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The Species of *Oryzomys (Oligoryzomys)* in Paraguay and the Identity of Azara's *"Rat sixième ou Rat à Tarse Noir"*

by
Philip Myers
and
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Mammal Division, National Museum of
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WILLIAM D. HAMILTON, EDITOR

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INTRODUCTION

Members of the subgenus *Oligoryzomys,* genus *Oryzomys,* are an important component of small mammal communities in the neotropics; nevertheless, their systematics are poorly understood. Tate (1932b) listed 44 named forms, many known from a single locality or from one or a few specimens, and at least three species have been described since. Many of these names will prove to be synonyms, but because of its complexity and the lack of material, *Oligoryzomys* has yet to be revised.

A further impediment to understanding the systematics of *Oligoryzomys* is our inability to confidently assign species to early specific epithets. The first description of an *Oligoryzomys* was by Azara (1801, 1802), who described the mammals he found in Paraguay but did not provide scientific names or designate type specimens. Subsequently, other authors — among them Fischer (1814), Illiger (1815), Olfers (1818, *fide* Hershkovitz, 1959), and Desmarest (1819) — provided names for many of Azara's descriptions. As far as we can determine, however, they based their taxa solely on Azara's writings, without seeing any of his specimens, and they did not designate types. These names, together with other taxa described in the 1800's, have seriously confused the systematics of *Oryzomys* in South America. The resulting nomenclatural morass is readily evident in the literature and in systematic collections, wherein names such as *nigripes, longitarsus, longicaudatus, flavescens,* and *eliurus* are inconsistently applied. Moreover, the taxonomic treatment accorded *Oligoryzomys* is decidedly uneven. For example, Cabrera (1961) retained nine species of small *Oryzomys* (he did not recognize *Oligoryzomys* as a subgenus), yet Hershkovitz (1966) allocated all South American *Oligoryzomys* to the species *nigripes.*

Extensive new collections from Paraguay (see Fig. 1), including localities near Atyrá, where Azara (1801) obtained his specimens of *Oligoryzomys (rat à tarse noir,* vol. 2:98), have allowed us to identify three species of *Oligoryzomys* from that country. Only two of these occur in the vicinity of Atyrá and thus might have been the basis for Azara's description. In this paper we attempt: 1) to identify and properly diagnose Azara's *rat à tarse noir;* 2) to clarify the systematics of species of *Oligoryzomys* from Paraguay; and 3) to review the status and relationships of some related forms from other parts of South America.

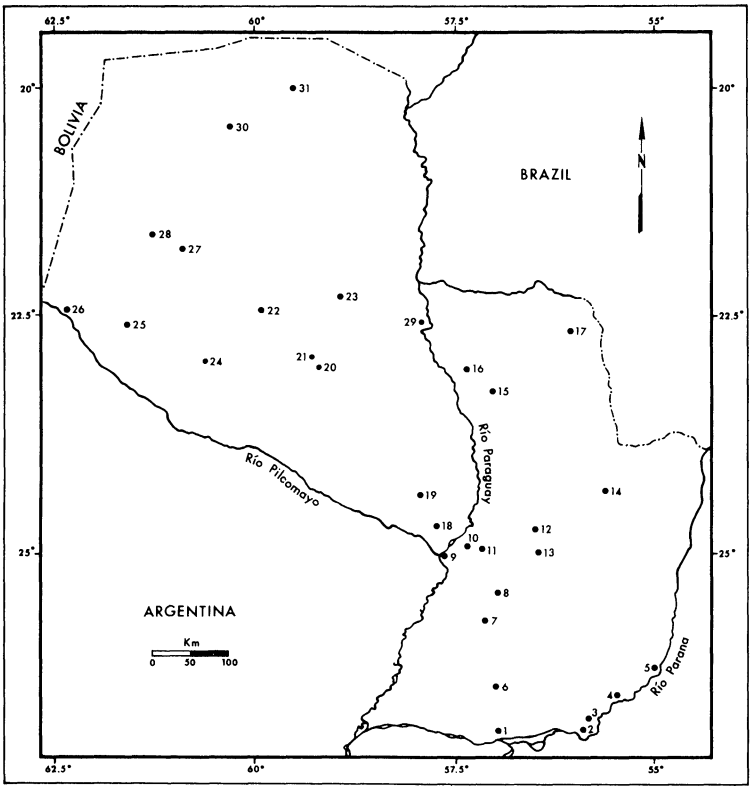

Fig. 1. Map of collecting localities in Paraguay. 1=Misiones, 2 km by rd. NE Ayolas; 2=Itapúa, 8 km W Encarnación; 3=Itapúa, 20 km by rd. NNE Encarnación; 4=Itapúa, Río Pirapó; 5=Itapúa, vic. San Rafael; 6=Misiones, 2.7 km N San Antonio; 7=Paraguarí, Parque Nacional Ybycuí; 8=Paraguarí, Sapucay; 9=Central, Asunción; 10=Central, 17 km by rd. E Luque; 11=Cordillera, 1.6 km by rd. S. Tobatí; 12=Caaguazu, 24 km NNW Carayaó; 13=Caaguazu, 25 km by rd. N Coronel Oviedo; 14=Canendiyu, vic. Curuguaty; 15=Concepción, 40 km by rd. E Concepción; 16=Concepción, Río Aquidabán at Paso Horqueta; 17=Amambay, vic. Cerro Corá; 18=Presidente Hayes, 24 km NNW Villa Hayes, La Golondrina; 19=Presidente Hayes, 69 km by rd. NW Villa Hayes; 20=Presidente Hayes, vic. Río Verde; 21=Presidente Hayes, vic. Juan de Zalazar; 22=Boquerón, vic. km 419 Trans Chaco Hwy; 23=Presidente Hayes, 85 km E Loma Plata; 24=Boquerón, Estancia Pirazal; 25=11 km NW Fortín Teniente Pratts Gil AF Base; 26=Boquerón, Dr. Pedro P. Peña; 27=Nueva Asunción, 19 km by rd. WSW km 588 Trans Chaco Hwy, Copagro; 28=Nueva Asunción, Teniente Ochoa; 29=Presidente Hayes, Puerto Piñasco; 30=Chaco, 50 km WNW Fortíin Madrejón, Cerro León; 31=Chaco, 123 km E Mayor Pablo Lagerenza, Agua Dulce.

ACKNOWLEDGMENTS

Many people and organizations have played important roles in the development of this report, and in the faunal survey of Paraguayan mammals from which it arises. Field work was supported by grants to the senior author from the Rackham Foundation, University of Michigan, and NSF DEB 77 04887. The Paraguayan Minister of Agriculture and Livestock, Ing. Agr. Hernando Bertoni, facilitated our obtaining permits and provided much encouragement. Personnel of the Servicio Forestal Nacional, especially Ing. H. Moreno and the director, Ing. P. Calabrese, kindly allowed us to carry out surveys in several national parks. The U.S. Military Attache, Col. Charles Wallis, helped us in obtaining permits for travel within Paraguay. Ed and Judy Borjesson, Robert Eaton, and Antonio Espinosa kindly permitted us to work on their ranches, and made life in the field much easier with their hospitality. The study benefitted immeasurably by the encouragement and practical assistance of Mr. and Mrs. Philip Myers, Jr., in Asunción. In the field we were ably and enthusiastically assisted by G.K. Creighton, F.S. Dobson, C. King, P. Kreisberg, L.G. Myers, P. Myers IV, R.M. Myers, T. Nelson, R.W. Storer, R.S. Voss, and R.M. Wetzel. Curators at several museums in the U.S. have aided us both with specimens and discussion; these include A.L. Gardner (USNM), G.G. Musser (AMNH), J.L. Patton (MVZ), D.O. Straney (MSU), R. Timm (FMNH), and R.M. Wetzel (UCM). A.L. Gardner and L. Heaney made extensive and valuable editorial suggestions. Finally, we thank M. Orsen and M. Van Bolt for assistance with the preparation of figures; D.O. Straney for providing us with a computer program to estimate the relative contribution of age and sexual variation; and personnel of the Statistical Research Laboratory, University of Michigan, for advice on the statistical techniques used.

METHODS

MEASUREMENTS.–Twenty cranial measurements were taken to the nearest 0.01mm by means of a craniometer (Anderson, 1968), as follows (measurements not defined below are self explanatory or follow Musser, 1979, though some abbreviations differ from his):

ZygoNot, zygomatic notch: from the anterior to posterior margin of the zygomatic notch.

LRostrum, length of rostrum.

GLS, greatest length of skull.

Zygo, zygomatic breadth.

BB, breadth of braincase.

IOC, interorbital constriction (breadth).

MM, breadth across molars: measured as greatest breadth from labial side of one upper molar toothrow to the labial side of the other.

LincFor, length of incisive foramen.

PalBrid, length of palatal bridge.

Bulla, length of bulla.

LM^1, LM^2, LM^3, crown lengths of M^1, M^2, and M^3.

WM^1, WM^2, WM^3, crown widths of M^1, M^2, and M^3.

NasProj, nasal projection: measured from lateral view with skull pressed to a plexiglass plate (ventral surface in contact with plate); distance (parallel to plate) from tip of nasals to face of incisors.

Diastema: measured with skull in above position, distance from cutting edge of incisors to the inflexion in the anterior face of M^1 at the gum line, or, in extremely worn teeth, to the anterior edge of the crown.

Max, length of maxillary toothrow: measured in the above position, distance from the inflexion in the anterior surface of M^1 to the posterior end of M^3.

HBulla, height of bulla.

Body measurements were taken either by the senior author or under his supervision; those taken by other investigators were not entered into the analyses. A copy of the original data matrix can be obtained from the senior author.

AGE CLASSES.–Specimens were divided into age classes on the basis of toothwear (dental terminology follows Reig, 1977):

Age class I: M^3 newly erupted or not fully erupted, M^2 unworn;

Age class II: M^3 slightly to moderately worn, but occlusal surface not flat; M^2 slightly worn; internal part of mesoflexus of M^2 cut off from external part and forming an enamel island;

Age class III: M^3 flat or slightly concave, although paracone may still rise above surface; enamel island formed by mesoflexus of M^2 well isolated; M^1 and M^2 appearing substantially worn;

Age class IV: surface of M^3 concave; enamel island formed from mesoflexus of M^2 obliterated; teeth strongly worn but main cusps still discernable;

Age class V: surfaces of M^1 and M^2 flat or concave, most or all of folding pattern obliterated by wear.

Males in age class I had small testes, the pelage of individuals of both sexes usually indicated immaturity, and many were obviously not fully grown. Animals in age class I were excluded from further statistical treatment except as noted in the analyses of patterns of variation that follow.

Samples with fewer than five adults (age class II or older) were excluded from the analyses of geographic variation and phenetic relationships. To increase some samples, we combined several localities on the basis of geographic proximity and similarity of habitat. Thus the sample labelled Paraná is a combination of localities 1-5; Ybycuí, 6-7; Central 9-11; Carayaó, 12-13; Zalazar, 20-21; and Copagro, 27-28 (see Fig. 1).

STATISTICAL METHODS.–We used statistical routines from BMD (Biomedical Computing Program, Health Science Computing Facility, University of California, Los Angeles) and MIDAS (Statistical Research Laboratory, University of Michigan, Ann Arbor), and a program provided by D.O. Straney for estimating variance components.

Sexual dimorphism and differences in age structure among populations are conspicuous features in *Oligoryzomys* populations. Both are common to many species of mammals but rarely are treated appropriately. Here we have used the method outlined by Straney (1978) to estimate the contribution of age and sex to total variation.

Sexual dimorphism was evident from inspection of the data and from ANOVA. The average difference between males and females is small, however, with males 2-3% larger. ANOVA is sensitive to minor differences in means, especially if sample sizes are large (Straney, 1978). We wished to know not only if significant dimorphism occurred, but if that dimorphism contributed substantially to total character variation. We analyzed six characters (Table 1), chosen to contrast some variables exhibiting substantial age variation (*e.g.*, greatest length of skull) with some having little age variation (*e.g.*, length of maxillary toothrow); and similarly for substantial sexual variation (*e.g.*, zygomatic breadth) *vs.* little sexual variation (*e.g.*, width of interorbital constriction). Only animals in age classes II-IV, which normally would be considered adults, were analysed. Results for a large collection of *O. nigripes* from one locality are presented in Table 1. Age was responsible

TABLE 1
RESULTS OF ANALYSIS OF SEX AND AGE VARIATION USING STRANEY'S (1978) METHOD
(excluding Age Class I)

Variable	Percent contribution of			
	Age	Sex	Interact.	Error
		Oryzomys nigripes		
GLS	70**	0	0	30*
Zygo	65**	0	5	30*
IOC	7	0	0	93**
Bulla	10	0	0	90**
Max	0	1	0	99**
LM^2	22	1	0	77**
		Oryzomys, new species		
GLS	29*	0	0	71**
Zygo	21	0	0	79**
IOC	3	0	0	97**
Bulla	0	0	0	100**
Max	14	0	0	86**
LM^2	40*	0	0	60*
		Oryzomys fornesi		
GLS	52*	8	0	40*
Zygo	25	8	0	67**
IOC	0	0	0	100**
Bulla	1	0	0	99**
Max	0	0	0	100**
LM^2	8	0	0	92**

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

TABLE 2
TWO-WAY ANOVA FOR NONGEOGRAPHIC VARIATION IN POPULATIONS OF *O. NIGRIPES* AT YBYCUI

Character	error df	F (sex)	F (age)	F (interaction)
GLS	43	13.69***	32.09***	.23
Zygo	47	16.37***	34.76***	2.19
IOC	48	1.61	2.44	.01
Bulla	48	2.30	3.76*	.37
Max	49	4.70*	.32	.33
LM^2	49	3.61	5.21**	.55

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

for a substantial fraction of the total variation in some, but not all, characters (Table 1). In all but length of M^2, the value of the character increased with age, while LM^2 tended to decrease due to toothwear. In no character was the proportion of the total variation accounted for by sex significantly different from zero despite the presence of significant differences between sexes in several characters (Table 2). Moreover, inspection of frequency histograms, and the results from Liliefors tests (Conover, 1971) on the most frequent age classes (II+III) for the same six characters, revealed no deviation from normality when both sexes were included. Accordingly, we combined measurements from males and females in our phenetic analyses.

