species are quite recent. The high degree of phenetic distinctiveness of *Nesoryzomys* relative to other oryzomyines argues for a more ancient origin, especially since *O. bauri* is nearly identical in all respects to the mainland *O. xantheolus*. The available biochemical data also support this contention. Two estimates have been proposed as a basis for using the largely time dependent nature of protein change as an "evolutionary clock." One is based on the number and rate of amino acid substitutions in proteins detected by electrophoresis (see Nei 1975, for review) such that time in years (t) since divergence is estimated as $t = 5\text{x}10^6 D$, where D is Nei's genetic distance measure. The second is based on the concordance between distance measures based on electrophoresis and the albumin immunological distance (see Wilson et al. 1977; Sarich and Cronin 1976). In the latter, a Nei D-value of 1 is estimated to correspond to 20-25 million years.

The D-value for *N. narboroughi*–*O. bauri* or *N. narboroughi*–*O. xantheolus* comparisons is about 0.62 (an exact measure is not possible since the electrophoretic data for the three species are not totally equivalent). By Nei's methods, this suggests an origin of *Nesoryzomys* around 3 to 3.5 million years ago. The Sarich and Cronin method provides a considerably higher estimate of divergence time, on the order of 12.4 to 15.5 million years. We are inclined to favor the more recent of these two possibilities for the following reasons. For one, all current estimates based on magnetic reversal sequences and sea floor spreading place the origin of the islands at 4+ million years (see Cox, this volume). Hence, the Nei estimation falls well within this time limit. The alternative requires origin prior to the formation of the Galapagos and is considered less likely. This necessitates origin and radiation of *Nesoryzomys* on the mainland prior to colonization of the Galapagos with subsequent extinction in its place of origin, an hypothesis we find difficult to accept. In any event, the great morphological uniformity among the taxa of *Nesoryzomys* (see below) suggests but a single immigration to the islands, be it of pre-*Nesoryzomys* or *Nesoryzomys* form, with subsequent radiation.

The origin of *O. bauri*–*O. galapagoensis* is surely a more recent development. Electrophoretically, *O. bauri* differs in only a minor fashion at two loci from *O. xantheolus*, and in nearly all morphological analyses the two taxa are barely separable. To our knowledge, this close relationship was first observed by Gyldenstolpe (1932). *O. bauri* is so similar to *O. xantheolus* that we would not be surprised if future studies showed that it was introduced to the Galapagos within the last few hundred to a thousand years, perhaps by aboriginal sailors coursing the west coast of Peru.

Taxonomic Status of the Endemic Species

We have postponed to this point any discussion as to the validity of the various species of endemic rats in the archipelago. Each new island form discovered in the past has been accorded specific status as a matter of course, and no critical examination of the entire group has ever been made. The demonstration of the biological basis for the specific assignment of these forms is, however, impossible. In the first place, except for the sympatric nature of *N. darwini* and *N. indefessus* on Santa Cruz, all species are restricted to allopatric distributions on single islands. Hence, the "test of sympatry" has only been established once. Secondly, since only one species of each of the two endemic groups remains extant, it will never be possible to perform breeding or other experiments to assess the level of reproductive compatibility among the various island forms. We are left, therefore, with the necessity of assessing species status within the complex as a whole on purely morphological grounds. Since this is unsatisfactory in that the results remain equivocal, we here merely characterize the extent of variation among the included taxa and provide our personal biases as to the systematic meaning of this variation pattern.

The assessment of morphological variability within and between the various endemic forms was made by discriminant function analysis based on the 28 quantitative characters and by spectrophotometric analysis of pelage color. The latter analysis was limited to taxa in the genus *Nesoryzomys* since skins of *O. galapagoensis* were not available for study.

A plot of the first and second discriminant functions for the seven taxa examined is given in Fig. 12. Combined, these axes account for 84.2% of the variance seen in the analysis (Table 4). All of the Galapagoan rats are included along with *O. xantheolus* from coastal Peru; the single specimen of *O. galapagoensis* is the holotype from the British Museum (Natural History), kindly measured for us by Dr. John Pizzimenti. The strong separation of *Nesoryzomys* from *Oryzomys* proper is again apparent, but such is not the main point of the graph. It is clear that there are really three, and only three morphological groupings represented. First, the type of *O. galapagoensis* falls well within the cluster of *O. bauri* individuals and is thus inseparable from that form. These two also link closely with *O. xantheolus*, again a reflection of the overall high level of similarity between these species seen in other analyses. This group of three species is then separated from all *Nesoryzomys* along the first discriminant axis. Second, *N. darwini* is clearly differentiated from other members of that genus, with separation achieved along the second axis. The third group thus contains the remaining three forms of *Nesoryzomys* (*swarthi, indefessus*, and *narboroughi*). Among the latter group, *N. indefessus* and *N. narboroughi* are almost totally overlapping in individual placement while the four known individuals of *N. swarthi* are separate from that pair.

