The Neotropical rodent genus *Rhipidomys* (Cricetidae:
Sigmodontinae) - a taxonomic revision

Christopher James Tribe

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ABSTRACT

South American climbing mice and rats, *Rhipidomys*, occur in forests, plantations and rural dwellings throughout tropical South America. The genus belongs to the thomasomyine group, an informal assemblage of plesiomorphous Sigmodontinae. Over 1700 museum specimens were examined, with the aim of providing a coherent taxonomic framework for future work. A shortage of discrete and consistent characters prevented the use of strict cladistic methodology; instead, morphological assessments were supported by multivariate (especially principal components) analyses. The morphometric data were first assessed for measurement error, ontogenetic variation and sexual dimorphism; measurements with most variation from these sources were excluded from subsequent analyses.

The genus is characterized by a combination of reddish-brown colour, long tufted tail, broad feet with long toes, long vibrissae and large eyes; the skull has a small zygomatic notch, squared or ridged supraorbital edges, large oval braincase and short palate. Three main divisions of the genus are recognized. The *R. fulviventer* section contains four species - *fulviventer, wetzeli, caucensis* and *ochrogaster* - inhabiting montane forests in the northern Andes and Guiana Highlands of Colombia and Venezuela; they share grey-based ventral pelage, dark extremities, a rounded interorbital region, broad braincase, and (except for *caucensis*) a primitive carotid circulation pattern; *R. fulviventer* consists of a chain of isolated subspecies, including *venustus*. The monospecific *R. macconnelli* section is restricted to the Guiana Highlands of Venezuela; it differs in certain external characters - darker colour (especially ventrally), longer

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metatarsals, bicoloured tail - but is similar cranially. The *R. leucodactylus* section is usually paler with broad feet, stronger cranial ridges and a derived carotid circulation pattern, and occurs mainly at lower levels. It contains 13 species: *couesi, leucodactylus, modicus, austrinus, latimanus* (including *venezuelae*), *nitela, emiliae, macrurus, mastacalis* and four as yet unnamed. Three species occur in NE Brazil; in SE Brazil the material currently available does not permit a clear-cut arrangement.

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Fig. 1.1 - *Rhipidomys mastacalis* from Fazenda União, Casimiro de Abreu, Rio de Janeiro, Brazil (Universidade Federal do Rio de Janeiro, Laboratório de Ecologia, no. FU 19). Photo: Lena Geise.

CHAPTER 1 - INTRODUCTION

The native rats and mice of the Neotropics are commonly placed in the subfamily Sigmodontinae (*sensu* Reig, 1980), either within the extensive family Cricetidae, which also includes the Eurasian hamsters and other essentially Old World or Nearctic groups, or in an even more encompassing Muridae (see Chapter 2). The sixty or so genera in the subfamily contain about 300 species (data from Musser & Carleton, 1993, plus subsequent additions) confined almost entirely to South America and Central America as far north as Mexico, with only a handful of species in two genera reaching the United States. This taxonomic diversity is reflected ecologically, with arboreal, terrestrial, fossorial and even semi-aquatic forms inhabiting sylvan (forest) and pastoral (savanna, etc.) habitats. Although the number of systematic studies of taxa from single species to tribal level has increased in recent years, relatively little attention has been paid to the often common but little known forest forms (Pine, 1982). This is especially true of the more arboreal genera such as *Oecomys* and *Rhipidomys*, and the latter genus has been mentioned as being in particular need of revision (Cabrera, 1961; Pine, 1982). On the basis of personal examination of the majority of the *Rhipidomys* specimens held in museum collections in Europe and the Americas and the critical collation of published data, I hope to achieve and to put across here an understanding of the genus that will serve as a foundation for future systematic and ecological research.