Inspection of frequency histograms of age classes strongly suggested differences among populations in age structure. Both sexual differences in age structure at a single locality (Fig. 2) and geographic differences in age structure (Fig. 3) were found. Differences in age structures are expected among populations that undergo episodic breeding (including at least *O. longicaudatus,* Schneider, 1946). Analysis by Straney's (1978) method demonstrated that age accounts for a large proportion of the variation of some characters (Table 1), so that differences in age structure among populations cannot be ignored. Two-way ANOVAs (BMD×64, which permits unbalanced cells) were used on data classified by sex and age to test for the significance of sexual differences, and on data classified by age and locality to test for geographic variation. Obviously immature animals (age class I) were excluded and, because BMD×64 does not allow empty cells, age classes III, IV, and V generally were combined and contrasted with age class II.

The substantial age variation made difficult the scanning of population means for geographic trends, and added unwanted variation to the clustering procedures. For example, small average measurements of a population might be due to geographic variation, or to an unusually large number of young adults in the population, or to a sex ratio favoring females, the smaller sex. We employed covariance analysis, using age (toothwear class) as covariate, to provide reasonable estimates of each variable for comparing popula-

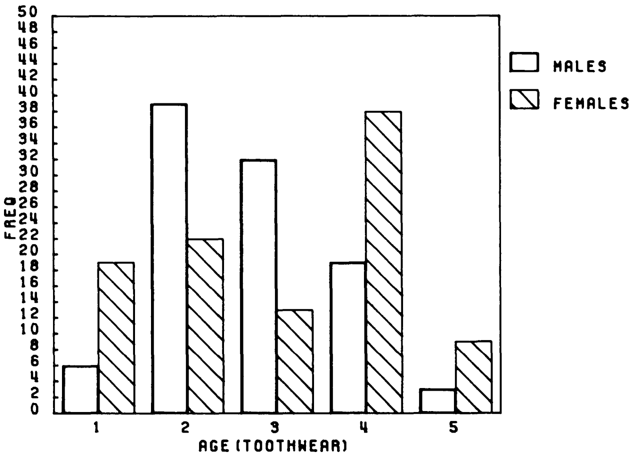

Fig. 2. Histogram showing sexual differences in age structure in populations of *Oryzomys nigripes* at Ybycuí National Park; columns show percentage of population in each age class.

tions differing in average age. All animals, including those in age class I, were considered in this analysis, which calculates means "adjusted" to compensate for differences in age among populations. It affected most strongly those variables that obviously change most with age; others, such as most tooth measurements, which show little or no relationship to age, were unchanged.

Several assumptions are made in using a covariance analysis. Slopes for the regression of the dependent variable examined on age must be the same for each population. This was generally true; for the few variables where equality was rejected, covariance had no significant effect on the means and the "unadjusted" values were used. A more serious problem is that growth is not linear. Furthermore, our age classification used an ordinal rather than interval scale because absolute ages were not known; the amount of growth occurring in class I, for example, may not be the same as that in other classes. Scatter plots of variables against age class revealed monotonically increasing and generally linear relationships for those variables in which the inclusion of age significantly modified the means. Therefore, we believe use of covariance is justified and was helpful in this case, though perhaps the levels of significance for differences of the adjusted means should be viewed with suspicion. Accordingly significance levels are not reported below. The use of covariance analysis clearly is not justified except when the above assumptions are met, and we do not recommend general uncritical use of the method.

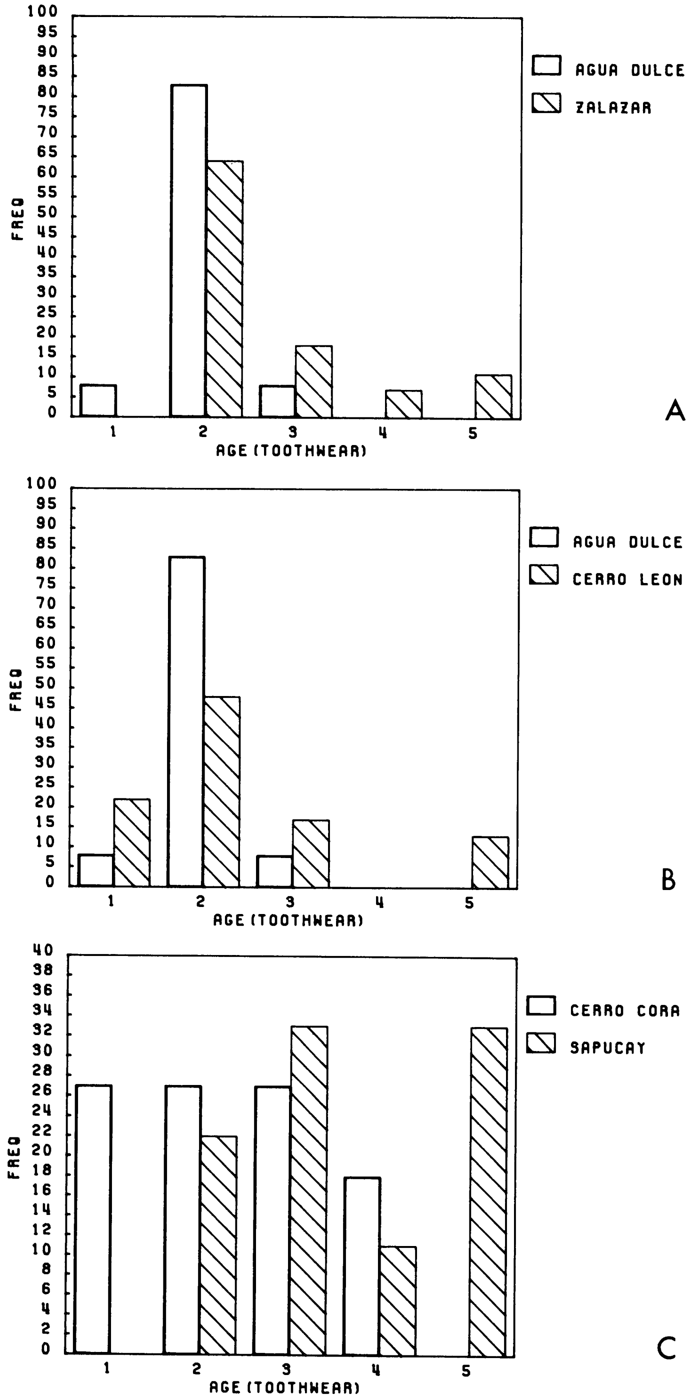

Fig. 3. Histogram showing geographic differences in age structure of *Oligoryzomys* populations; columns show percentage of population in each age class. A. *O.* new species, Agua Dulce *vs.* Zalazar. B. *O.* new species, Agua Dulce *vs.* Cerro León. C. *O. nigripes,* Cerro Corá *vs.* Sapucay.

KAROTYPES.–To decrease the field supplies for preparation of karyotypes and to increase the number of animals processed, the senior author combined the technique developed by Patton (1967) with a method often used for the preparation of testis tubules for analysis of meioses. The revised procedure requires no centrifuging, and the tissues are returned to the lab preserved in Carnoy's fixative (obviating the need for preparation of slides in the field). The technique proved useful in that large numbers of animals were processed easily and quickly. The quality of the karyotypes, however, suffered somewhat. The rate of cell fragmentation was high, and the degree of spreading of cells was sometimes less than optimal.

The object of the revised technique is to leave the marrow cells attached to bone rather than in suspension. See Patton (1967) for details of times and solutions for *in vivo* culturing. Remove the femur and split it lengthwise with scissors. Breaking the bone into smaller pieces may be helpful, particularly for larger animals. Place the pieces in hypotonic citrate in a 15mm centrifuge tube and incubate for about 10 minutes. Pour off the citrate solution; a small amount will remain around the tissue at the bottom of the tube. Slowly dribble in Carnoy's fluid. After approximately five minutes agitate the solution gently to mix thoroughly. After 10-15 minutes change the Carnoy's fixative, wait 2-3 minutes, and change it again. Place the tissue, still attached to the femur, in a labelled 1 dram screw-cap vial filled with Carnoy's fluid.

On returning to the laboratory, scrape a small amount of marrow from the bone and place it in a few drops of 60% acetic acid. Tease it apart, and aspirate gently with a pipette several times to break up clumps. Pipette drops of the suspension on to a warm (40° C) slide, allow it to sit for a few seconds, and pipette off the remaining fluid. We repeat the procedure several times for each slide, attempting to cover the slide while minimizing overlap of the resulting rings of cells. Allow the slides to dry, and stain with Giemsa as usual. Slides have been prepared from material stored in Carnoy's fluid for over 6 months. C-banding of chromosomal material prepared in this manner has been moderately successful.

Oryzomys, subgenus *Oligoryzomys*

A general description of Paraguayan *Oligoryzomys* follows.

EXTERNAL CHARACTERS.–Brown dorsally, individual hairs with basal half or more plumbeous, distal part brown on most hairs, but black in some, resulting in the appearance of black lining on a brown base. Color of crown of many individuals grayer; rump darker, sometimes redder (especially older animals); sides paler; venter distinctly paler than sides, either white, grayish, or buffy, with individual hairs plumbeous basally. Youngest animals much grayer than adults, although tips of dorsal hairs are brown and ventral hairs, grayish white. Tail unicolored to weakly bicolored, scantily clad with short hairs; no or weakly developed pencil; length of tail in adults averages 128% (111% - 171%) head-body length. Feet white above, soles dark; terminal tufts of hairs on toes moderately developed; first hind toe (minus claw) does not reach distal end of first phalanx; fifth hind toe (minus claw) reaches or exceeds joint between first and second phalanges of fourth; postdigital plantar pads 1-4 large, five small, intertarsal pad intermediate; length of hind foot averages 25.5% (19.0% - 32.2%) of head-body length in adults. Pinnae internally covered with fine hairs, which in all Paraguayan species usually are orangish over at least part of their length; pinnae sparsely to moderately haired externally, hairs at base of pinnae pale, those towards tips and anterior margin darker; ears moderately large, averaging 67% (48% - 83%) length of hind foot.

CRANIAL.–(Fig. 4). Braincase moderately large; rounded in young animals and with weak temporal and occipital ridges developing in older; interparietal large; interorbital region hour-glass shaped, least width less than width of rostrum, sides squared but not conspicuously ledged; zygoma moderately flared and slightly convergent anteriorly; incisive foramina extending to level of first molars; palate ends at or behind level of last molar, length of palate equal to or slightly less than breadth across molar rows (from labial edge to labial edge); post-palatal foramina present, but not recessed in deep pits; parapterygoid plates at level of posterior end of pterygoids broader than mesopterygoid fossa, external borders slightly convex; sphenofrontal foramen and squamosal groove absent; stapedial foramen present and large; sphenopalatine vacuities, postglenoid and subsquamosal foramina present; bullae medium-sized, approximately equal in length to toothrow.

DENTAL.–The descriptions of oryzomyine teeth given by Hershkovitz (1944, 1960), Langguth (1963), and Massoia (1973) adequately characterize the Paraguayan species, which differ slightly and only in size of teeth (Table 13).

REPRODUCTION.–A minimum of five reproductive tracts of adult males of each of the Paraguayan species was dissected and compared with tracts of *O. flavescens* from Buenos Aires, *O.l. longicaudatus* from Coquimbo Province, Chile, and *O.l. philippii* from Malleco Province, Chile. The glans penis and baculum of *O. flavescens* from Argentina were described by Hooper and Musser (1964) and closely resemble the Paraguayan species. The only differences detected among the Paraguayan forms are in absolute size of the glans and baculum. The male accessory glands are as described by Voss and Linzey (in press) for oryzomyines. Preputial glands are present in at least some individuals of each species, though they may be poorly defined. In a few males the neck of the gland appears incompletely subdivided, perhaps indicating two pairs of preputials as in some other South American cricetines.