These results are fully consistent with the available published record of opinion on the status of these species. The likelihood of conspecificity of *O. bauri* and *O. galapagoensis* was intimated by Heller (1904:240) and Osgood (1929), and the two were placed in synonymy by Cabrera

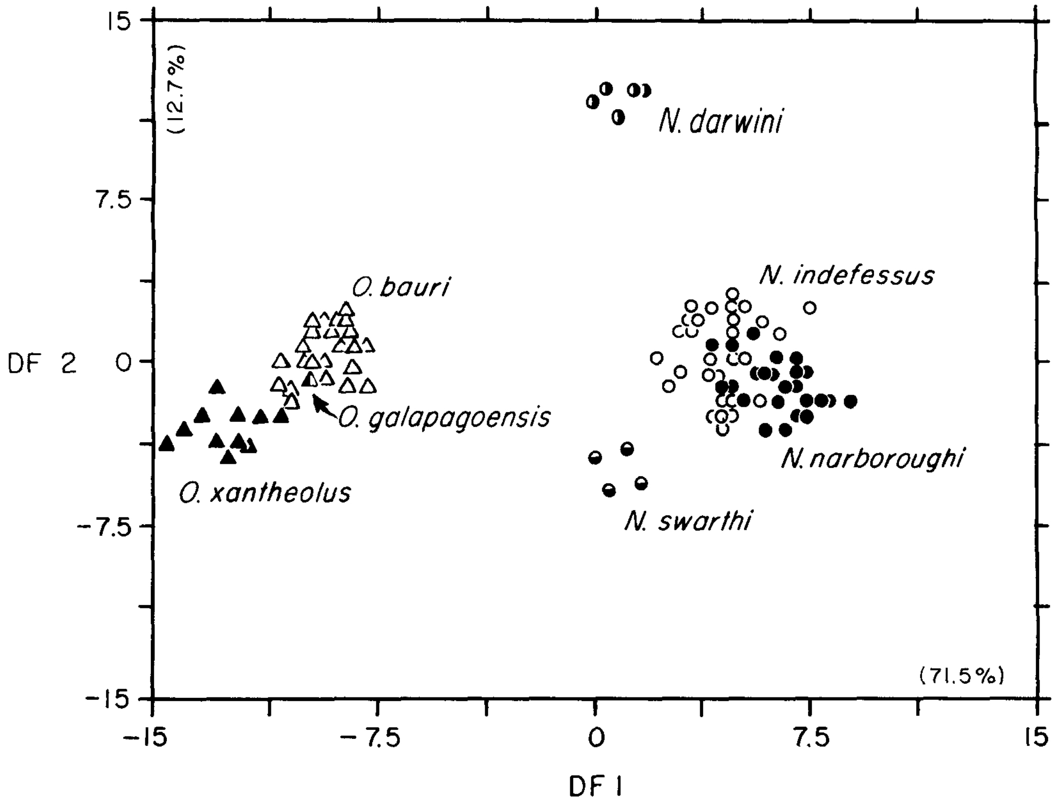


Fig. 12. Plot of the first two Discriminant Function axes comparing the six endemic Galapagos taxa with *O. xantheolus* from the Peruvian coast. The single specimen of *O. galapagoensis* is the holotype; its placement is based on analysis of only 14 of the 28 quantitative characters used for the remaining species.

(1961). Based on the present analysis, we see every reason to argue for this point of view. A similar stand can be made relative to the three large-bodied taxa of *Nesoryzomys*. Orr (1938) was the last author to characterize these species. He noted that *N. indefessus* and *N. narboroughi*, while virtually indistinguishable cranially, were separable primarily on the basis of pelage color. Color differences between the taxa are in the nature of a continuum (see Fig. 13). Complete overlap occurs in color characteristics between *N. indefessus* and *N. swarthi* and, while *N. narboroughi* is noticeably darker than the other taxa, some overlap between it and *N. indefessus* is apparent (Table 5 and Fig. 13). *N. swarthi* possesses certain characters in common with both of the others, being most distinct cranially. As a collective group, however, the three large forms differ much less among themselves than any differ from *N. darwini*. These statements are clearly supported by the discriminant and colorimetric analyses reported here. It is arguable, therefore, that the three large forms of *Nesoryzomys* should best be considered members of a single species characterized by a level of intraspecific variation expected of allopatric populations inhabiting ecologically quite distinct islands. For example, the blackish pelage of *N. narboroughi*, its major distinguishing feature, is to be expected for a form living largely on a black lava substrate. We are thus of the opinion that *N. narboroughi, N. indefessus,* and *N. swarthi* are most realistically considered only slightly to moderately delineated races of a single biological species, for which the name *indefessus* has priority.