Known by English-speaking taxonomists as South American Climbing Mice, the species of *Rhipidomys* are generally included among *ratos arborícolas* ("tree rats") in Portuguese, or *ratas arborícolas* in Spanish; a few more specific local names have also been recorded. The fact that forty-two species and subspecies referrable to the genus have been described testifies to the diversity it contains. The range of the genus covers most of tropical South America, from the Paraguaná peninsula in northern Venezuela, at nearly 12°N, to São Paulo state in southeastern Brazil and Jujuy province in northwestern Argentina, both of which lie at approximately 24°S. It also occurs just within the borders of Panama and on certain islands off the Venezuelan coast, including Trinidad. Within these latitudes no representatives have been found in the dry coastal areas west of the Andes in Peru and Chile or in the cold and treeless zones of the high Andes; over the rest of the area, however, the genus probably occurs wherever there is suitably moist forest habitat. Even isolated mesic patches in the dry scrub of the caatinga or riparian gallery forests a few metres wide in the midst of the savanna-like cerrados will support

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populations, whereas the species inhabiting the often treeless summits of the sandstone tepuis in the Guiana Highlands has applied its scansorial abilities to rock faces and crevices.

Data from specimen labels and field notes show that *Rhipidomys* are often found among the rafters or in the thatch of human dwellings, and species may locally be considered pests in cacao, coffee and other plantations: the holotype of the type species, *R. leucodactylus*, was in fact caught in a pineapple field (Tschudi, 1845). Yet few published works have dealt exclusively with members of the genus (Guillotin & Petter, 1985; Cerqueira et al., 1989; Montenegro-Díaz et al. 1991; Zanchin et al., 1992a; Svartman & Almeida, 1993). *Rhipidomys* species are frequently cited as members of rodent communities, and some works of community scope provide valuable data on their ecology and life histories (e.g., Davis, 1947; Aagaard, 1982); but capture frequencies are generally too low to yield much information (e.g., Everard & Tikasingh, 1973; Mello & Moojen, 1979; Dietz, 1983; August, 1984; Díaz de Pascual, 1984; Malcolm, 1988; Stallings, 1988; O'Connell, 1989).

Their arboreal habits have meant that relatively few *Rhipidomys* specimens have been captured for scientific collections, despite their widespread occurrence and sporadic status as agricultural pests. In certain localities they may be present at relatively high densities: witness G.H.H. Tate's extensive series of Venezuelan *R. macconnelli* and *R. venezuelae* (American Museum of Natural History collection). Elsewhere they may be either extremely scarce or just trap-shy: for example, only one individual of *R. mastacalis* was captured in 57,120 trap-nights (18,360 of which were arboreal), during a seventeen-month study in forests in eastern Minas Gerais, Brazil (Fonseca & Kierulff, 1988), while at Paracou, French Guiana, a single *R. nitela* was shot unexpectedly in a bat roost although none had been captured in two years of trapping (R. S. Voss, personal communication). Probably no more than 2000 specimens exist in collections worldwide, a rather small total for a speciose and widespread genus. The 1734 specimens I have examined include a few large series (i.e. collections made at a single locality over a continuous, usually short period of time), but the majority of collecting localities are represented by only one or very few individuals.

Whatever the methods and data sets used, taxonomic judgements have to be based ultimately on similarities and differences exhibited by the specimens. The variation between individuals must be broken down as far as possible into its component parts: within-species variation of individual, ontogenetic, sexual and geographic origin must be

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recognized as such and distinguished from variation that characterizes species. This is most easily accomplished when large series of specimens are available from numerous localities throughout the range of the organism under study. Such ideal conditions are, however, rarely encountered except in studies of very limited scope. In the present case, as in many if not most studies of mammalian taxonomy, the material available is far from ideal; it could be improved only with a considerable investment in fieldwork throughout tropical South America. For now, the lack of large series of *Rhipidomys* from many key areas and within many species of the genus means that rigorous statistical testing of certain hypotheses is not possible.

Much has been written in recent years about species concepts in biology (reviewed by Häuser, 1987). Most authors agree that while the genus and higher categories are artificial constructs based on particular concepts of phylogeny or other classificatory criteria, the species is a natural grouping with a real existence in nature. The unity of the species is ultimately derived from the reproductive potential of its members. The "biological" species concept developed by Mayr and Dobzhansky from the late 1930s onwards, for example, requires reproductive isolation between populations for them to be assigned the rank of separate species; in contrast, the "recognition" concept (Paterson, 1985) emphasizes the unity of a reproductive pool of individuals without regard to other groups.