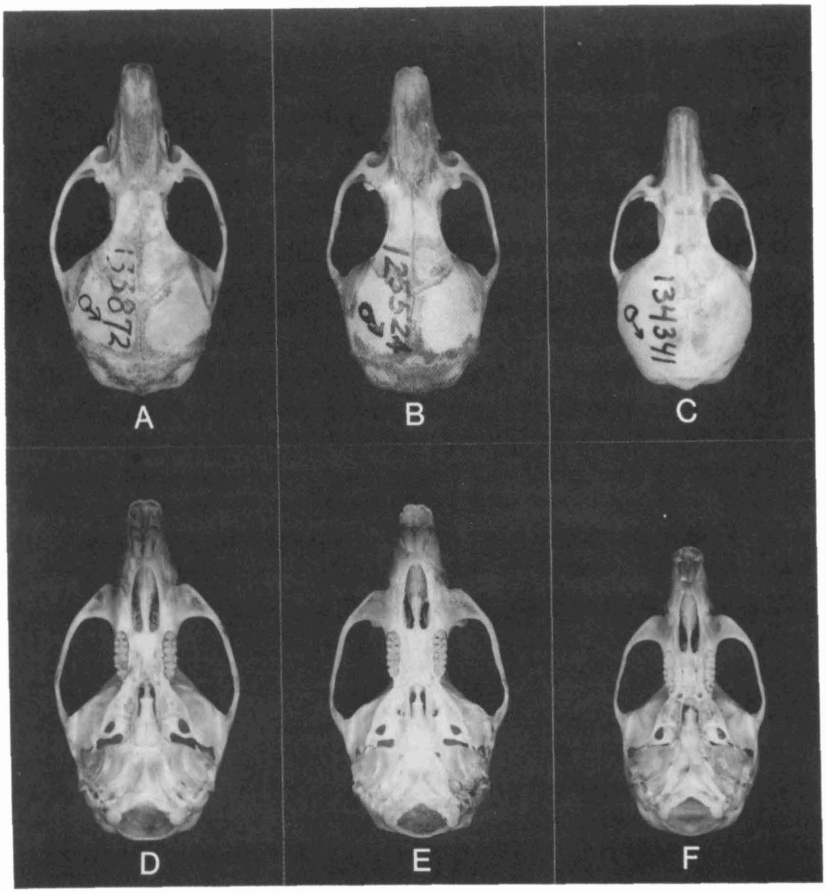

Fig. 4. Dorsal and ventral views of crania. A,D. *Oryzomys nigripes;* neotype, UMMZ 133872, B, E. *O.* new species; holotype, UMMZ 125524. C,F. *O. fornesi;* UMMZ 134341, captured at La Golondrina, Dept. Presidente Hayes, Paraguay.

Individuals of both sexes of the three Paraguayan species appear to reach sexual maturity while in age class II.

FOOD HABITS AND STOMACH MORPHOLOGY.–A cursory examination of the contents of the stomachs of at least five individuals of each of the Paraguayan species was made. No detailed analysis was attempted because most mice were live-trapped and held for a period of time before preparation. All stomachs contained vegetable material and small amounts of insect chitin.

Stomach morphology is similar to that reported for *O. nigripes* (Carleton, 1973). No difference among the species was detected.

COMPARISONS.–Members of the subgenera *Oligoryzomys* and *Microryzomys* are distinguished from other *Oryzomys* primarily by their small size. The distinctiveness of *Microryzomys* and *Oligoryzomys* from one another has been questioned. Tate (1932b) placed *Microryzomys* in synonomy under the subgenus *Oligoryzomys*, while Osgood (1933) argued that, of the two, *Microryzomys* is more highly differentiated from other *Oryzomys*. We agree with Osgood that *Microryzomys* is distinctive and deserving of subgeneric status. It differs from *Oligoryzomys* as follows: more slender rostrum, shallow zygomatic notch; shorter, rounded braincase; sphenofrontal foramen and squamosal groove present; and karyotype with a low FN/2*n* ratio.

The basis for formal recognition of *Oligoryzomys* is weaker than for *Microryzomys*. As pointed out by Ellerman (1941:342), who recognized the subgenus, species commonly are assigned to *Oligoryzomys* based on their size and their "combination of relative rather than absolute characters." Recent descriptions of the glans penis (Hooper and Musser, 1964) and the karyotype (Gardner and Patton, 1976) buttress this statement. Cabrera (1961) suggested that *Oligoryzomys* species are too weakly differentiated from members of the subgenus *Oryzomys* to deserve formal status. We agree with Gardner and Patton (1976), however, that the group is cohesive and should stand alone, even though absolutely diagnostic characters have not been found. Our data on karyology conform with the pattern presented by Gardner and Patton (1976) and reinforce their conclusion.

Oryzomys nigripes (Olfers, 1818)

NOMENCLATURE.–The name *nigripes* was first given to Azara's *rat à tarse noir* (=*colilargo* in the 1802, Spanish, edition) by Olfers (1818). To our knowledge, no types have been designated or described for any of Azara's *Oryzomys* (*rat troisième ou angouyá, rat seconde ou rat á grosse tête,* and *rat sixième ou rat á tarse noir*). Two problems immediately confront the systematist interested in Paraguayan *Oryzomys:* (1) priority and acceptability of names, and (2) assignment of species to names based on Azara's descriptions.

Regarding the appropriateness of the various names for *rat à tarse noir,* Langguth (1966) made two points that are relevant here. First, Illiger's (1815) descriptions are inadequate and should be considered *nomina nuda* (a point made earlier by Hershkovitz, 1959). Second, Fischer's (1814) *Mus tarso nigro* antedates Olfer's (1818) *Mus nigripes,* the name currently accepted for this taxon (Hershkovitz, 1959). Fischer's *tarso nigro* has not appeared as a senior synonym for well over the 50 years required by the code. Olfer's *nigripes,* on the other hand, is used widely in the literature and in collections. More importantly, as noted by Sabrosky (1967), Fischer's (1814) names are not properly available because he did not consistently use binomial nomenclature in accordance with Article 11(c) of the Code. For example, his use of *Mus tarso nigro* and *Mus laucha et lauchita* indicates that he simply listed and translated verbatim names from the literature. Moreover, Fischer sometimes employed names in the synopsis to his work that are different from those appearing in his text. Due to these problems we consider Fischer's *Mus tarso nigro* invalid.

For further discussion of the history of the nomenclature of this taxon see Tate (1932a, b), Hershkovitz (1959), Langguth (1966), and Massoia (1973).

Regarding the assignment of an actual taxon to *rat à tarse noir,* the description provided by Azara is lengthy and detailed but unfortunately includes many characters shared with other South American cricetines. This led Massoia (1973) to suggest that the name *nigripes,* considered by many the appropriate specific epithet for *rat à tarse noir* (and presumably other names applied to Azara's description of that species), be designated a *nomen dubium.* Recent Paraguayan collections, including those from the vicinity of Atyrá, where Azara obtained his specimens of *rat à tarse noir,* have allowed us to identify with a high degree of confidence the animal that Azara described.

Azara clearly described an *Oligoryzomys.* No other Paraguayan rodent, native or introduced, young or old, has a similar combination of small size, tail substantially longer than head-body, brown dorsum, and whitish venter. Two species of *Oligoryzomys* are distributed over eastern Paraguay; both occur near Atyrá. One is small, has especially small ears, and in our experience is uncommon and restricted to grassy marshes. The larger species is much more common, has proportionately larger ears, and occurs in a variety of habitats.

Much of the confusion surrounding *rat à tarse noir* arises from Azara's measurements of the body and tail, which are too small to represent an adult of any species of rodent at Atyrá. In the University of Michigan collection, the closest fit to Azara's measurements was obtained with two young of the larger species of *Oligoryzomys* at Atyrá, which have total and tail lengths near Azara's (total length=140, 164mm *vs.* Azara's 148.9mm; tail length= 82, 97mm *vs.* 76.7mm; Table 3). No young of comparable age was available for the smaller species; the youngest animal examined has total length=161 and tail length=89. The young of the large species have a gray venter and grayish-brown back, while the smallest individual of the small species is dark grayish buff on the belly and grayish brown dorsally. Young of both species are thus unlike Azara's mice, which had whitish venters and cinnamon-brown backs. Adults of the larger species at Atyrá have grayish white venters and brown or reddish brown backs, while adults of the smaller species have buffy or grayish buffy bellies and brown backs. Given these color differences it is apparent that Azara examined adults, not juveniles, of one of these species, suggesting that the body and tail measurements are erroneous. Further, Azara (1801, vol. 2:100) reported several ear measurements. Of these we could duplicate only the measurement of distance between the ears, which Azara gives as 18mm. This dimension characterizes adults of the larger species, and distinguishes them from adults of the smaller species. If the body and tail measurements are rejected, then on the basis of belly color and the measurement between the ears a case for the identity of Azara's species with the larger of those present at Atyrá is made.

A much stronger argument can be constructed, however, based on the detailed description given by Azara, and in particular on his comparison of

TABLE 3
MEASUREMENTS OF *OLIGORYZOMYS*[1]

Species	Total	Tail	Body	Hind foot[2]	Between ears[5]	Source of measurements
nigripes	148.9	76.7	72.2	23.7	18	Azara (1801)
longitarsus	174	95.7	78.3	19.6	....	Rengger (1830)
eliurus	230.6	130.5	100.1	....	....	Wagner (1845)
fornesi[3]	188.0 (165-212)	105.5 (93-118)	83.0 (60-95)	23.7 (21-26)	13.2 (11-14)	This study
nigripes[4]	224.8 (161-270)	125.5 (100-149)	99.3 (78-116)	24.8 (21-28)	17.4 (15-19)	This study

[1]measurements in mm: one *pouce* = 27.07mm; 1 *zoll* = 26.1mm (Hershkovitz, 1975)
[2]*tarsus* of Rengger
[3]mean and range of 50 adult specimens
[4]mean and range of 80 adult specimens
[5]measured as distance between ear notches on fluid-preserved specimens; mean and range of 5 adult specimens

the *rat à tarse noir* with the house mouse, *Mus musculus,* of which he had a specimen at hand. Careful reading of Azara's account, with examples of *M. musculus* and the two species of *Oligoryzomys* at hand, leaves no doubt that Azara described the larger of the species at Atyrá. The statement that *rat à tarse noir* has head and feet larger than those of a house mouse is decisive. No individuals of the smaller species of *Oligoryzomys* reach this size, while most animals of the larger species at age class III or older exceed *M. musculus* in size, especially in their heads and feet (which are proportionately as well as absolutely larger than those of *Mus*). Finally, Azara's specimens came from gardens, habitat characteristic of the larger, but not the smaller, species in Paraguay. Although we believe the body and tail measurements given by Azara are erroneous, we accept the remainder of his description as an accurate description of the larger of the two species occurring in that area. Therefore, we assign the name *Mus nigripes* Olfers, 1818 to the larger species.

NEOTYPE.–University of Michigan Museum of Zoology number 133872, an adult male preserved as skin and skull with body in fluid, plus karyotype; collected on 20 June 1979 by P. Myers (field no. 3930); captured on the floor of subtropical forest at Ybycuí National Park, Department Paraguarí, Paraguay. A specimen was chosen from this site, which lies approximately 85km SSE Atyrá, because the habitat is similar to that originally present at Atyrá (but now largely destroyed), because a large series of this species was available to us from that locality, and because the populations inhabit a protected area and are likely to remain available to investigators.

DIAGNOSIS.–A medium-sized species of the subgenus *Oligoryzomys* characterized by grayish-white venter with white-tipped hairs (occasionally mixed with buffy hairs), often with an orangish pectoral band; long ears; lack of supraorbital shelf; relatively long toothrow; weak development or complete absence of preputial glands; and $2n=62$. In Paraguay it is distinguished from *O. fornesi* by toothrow > 3.3mm, length of bulla > 3.3mm, larger rostrum, and longer ears (> 14mm) which are less densely furred on the inner surface, as well as by its karyotype, preferred habitat, and the absence or weak development of preputial glands. A similar species of *Oligoryzomys* (described below) inhabits western Paraguay; it can be distinguished from *nigripes* by its paler, yellower dorsal color, whiter venter, which never has a pectoral band; hairs of throat usually white to base; complete or almost complete absence of a dark basal band on the same hairs internally clothing the pinnae (prominent in *nigripes*); and by its karyotype (Fig. 5).

DISTRIBUTION.–In Paraguay, *O. nigripes* occurs east of the Paraguay River and is generally absent from extensive grasslands and marshes. We have assigned specimens from several localities in Dept. Misiones and one in Dept. Chaco, Argentina to this species, but the limits of distribution of *nigripes* are not yet defined.

EXTERNAL CHARACTERS.–As previously described under *Oligoryzomys* and as follows (capitalized color terms from Ridgway, 1912): middle of dorsum and rump Tawny to Isabella, approaching Dresden Brown on head; older individuals Hazel to Vinous Rufous over rump; all individuals at least moderately lined with black, lining most distinct on head; cheeks often orange; paler and less heavily lined on sides of body, many individuals with a narrow but fairly distinct orange-brown lateral line separating dorsum and venter; hairs on chin white to base, but white-tipped with basal 2/3 - 3/4 gray on throat and rest of venter, where hairs occasionally washed with buff; basal gray usually visible, giving belly a frosted appearance; orange pectoral band often present. Tail unicolored or weakly bicolored, 126% (112 - 150%) of head-body length. Feet relatively small, length 24.5% (21.5 - 27.9%) of head-body. Ears long, 70% (59 - 82%) length of hind foot, hairs on inside each with basal 50% or less black or brown, distal part orangish or tan.

