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A Review of the Genus *Isothrix* (Rodentia, Echimyidae)

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ABSTRACT

Two species of the echimyid rodent genus *Isothrix* are recognized within the Amazon and upper Orinoco basins of South America based on color and color pattern, bacular morphology, cranial morphometrics, and karyotype. These represent significant departures in the previously recognized name combinations: *I. bistriata* Wagner, with two

geographic races (*bistriata* [including *villosa* Deville, *negrensis* Thomas, *molliae* Thomas, and *boliviensis* Petter and Cuenca Aguirre] and *orinoci* Thomas), and *I. pagurus* Wagner. No localities of sympatric contact between these two species are known, although their ranges come very close in the general vicinity of Manaus in central Brazil.

INTRODUCTION

The genus *Isothrix* contains arboreal rats of moderate body size that are a well-marked component of the morphologically and ecologically diverse neotropical rodent family Echimyidae. Erected by Wagner in 1845 to accommodate three species, it is characterized by a pelage lacking spines, a bushy tail, and teeth with complex, irregular re-entrant angles and enamel folds. The combination of soft-haired pelage and bushy tail differentiates *Isothrix* from other echimyid rodents that have similar occlusal patterns (for example, *Echimys* Cuvier [1809] and *Mesomys* Wagner [1845]). *Diplomys* Thomas (1916a), also a soft-haired form without spines, differs from *Isothrix* by its rather simple teeth with

transverse plates which persist into advanced age.

Despite the relative distinctness of *Isothrix* as a generic unit, however, no clear understanding of its component taxa is currently available. Specimens of this genus are rare in collections, a state which has resulted in the description of geographic units at the specific or subspecific levels without benefit of proper comparisons to permit a realistic assessment of individual relative to geographic variation. The present paper was motivated by the existence of large series of *Isothrix* from three general areas of the Amazon Basin and adjacent Venezuela, mostly in the collections of the American Museum of Natural History.

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These allow us to examine for the first time both individual variation and geographic trends, and thus to make a better assessment of the taxonomic diversity within the genus.

TAXONOMIC HISTORY OF *ISOTHRIX*

Nine names have been proposed as taxa within the genus *Isothrix*. Wagner (1845), in the original definition of the genus, described three species: *bistriata*, with type locality Rio Guapore, Mato Grosso, Brazil; *pachyura*, type locality not identified (but subsequently designated as Cuiaba, Mato Grosso, Brazil by Cabrera [1961]); and *pagurus*, type locality Borba, Rio Madeira, Amazonas, Brazil. In 1848 Wagner renamed *pachyurus* as *crassicauda* without reason. A fourth species, *villosa*, was proposed by Deville (1852), based on Castlenau's specimen from Sarayacu Mission, Rio Ucayali (not Rio Urubamba as given in Cabrera [1961]), Loreto, Peru. Subsequently, Oldfield Thomas described three forms as subspecies of either *bistriata* (*orinoci* [Thomas, 1899] and *negrensis* [Thomas, 1920]) or *villosa* (*molliae* [Thomas, 1924]). Finally, the name *boliviensis* was recently proposed as a Bolivian subspecies of *bistriata* by Petter and Cuenca Aguirre (1982).

The named form *pictus* (Pictet, 1843), a soft-haired echimyd from coastal Bahia, eastern Brazil, has been varyingly placed in the genus *Isothrix* (for example, Waterhouse, 1848; Ellerman, 1940; Cabrera, 1961), in a monotypic genus *Nelomys* (Pictet, 1843; Goldman, 1916; Thomas, 1916a), or in *Echimyris* (Tate, 1935; Moojen, 1952). This difference of opinion results from *pictus* combining simple laminated upper cheek teeth (characteristic of *Diplomys*) with the complex lower teeth of *Isothrix* and *Echimyris*. We follow Cabrera (1961) and Honaki, Kinman, and Koepl (1982) in placing *pictus* within *Isothrix*, but do not consider it further.

Most recent authors (for example, Honaki, Kinman, and Koepl, 1982; Petter and Cuenca Aguirre, 1982) have followed the taxonomic arrangement given by Cabrera (1961) in recognizing three species, as follows:

- Isothrix bistriata bistriata* Wagner, 1845
- bistriata pachyura* Wagner, 1845
- bistriata pagurus* Wagner, 1845
- bistriata orinoci* Thomas, 1899

- bistriata negrensis* Thomas, 1920
- Isothrix villosa villosa* (Deville, 1852)
- villosa molliae* Thomas, 1924
- Isothrix pictus* (Pictet, 1843)

This view has been accepted even though Oldfield Thomas suggested that several of these named forms most likely represented the same taxon. In 1928, for example, he stated that *I. v. villosa* and *I. v. molliae* from northern Peru were the same entity, and both in 1916 and 1928 he suggested that *I. villosa* might in fact grade into *I. bistriata* and thus would represent only an upper Amazon subspecies of the latter.

METHODS AND ABBREVIATIONS

Ninety-six specimens of *Isothrix* from eastern Peru, eastern Bolivia, southern Venezuela, and central Brazil were examined in this study. Eighty-four of these were considered adults by the criteria given below. Standard external measurements were missing from the labels of most specimens, so analyses of individual and geographic variation were based on external color and color pattern and morphometric variables of the cranium. For the cranium, the following 19 measurements were taken from each skull with dial calipers reading to 0.05 mm: (1) greatest length of skull [GSL]; (2) basilar length of Hensel [BaL]; (3) zygomatic breadth [ZB]; (4) mastoid breadth [MB]; (5) least interorbital constriction [IOC]; (6) rostral length [RL]; (7) nasal length [NL]; (8) rostral width [RB]; (9) rostral depth [RD]; (10) diastema length [D]; (11) palatal length A [PLA]; (12) palatal length B [PLB]; (13) maxillary tooth row length [MTRL]; (14) maxillary breadth [MaxB]; (15) incisive foramen length [IFL]; (16) bullar length [BuL]; (17) post palatal length [PPL]; (18) cranial depth [CD]; and (19) mesopterygoid fossa width [MPFW]. Each of these measurements is described and figured by Patton and Rogers (1983) for the related genus *Proechimys*.