The application of either concept in a taxonomic study is fraught with difficulty. The recognition model requires detailed assessment of the subtle complexities of the specific mate recognition system (SMRS) of the animal. In addition to the visual recognition of the external morphology of a potential mate, which we may be able to achieve very imperfectly with a museum specimen, the mammalian SMRS will include detection of auditory, olfactory and behavioural signals which cannot be preserved in collections. In the absence of very carefully conducted field observations and experimentation, species definitions must therefore rely on the assumed importance to the SMRS of the external morphology of the animal, as shown by skin characters and skeletal proportions. Difficulties of a similar scale are involved in the use of the biological species concept, particularly when the genus has been as poorly sampled throughout its range as in the case of *Rhipidomys*. Evidence of gene flow (or the lack of it) between wild populations, and/or laboratory breeding experiments are required to demonstrate reproductive isolation between species, except in the (taxonomically non-trivial) case of geographical barriers. And at a higher level, if genera are to be distinguished on the basis

of an inability to produce even sterile hybrid offspring (Van Gelder, 1977), similar experimentation is needed to confirm whether *Rhipidomys* is indeed distinct from *Thomasomys*. In the present study of preserved museum specimens for which molecular data are unavailable, allocation to genus and species according to genetic inheritance has to be based upon morphological characters, seen as imperfect phenotypic expressions of the genome. Thus, whether one accepts a biological or a recognition species concept, in practice one can distinguish only morphospecies on the basis of the phenotypes of the specimens available.

Of the many names proposed for taxonomic categories between the levels of subgenus and species and between species and subspecies, several have unfortunately been redefined or used in a different sense by subsequent workers, with the result that the area is cluttered with partly synonymous yet subtly distinct terms. What would seem to be the most useful categories are: a) superspecies (Mayr, 1931, based on Rensch, 1929), redefined by Amadon (1966:245) as "a group of entirely or essentially allopatric taxa that were once races of a single species but which have now achieved species status"; b) allospecies (Amadon, 1966), the vicariant component units of a superspecies; c) semispecies (in the amended sense of Mayr, 1963, as argued on pp. 501-2 and in the second part of his definition on p. 671), "populations that have acquired some, but not yet all, attributes of species rank; borderline cases between species and subspecies" (equivalent to the "megasubspecies" of Amadon & Short, 1976); and d) megaspecies (Crawford-Cabral, 1986), for a taxon composed of semispecies. These concepts may be referred to here in discussions of the relationships between taxa, but since they are not recognized in the International Code of Zoological Nomenclature (1985), they will not be used in any formal sense. In any case, there is often insufficient evidence on which to select the most appropriate category. When, as in the case of *Rhipidomys*, taxa are represented in museum collections by small, widely separated samples, it is often impossible to say whether the variation seen in a particular character is evidence of specific or subspecific distinction, represents points on a cline within a single species, or is just individual "noise" (Corbet, 1970). The taxonomic decision taken in each case is influenced by the congruence of other characters and by biogeographical inferences drawn from environmental data and similar distributions of other taxa.

The ultimate aim of this study is to provide a taxonomic framework for the genus based on the data currently available. Concomitantly, specific areas for future work will be highlighted, in particular the need for reinforcement of existing inadequate samples,

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collecting in intermediate localities to elucidate the relationships between apparently separate populations, assessment of ecological differences between sympatric species, and investigation of predicted occurrences of taxa. The accumulation of such data will in turn lead to the refinement of the framework proposed herein.

Chapter 2 deals with the taxonomic context of *Rhipidomys*, situating the genus within the Rodentia and Muroidea and especially within the Sigmodontinae. In the following two chapters I describe the material examined and the methods of analysis used, together with the results of preparatory numerical techniques including assessments of measurement error and sexual and ontogenetic variation. The results of examination and analyses are presented in the remaining chapters. The purpose of Chapter 5 is to define and delimit *Rhipidomys*, contrasting it with other genera of Sigmodontinae. In Chapter 6 the variation that exists within the genus is examined and its included species are assessed on the basis of visual, morphometric and biogeographical data. This information is drawn together in the Taxonomic Synthesis of Chapter 7 to provide formal, synthetic diagnoses and descriptions of *Rhipidomys* and its constituent species, together with synonymies and other information. Conclusions and directions for future work form Chapter 8.