KARYOTYPE.–$2n=62$, FN=80 (Fig. 5). Thirty-five individuals (15 females and 20 males) from five localities (Curuguaty 20; Ybycuí 10; Paraná 3; Carayaó 1; Cerro Corá 1) were karyotyped. No variation in $2n$ or FN was noted. The X chromosome is a medium-sized acrocentric; the Y, a small acrocentric. The idiogram appears identical in gross morphology to that described for *eliurus* from São Paulo, Brazil (Yonenaga *et al.*, 1976), including the occurrence of a possible pericentric inversion in the third pair of biarmed elements (Fig. 5) in some individuals.

MEASUREMENTS AND DESCRIPTION OF NEOTYPE.–Total length 219; tail 119; hind foot 26; ear 18; Depth of zygomatic notch 1.40; length of rostrum 7.76;

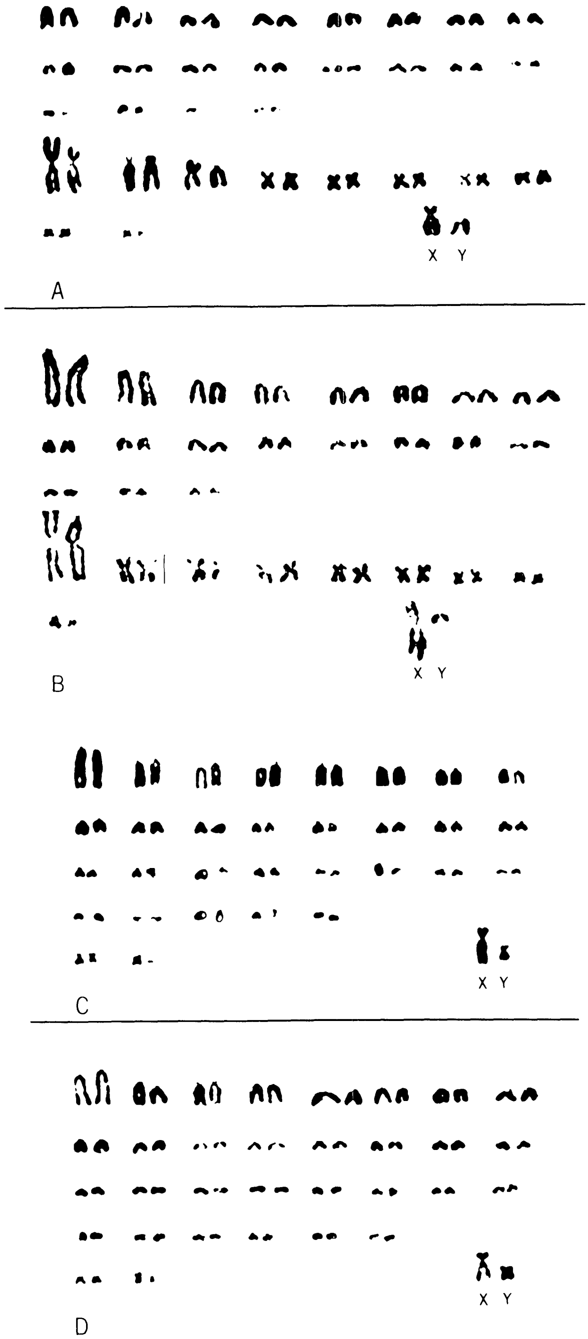

Fig. 5. Karyotypes of Paraguayan *Oligoryzomys*. A. *Oryzomys nigripes*. B. *O.* new species C.D. *O. fornesi*.

greatest length of skull 25.74; zygomatic breadth 14.06; breadth of braincase 11.55; interorbital constriction 3.81; breadth across molars 4.78; length of incisive foramen 4.95; palatal bridge 3.69; length of bulla 3.60; length of M^1 1.68; length of M^2 1.11; length of M^3 .82; width of M^1 1.05; width of M^2 1.10; width of M^3 .90; nasal projection 1.89; diastema 5.81; length of maxillary toothrow 3.59; height of bulla 2.85. Descriptive statistics, based on large samples of *nigripes,* are given in Table 13.

The neotype is an adult in age class II. The dorsum is approximately Tawny, moderately lined with black. The cheeks and pectoral band are distinctly orangish. The venter is whitish, but with a faint buffy wash.

NONGEOGRAPHIC VARIATION.–Color within a population is remarkably variable; some variation is attributable to age, none to sex.

Two sets of morphometric data were analyzed. First, a limited set of characters was measured from a large sample (n=62) captured within a two-week period in June at Ybycuí National Park. Individuals were classified by age (classes II and III compared to classes IV plus V combined) and sex and considered in a 2-way ANOVA. Significant differences among age classes were seen in four of six variables, and between sexes also in four of six variables (Table 2). Analysis by the method of Straney (1978), however, shows age contributes substantially and significantly to variation in two out of six characters, whereas the effect of sex is small or undetectable relative to total variation (Table 1).

A second set of ANOVA's was performed to include all variables. To increase sample size, several sites from central Paraguay were combined; and to prevent empty cells age classes III-V were lumped to be contrasted with age class II. The results were similar to those from the Ybycuí population (Table 4). Seven characters show significant age variation, and seven significant sexual variation. For several characters, F(sex) is larger than F(age), suggesting a relatively large contribution to total variation by sex. In these cases, however, analysis by Straney's (1978) method revealed that neither sex nor age adds significantly to total variation.

GEOGRAPHIC VARIATION.–No geographic variation in color was detected.

Two-way analyses of variance of 20 cranial measurements (Table 5) classified by age and locality revealed significant geographic variation in only two variables (nasal projection and length of bulla). For most there is a slight, statistically insignificant, tendency for specimens from more central populations (Ybycuí, Curuguaty) to be larger than those from farther south (Paraná) or north (Cerro Corá) (Table 6). Populations of *eliurus* from Itapetininga and Casa Grande, São Paulo, differ from the Paraguayan populations of *nigripes* only in their slightly smaller average size, especially as evidenced by their teeth; the differences were not statistically significant.

REPRODUCTION.–An average of 3.57 embryos (range, 2-5) was recorded in a sample of 21 pregnant females. Most trapping was carried out between early June and late August, precluding a determination of breeding season.

TABLE 4
NONGEOGRAPHIC VARIATION IN *O. NIGRIPES*[a]
RESULTS OF TWO-WAY ANOVAs

Character	Error df	F(sex)	F(age)	F(interaction)
ZygoNot	44	2.67	1.71	1.29
LRostrum	44	4.49*	14.70**	1.36
GLS	43	6.82*	6.91*	.73
Zygo	42	11.62**	5.37*	1.69
BB	42	10.41**	1.46	.86
IOC	44	3.97	1.56	3.88
MM	43	3.36	8.44**	.13
LincFor	44	6.75*	12.63***	.14
PalBrid	43	.00	6.94*	2.89
Bulla	43	1.61	.29	.74
LM^1	44	1.33	.14	1.01
LM^2	44	6.87*	3.82	.43
LM^3	44	1.81	2.84	.13
WM^1	44	3.14	3.41	.02
WM^2	44	2.80	.92	.52
WM^3	44	.51	.05	.34
NasProj	44	.13	.91	.56
Diastema	44	9.86**	26.73***	.53
Max	44	2.62	.01	1.65
HBulla	43	1.55	.51	.04

[a] based on localities Ybycuí, Carayaó, and Canendiyu combined. df (age) = 1; df (sex) = 1.
* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

TABLE 5
GEOGRAPHIC VARIATION IN *O. NIGRIPES*[a]
RESULTS OF TWO-WAY ANOVAs

Character	Error df	F(age)	F(place)	F(interaction)
ZygoNot	82	2.15	.55	1.38
LRostrum	80	17.73***	.87	1.17
GLS	78	15.51***	1.51	1.04
Zygo	78	16.14***	1.02	1.12
BB	79	.12	1.86	1.88
IOC	82	2.84	.38	.46
MM	81	14.30***	.86	.90
LincFor	82	9.81**	.68	.19
PalBrid	81	10.26**	1.11	.43
Bulla	72	.00	5.51**	.68
LM^1	81	1.12	1.83	.93
LM^2	81	4.03*	.81	1.39
LM^3	80	1.62	1.09	.49
WM^1	81	2.97	1.17	1.24
WM^2	81	5.35*	1.99	1.79
WM^3	80	2.03	2.06	2.12
NasProj	80	3.64	3.17*	2.35*
Diastema	82	23.26	1.32	1.04
Max	80	1.44	1.84	.86
HBulla	73	.56	.63	.21

[a] sites include Paraná, Ybycuí, Carayaó, Curuguaty, Cerro Corá, Itapetininga, and Casa Grande. df (place) = 6; df (age) = 1. * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

TABLE 6
GEOGRAPHIC VARIATION IN *O. NIGRIPES*[a]

Population	n	GLS	Bulla	NasProj	L M^1	L M^2	W M^1	W M^3
Paraná	10	24.36	3.54	1.57	1.70	1.14	1.02	.88
Ybycuí	22	25.19	3.59	1.65	1.64	1.13	1.02	.87
Carayaó	6	25.72	3.55	1.79	1.68	1.13	1.03	.88
Curuguaty	22	25.12	3.39	1.65	1.70	1.13	1.02	.87
Cerro Corá	11	25.15	3.42	1.71	1.64	1.13	1.02	.88
Itapetininga	3	24.61	3.50	1.51	1.58	1.01	.92	.81
Casa Grande	9	24.29	3.48	1.44	1.59	1.10	.98	.81

[a] Character means "adjusted" for the effect of age by covariance analysis.

In a sample of 39 females collected in June 1979 in Ybycuí National Park, 16 were pregnant or lactating. Of 29 females taken in Canendiyu Department in early and mid-July, 1979, one was lactating and none was pregnant. In samples of 13 females taken at the same locality in mid-August, 1978, and in Itapuá Department in late July and early August, 1978, 8 of 13 and 3 of 8 females, respectively, were pregnant or lactating. These data suggest a mid-winter hiatus in breeding in July, though the possibility of variation in the timing of breeding between localities or years cannot be excluded.

Preputial glands are poorly defined or absent in adult male *nigripes* in breeding condition. Males with enlarged, scrotal testes and epididymidal sperm were taken in each sample.

ECOLOGICAL NOTES.–*Oryzomys nigripes* primarily inhabits forests and areas of second growth (Fig. 6). Very high densities may also occur in newly cleared fields where trunks remain and coarse weeds and shrubs have invaded. Individuals commonly were taken in traps set on the ground and in trees 10m or more above the forest floor. Their arboreal proclivity is further suggested by their relatively shorter feet compared to those of *fornesi,* which appears to be strictly terrestrial (Hershkovitz, 1960). *Oryzomys nigripes* shares its habitat in eastern Paraguay with other rodents such as *Oryzomys capito, O. nitidus, O. ratticeps, O. buccinatus, O. concolor, Nectomys squamipes, Akodon cursor, A. nigrita, A. lasiurus, Calomys musculinus,* and *Trichomys aperiodes.*

The common *Oligoryzomys* throughout most of the Chaco (including parts of Paraguay, Bolivia, Argentina, and Brazil) represents an undescribed species.

Oryzomys chacoensis, new species

HOLOTYPE.–University of Michigan Museum of Zoology number 125524, an adult male preserved as a skin and skull with body in fluid, plus karyotype; collected at 419km by road NW Villa Hayes (alongside the Trans Chaco Highway), Dept. Boquerón, Paraguay; captured on the ground in a strip of dry grass bordering a small artificial pond and surrounded by chacoan thorn scrub, on 29 July 1977 by P. Myers (field no. 2872). Two addi-

Fig. 6. Habitat of *Oryzomys nigripes;* Paraná rainforest and agricultural clearing near San Rafael, Dept. Itapúa, Paraguay.

tional specimens (UMMZ 125525-6), both males, were captured with the holotype.

DIAGNOSIS.–A medium-sized species of the subgenus *Oligoryzomys* unique in its whitish underside with hair white to the base on the chin and throat, relatively long ears having hairs on inner surface with unusually short or absent dark basal bands, small but distinctive tufts of orangish hairs anterior to the ears, and karyotype with $2n=58$, FN=74. Differences from *nigripes* are described under that species. *Oryzomys chacoensis* can be distinguished from *fornesi,* with which it occurs sympatrically, by its larger size (maxillary toothrow usually > 3.3mm, ears usually > 15mm), characteristic karyotype, lack of preputial glands, and in most specimens by its lack of buff on the belly. Its karyotype, white venter, and lack of preputial glands also distinguish it from *O. longicaudatus. Oryzomys chacoensis* differs from *O. chaparensis* Osgood (1916) primarily in color pattern: the type of *chaparensis* is much darker and less hispid dorsally, yellowish ventrally, lacks the orange tufts anterior to the ears, and has a grayish throat. The distal portions of the nasals of the holotype flare laterally to an extent not seen in *chacoensis.* Unfortunately *chaparensis* is known only from the type, an old animal (age class IV), and a paratype, which is young (class I); the karyotype and state of the preputial glands are unknown. According to the collector's field notes, the type of *chaparensis* was trapped in wet, dense tropical vegetation (R.H. Becker, notes in the Field Museum of Natural History); this habitat is unlike the dry thorn shrub and grassland inhabited by *chacoensis.*

DISTRIBUTION.–This species is common throughout the Paraguayan chaco. Specimens from the chaco of Bolivia (Depts. Beni, Santa Cruz and Tarija), and Argentina (Prov. Formosa), and from southwestern Mato Grosso in Brazil also represent this species.