Variation in bacular dimensions was examined from cleared and stained glands, prepared as in Hooper (1959). Specimens were aged according to nine categories of tooth eruption and wear patterns: (I) dP⁴ erupted, M¹ erupted but below occlusal level; (II) M¹ to occlusal level, M² erupting; (III) M³ erupt-

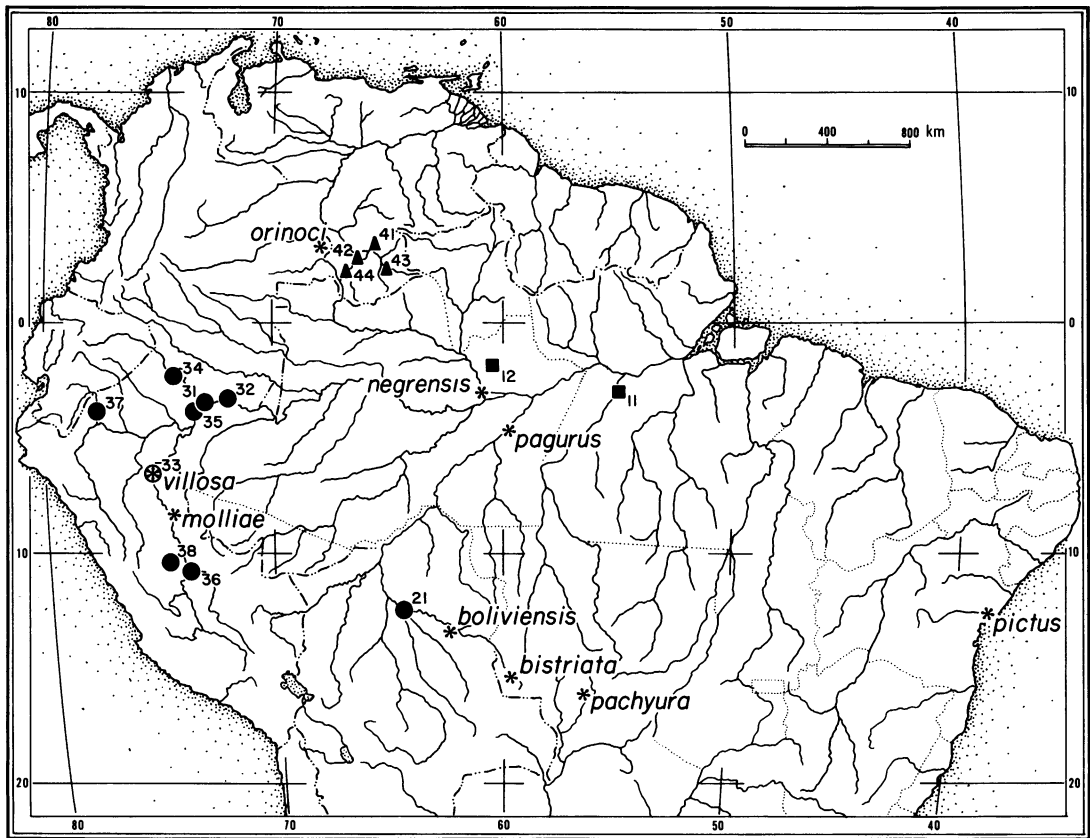


FIG. 1. Sampled localities of *Isothrix* specimens examined in this report; numbered localities are as identified in the text. The type localities for all named forms are indicated by asterisks.

ing; (IV) median re-entrant fold confluent with primary fold on dP^4 to M^3 ; (V) median fold separate on dP^4 , open on M^1 through M^3 ; (VI) median fold open on M^2 through M^3 ; (VII) median fold open only on M^3 ; (VIII) median fold separate from primary fold on all teeth; and (IX) entire tooth row worn, all folds isolated. Age classes V through IX were considered to represent adult individuals, although no data are available on individual reproductive status in each of the various age classes recognized.

The degree of non-geographic variation due both to age and sex was assessed by two-way analysis of variance (ANOVA) following the suggestion of Leamy (1983). One-way ANOVAs were utilized to assess the significance of single character variation within a taxon over a geographic area and to examine the

degree of character difference between the named forms recognized by Cabrera (1961) and others. Finally, overall geographic trends and degrees of differentiation between localities were examined by the multivariate procedure of discriminant function analysis. The statistical routines of SAS (Barr et al., 1982) and SPSS (Nie et al., 1975) were used for all analyses. Samples from each locality were considered as separate entities in the examination of both univariate and multivariate geographic trends.

Karyotypes from two individuals, one from northern Peru and one from central Brazil, were prepared following the technique of Patton (1967).

Specimens forming the basis of this report are in the collections of the American Museum of Natural History, New York (AMNH),

TABLE 1
Non-geographic Variation for Cranial Variables
in a Combined Sample of *Isothrix* from Northern
Peru (Localities 31 to 34)^a