TABLE 4. STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS FOR THE FIRST THREE VECTORS

Character	I	II	III
ToL	- .6821	1.2174	.2567
TaL	-1.5331	-1.0539	-1.2329
HF	.7011	-1.1558	- .0457
E	.1903	- .5428	.5565
ON	3.8579	-1.9442	.4998
BaL	-2.0264	2.0423	-3.9496
BB	.1684	.5527	.7720
ZB	- .1490	-2.3254	.2986
RL	1.3083	.8201	-1.1713
DL	.7736	.5153	.6727
CD	.0512	- .0511	- .0856
ACH	- .3800	- .3991	- .4042
BCL	.2569	-1.4193	- .3778
IOC	- .4261	.3445	- .6799
RW	- .6997	.5934	.3418
MTRW	.7579	.2436	.5581
MTRL	.0075	.2381	.5364
BuL	- .1817	- .0219	.5875
RD	.6353	- .7008	.5875
mTRL	- .1290	- .5172	.9102
RH	.3747	.1840	- .2475
ZPW	- .8335	.2426	.7077
IFL	- .8904	- .4653	1.1189
1L	- .3230	- .5330	.5895
2L	- .2295	.0237	.0752
3L	.0561	.4336	-1.0261
MPFW	- .6686	- .6560	.5288
MPFL	-1.3695	.1760	.5788
% total variance	71.5	12.7	10.5
Eigenvalue	52.035	9.267	7.706

TABLE 5. THREE COLOR VARIABLES OF THE PELAGE OF THE FOUR TAXA OF *NESORYZOMYS* FROM THE GALAPAGOS ISLANDS[1]

CHARACTER	*Nesoryzomys indefessus* N=29	*Nesoryzomys narboroughi* N=26	*Nesoryzomys darwini* N=3	*Nesoryzomys swarthi* N=3
Brightness	8.3±0.19 6.46-10.67	5.57±0.11 4.30-6.59	7.52±0.74 6.60-8.99	7.99±0.57 7.11-9.05
Dominant wavelength	583.6±0.12 582-585	583.5±0.32 580-587	585.0±1.15 583-587	583.2±0.33 583-584
Purity	27.50±0.60 18.8-33.3	13.07±0.90 6.1-25.9	28.90±0.78 27.4-30.0	26.20±2.81 21.2-30.9

[1] Mean ± one standard error and range are given.