EXTERNAL CHARACTERS.–Dorsum Clay color, heavily lined with black, darkest over shoulders; head grayer, very heavily lined with black; cheeks brown or gray, occasionally with some orange; sides clearer; venter contrasts sharply with sides (the orangish lateral line separating dorsum and venter in many *nigripes* is usually absent or at least less distinct), white or occasionally washed buffy, basal half of hairs plumbeous, except on chin and throat where hairs are white to base. Old individuals redder, approximately Burnt Sienna, and dorsum less heavily lined with black. Pelage of young woolier; color grayer but still strongly brown; lining of back less distinct. Tail weakly bicolored, averaging 131% (112 - 171%) of head-body length. Feet average 25% (19 - 32%) head-body length. Pinnae heavily furred on inside, hairs orangish over most of length (basal 1/3 or less dark), distinctive tufts of orangish hairs usually just anterior to ear notch; pinnae 69% (52 - 83%) length of hind foot.

KARYOTYPE.–$2n=58$, FN=74 (Fig. 5). Sixteen individuals (4 females, 12 males) from three localities (Madrejón, 11; km 419, 3; La Golondrina, 2) were examined. No variation in $2n$ or FN was found. The X is a large submetacentric; the Y, a medium-sized acrocentric.

MEASUREMENTS AND DESCRIPTION OF HOLOTYPE.–Total length 253; tail 149; hind foot 26; ear 16; depth of zygomatic notch 1.47; length of rostrum 7.88; greatest length of skull 25.65; zygomatic breadth 13.94; breadth of braincase 10.99; interorbital constriction 3.85; breadth across molars 4.69; length of incisive foramen 4.88; palatal bridge 4.19; length of bulla 3.25;

TABLE 7
NONGEOGRAPHIC VARIATION IN *O. CHACOENSIS*[a]
RESULTS OF TWO-WAY ANOVAs

Character	Error df	F(sex)	F(age)	F(interaction)
ZygoNot	50	.03	10.36**	3.28
LRostrum	49	4.49*	13.29***	.05
GLS	49	3.89	14.82***	.01
Zygo	50	1.79	11.03**	.18
BB	50	.19	.45	.33
IOC	50	4.20*	4.15*	.00
MM	49	.04	21.48***	.00
LincFor	50	1.77	18.43***	1.01
PalBrid	50	2.60	.52	.53
Bulla	50	1.43	1.09	.15
LM^1	50	3.10	.03	.28
LM^2	50	.00	3.47	.01
LM^3	50	1.75	2.24	.47
WM^1	50	.49	.97	.57
WM^2	50	.53	.11	4.50*
WM^3	50	.90	.03	1.26
NasProj	49	.24	.53	.19
Diastema	50	5.84*	35.83***	1.55
Max	50	3.55	2.23	1.23
HBulla	50	.57	1.28	.03

[a] based on localities Copagro, Km 419, and Zalazar combined. df (age) = 2; df (sex) = 2.
* p ≤ .05, ** p ≤ .01, *** p ≤ .001

length of M^1 1.70; length of M^2 1.14; length of M^3 .85; width of M^1 1.03; width of M^2 1.02; width of M^3 .87; nasal projection 1.73; diastema 6.14; length of maxillary toothrow 3.45; height of bulla 2.77. Descriptive statistics of all specimens measured are given in Table 13.

The holotype is a young adult in age class II. The dorsum is near Clay, moderately heavily lined with black; the cheeks and sides lack orange; the venter is white with no buff. In other respects the holotype agrees with the description given above under External Characters.

NONGEOGRAPHIC VARIATION.–Analyses like those performed for *nigripes* were applied to a sample formed by combining populations from the middle of the north-south range of the species (Zalazar, Km 419, and Copagro). Significant age variation was found in 8 of 20 variables; significant sexual differences were seen in only three (Table 7). Analysis by Straney's (1978) method showed a significant contribution to overall variation by age for two characters of the six examined and by sex for none of six (Table 1).

GEOGRAPHIC VARIATION.–No geographic variation in color was detected.

Populations from Cerro León and Agua Dulce in the northern chaco, Copagro in the west, Zalazar in the middle chaco, and La Golondrina in the southeast were sufficiently large to be included in two-way analyses of

TABLE 8
GEOGRAPHIC VARIATION IN *O. CHACOENSIS*[a]
RESULTS OF TWO-WAY ANOVAs

Character	Error df	F(age)	F(place)	F(interaction)
ZygoNot	80	7.70**	2.06	1.17
LRostrum	77	9.73**	3.67**	1.51
GLS	77	14.48***	4.59**	1.03
Zygo	80	19.36***	5.12**	1.63
BB	80	.52	3.50*	1.03
IOC	80	2.05	1.67	1.19
MM	79	9.59**	1.22	1.34
LincFor	80	11.55**	1.12	2.74*
PalBrid	80	.51	6.91***	1.18
Bulla	80	.02	.62	1.07
LM^1	80	.72	5.54***	.66
LM^2	80	5.92*	3.52*	2.63*
LM^3	80	.00	1.23	1.55
WM^1	80	1.81	1.81	.33
WM^2	80	.99	2.49	.60
WM^3	80	.00	.92	.48
NasProj	77	.00	.92	2.69*
Diastema	80	18.09***	5.52***	1.48
Max	80	.01	.90	1.70
HBulla	80	.54	1.77	.56

[a] sites include Cerro León, Agua Dulce, Copagro, Zalazar, and Golondrina.
df (place) = 4; df (age) = 1. * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

variance. Considerably more geographic variation was detected in *chacoensis* than *nigripes*, with eight of 20 characters varying significantly (Table 8). The trend is for animals in the middle of the range (Zalazar and, to a lesser extent, Copagro) to be smaller in most variables than animals at the periphery. Samples from Cerro León or Agua Dulce averaged largest in most of the eight dimensions that varied significantly (Table 9).

REPRODUCTION.–An average of 4.6 embryos (range 2-5) was recorded for 10 pregnant females. At Copagro six of 15 females taken in late January and early February were pregnant, while only one of 32 taken from late May through mid-June was pregnant. In samples taken at Cerro León and Agua

TABLE 9
GEOGRAPHIC VARIATION IN *O. CHACOENSIS*[a]

Population	n	LRostrum	GLS	Zygo	BB	PalBrid	LM^1	LM^2	Diast.
Cerro León	18	7.51	24.93	13.02	11.18	4.21	1.73	1.15	5.79
Agua Dulce	11	7.22	24.56	13.00	11.25	4.10	1.72	1.14	5.54
Copagro	26	7.23	24.04	12.52	10.93	3.84	1.64	1.10	5.48
Zalazar	26	7.31	24.48	12.79	11.11	4.14	1.69	1.12	5.71
Golondrina	6	7.31	24.42	12.63	11.24	4.26	1.66	1.10	5.58

[a] Character means "adjusted" for the effect of age by covariance analysis.

Dulce in mid-July, four of 10 females were pregnant. As with *nigripes,* the pattern of sampling precluded determination of the breeding season; however, few animals breed in early winter (June).

Preputial glands were absent in most adult males, but present, although weakly defined, in a few. Males with enlarged, scrotal testes and epididymidal sperm were included in each sample.

ECOLOGICAL NOTES.–*Oryzomys chacoensis* is ubiquitous in the thorn scrub and grassland of the northern and western chaco, with highest densities found in grassland (Fig. 7). In the lower, wetter chaco it is found in forest and dry grassland, but not in wet marshes, where *fornesi* occurs. Traps set in bushes and low trees occasionally caught *chacoensis.* Like *nigripes,* the hind feet of *chacoensis* are relatively short compared to those of the more terrestrial *fornesi. Oryzomys chacoensis* coexists with *Graomys griseoflavus, Andalgalomys pearsoni, Calomys callosus, C. laucha, Akodon varius, A. lasiurus,* and *Oryzomys concolor.*

Oryzomys chacoensis joins an already substantial list of mammals known to be endemic to the chaco, including *Catagonus wagneri, Pseudoryzomys wavrini, Andalgalomys pearsoni, Graomys griseoflavus chacoensis, Akodon varius toba, Ctenomys conoveri,* and *Cabassous chacoensis.*

Fig. 7. Habitat of *Oryzomys chacoensis;* grass and thornscrub near Cerro León, northern chaco, Paraguay.

Oryzomys fornesi Massoia, 1973

NOMENCLATURE.–We use Massoia's name *fornesi* because his diagnosis clearly describes populations of the smallest species of *Oryzomys* in Paraguay. The type locality of *fornesi* (Argentina, Prov. Formosa, Naineck) is close to La Golondrina, one of our Paraguayan localities. Further study of the relationships of *fornesi* may uncover an older, valid synonym (see Discussion), but until that time, we have adopted a conservative course and apply the specific name used for populations geographically closest to those in Paraguay.

Oryzomys longitarsus (Rengger, 1830) may represent the earliest name for this species. No type specimen is known. The dimensions given by Rengger best fit *fornesi* (Table 3); nonetheless, most of Rengger's measurements fall within the range of overlap of adult *fornesi* and *nigripes*. Furthermore, the possibility that Rengger had a young animal cannot be excluded on the basis of his description and is suggested by the ash gray *(aschgrau)* color of the belly. This color is descriptive of the venter of young of either species, as well as adult *nigripes*, but not the usually buffy venter of adult *fornesi*. Finally, the habitat (bank of the Paraguay River) mentioned by Rengger could have contained either species. Much of the river bank is forested, characteristic habitat of *nigripes*, while some is bordered by marshes, habitat of *fornesi*. We see nothing allowing nearly as strong a statement concerning the identification of *longitarsus* as was possible for Azara's *rat à tarse noir* and recommend that *Mus longitarsus* Rengger, 1830, be considered a *nomen dubium*.

DISTRIBUTION.–*Oryzomys fornesi* occurs throughout eastern Paraguay and has been taken as far west as Zalazar in the Paraguayan chaco. Its northern and southern limits are unknown, but clearly include all of Paraguay east of the Paraguay River. Also, specimens from São Paulo and Minas Gerais, Brazil and Beni, Bolivia appear to be this species.

EXTERNAL CHARACTERS.–Dorsum Saccardo's Umber or Tawny Olive to Russet, usually heavily lined black; sides clearer, the orangish lateral stripe seen in some *nigripes* is absent or indistinct; hairs on chin white to base, throat variably white to gray; venter whitish or grayish, washed buffy in most specimens, basal 1/3 - 2/3 of hairs plumbeous; pectoral band usually absent, but weakly defined in some specimens; cheeks orangish, brown, or gray. Tail weakly bicolored, 128% (111 - 154%) length of head-body. Feet relatively long, 28.5% (24.2 - 32.2%) length of head and body. Pinnae densely furred internally, hairs with basal half dark, distal part orange; hairs on outside moderately dense; length of ears 59.0% (50.0 - 69.6%) of length of foot.

KARYOTYPE.–$2n$=62-66, FN=64-68 (Fig. 5). The karyotypes of 12 individuals (7 males, 5 females) from three localities (Curuguaty, 5; Carayaó, 4; La Golondrina, 3) were examined. Each is characterized by four small metacentric-submetacentric chromosomes and a graded series of 58-62 acrocentric or subtelocentric chromosomes. In our samples three individuals had $2n$=62, FN=64; one, $2n$=64, FN=66; five, $2n$=65, FN=67; two, $2n$=66, FN=68; and one, either $2n$=65, FN=67 or $2n$=66, FN=68. In all but one, the X chromosome was a large submetacentric or subtelocentric; it appeared to be a large acrocentric in the odd individual ($2n$=62). The Y is a small submetacentric. No geographic pattern is apparent to explain the variation in diploid number; several morphs were found in each of the three populations examined.

Yonenaga *et al.* (1976) reported a chromosomally polymorphic *Oryzomys* sp. from the states of São Paulo or Rio de Janiero, Brazil, with $2n$=64 and 66, which may be this species. Similarly, Gardner and Patton (1976) reported a $2n$=64, FN=66 karyotype for *Oligoryzomys* from localities in Peru. Brum (1965, *fide* Gardner and Patton, 1976) gave $2n$=60, FN=66 for *flavescens*. Each of these configurations, with their low number of biarmed pairs, is much more similar to Paraguayan *fornesi* than to *nigripes* or *chacoensis*.

NONGEOGRAPHIC VARIATION.–Populations from the center of eastern Paraguay (Ybycuí, Central, Canendiyu, Carayaó) were combined for analysis of variance and examination by Straney's (1978) method. The resulting sample size, however, is small (n=27). Significant variation was seen in five of 20 characters for both age and sex (Table 10). Analysis by Straney's method revealed a significant contribution to total variation by age in only one variable of six, and none by sex (Table 1).