Variable ^b	Age	Sex	Age × Sex	Residual
GSL	ns ^c (24.6)	ns (7.9)	ns (0.0)	(67.5)
BaL	ns (22.6)	ns (11.5)	ns (0.0)	(65.9)
ZB	* ^d (15.9)	* (13.5)	ns (11.0)	(59.6)
MB	ns (0.0)	* (7.2)	* (33.6)	(59.2)
IOC	* (28.3)	ns (4.2)	ns (0.0)	(67.5)
RL	* (28.0)	ns (1.2)	ns (0.0)	(70.8)
NL	ns (16.7)	ns (4.1)	ns (0.0)	(82.2)
RW	ns (11.8)	ns (6.0)	ns (0.0)	(82.2)
RD	ns (1.2)	ns (0.0)	ns (0.0)	(98.8)
D	ns (15.0)	ns (9.6)	ns (0.0)	(75.4)
PLA	ns (12.2)	ns (3.9)	ns (0.0)	(83.9)
PLB	ns (6.5)	ns (0.0)	ns (0.0)	(93.5)
MTRL	ns (0.0)	ns (0.0)	ns (8.9)	(91.1)
MaxB	ns (0.0)	ns (0.0)	ns (22.0)	(78.0)
IFL	ns (10.9)	ns (13.7)	ns (0.0)	(75.4)
BuL	ns (0.3)	ns (14.6)	ns (0.0)	(85.1)
PPL	ns (5.1)	ns (15.1)	ns (0.0)	(79.8)
CD	ns (8.0)	ns (9.9)	ns (0.0)	(82.1)
MPFW	ns (7.5)	* (25.1)	ns (0.0)	(67.4)
Mean	(11.29)	(7.76)	(3.97)	(76.98)

^a The significance level due to age, sex, and the interaction between age and sex is given for each variable based on a two-way ANOVA; the proportion of variation attributed to each component as well as the residual variation is given in parentheses.

^b See text for full description of each variable.

^c Non-significant.

^d $p < 0.05$.

the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). In addition, three holotypes in the British Museum (Nat. Hist.), London, were examined: *orinoci* Thomas (BM[NH] 99.9.11.45), *negrensis* Thomas (BM[NH] 20.7.1.20), and *molliae* Thomas (BM[NH] 24.2.22.25).

Figure 1 provides the mapped localities for material examined in this report; a two-digit locality code is employed to signify both country and specific locality. All type localities are indicated. Localities and their designations are as follows:

Locality 11—BRAZIL: Para; Rio Tapajoz, Igarape Brabo (2, AMNH), Rio Tapajoz, Inajataba (8, AMNH), Rio Tapajoz, Igarape

Amorin (5, AMNH), Rio Tapajoz, Limoal (1, AMNH).

Locality 12—BRAZIL: Amazonas; 80 km N (by rd) Manaus (1, USNM).

Locality 21—BOLIVIA: Beni; Rio Itenez at Costa Marques (1, AMNH).

Locality 31—PERU: Loreto; Pto. Indiana, Rio Amazonas (25, AMNH).

Locality 32—PERU: Loreto; Orosa, Rio Amazonas (5, AMNH).

Locality 33—PERU: Loreto; Sarayacu, Rio Ucayali (14, AMNH).

Locality 34—PERU: Loreto; Boca Rio Curaray (1, AMNH).

Locality 35—PERU: Loreto; Rio Itaya near Iquitos (1, AMNH).

Locality 36—PERU: Ucayali; Lagarto, Rio Alto Ucayali (5, AMNH), Boca Rio Urubamba (1, AMNH).

Locality 37—PERU: Amazonas; La Poza, Rio Santiago (3, MVZ).

Locality 38—PERU: Pasco; Nevati Mission (1, AMNH).

Locality 41—VENEZUELA: Amazonas; Boca del Rio Ocampo, Rio Orinoco (4, AMNH).

Locality 42—VENEZUELA: Amazonas; Rio Casiquiare, Orilla Izquierda El Meray (2, AMNH), Casiquiare Canal, Capibara (1, USNM).

Locality 43—VENEZUELA: Amazonas; Rio Orinoco, Cerro Duida (6, AMNH).

Locality 44—VENEZUELA: Amazonas; Esmeralda, Mt. Duida, 335 m (10, AMNH), 68 km SE Esmeralda, Boca Mauaca (4, USNM).

RESULTS OF ANALYSES

UNIVARIATE CRANIAL ANALYSES: Non-geographic variation was examined for samples from the combined region of northern Peru (localities 31–34) for which the largest samples were available (21 males, 19 females). Two-way ANOVA assessed the level of significance of age, sex, and age-sex interaction for each individual cranial variable, and the VARCOMP procedure of SAS apportioned the total variation of each character into age, sex, interaction, and residual components. As is evident in table 1, there is only minimally significant expressed variation due to specimen age, sex, or the interaction of these two

variables; only three variables show either age or sexual variation and only one variable shows a significant interaction, all at the 0.05 level. The low level of non-geographic variation is clearly evident from the variance component estimations. Less than 12 percent of the total variance averaged across all characters is attributable to age, less than 8 percent to sexual dimorphism, and less than 4 percent to their interaction. Fully 77 percent of the variation is residual, or due to other factors. Therefore, there is statistical justification for combining all adult individuals within localities in subsequent analyses.

Univariate geographic trends were assessed by one-way ANOVAs (1) within the samples from Peru-Bolivia and Venezuela, respectively; (2) between the samples from these two geographic regions; and (3) between the available samples from all areas. The rationale for this "hierarchical" procedure is as follows: The first level permits a test of the amount of variation within limited geographic regions and, thereby, examines the degree of regional homogeneity in the available samples. This is desirable because of the small sample sizes. The second analysis directly assesses the degree of differentiation between samples traditionally allocated to the separate species, *I. villosa* and *I. bistrata*, but for which Thomas (1916b, 1928) suggested possible conspecificity. Finally, the third analysis includes the sample from central Brazil (locality 11), specimens of which are clearly distinct in pelage characters in comparison with *villosa* and *bistrata* (see below).

Table 2 summarizes the level of character differentiation in each of the above three analyses. As is evident, character differentiation is minimal to non-existent within the combined localities of Peru and Bolivia (localities 21 and 31 to 38) or Venezuela (localities 41–44). Only three of 19 and five of 19 variables, respectively, show significant geographic variation within each region, and then only at $p < 0.05$. Thus, the combined geographic regions are virtually homogeneous within themselves, with little or no geographic character variation exhibited.