CHAPTER 2 - THE SYSTEMATIC CONTEXT

2.1 - *Muroidea*

The traditional division of the Rodentia into three suborders (Sciuromorpha, Myomorpha and Hystricomorpha) dates essentially from the work of Brandt (1855), who was the first to use the osteology and associated myology of the rodent masticatory apparatus as a formal basis for classification. Brandt's arrangement (which originally also included the Lagomorpha as a fourth suborder of Rodentia) is today seen as a rather over-simplified representation of rodent relationships. The majority of extant rodent taxa are now regarded as forming five main clades (Catzeflis et al., 1992): Protrogomorpha (sewellel), Sciuromorpha (squirrels, beavers, etc.), Myomorpha (rats, jerboas, etc.), Phiomorpha (African cane rats), and Caviomorpha (capybara, chinchilla, etc.) The relations of the dormice (Myoxidae) are somewhat ambiguous, since they have certain cranial foramina and macromolecular traits in common with Myomorpha, but share some middle ear structures with Protrogomorpha and Sciuromorpha (Flynn et al., 1985; Lavocat and Parent, 1985; Wahlert, 1985). They are now considered to form a basal branch (superfamily Myoxoidea) within the Myomorpha (Wahlert et al., 1993), a taxon which also includes the Muroidea (rats, mice, etc.), Dipodoidea (birch mice and jerboas) and Geomyoidea (pocket gophers, kangaroo rats, etc.), united on the basis of myological, skeletal and dental evidence (Flynn et al., 1985).

For many years the contents of Muroidea Miller and Gidley, 1918, varied from author to author, especially as regards the question of whether or not the dormice should be included; Simpson (1945) finally removed them. This paved the way for recognition of the loss of the fourth upper premolar as the character defining the monophyly of Muroidea in its broadest sense, with true myomorphy being the most distinctive apomorphic trait of advanced muroids since the Oligocene (Flynn et al., 1985). Carleton and Musser (1984) provide a thorough diagnosis of the superfamily.

Within the Muroidea as currently understood, the ranking and arrangement of the constituent groups also varies considerably between different authors' classifications, particularly where the union or separation of the Muridae and Cricetidae is concerned. This lack of agreement is due in large part to the frequent parallelism, convergence and secondary losses that occurred in the evolution of the various groups, masking their true phylogenetic relationships (e.g., Ellerman, 1941; Simpson, 1945; Carleton, 1980; Carleton and Musser, 1984). When Carleton and Musser (1984) placed all muroid rodents

into fifteen subfamilies within a single, all-embracing family Muridae, they stated clearly that theirs was a conservative position which "reflects not our conviction that this is the preferred nomenclature, but rather our uncertainty of the hierarchical pattern" (p. 300).

Such an arrangement, however, wastes the opportunity of using the family category to express at least some of the considerable variation among muroids. Simpson (1945) placed most muroid taxa into the two large families Cricetidae and Muridae, using two more families (Spalacidae and Rhizomyidae) for more divergent forms. Chaline, Mein and Petter (1977) split the muroids into eight families, placing Simpson's Spalacidae within the Cricetidae, but extracting from the latter taxon the Nesomyidae, Gerbillidae and Arvicolidae, while the Dendromuridae and Cricetomyidae were removed from the Muridae. In recognizing a total of eleven families on the basis of the palaeontological appearance of apomorphies, Flynn et al. (1985) disagreed especially with respect to the Spalacidae (which they considered a separate lineage from the Cricetidae) and Arvicolidae (which they regarded as a polyphyletic group of advanced Cricetidae).

Simpson's (1945) Cricetidae embraced voles and lemmings, gerbils and other groups, in addition to hamsters and New World rats and mice; the last formed the tribe Hesperomyini, which together with the Cricetini (hamsters) and Myospalacini (East Asian mole rats) made up the subfamily Cricetinae. Having removed most of Simpson's other subfamilies from the Cricetidae, Chaline et al. (1977) raised the Hesperomyini and other tribes to the rank of subfamilies, on an equal footing with the Spalacinae. Under the name Sigmodontinae Wagner, 1843 (a name demonstrated by Hershkovitz, 1966b, and Reig, 1980, to have priority over Hesperomyinae Murray, 1866), Carleton and Musser (1984) included the New World rats and mice as one of their fifteen subfamilies of Muridae.