GEOGRAPHIC VARIATION.–No geographic variation in color pattern was detected.

TABLE 10
NONGEOGRAPHIC VARIATION IN *O. FORNESI*[a]
RESULTS OF TWO-WAY ANOVAs

Character	Error df	F(sex)	F(age)	F(interaction)
ZygoNot	23	.23	2.04	.03
LRostrum	22	8.61**	14.18***	.11
GLS	21	21.60***	15.73***	.21
Zygo	21	7.36*	3.50	.41
BB	22	3.42	.85	.16
IOC	23	1.88	.20	.23
MM	23	.02	6.70*	.17
LincFor	23	.04	.61	.16
PalBrid	23	11.44**	1.47	.41
Bulla	23	1.20	2.32	.12
LM^1	23	1.06	3.64	.62
LM^2	23	3.42	.06	1.34
LM^3	23	.46	3.24	2.41
WM^1	23	2.26	1.83	.81
WM^2	23	.25	1.44	.80
WM^3	23	.01	2.85	.76
NasProj	21	.11	.81	2.06
Diastema	23	6.09*	7.01*	.52
Max	23	3.36	7.00*	3.36
HBulla	22	3.81	1.23	.00

[a] localities Carayaó and Canendiyu combined. df (age) = 1; df (sex) = 1.
* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$.

Two-way analyses of variance were performed for each cranial variable, contrasting the populations at Carayaó, Curuguaty, La Golondrina, and Itapetininga-Casa Grande (these two samples combined), and age class II with classes III to V combined. Significant geographic variation was seen in only three characters (Table 11); sample size, however, was small. The population samples from Brazil averaged larger in 13 of 21 cranial measurements; animals from La Golondrina, Paraguay were smaller (Table 12).

TABLE 11
GEOGRAPHIC VARIATION IN *O. FORNESI*[a]
RESULTS OF TWO-WAY ANOVAs

Character	error df	F(age)	F(place)	F(interaction)
ZygoNot	42	.00	5.03**	1.79
LRostrum	39	6.48*	2.13	.33
GLS	38	3.68	2.88*	.67
Zygo	40	.37	1.60	2.02
BB	41	.51	.88	.84
IOC	42	.81	1.02	1.77
MM	42	5.16*	.57	1.67
LincFor	42	.22	2.63	.96
PalBrid	41	.00	1.30	.26
Bulla	40	.01	1.81	2.35
LM^1	42	.22	2.63	1.17
LM^2	42	.33	1.21	.69
LM^3	42	.02	.44	1.38
WM^1	42	.06	1.44	.48
WM^3	42	.36	2.89*	.82
WM^3	42	.15	1.39	.91
NasProj	38	.77	.86	.28
Diastema	42	1.06	1.99	1.31
Max	42	.03	2.24	2.12
HBulla	40	1.56	1.18	2.55

[a] sites include Carayaó, Curuguaty, La Golondrina, Itapetininga, and Casa Grande. The last two were lumped to form a single stratum. df (place) = 3; df (age) = 1.
$^{*}p \leqslant .05$, $^{**}p \leqslant .01$, $^{***}p \leqslant .001$

TABLE 12
GEOGRAPHIC VARIATION IN *O. FORNESI*[a]

Population	n	ZygoNot	GLS	WM^2
Carayaó	9	1.14	22.77	.89
Curuguaty	17	1.08	22.40	.91
Golondrina	9	.98	21.94	.86
Itapetininga	7	1.06	23.90	.89

[a] Character means "adjusted" for the effect of age by covariance analysis.

REPRODUCTION.–Preputial glands were well defined in all adult males dissected, in contrast to the condition in *chacoensis* and *nigripes*. The glands are longer than the body of the glans penis and easily visible macroscopically, whereas those in *chacoensis* and *nigripes*, if present, are shorter than the glans and so diffuse as to require magnification to verify their presence.

Pregnant females bore an average of 3.25 embryos (range 3-4; n=4). Pregnant females were taken in June (one of one), July (two of six), and September (one of one).

ECOLOGICAL NOTES.–*Oryzomys fornesi* appears to be restricted to wet marshes (Fig. 8). Individuals were taken on the ground, on fruiting bromeliads a few inches above the ground, and on floating mats of grass. Small rodents sharing these habitats include *Akodon cursor*, *A. lasiurus*, *A. azarae*, *Calomys callosus*, *Holochilus brasiliensis*, *Nectomys squamipes*, *Pseudoryzomys wavrini*, and *Scapteromys tumidus*.

MORPHOLOGICAL SIMILARITIES AMONG THE SOUTHERN SOUTH AMERICAN SPECIES

Our efforts to determine the relationships among the Paraguayan species and other *Oligoryzomys* have been frustrated by a lack of discernable

Fig. 8. Habitat of *Oryzomys fornesi*; marsh near Zalazar, central chaco, Paraguay.

TABLE 13
MEANS AND RANGES OF SKIN AND SKULL MEASUREMENTS[a]

Measurements	*O. nigripes*[b] n=80	*O. chacoensis*[b] n=90	*O. eliurus*[c] n=24	*O. longi-caudatus*[d] n=65	*O. fornesi*[b] n=50	*O. flavescens*[e] n=27
Total	224.75 (161-270)	223.40 (185-280)	....	....	188.02 (165-212)	....
Tail	125.51 (100-149)	128.99 (105-150)	....	....	105.50 (93-118)	....
Hind Foot	24.76 (21-28)	24.76 (18-30)	....	....	23.66 (21-26)	....
Ear	16.72 (14-20)	16.56 (13-19)	....	....	13.84 (12-16)	....
ZygoNot	1.22 (.91-1.65)	1.30 (.90-1.82)	1.15 (.85-1.71)	1.36 (1.08-1.69)	1.09 (.81-1.35)	1.22 (.93-1.57)
LRostrum	7.61 (6.44-8.80)	7.38 (6.35-8.58)	7.45 (6.55-8.45)	7.75 (6.97-8.87)	6.44 (5.56-7.35)	6.67 (5.75-7.92)
GLS	25.45 (22.93-28.06)	24.59 (22.12-27.79)	24.98 (23.19-27.06)	25.91 (23.83-28.37)	22.51 (20.63-24.73)	23.43 (22.09-26.04)
Zygo	13.31 (11.91-15.06)	12.86 (11.12-14.84)	13.10 (11.94-13.95)	13.65 (12.16-15.05)	11.87 (10.63-12.88)	12.29 (11.62-13.49)
BB	11.06 (10.19-11.87)	11.13 (10.14-11.85)	11.15 (10.82-11.58)	11.62 (11.09-12.36)	10.49 (9.83-11.17)	10.82 (10.35-11.54)
IOC	3.66 (3.25-4.30)	3.77 (3.39-4.17)	3.69 (3.37-3.99)	3.62 (3.30-3.87)	3.39 (2.94-3.70)	3.44 (3.16-4.27)
MM	4.60 (3.92-5.01)	4.48 (4.14-4.85)	4.59 (4.29-5.62)	4.88 (4.23-5.37)	4.20 (3.90-4.53)	4.35 (4.08-4.82)
LincFor	4.84 (4.00-5.99)	4.59 (3.88-5.41)	4.74 (4.27-5.13)	5.44 (4.60-6.15)	4.26 (3.53-4.68)	4.78 (4.23-6.65)
PalBrid	4.15 (3.60-4.78)	4.09 (3.41-4.93)	4.13 (3.54-4.59)	4.17 (3.68-4.77)	3.71 (3.08-4.33)	3.73 (3.28-4.27)
Bulla	3.53 (3.20-3.87)	3.53 (3.19-3.81)	3.50 (3.32-3.73)	3.66 (3.40-4.60)	3.18 (2.92-3.38)	3.25 (3.02-3.72)

TABLE 13, continued
MEANS AND RANGES OF SKIN AND SKULL MEASUREMENTS[a]

Measurements	*O. nigripes*[b] n=80	*O. chacoensis*[b] n=90	*O. eliurus*[c] n=24	*O. longicaudatus*[d] n=65	*O. fornesi*[b] n=50	*O. flavescens*[e] n=27
LM¹	1.67 (1.47-1.94)	1.69 (1.52-1.91)	1.61 (1.43-1.73)	1.67 (1.49-1.82)	1.45 (1.32-1.60)	1.55 (1.44-1.86)
LM²	1.13 (.94-1.24)	1.11 (.95-1.24)	1.08 (.93-1.20)	1.15 (.97-1.27)	.98 (.85-1.12)	1.09 (.89-1.18)
LM³	.83 (.72-.94)	.83 (.66-.95)	.80 (.69-.93)	.90 (.76-1.02)	.73 (.63-.86)	.81 (.60-.90)
WM¹	1.02 (.88-1.13)	.99 (.88-1.11)	.98 (.91-1.08)	1.09 (.97-1.20)	.90 (.80-1.00)	.94 (.87-.98)
WM²	1.02 (.85-1.17)	.97 (.83-1.07)	.97 (.91-1.07)	1.07 (.95-1.08)	.89 (.78-1.00)	.94 (.87-.98)
WM³	.87 (.72-.96)	.84 (.67-.97)	.82 (.71-.94)	.91 (.79-1.02)	.76 (.68-.84)	.83 (.76-.87)
NasProj	1.67 (1.20-2.17)	1.59 (1.00-1.88)	1.47 (1.04-1.86)	1.26 (.92-2.05)	1.30 (.81-1.59)	1.35 (1.01-1.72)
Diastema	5.97 (4.96-7.17)	5.68 (4.81-6.89)	5.83 (5.11-6.65)	6.34 (5.53-7.59)	5.26 (4.27-5.93)	5.32 (4.85-6.96)
Max	3.52 (3.21-3.82)	3.49 (3.14-3.87)	3.42 (3.20-3.67)	3.59 (3.27-3.89)	3.09 (2.81-3.31)	3.30 (2.90-3.48)
HBulla	2.90 (2.43-3.88)	2.78 (2.49-3.33)	2.95 (2.65-3.23)	3.07 (2.31-3.58)	2.56 (2.18-2.95)	2.80 (2.54-3.08)

[a]animals in age class I are excluded.
[b]all Paraguayan samples.
[c]samples from Itapetininga and Casa Grande, São Paulo, Brazil.
[d]samples of *O. l. philippi* from the following provinces in Argentina: Chubut, Neuquen, Rio Negro, and Santa Cruz; and the following provinces in Chile; Aruaco, Coquimbo, Santiago, Valdivia.
[e]samples from Buenos Aires, Argentina.

character variation. Examination of cranial and postcranial skeletons and several soft anatomical systems uncovered minimal variation, mostly continuous in nature and poorly suited for evolutionary analyses. We have used the cranial measurements in phenetic schemes, together with other evidence, to formulate a preliminary hypothesis of the systematic relationship of these species.

"Adjusted" means were calculated by covariance analysis for each population sample exceeding five individuals: four populations of *fornesi* (three from Paraguay and one from Brazil), six populations of *nigripes* (from Paraguay), two populations of *eliurus* (Brazil), five populations of *chacoensis* (Paraguay), three populations of *O. longicaudatus philippii* (southern Argentina), and one population each of *longicaudatus longicaudatus* (Tucumán, Argentina) and *flavescens* (near Buenos Aires, Argentina). The resulting 22 × 23 matrix was subjected to principal components analysis (using the covariance matrix) and to clustering (using standardized, unweighted data, an average distance algorithm, and the Euclidean metric). The statistical manipulations were then repeated, using means "unadjusted" by covariance analysis.

Principal components analysis of the adjusted means yielded several clusters (Fig. 9, Table 14). The first axis appears to represent size.