In the comparison of Peruvian-Bolivian samples (mostly assignable on present grounds to *I. villosa*) and Venezuelan *I. bistrata*, the level of character differentiation

TABLE 2
Univariate Levels of Geographic Variation within Samples of *Isotrix*, Based on One-way Analysis of Variance

Variable ^a	Within Peru-Bolivia	Within Venezuela	Between Peru-Bolivia and Venezuela	Between Peru-Bolivia, Venezuela, and Central Brazil
GSL	ns ^b	ns	ns	**** ^e
BaL	ns	*	ns	***
ZB	* ^c	*	ns	***
MB	ns	*	ns	***
IOC	ns	ns	*** ^d	***
RL	ns	*	ns	***
NL	ns	*	*	***
RW	ns	ns	ns	***
RD	*	ns	*	***
D	ns	ns	ns	***
PLA	ns	ns	ns	***
PLB	ns	ns	***	***
MTRL	ns	ns	ns	***
MaxB	ns	ns	*	***
IFL	*	ns	*	***
BuL	ns	ns	ns	***
PPL	ns	ns	*	***
CD	ns	ns	**	***
MPFW	ns	ns	ns	*

^a See text for full description of variables.

^b ns = non-significant.

^c * = $p < 0.05$.

^d ** = $p < 0.01$.

^e *** = $p < 0.001$.

is somewhat greater relative to that within each geographic region. Eight of the 19 variables show significant differences between these two regions, five at the 0.05 level, two at the 0.01 level, and one at the 0.001 level (table 2). Of the characters which do show significant geographic variation, only two of these exhibit any apparent geographic pattern. The Venezuelan samples consistently have both the longest nasals (character NL) and shortest palates (character PLB) relative to Peruvian samples, with a sizeable gap between them (table 3).

Finally, when the comparison incorporates all available samples from the three geographic regions of Peru-Bolivia, Venezuela, and central Brazil, all characters show highly

TABLE 3

Minimally Non-significant Geographic Subsets of *Isothrix* Population Samples from Peru-Bolivia and Venezuela for Those Two Variables that Show Geographic Patterns^a

Char- acter	Mean	Locality	Char- acter	Mean	Locality
NL	17.50	43 I	PLB	8.72	32 I
	17.20	41 II		8.52	31 III
	16.98	44 II		8.25	37 IIII
	16.95	42 II		8.18	33 IIII
	16.35	33 III		8.14	36 IIII
	16.32	31 III		7.54	43 IIII
	16.22	32 III		7.36	44 IIII
	15.53	36 III		7.05	42 II
	14.60	37 I		6.93	41 I

^a Based on Duncan's multiple range test with $\alpha = 0.05$.

significant differentiation (18 of 19 at $p < 0.001$; table 2), with central Brazilian specimens smaller in 16 of the 19 measurements. Clearly, therefore, on a univariate level, there is virtually no differentiation among localities within each of the three regional samples; only relatively slight differentiation is present in the comparison between Peru-Bolivia and Venezuela samples of *I. villosa* and *I. bistriata*, respectively, while the central Brazilian animals are sharply differentiated from all others.

MULTIVARIATE CRANIAL ANALYSIS: A step-wise discriminant function (DF) analysis was performed to determine the degree of multivariate separation among samples within and between each geographic region. Analyses were performed considering each locality as a separate a priori group and with localities combined into the three major geographic units as a priori groups. The results of these two analyses did not differ, and only the first will be presented here.

Eighteen discriminant functions were extracted, but only the first three functions had eigenvalues greater than 1.0. These three functions account for slightly more than 78 percent of the total variance in the data, with 49 percent attributable to DFI alone (table 4). Most of the total variance in the samples relates to both absolute and proportional size differences involving the rostrum and palate: nasal and rostral length measures contribute

TABLE 4

Standardized Canonical Discriminant Functions for Geographic Samples of *Isothrix*

Variable ^a	DFI	DFII	DFIII
GSL	-1.477	-0.285	-2.516
BaL	-0.636	2.085	1.487
ZB	0.156	0.057	-0.720
MB	0.457	-0.084	0.163
IOC	-0.087	0.381	-0.590
RL	2.111	-1.183	-3.790
NL	-3.684	4.393	1.427
RW	-0.031	-0.006	-0.225
RD	0.604	-0.782	1.775
D	1.219	-0.244	0.167
PLA	1.537	-1.565	1.113
PLB	-0.011	-4.494	0.213
MTRL	0.764	-1.092	0.219
MaxB	0.003	-0.208	-0.494
IFL	-0.056	-0.203	-0.561
BuL	0.419	-0.254	1.380
PPL	0.414	0.181	-0.899
CD	0.436	0.319	1.724
MPFW	-1.215	0.520	0.450
Eigenvalue	5.984	2.414	1.093
% variance explained	49.04	20.11	8.95

^a See text for full description of variables.

to most of the differentiation along DFI while NL and palatal length (PLB) contribute to discrimination along the second axis (table 4). Thus, this multivariate view is consistent with the results of the univariate analyses.