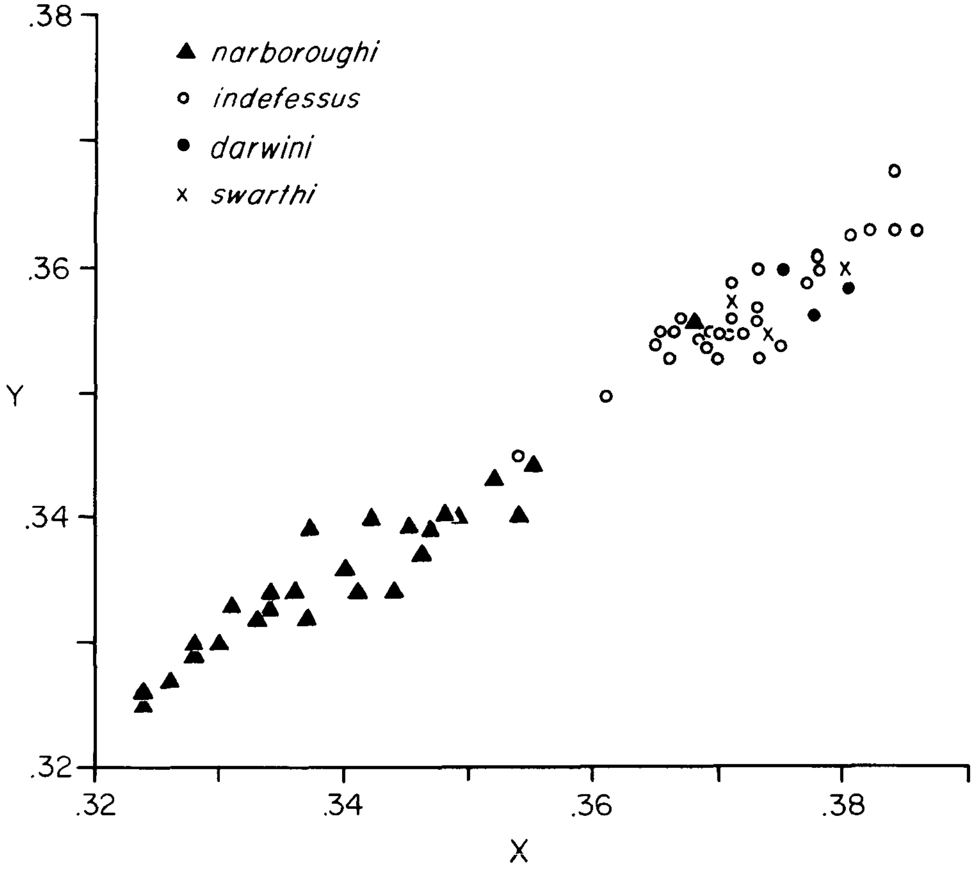


Fig. 13. Chromaticity diagram showing the distribution of trichromatic coefficients, x and y, for the four taxa of *Nesoryzomys*. Note the essentially linear spread of values with complete overlap between *N. indefessus*, *N. swarthi*, and *N. darwini*, and marginal overlap between *N. indefessus* and *N. narboroughi*. The white point (I.C.I. Illuminant C) is at x=.3163, y=.3101.

ACKNOWLEDGMENTS

This report is a contribution of the Charles Darwin Foundation. It could not have been completed without logistical and other support of the Direccion General de Desarrollo Forestal and Parque Nacional Galápagos, Ecuador, and the Charles Darwin Research Station, Galápagos. We are exceedingly grateful to Mrs. Carol P. Patton and Dr. Philip Myers for assistance in the field; Drs. Alfred L. Gardner, John W. Wright, and Philip Myers for relevant discussions; Dr. Peter Kramer and Mr. Craig MacFarland for logistical support at the Darwin Research Station; Dr. Luis de la Torre, Field Museum of Natural History, and Mrs. Jacqueline Schonewald, California Academy of Sciences, for permitting examination of specimens in their care; and Dr. John J. Pizzimenti for measuring the holotype of *O. galapagoensis* in the British Museum (Natural History). Illustrations were drawn by Mr. Gene M. Christman of the Museum of Vertebrate Zoology. Financial support was made available by the Janss Foundation, the Museum of Vertebrate Zoology, the Penrose Fund of the American Philosophical Society, and a Biomedical Sciences Support Grant from the U.S. Public Health Service.

RESUMEN

La fauna nativa de roedores en el archipiélago de las Galápagos consiste en siete especies pertenecientes al grupo generalizado de las "ratas de arroz" neotropicales de la familia Cricetidae. Esta especies forman tres complejos diferentes, siendo cada uno de ellos definido con rango genérico o subgenérico: (1) *Oryzomys* (*sensu stricto*), incluyendo *galapagoensis* (conocida solamenta en la Isla San Cristóbal) y *bauri* (de la Isla de Santa Fe); (2) *Nesoryzomys*, que incluye a las especies *narboroughi* (de la Isla Fernandina), *swarthi* (de la Isla Santiago), *darwini* (de la Isla Santa Cruz), y *indefessus* (de las islas Santa Cruz y Baltra); y (3) *Megalomys curioi* (de la Isla Santa Cruz). *Megalomys* conocido solamente por material subfósil no va ha ser tratado en este trabajo. Cuatro de las restantes seis especies están probablemente extintas ya que solo se conocen actualmente poblaciones activas de las especies *O. bauri* y *N. narboroughi*.