TABLE 14
RESULTS OF PRINCIPAL COMPONENT ANALYSIS

Character	First principal component	Second principal component	Third principal component
ZygoNot	.2014	−.0374	−.5742
LRostrum	.2414	.1025	.1256
GLS	.2456	.0535	.1688
Zygo	.2430	.0019	.1685
BB	.2326	−.0841	−.2972
IOC	.1777	.4476	−.3369
MM	.2334	−.1967	.0993
LincFor	.2031	−.3997	.0964
PalBrid	.2233	.2083	−.0700
Bulla	.2361	.0503	−.0912
LM^1	.2273	.2397	−.1343
LM^2	.2336	.0247	−.0525
LM^3	.2309	−.1748	−.2154
WM^1	.2346	−.1174	.8382
WM^2	.2385	−.1191	.1970
WM^3	.2376	−.0974	.1332
NasProj	.0955	.6070	.4012
Diastema	.2276	−.1306	.1732
Max	.2418	.1177	−.0070
HBulla	.2181	−.0999	.2041
Cumulative % Variance	79.3	88.8	91.8

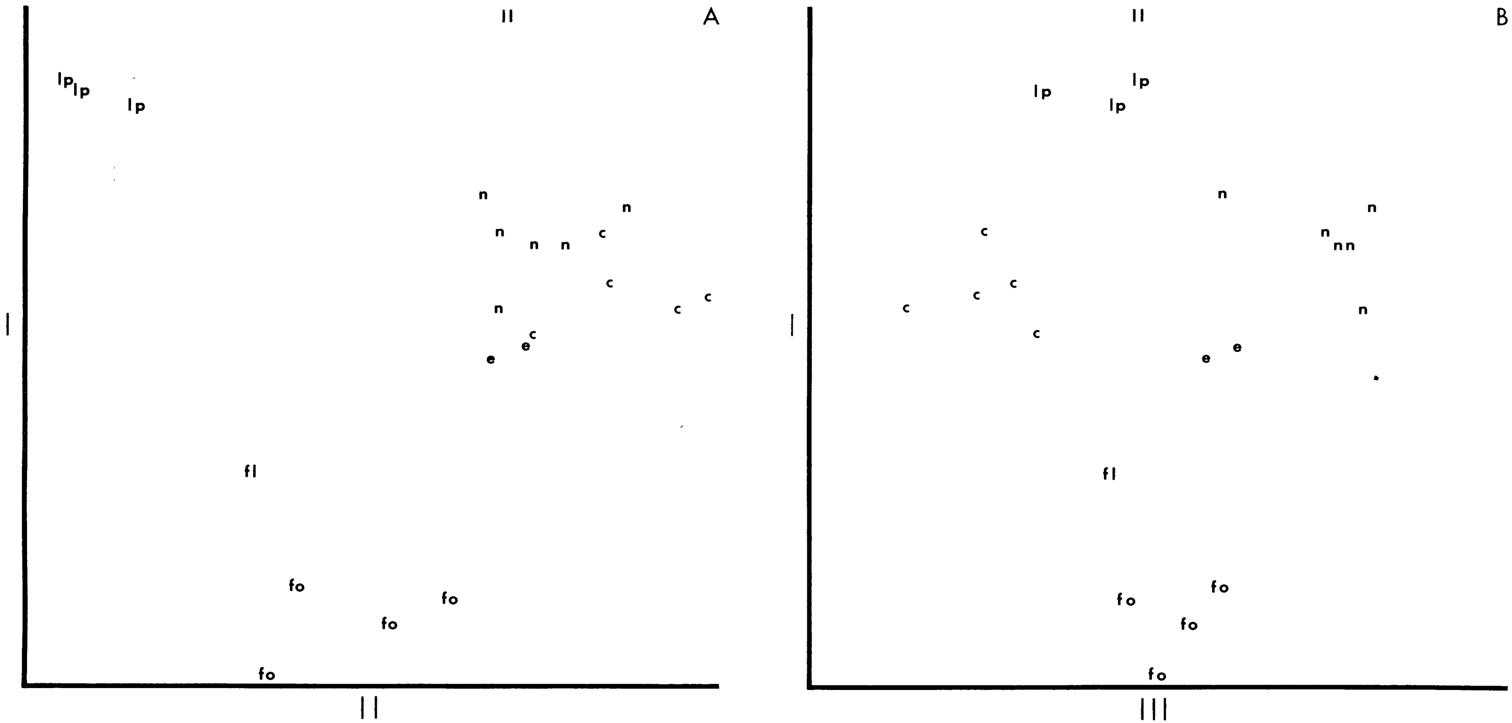

Fig. 9. Scatter plot of principal component I *vs* II (A) and I *vs* III (B) for 22 populations of *Oligoryzomys*. c=*chacoensis*, e—*eliurus*, fl=*flavescens*, fo=*fornesi*, 11=*I. longicaudatus*, lp=*longicaudatus philippii*, n=*nigripes*.

The second emphasizes length of nasal projection, breadth of interorbital constriction, and length of the incisive foramen, while the third weights most heavily the width of M^1, length of zygomatic notch, length of nasal projection, and interorbital constriction. Populations of *fornesi* form a group, as do the populations of *longicaudatus philippii*. *Oryzomys flavescens* lies close to *fornesi*. *Oryzomys l. longicaudatus* clusters near *longicaudatus philippii* on the first and third axes, but is separated on the second. *Oryzomys nigripes* and *chacoensis* form a single cluster on the first and second axes, but are separated from each other on the third. The Brazilian samples called *eliurus* lie close to *nigripes* on all three axes.

Clustering of adjusted means mirrored this arrangement (Fig. 10). The first branch divides *fornesi* and *flavescens* from the other species. Of the Paraguayan populations of *fornesi*, the two from eastern Paraguay resemble each other more than either resembles the population in the chaco (La Golondrina). The population from Itapetininga, São Paulo, is included in this group. The next major branch separates *longicaudatus* ssp. from *nigripes, eliurus,* and *chacoensis*. The northern population of *longicaudatus,* within the range of *longicaudatus longicaudatus* according to Osgood (1943), is distinct from the southern populations, *longicaudatus philippii,* which cluster tightly. In the *chacoensis-nigripes-eliurus* cluster, the Brazilian samples (Itapetininga and Casa Grande) come off first, followed immediately by a split between *chacoensis* and *nigripes*. Within *nigripes* the samples from ecologically similar habitats in central and northern Paraguay are separated from the one from the Paraná rain forests. Within *chacoensis,* the far-western Copagro sample links at the lowest level of similarity. Its habitat is substantially more xeric than that of the other populations of *chacoensis*. The next furcation separates the sample from La Golondrina, which inhabits a distinctive, seasonally wet area along the Paraguay river. The remaining samples are from populations inhabiting rather similar thorn scrub in the middle longitudes of the chaco.

Clustering was repeated using "unadjusted" means. The results were similar, with the following exceptions. First, the population of *chacoensis* at Cerro León, composed of relatively old individuals, clustered with *nigripes* (which tends to be slightly larger than *chacoensis*). Second, the clear relationship within species between the pattern of clustering and the ecological and geographical relationships of the populations described above completely disappears.

DISCUSSION

The phenetic data, karyotypic evidence, pattern of occurrence of preputial glands, and our general impression from examining these and other *Oligoryzomys,* all support recognition of two major groups of southern *Oligoryzomys:* one (*fornesi* and *flavescens*) characterized by small size, proportionately short, narrow rostra, small ears and teeth, large preputial glands, and a low FN/2*n* ratio; and a second (*chacoensis, eliurus, longicaudatus,* and

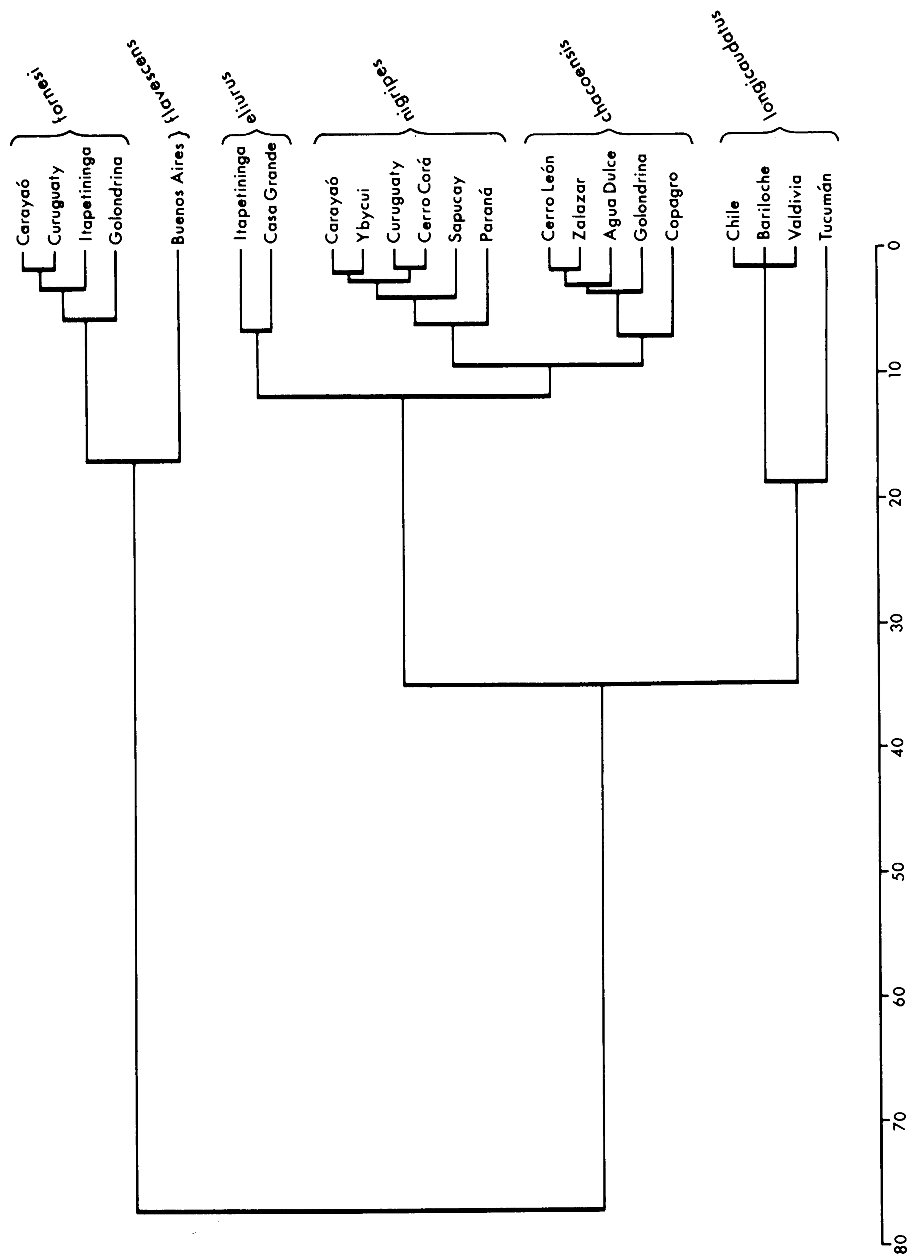

Fig. 10. Phenetic clustering (UPGMA) of "adjusted" means of 22 populations of *Oligoryzomys*.

nigripes) containing larger, longer-eared, larger toothed, mice with a high FN/2*n* ratio and either with or without conspicuous preputial glands.

Several problems arise regarding the *chacoensis-eliurus-longicaudatus-nigripes* assemblage. Were it not for their distinctive karyotypes and the substantial chromatic differences in pelage we would suggest a subspecific level of differentiation for *nigripes* and *chacoensis*. Evidence of interbreeding was not found, however, and seems unlikely given the karyologic divergence. If intergradation does exist, it must be restricted to a narrow zone, because the two forms maintain their identities at nearby localities on either side of the Paraguay River (Fig. 1). This river is crossed frequently by floating mats of vegetation and has a history of meandering, so that "islands" of eastern Paraguay become annexed to the chaco, and *vice versa*. Therefore, it is likely that our hypothesis of specific differentiation can be tested by searching for populations in sympatry or parapatry along this river. We consider a series of three *Oligoryzomys* from Las Palmas, Chaco, Argentina, a site on the west bank of the Paraná River near its confluence with the Paraguay, to be *nigripes*. More specimens, especially ones of known karyotype, are needed from this region.

We believe *nigripes* and *eliurus* are at most subspecifically distinct, based on the fairly high phenetic similarity of populations from near the type locality of *eliurus* to those of *nigripes* (as well as *chacoensis)*, and the karyotypic identity reported for them. Analysis of specimens from localities between São Paulo, Brazil and Paraguay is needed, however, to support formal recommendation of synonomy.

Oryzomys longicaudatus is more similar to *nigripes* and *chacoensis* than to *fornesi* and *flavescens*, a resemblance first recognized by Thomas (1926). This resemblance is evident from the karyotype of *longicaudatus philippii*, with its relatively high number of biarmed elements (Gallardo and Gonzalez, 1976), as well as from the phenetic analyses of cranial characters. Specimens of *longicaudatus* share the characters of relatively large ears and small hind feet with specimens of *nigripes* and *chacoensis*. On the other hand, examples of *longicaudatus philippii* from Malleco Province and *l. longicaudatus* from Coquimbo Province, Chile, possess well-defined preputial glands, which are lacking or only poorly developed in *nigripes* and *chacoensis*. Again, additional material is needed before the degree of relationship can be resolved. The relatively large phenetic difference discovered between *O. l. longicaudatus* and *O. l. philippii* invites further attention, as does the entire Andean complex of *longicaudatus*-like forms (e.g., *destructor, stolzmanni, spodiurus, maranonicus)*. Langguth (1963) postulated that *longicaudatus* is related to *delticola* Thomas of Uruguay, a species not included in our study.

Oryzomys fornesi and *flavescens* resemble one another in cranial characters (Fig. 4), relatively large feet, and short, densely furred ears (see Langguth, 1963, for ear and foot proportions of *flavescens)*. These two species share well-developed preputial glands and similar, though not identical, karyotypes. It seems likely that further study will verify a close relationship between *fornesi* and *flavescens* compared to other *Oligoryzomys*. Is recognition of *fornesi* as specifically distinct justified? *Oryzomys fornesi,* including both Paraguayan and Argentina specimens, is markedly smaller than *flavescens* and differs in a number of cranial dimensions (Massoia, 1973). Unfortunately Massoia's comparisons are based on allopatric populations separated by a large distance (northern Argentina *vs.* the vicinity of Buenos Aires). Further collections are much needed, especially along the Paraná River between Corrientes and Buenos Aires. Karyotypes of *flavescens* from these areas also might shed light on the level of differentiation of these taxa. Pending the outcome of such studies, however, we prefer to use the specific name *fornesi* for populations in the Paraguay/Paraná drainage of northern Argentina, Paraguay, and Brazil.