Figure 2 presents a plot of the discriminant scores for individuals from each separate locality. Three groups of localities are visually apparent, with the sample from the Rio Tapajoz in central Brazil (locality 11) most differentiated. The Venezuelan (localities 41–44) and Peruvian-Bolivian (localities 21 and 31–38) samples are less differentiated, although they are non-overlapping along the first two axes. Individual samples within either of these two regions are virtually identical. This visual perspective is supported by a multivariate analysis of variance comparing the Mahalanobis distances between group centroids (table 5). Only four of 31 two-way locality comparisons within the Peruvian-Bolivian or Venezuelan geographic units show significant F-values, whereas 20 of 32 com-

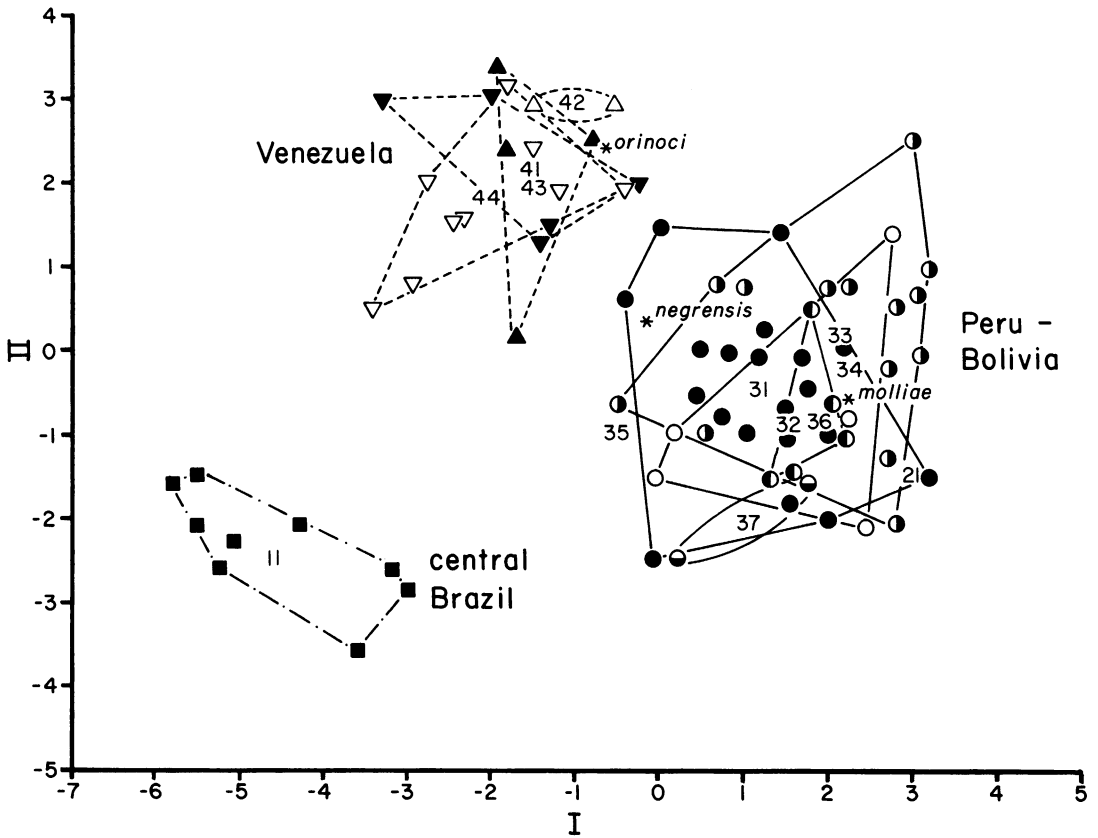


FIG. 2. Plot of the first two discriminant functions for geographic samples of *Isothrix*: circles represent localities from Peru and Bolivia; triangles those from Venezuela; and squares those from central Brazil. Centroids for each locality are indicated by their respective numerical designations (see text). The placement in discriminant space of the holotypes for three named forms is illustrated.

TABLE 5
Summary of Differentiation between Geographic Samples of *Isothrix*^a

Geographic Region Being Compared	Number of Pair-wise Comparisons	D ² ± st dev	Number of Significant Comparisons
Within Peru-Bolivia	28	1.328 ± 0.463	3 @ p < 0.05 1 @ p < 0.01
Within Venezuela	5	0.386 ± 0.157	0
Between Peru-Bolivia and Venezuela	32	3.012 ± 0.836	6 @ p < 0.05 6 @ p < 0.01 8 @ p < 0.001
Between Peru-Bolivia and central Brazil	8	6.385 ± 1.443	2 @ p < 0.01 6 @ p < 0.001
Between Venezuela and central Brazil	4	4.660 ± 0.870	4 @ p < 0.001
Between Peru-Bolivia-Venezuela and central Brazil	12	5.810 ± 1.662	2 @ p < 0.01 10 @ p < 0.001

^a Based on a multiple analysis of variance of sample pair-wise Mahalanobis distances (D²), with df_{51,15}.