2.2 - New World Cricetids

In none of the above-mentioned classifications is there any attempt to make further subdivisions of the New World rats and mice. There is evidence, however, that this assemblage consists of at least two separate groups, which for convenience in the following discussion I shall refer to as Neotropical cricetids and North American cricetids. The latter group ranges from Yukon and Labrador south to Panama, with two genera (*Reithrodontomys* and *Tylomys*) extending into the northern Andes of South America; Hershkovitz's (1966b) peromyscine group or Peromyscini, Reig's (1980) Neotominae, and the neotomine-peromyscines of other authors are approximate equivalents. The Neotropical cricetids are also referred to as Sigmodontinae (in a restricted sense of the

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name: e.g., Reig, 1980; Steppan, 1995), South American cricetines (e.g., Marshall, 1979; Carleton, 1980) or South American sigmodontines (Carleton and Musser, 1984). They occur throughout the Neotropical region, and two genera (*Oryzomys* and *Sigmodon*) range into the southern and eastern United States.

The idea that such a division between Neotropical and North American cricetids might exist was first aired by Rinker (1954) in his myological study of four genera found in North America. He discovered that *Sigmodon* and *Oryzomys* shared similarities in muscle anatomy with each other which were not shared by *Neotoma* and *Peromyscus*, and vice versa. He concluded that the most plausible explanation for the character distribution was that each of these pairs had a common ancestor not shared by either of the other genera. However, not having made consistent use of an outgroup to aid in the polarization of characters, he was unable to draw firmer conclusions.

The study which attracted most attention to the possible dichotomy was that of Hooper and Musser (1964) on the glans penis in Neotropical cricetines, which drew for comparison on the results of Hooper's previous studies of mainly New World rodents published from 1958 onwards (e.g., Hooper, 1958; Hooper and Hart, 1962). They discovered that members of the Neotropical group generally possessed a complex glans, ornamented with papillae and processes and containing sac-like sinuses and a baculum with three terminal digits. Similar characteristics were shared by North American microtines and many Old World muroid rodents. In North American cricetids, however, the glans was simpler, with vascularized spongy tissue instead of the sinuses, little ornamentation, and a baculum without lateral digits. Within these two basic plans, many smaller variations allowed species and genera to be grouped on the basis of shared similarities. The presence of the complex phallus in several other muroid taxa implied that this was the primitive condition, and that the simple type was derived by means of secondary loss or reduction of the papillae and lateral bacular digits. Thus the North American cricetids might form a monophyletic group separate from the Neotropical genera.

The distribution of stomach morphologies among New World mice shows certain parallels with that of the simple and complex types of penis. Carleton (1973) showed that whereas most neotomine-peromyscines had a bilocular stomach all other species he examined had a unilocular one in which the antrum and corpus were broadly confluent (regarded as the primitive condition). The phyletic correspondence between stomach and glans penis types was not perfect, however, because certain mainly Central American

"simple penis" genera - *Tylomys*, *Ototylomys*, *Scotinomys*, *Baiomys* and possibly *Ochrotomys* - all had unilocular stomachs. The area of the stomach lining covered by glandular epithelium also varied considerably between genera, and even between apparently congeneric species in some cases. Most unilocular stomachs were hemiglandular, with glandular epithelium lining the whole antrum, but in a few it was restricted to a band (ichthyomyines), a disc (*Scapteromys*) or a separate pouch (*Oxymycterus*). Most bilocular stomachs were discoglandular, although *Onychomys* and certain *Peromyscus* species had a glandular pouch convergent with that of *Oxymycterus*. Thus stomach morphology alone was insufficient to provide a clear separation between the Neotropical and North American cricetids, although, if Carleton's (1973) polarization of characters is correct, the bilocular arrangement does suggest monophyly for the majority of the latter group.

From his study of male accessory reproductive glands in muroid rodents, Arata (1964:28) concluded that his results supported the dichotomy of simple/complex penis forms, and other authors have cited his work as so doing. However, as Voss and Linzey (1981:23) pointed out, the data are consistent with but do not confirm the hypothesis. They found that Neotropical genera varied little in accessory gland complement, whereas North American cricetids showed far greater variability (i.e. had many apomorphies, according to their polarization of characters), but such a character distribution did not necessarily imply the monophyly of either group.