El tiempo, patrones de radiación biológica y relaciones filogenéticas de *Oryzomys* y *Nesoryzomys* son estudiados por medio de investigaciones cariológicas, bioquímicas y anatómicas de las dos únicas especies vivientes, y por análisis multivariable de caracteres morfométricos de ejemplares, preservados en colecciones de museos, pertenecientes a todas las especies. Nuestros datos sugieren lo siguiente: a) *Nesoryzomys* es una unidad claramente distinta y debe ser reconocida a nivel genérico; b) se pueden definir al menos dos invasiones, independientes una de la otra, a las islas, en donde *Nesoryzomys* representa un colonizador más temprano, seguido bastante más tarde por *Oryzomys* (*s. s.*); c) ambos grupos de *Oryzomys* son immigrantes bastante recientes y son indudablemente derivados de *O. xantheolus* de los valles fluviales de la región costera de Perú, o de un antepasado común; d) el origen de *Nesoryzomys* es poco claro actualmente; e) las especies de mayor tamaño del género *Nesoryzomys* (*narboroughi, swarthi* e *indefessus*) deberían ser consideradas razas de una misma especies que se diferencian solamente por el color del pelaje; f) similarmente, *O. galapagoensis* y *O. bauri* deberían ser consideradas conespecíficas.

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APPENDIX I

Specimens Examined

All specimens of Galapagos endemic rats utilized in this report are represented by standard museum preparations and are deposited in either the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); the California Academy of Sciences, San Francisco (CAS, or SU if part of the Stanford University collection housed by that institution); or the Field Museum of Natural History, Chicago (FMNH). Localities and sample sizes follow:

Nesoryzomys narboroughi Heller, 1904. Isla Fernandina: Punta Espinosa (23♂, 20♀ - MVZ 125476-125477, 133122-133129, 145382-145391; CAS 2505-2515, 2479, 2483, 2485-2488, 13273-13274, 13276, 13278-13279); Mangrove Point (9♂, 10♀ - FMNH 30832-30841, 30843-30844; SU 2468-2474).

Nesoryzomys indefessus (Thomas, 1899). Isla Santa Cruz: Academy Bay (22♂, 15♀ - FMNH 30847-30849, 30852-30855, 30847, 30869; CAS 2527-2532, 2534-2547, 2549-2553, 2575-2576); Conway Bay (7♂, 2♀ - FMNH 30869-20875, 20877, 30869); North Santa Cruz (3♂, 2♀ - SU 2463-2467). Isla Baltra: (16♂, 9♀ - FMNH 30859-30868; CAS 2490-2498; SU 2454, 2457-2461).

Nesoryomys darwini Osgood, 1929. Isla Santa Cruz: Academy Bay (4♂ - FMNH 30828-30829; CAS 2533, 2548); Conway Bay (1♂ - FMNH 30831).

Nesoryzomys swarthi Orr, 1938. Isla Santiago: Sullivan Bay (4♂ - CAS 2556, 2561-2563).

Oryzomys bauri J. A. Allen, 1892. Isla Santa Fe: northeast coast (18♂, 19♀ - MVZ 125469-125470, 145372-145381; FMNH 49012-49013, 51756-51757, 51761-51770; CAS 2478, 2480-2482, 2489; SU 2449-2453).

APPENDIX II

Remarks on the Current Status of Galapagos Endemic Rats

Oryzomys galapagoensis (Waterhouse, 1839)

This rat was collected by Darwin from Chatham (=San Cristóbal) Island during his visit in 1835 and was subsequently described by Waterhouse in 1839. Darwin noted that the species was abundant, but no subsequent expedition has secured specimens. Heller (1904) considered the species extinct, or if indeed extant, that it must be restricted to the barren eastern end of the island where Darwin secured his specimens. No mammalogical investigations of this section of the island have been made, to our knowledge, since Darwin's visit. Nevertheless, it is very doubtful that *O. galapagoensis* remains extant. Both *Rattus rattus* and *Mus musculus* have been introduced to the island, the former prior to 1891 (see Patton, et al. 1975).

Oryzomys bauri J. A. Allen, 1892

Specimens of this species were collected on Barrington (=Santa Fe) Island by Dr. G. Baur on the Salisbury Expedition in 1892, and subsequently described by Allen in 1892. Dr. Baur noted that the animal was common in all major habitats and all subsequent workers have held the same opinion. Brosset (1963) estimated a population size of from 1000-2000 individuals in 1962. The species breeds during the rainy season, from January through April (Rosero Posso 1975). No introduced rats have ever been recorded from the island. In its current abundant state, *O. bauri* is in no danger of extinction.

Nesoryzomys indefessus (Thomas, 1899)

This species was first collected by Webster and Harris of the Rothschild Expedition in 1897 on Indefatigable (=Santa Cruz) Island. It was originally described as *Oryzomys indefessus* by Oldfield Thomas in 1899. Heller (1904), as a member of the Hopkins-Stanford Expedition of