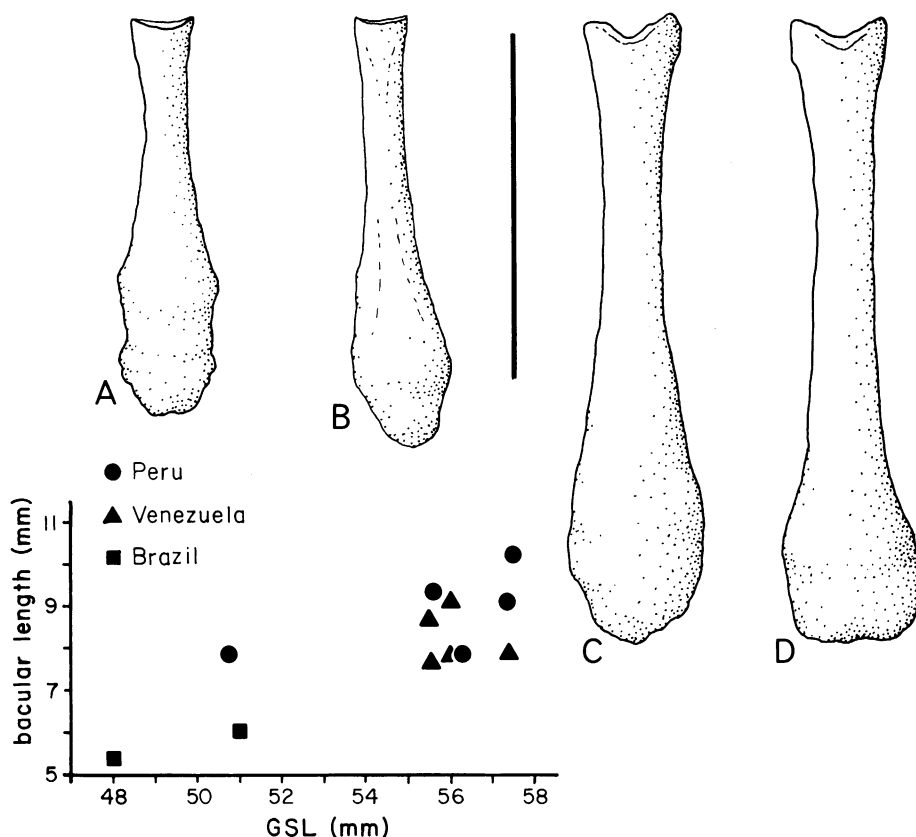


FIG. 3. Representative bacula for *Isothrix* specimens from central Brazil (A = AMNH 94885; B = AMNH 95652; locality 11), Venezuela (C = AMNH 78114; locality 41), and Peru (D = AMNH 74072; locality 32). Bar = 5 mm. The inset graph illustrates the proportional difference in bacular length in relation to overall body size, as indexed by greatest skull length (GSL), among the three geographic samples.

parisons between these two units are significantly different. All 12 pair-wise distances between the Peruvian-Bolivian-Venezuelan samples and that from central Brazil were found to be highly significantly different. Again, these multivariate results mirror the patterns of character differentiation within and between geographic samples based on the univariate analyses.

BACULAR VARIATION: Cleared and stained glands are available from a total of 12 specimens representing the three geographic areas herein considered: Peru ($N = 5$), Venezuela ($N = 5$), and central Brazil ($N = 2$). The baculum of *Isothrix* has not been previously figured, to our knowledge (see Didier, 1962, for a synopsis of bacular variation in echimyid rodents). General bacular form is the same

in all specimens available, regardless of taxon or locality: an elongate bony structure, with a rather bulbous proximal base tapering to a narrow distal tip which, in specimens from Peru and Venezuela but not those from central Brazil, has a moderate median notch (see fig. 3). A simple, shallow, triangular cartilaginous tip is present. In lateral view the baculum is straight. The tip is rather ovoid in cross-section; a slight ventral groove develops at midshaft and extends to near the base. This general bacular type is characteristic of most echimyid rodents, notably *Echymys*, *Diplomys*, *Thrinacodus*, and *Dactylomys*, as well as several species of *Proechimys* (see Didier, 1962; Patton and Gardner, 1972; also, Patton, unpubl. data).

Despite an overall similarity in bacular

TABLE 6
Measurements (in Millimeters) of Bacula in Geographic Samples of *Isothrix*
(Mean plus or minus one standard deviation are listed for each measurement.)

Geographic Region	Age	N	Bacular Length	Width at Tip	Width at Base
Central Brazil	8	2	5.83 \pm 0.54	0.86 \pm 0.14	1.14 \pm 0.01
Peru	6	2	7.28 \pm 0.76	1.28 \pm 0.01	1.67 \pm 0.12
	7	1	7.95	1.04	1.51
	8	2	9.56 \pm 0.60	1.51 \pm 0.10	2.26 \pm 0.06
Venezuela	7	1	7.76	1.45	2.00
	8	4	8.37 \pm 0.67	1.43 \pm 0.16	2.05 \pm 0.30

shape, the baculum of the two specimens from central Brazil is proportionally shorter than that of Peruvian or Venezuelan specimens, even when allowing for individual age differences (see fig. 3 and table 6). It is not possible to differentiate the bacula of Peruvian and Venezuelan specimens on either absolute or relative size (fig. 3).

COLOR AND COLOR PATTERN: Only two geographic entities are evident on the basis of sharply distinguishable color patterns. All specimens from Venezuela, Peru, and Bolivia are characterized by a grizzled, yellowish gray head with a distinct pair of black or dark brown supraorbital stripes extending onto the nape of the neck, and a pale creamy patch on the forehead between these stripes. The dorsum is rather uniformly grizzled yellow-brown, often with a dark middorsal patch. The venter is uniformly pale yellow to buff, with basal gray showing in many specimens. The tail is varying colored, almost always pale auburn to yellow at the base but darkening to black at the tip. In only one specimen does the distal portion of the tail lack black; in all others the black portion encompasses at least the terminal one-fourth of the tail, usually one-half or more (72 of 76 specimens). It is not possible to separate specimens from Peru or Bolivia from those from Venezuela on the basis of any consistent color feature. Thomas (1920) distinguished *negrensis* primarily on the basis of black head stripes that fuse on the nape of the neck to form a broad black band. Such fusion, however, was seen in 14 percent of Peruvian specimens (8 of 57 examined) and in 46 percent of those from Venezuela (12 of 25 examined).

The specimens from central Brazil, however, show a radical departure in both color and pattern from those of Bolivia, Peru, or Venezuela. First, and most striking, these specimens lack even a hint of black supraorbital stripes, they have a reddish snout with that color extending to above and below the eyes, and, in adults, the tail grades uniformly from gray-brown at the base to yellow-brown toward the tip. Tail color of juveniles varies from uniformly gray-brown to dark brown. The tail thus not only lacks any black hairs, but shows the opposite color pattern, being lighter at the tip than the base in adults. The dorsal color ranges from grizzled yellow or gray-brown from the forehead to midback with the distal sides and rump distinctly russet. The venter is as in Peruvian-Venezuelan specimens, but generally paler.