Parasitological evidence has also been brought to bear on the question of a phylogenetic separation within the New World rats and mice. Through coevolution, parasites (and ectocommensals such as amblyopinine beetles) may show phylogenetic parallels with their hosts or at least distribution patterns concordant with host phylogenies. Slaughter and Ubelaker (1984) list the presence of nematodes of the genus *Parastrongylus* in diverse Old World rodents, in three Neotropical cricetid genera, but in no North American ones. They interpret this distribution to support the hypothesis that the Neotropical and North American cricetids originated from different Eurasian migratory stocks, but as Baskin (1986) pointed out, the evidence is not substantial enough for such an inference to be drawn. Slaughter and Ubelaker's (1984) hypothesis does not account for the parasite's apparent absence from the other fifty-odd Neotropical cricetid genera, nor for its occurrence in Panama in a greater proportion of captured individuals of *Liomys*, a geomyoid rodent, than of the cricetids *Oligoryzomys* or *Zygodontomys*. Clearly, a thorough investigation of nematode infestations in many more genera and species of

New World rodents is called for before the data can be used to support phylogenetic and zoogeographical hypotheses.

Wenzel and Tipton (1966) found that the ectoparasites (especially mites and fleas) infesting Neotropical cricetids in Panama belonged to groups confined to or centred in South America, and differed taxonomically from those infesting North American genera. However, environmental constraints on the distribution of these ectoparasites must be considered: in the case of *Polygenis* fleas, for instance, it appears that they are confined mainly to tropical lowlands, where their principal hosts are Neotropical rodents, but the few North American cricetids found in tropical forest habitats may also carry them (Carleton, 1980:138). Thus the specialization of ectoparasites on one group of hosts may be mediated by environmental rather than phylogenetic factors.

Carleton (1980) applied cladistic methodology to elucidate phylogenetic relationships in the neotomine-peromyscine rodents, using the distributions of 79 characters in 75 species, of which 49 were neotomine-peromyscines and 13 were Neotropical cricetids. In reassessing the phallic data, he found that both the simple- and the complex-penis groups embraced a considerable range of phallic morphologies and that there was a certain degree of intergradation between them. He concluded that there was insufficient evidence for the division of New World cricetids into two monophyletic assemblages. Instead, his Wagner tree analysis (Carleton, 1980, fig. 41) placed *Tylomys* and *Ototylomys* with *Nyctomys* in a clade separated basally from the remainder; the next branching split the Neotropical group from the neotomines and most peromyscines; but the North American genera *Ochrotomys*, *Baiomys* and *Scotinomys* were positioned at the base of the South American branch. Given the lack of a clear dichotomy corresponding to the simple- versus complex-penis arrangement of Hooper and Musser (1964), Carleton (1980) opted for twelve informal groupings at tribal level, four (neotomine, peromyscine, baiomyine and tylomyine) corresponding to the North American cricetids and eight to the Neotropical cricetids.

Further evidence for the distinctness of the Neotropical and North American groups was presented by Catzeflis et al. (1993) in their discussion of DNA-DNA hybridization results for muroid rodents. Using the *Mus/Rattus* split, timed by fossil evidence at 10 million years ago (Mya), to calibrate the rate of nucleotide substitution in the superfamily, they found that the Neotropical cricetids (represented by *Akodon, Sigmodon, Phyllotis, Oryzomys, Zygodontomys*) diverged from the North American group (represented by *Peromyscus, Neotoma, Tylomys*) roughly 12 Mya. This was approximately

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the same time as the latter group split from the Arvicolinae (Microtinae), in an unresolved trichotomy.

A subdivision of the New World cricetids into two or more groups therefore appears well supported, but it is not so simple as a cursory examination of the penile morphologies presented by Hooper and Musser (1964) might suggest. The first main modification required is the removal of two pairs of mainly Central American genera - *Tylomys* and *Ototylomys*, and *Nyctomys* and *Otonyctomys* - from the North American and Neotropical assemblages respectively, to form a separate clade equivalent to Carleton's (1980) tylomyine group, which was given subfamily rank as Tylomyinae by Reig (1984). Although *Nyctomys* has often been placed within the Neotropical thomasomyine group (e.g., Hershkovitz, 1944, 1962), Thomas long ago suggested, on the basis of its molar morphology, that it might "possibly be an offshoot of the *Peromyscus* stock, with no close relationship to *Rhipidomys* [a thomasomyine] at all" (Thomas, 1906: 445). Hooper and Musser (1964) considered *Nyctomys* to be a highly differentiated outlier of the South American (i.e., complex-penis) group, and saw a resemblance of its glans with that of *Tylomys* and *Ototylomys*. Hershkovitz (1966b: 734) later regarded both *Nyctomys* and *Otonyctomys* as "possibly relicts of the archaic North or Middle American stock from which the complex-penis-type thomasomyines may be derived on the one hand, and from which simple-penis-type peromyscines diverged on the other", thus recognizing their distinctness from other New World mice. *Nyctomys* also differs from other Neotropical cricetids (except, presumably, *Otonyctomys*) in its male accessory gland complement (Arata, 1964; Voss and Linzey, 1981), its retention of an entepicondylar foramen in the humerus (Carleton, 1980), and its chromosome morphology (Haiduk et al., 1988).