In addition to *flavescens,* several other nominal forms of *Oligoryzomys* seem to bear close relationship to *fornesi* and form part of the same complex. The holotypes of *Oryzomys delicatus* Allen and Chapman 1897 (Trinidad, Caparo), *O. tenuipes* Allen 1904 (Venezuela, Mérida), *O. munchiquensis* Allen 1912 (Colombia, Cauca, La Florida), and *O. microtis* Allen 1916 (Brazil, Amazonas, Lower Rio Solimõens) all possess relatively small ears and a small, delicate skull with short rostrum and toothrow. The possibility that one or more of these taxa is conspecific with *fornesi* and/or *flavescens* from southern South America deserves further investigation. It is probably this complex, not some member of the *nigripes-longicaudatus-chacoensis* assemblage, that is aligned with *Oryzomys fulvescens* of Central America. This conclusion is also implied by Handley (1976), who listed under *fulvescens* the small *Oligoryzomys* in Venezuela, populations previously assigned to *delicatus* and *tenuipes.*

Hesperomys pygmaeus Wagner 1845 (type locality Ypanema, eastern Brazil) may also be a member of this assemblage. Thomas (1902) synonomized *pygmaeus* with *eliurus,* claiming it was a juvenile of the latter species. Nevertheless, Wagner (1847) and Gyldenstolpe (1932) both described the cinnamon or yellowish cast of the belly, which is found in *fornesi* and *flavescens* but is not characteristic of most *eliurus.* Wagner also (1847) mentioned the densely furred ears, another characteristic of *fornesi* and *flavescens.* In view of this and the common coexistence of two species of *Oligoryzomys* documented here, we believe the status of *pygmaeus* and its relationship to the *fornesi-flavescens* group needs to be reappraised. A more substantive recommendation must await examination of the type and further collections from the type locality.

Two other species pertinent to our discussion of South American *Oligoryzomys* are Allen's (1916) *utiaritensis* and *mattogrossae* from Utiarity, Mato Grosso, Brazil. Allen based his descriptions on only two specimens of each form, and Goodwin (1953) advanced the idea that the specimens of *mattogrossae* were simply individual variants of *utiaritensis.* Accordingly Cabrera (1961) synonomized the former under *utiaritensis.*

Examination of the type material suggests that two species are represented at the type locality and that Allen's type series may be composites, as follows. The holotype of *utiaritensis* (AMNH 37541, adult female) strongly resembles *nigripes* from Paraguay in its grayish belly, length of tail (120mm), and size of skull. Likewise, the skin of the paratype (AMNH 37540, young adult female) is similar in size and color to examples of *nigripes*. However, the skull of this individual (which is damaged) resembles our series of *fornesi* and other small-toothed *Oligoryzomys*. Certain dimensions of the cranium, such as greatest length (22.6mm) and length of maxillary toothrow (3.0mm), as well as its general conformation, underscore this resemblance and raise the suspicion that the skin and skull are mismatched. Moreover, that none of the pieces of the broken skull were numbered establishes the potential for a mix-up.

The holotype of *mattogrossae* (AMNH 37542, male) has heavily worn molars, indicating an extremely old animal. Nevertheless, certain cranial features (zygomatic breadth and width of braincase) are much smaller than generally observed in individuals of *nigripes* of comparable age, but not unusual in old *fornesi*. The dimensions of the skin (total length 210mm, tail 115mm), although at the upper extreme recorded for *fornesi* (Table 13), are not excessive in view of the specimen's apparent age. In addition, the buffy venter of the holotype resembles samples of *fornesi* and not *nigripes*. Allen's paratype of *mattogrossae* (AMNH 37100, adult female), on the other hand, fits more closely with series of *nigripes*. Therefore, we question the propriety of synonomizing *utiaritensis* and *mattogrossae* until their status can be clarified by additional collections from the type locality, preferably including karyotypes and animals preserved in fluid.

The opinion that two species, one medium-sized, the other small, are present in Allen's series from Mato Grosso conforms with our evaluation of *Oligoryzomys* in Paraguay and the investigations of others (*e.g.*, Langguth, 1963; Massoia, 1973) in other regions of South America. To determine the distributional limits of these forms and to decide which represent only regional variants of a single biological species remains a formidable task. We hope that the assignment of *Oryzomys nigripes*, Azara's *rat à tarse noir*, to a definite morphology will provide some progress and impetus toward these goals.

SPECIMENS EXAMINED

A total of 701 *Oligoryzomys* was examined from the following institutions: American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Museum of Comparative Zoology, Harvard (MCZ); The Museum, Michigan State University (MSU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); University of Connecticut Museum (UCM); University of Michigan Museum of Zoology (UMMZ); and U.S. National Museum of Natural History (USNM).

O. chacoensis: 123 from the following localities.

Argentina. Formosa: km 182, 10 mi NW Riacho Pilaga, 6 (USNM).

Bolivia. Beni: Mamoré, Tacuaral, 1 (USNM); Río Machupo, Las Penas, 1 (USNM). Tarija: 35 km by rd. SE Villa Montes, Taringuiti, 2 (UMMZ).

Brazil. Mato Grosso: Corumbá, 10 km NE Urucum, 2 (USNM); 48 km W Cáceres, Limão, west bank Río Jauru, 1 (USNM); Urucum de Corumbá, 3 (FMNH).

Paraguay. Boquerón: 410 km by rd. NW Villa Hayes, 1 (MVZ); km 419 Trans Chaco Hwy., 3 (UMMZ); Estancia Pirazal, 1 (UCM); Dr. Pedro P. Peña, 1 (UCM); 11 km NW Fortín Teniente Pratts Gil AF Base, 1 (UCM); Guachalla, Río Pilcomayo, 580 km W Asunción, 1 (FMNH). Chaco: 50 km WNW Fortín Madrejón, Cerro León, 23 (UMMZ); 123 km E Mayor Pablo Lagerenza, Agua Dulce, 12 (UCM). Nueva Asunción: 19 km by rd. WSW km 588 Trans Chaco, Copagro, 22 (UCM); Teniente Ochoa, 2 (UCM). Presidente Hayes: 69 km by rd. NW Villa Hayes, 1 (MVZ); 295 km by rd. NW Villa Hayes, Chaco Experimental Station, 4 (MVZ); 2 km N Río Verde, Juan de Zalazar, 12 (UCM); 8 km NE Juan de Zalazar, 6 (UMMZ); 24 km NNW Villa Hayes, La Golondrina, 10 (UMMZ); Puerto Piñasco, 1 (USNM); 85 km E Loma Plata, Estancia Laguna Porá, 2 (UCM); Río Pilcomayo, 15 m W Río Paraguay, 5 (FMNH).

O. chaparensis: 2 from the following locality.

Bolivia. Santa Cruz: Todos Santos, 1 (FMNH), 1 (AMNH).

O. eliurus: 36 from the following localities.

Brazil. Minas Gerais: Passos, 1 (USNM); Serra do Caparaó, Rio Caparaó, 3000 ft, 8 (AMNH); Fazenda Cardosa, 3360 ft, 7 (AMNH). São Paulo: Casa Grande, 18 (USNM); Itapetininga, 2 (USNM).

O. flavescens: 34 from the following localities.

Argentina. Buenos Aires: La Valle, 1 (USNM); 20 km S Buenos Aires, Ezeiza, 3 (MVZ); Punta Lara, 1 (UMMZ); Pdo. Berazategui, Hudson, 1 (UMMZ); Balcarce, km 67 Ruta 226, 22 (MSU). Tucumán: Concepción, 6 (USNM).

Uruguay. Montevideo: 1 (USNM). Maldonado: 1 (USNM).

O. fornesi: 102 from the following localities.

Bolivia. Beni: Mamoré, San Joaquin, 5 (USNM).

Brazil. Minas Gerais: Parque Nacional de Serra de Canastra 23 (MSU); Serra do Caparaó, Río Caparaó, 3000 ft, 3 (AMNH). São Paulo: Casa Grande, 3 (USNM); Itapetininga, 10 (USNM).

Paraguay. Caaguazu: 25 km by rd. N Coronel Oviedo, 1 (UMMZ); 24 km NNW Carayaó, 9 (UMMZ). Canendiyu: 6.3 km by rd. N Curuguaty, 8 (UMMZ); 13.3 km by rd. N Curuguaty, 11 (UMMZ). Central: 17 km by rd. E Luque, 1 (MVZ). Concepción: 40 km by rd. E Concepción, 1 (UMMZ); Río Aquidabán at Paso Horqueta, 2 (UMMZ). Cordillera: 1.6 km by rd. S Tobatí, 2 (1 MVZ and 1 UMMZ). Itapúa: 8 km W Encarnación, 2 (UMMZ). Misiones: 2 km by rd. NE Ayolas, 1 (UMMZ); 20 km W San Ignacio, San Pablo, 1 (USNM). Paraguarí: Parque Nacional Ybycuí, 6 (UMMZ). Presidente Hayes: 8 km NE Juan de Zalazar, 2 (UMMZ); 24 km NNW Villa Hayes, La Golondrina, 11 (UMMZ).

O. l. longicaudatus: 15 from the following localities.

Argentina. Tucumán: Concepción, 12 (USNM).

Chile. Coquimbo: 1.5 km N Paihuano, 1 (UMMZ); 2 km S Paihuano, 2 (UMMZ).

O. l. philippii: 126 from the following localities.

Argentina. Chubut: 5 km W Leleque, 2 (MVZ); Lago Puelo, 1 (MVZ); El Hoyo, La Catarata, 2 (MVZ). Neuquén: 20 km N Villa la Angostura, 3 (MVZ); 45 km SSE Chos Malal, 1 (MVZ). Río Negro: Bariloche, 2 (MVZ); 5 km S Bariloche, 3 (MVZ); 14 km W Bariloche, 18 (MVZ); La Veranada, 38 km SSW Bariloche, 3 (MVZ); Río Castaña Overo, 44 km W Bariloche, 14 (MVZ); Puerto Blest, 9 (MVZ); 19 km NNE El Bolsón, 5 (MVZ). Santa Cruz: 52 km WSW El Calafate, 2 (MVZ).

Chile. Arauco: 11 km NW Ranquil, 1 (MVZ); 7 km WNW Los Alamos, 4 (MVZ). Coquimbo: Fray Jorge, 1 (MVZ). Malleco: Parque Nacional Nahuelbuta, 26 (MVZ);

El Vergel, S Angol, 2 (MSU); 9 km NE Angol, 4 (MSU); 10 km WNW Angol, 2 (MSU); 15 km NW Angol, 2 (MSU); 18 km WNW Angol, 4 (MSU); 23 km W Angol, 2 (MSU); 24 km NW Angol, 2 (MSU); Relun, 26 km SW Capitán Pastene, 1 (MSU). Santiago: 10 km W Tiltil, Fundo Sta. Laura, 2 (MVZ). Valdivia: Parcela Escuela Normal, 8 (MVZ).

O. mattogrossae: 2 from the following localities.

Brazil. Mato Grosso: Papagaio River, Utiarity, 1 (AMNH); Guatsue, 1 (AMNH).

O. microtis: 9 from the following locality.

Brazil. Amazonas: Lower Río Solimõens (50 mi above the mouth), 9 (AMNH).

O. nigripes: 243 from the following localities.

Argentina. Chaco: Las Palmas, 3 (USNM). Misiones: Río Urugua-í, 30 km de Pto. Bertoni, 4 (FMNH); Caraguatay, 7 (FMNH); Río Paranay, 5 (FMNH).

Paraguay. Amambay: 28 km SW Pedro Juan Caballero, 8 (UMMZ); 4 km by rd. SW Cerro Corá, 3 (UMMZ). Caaguazu: 24 km NNW Carayaó, 4 (UMMZ); 25 km by rd. N Coronel Oviedo, 1 (UMMZ); Sommerfeld Colony no. 11, 2 (USNM); Tacuatí, Aca-Poí, 1 (USNM). Canendiyu: 13.3 km by rd. N Curuguaty, 78 (UMMZ). Central: 17 km by rd. E Luque, 2 (MVZ); Asunción, 1 (MCZ). Itapúa: 20 km by rd. NNE Encarnación, 1 (UMMZ); 3.5 km E San Rafael, 11 (UMMZ); 8 km N San Rafael, 5 (UMMZ); Río Pirapó, 5 (UCM). Misiones: 2.7 km N San Antonio, 1 (UMMZ); 36 km NE San Ignacio, San Francisco, 3 (USNM). Paraguarí: Sapucay, 8 (USNM); Parque Nacional Ybycuí, 90 (UMMZ).

O. spodiurus: 6 from the following locality.

Ecuador. Imbabura: near Penaherrera, Intag, 6 (UMMZ).

O. stoltzmani maranonicus: 1 from the following locality.

Peru. Catamarca: Hda. Limón, 10 mi W Balsas, 1 (FMNH).

O. utiaritensis: 2 from the following locality.

Brazil. Mato Grosso: Papagaio River, Utiarity, 2 (AMNH).

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