KARYOTYPES: Chromosome characters are available from only two individuals, one Peruvian specimen referable to *I. villosa* and one specimen of the central Brazilian form. The karyotype of the latter is illustrated in figure 4. The diploid number is 22, the number of autosomal arms 38. There are eight autosomal pairs of meta and submetacentrics, the fourth largest of which shows a distinct secondary constriction on the long arm, and one autosomal pair each of subtelocentrics and acrocentrics. The X-chromosome is a medium-sized submetacentric, and the Y is a small acrocentric. Differential staining for constitutive heterochromatin (C-bands; see inset, fig. 4) reveals only two pairs of autosomes with slight centromeric heterochromatin, whereas eight pairs exhibit telomeric heterochromatin on one (four pairs) or two

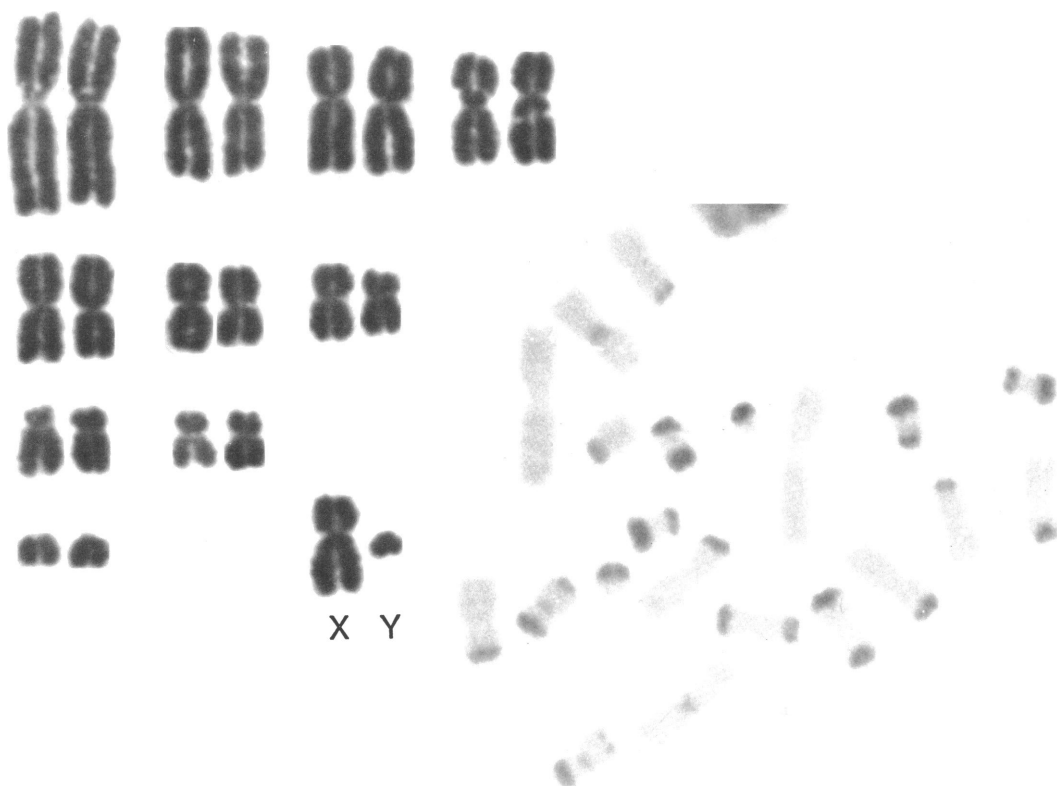


FIG. 4. The karyotype of *Isothrix pagurus* from 80 km N Manaus, Amazonas, Brazil ($2n = 22$, $FN = 38$; USNM 555639). Inset: a mitotic metaphase cell differentially stained for constitutive heterochromatin.

arms (four pairs). The short arm of the X-chromosome appears totally heterochromatic.

The chromosome preparations from the single Peruvian specimen are quite poor. Nevertheless, diploid number counts range from 54 to 58 and most of the chromosomes appear biarmed. These two karyotypes are quite distinct, equivalent to the differences seen among the most divergent species of *Proechimys* (Patton and Gardner, 1972; Reig, 1981), or even among other genera of echimyid rodents (for example, Yonenaga, 1975; Souza and Yonenaga-Yassuda, 1982).

COUNTERFOLD PATTERN OF THE CHEEK TEETH: In the most recent taxonomic study of *Isothrix*, Petter and Cuenca Aguirre (1982) focused solely on the number and pattern of re-entrant folds on both upper and lower cheek teeth for taxonomic conclusions. They

examined, however, only 15 specimens, representing eight named forms. Of these, *I. pictus* (Pictet) is rather easily distinguished by virtue of the simple and complete transverse plates of the upper teeth, an observation made by all previous authors (for example, Waterhouse, 1848; Thomas, 1916a, 1916b; Ellerman, 1940). However, despite the discussion of details differentiating the teeth of the named forms applied to the species *I. villosa* and *I. bistrata*, Petter and Cuenca Aguirre were unable to illustrate any dental features which can serve to separate consistently these taxa. Indeed, in the present analysis, the complete range of re-entrant fold number, details of position, and lateral versus lingual initial closure with wear can be observed among individuals within single localities. We, therefore, find no way to differentiate regional units on the basis of counterfold pattern, with the

exception of *I. pictus*. Certainly, the central Brazilian specimens, so distinctive in other characters, cannot be separated from those of Peru or Venezuela, nor can those from Peru or Venezuela be differentiated from each other.

MORPHOLOGICAL AND BEHAVIORAL NOTE: The single specimen collected by one of us north of Manaus in central Brazil was observed for a day in captivity. A striking feature of its behavior when at rest was a tendency to coil the tail tip in a tight downward spiral of one and a half loops. When climbing, it sometimes wrapped its tail longitudinally around the branch. These behaviors indicate a semiprehensile tail, a feature hitherto undescribed in echimyid rodents, and not present in *Mesomys* or *Dactylomys*, two other arboreal genera of this family that we have observed in the field.

TAXONOMIC CONCLUSIONS

The present analyses provide totally concordant results that clearly distinguish central Brazilian *Isotrix* from those elsewhere in the Amazon region of Venezuela, Peru, and Bolivia. This differentiation is trenchant, being based on cranial morphometric and bacular characters, color and color pattern, and karyotype with available specimens. There seems little doubt but that these respective samples represent distinct species. The question remains, therefore, regarding the proper allocation of names to these two taxa.

Although Wagner (1845) did not designate a type species for his genus *Isotrix*, Goldman (1916) selected *I. bistriata*, the first of Wagner's species, as the type for the genus. The type locality for this taxon is Rio Guapore, Mato Grosso, Brazil. Wagner's original description clearly ascribes to the holotype the color and pattern characteristic of all Venezuelan, Peruvian, and Bolivian specimens examined here. Most notably, the type is characterized by a pair of black stripes on the head and a black tail with a yellow base (Wagner, 1845, p. 146). It is, therefore, quite clear that the name *bistriata* should apply to animals with the black head stripes. Traditionally, however, there have been two recognized forms having this general color pattern on the head: *bistriata* and Peruvian *villosa*

(Deville), despite Thomas's (1916b, 1928) suggestion that these two taxa are likely conspecific. In color pattern of the head, body, and tail, and in tooth and bacular characters, samples applicable to these two named forms are indistinguishable, although they are separable on the basis of a multivariate analysis of cranial dimensions. Considering the overall high degree of similarity among these samples and their extreme level of difference from central Brazilian populations in the genus, it seems best to consider as members of the single species, *I. bistriata* Wagner, all Venezuelan, Peruvian, Bolivian, and Brazilian specimens of *Isotrix* with black stripes above the eyes. The geographic homogeneity within the regional samples from Peru and Bolivia on the one hand and Venezuela on the other, in combination with the degree of cranial distinctness of specimens from these two areas, argues for recognition of two subspecific units within *I. bistriata*. Since the type locality of *bistriata* is quite close to the Bolivian border, the Bolivian and Peruvian samples examined here are best referred to the nominant subspecies, *I. b. bistriata* Wagner. Thus, the names *villosa* (Deville) and *molliae* Thomas, with type localities in Peru, become junior synonyms. Clearly, the holotype of *molliae* falls within the morphological range exhibited by these geographic samples (see fig. 2). Although we have not examined the type of *boliviensis* Petter and Cuenca Aguirre (1982), we consider it likewise to be a synonym. The only name available for the Venezuelan samples is *orinoci* Thomas, so these specimens are referred to the subspecies *I. b. orinoci* Thomas. The named form *negrensis* Thomas (1920), with type locality at Acajatuba on the lower Rio Negro, near Manaus, Amazonas, Brazil, remains somewhat problematical. This form is clearly referable to *bistriata* on the basis of color pattern and cranial features (see Thomas, 1920 and fig. 2). The DF analysis places the type, and only examined specimen, within the *bistriata* samples from Peru and Bolivia rather than with Venezuelan *orinoci*. We, therefore, subsume *negrensis* within the subspecies *bistriata* until adequate samples become available for analysis. With better and geographically intermediate samples, the current distinction between *bistriata* and *orinoci* may in fact disappear into a more

smoothly distributed clinal relationship. Certainly, the nearly intermediate position of the holotype of *negrensis* in discriminant space relative to samples of *bistriata* and *orinoci* suggests such a possibility (fig. 2).

The specimens from the Rio Tapajoz in central Brazil examined here seem best referable to the species *I. pagurus* Wagner. Although Wagner's original description of this form (Wagner, 1845, p. 146) is lacking in detail, he does make reference to the fulvous snout and rust-colored hind parts, and makes no reference to black eye stripes. Unfortunately, Wagner's specimen of *pagurus* lacked a tail. The type locality of *pagurus* is given as Borba, near the mouth of the Rio Madeira, not far to the south of Manaus, where the single karyotyped specimen is from, or to the west of the Rio Tapajoz (see fig. 1).

GENUS *ISOTHRIX* WAGNER

Isothrix Wagner, 1845.

Nelomys Pictet, 1843 (part, not Cuvier, 1837).

Lasiuromys Deville, 1852.

GENOTYPE: *Isothrix bistriata* Wagner (designation by Goldman, 1916).

Isothrix bistriata bistriata Wagner

Isothrix bistriata Wagner, 1845.

Isothrix pachyura Wagner, 1845.

Lasiuromys villosa (Deville, 1852).

Isothrix bistriata negrensis Thomas, 1920.

Isothrix villosa molliae Thomas, 1924.

Isothrix bistriata boliviensis Petter and Cuenca Aguirre, 1982.

RANGE: Western and southwestern Amazon Basin from Mato Grosso in Brazil northwest through eastern Bolivia, eastern Peru, and western Brazil (localities 21 and 31 through 38; see map, fig. 1). Type locality: Rio Guapore, Mato Grosso, Brazil.

Isothrix bistriata orinoci Thomas

Loncheres (Isothrix) bistriatus orinoci Thomas, 1899.

RANGE: Upper Rio Orinoco, Rio Casiquiare, and upper Rio Negro of Venezuela and adjacent Colombia (localities 41 through 44; see map, fig. 1). Type locality: Maipures, upper Rio Orinoco, Intendencia Vichada, Colombia.

Isothrix pagurus Wagner

Isothrix pagurus Wagner, 1845.

RANGE: Amazon Basin of central Brazil, from Rio Madeira east to the Rio Tapajoz and north to the lower Rio Negro (localities 11 and 12; see map, fig. 1). Type locality: Borba, lower Rio Madeira, Amazonas, Brazil.

Isothrix pictus (Pictet)

Nelomys pictus Pictet, 1843.

RANGE: Coastal forests of eastern Brazil. Type locality: Bahia, Brazil (probably collected in the region north of the municipality of Ilheus [Fazenda Almada]; see Moojen, 1952).

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