The second problem with a dichotomous arrangement of the New World mice concerns the baiomyine group, in terms of both content and relationships. In Carleton's (1980) Wagner tree it lies marginally closer to the Neotropical cricetids than to the remaining North American genera, but in many respects it is intermediate between these two groups. This opinion is shared by Rogers and Heske (1984) in their study of chromosomal evolution in the North American genus *Scotinomys*, which, together with *Ochrotomys* and possibly *Baiomys*, they consider intermediate in this way. Carleton (1980) considers the phylogenetic affinity of the baiomyine group to be ambiguous, although Reig (1984) places it squarely within the Neotominae, dismissing similarities between *Baiomys* and the South American *Calomys* as mere convergence. Whether the baiomyines constitute a monophyletic grouping or not is uncertain. They may represent

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a separate clade equally deserving of subfamilial status, a basal clade within either the Neotominae or the Sigmodontinae (*sensu stricto*), or simply a paraphyletic assemblage of relatively plesiomorphous forms. Pending further investigations the baiomyine genera are probably best regarded as *incertae sedis* within the New World cricetid radiation.

Leaving aside the tylomyines and baiomyines, we are left with two core groups: the mainly North American Neotominae, comprising the neotomines and peromyscines (see Reig, 1980, for priority of the subfamily name); and the Sigmodontinae, restricted to the Neotropical cricetids without *Nyctomys* and *Otonyctomys*. Where the gross ranges of the two subfamilies overlap in Central America, sigmodontines generally occur at lower elevations than neotomines. Although the monophyly of these two core groups has not yet been strictly demonstrated, enough circumstantial evidence has accumulated (as discussed above) for this arrangement to be accepted as a working hypothesis. Henceforth, therefore, I shall use the name Sigmodontinae to refer to the Neotropical cricetids, characterized by absence of the entepicondylar foramen of the humerus, a double articulation of the first rib with the transverse processes of the seventh cervical and first thoracic vertebrae, and absence of an entoglossal process of the basihyal (Voss, 1993).

2.3 - Sigmodontinae: historical zoogeography

The zoogeographic history of the Sigmodontinae, and particularly the time of their arrival in South America, is an area of controversy fed by apparently conflicting evidence from different fields.

A brief review of the geological history of South America is pertinent here. On the break-up of Gondwanaland in the late Cretaceous, the South American plate drifted westwards away from all other landmasses, allowing its fauna to evolve in isolation for some sixty million years. As South America rode up over the Cocos/Nazca plate, which underlies the eastern Pacific ocean, tectonic forces during the Miocene and Pliocene especially caused the uplift of its western edge, building the Andean chain and affecting climatic and drainage patterns throughout the continent. Meanwhile, it had gradually moved closer to the southern peninsula of North America, which had been extended southwards in the latest Cretaceous by the southeastward movement of the Chortis block to its current position forming Honduras and northern Nicaragua (Gose, 1985). During the middle Miocene, about 12 Mya, a major uplift of the Panama sill led to the formation of an island arc (corresponding to the present-day Serranía de San Blás-Darién) between North and South America. During a second major episode of uplift in the Pliocene (3.7-

3.1 Mya) the Panama isthmus finally emerged, ending South America's period of terrestrial isolation (Duque-Caro, 1990).

The mammalian fauna of South America may be conveniently divided into three main groups according to their time of appearance in the continent. These "strata" (Simpson, 1980), however, should not be interpreted as discrete units within which the component taxa are united by a common history; they may in fact have had diverse origins (Reig, 1981). The first stratum consists of those mammals present in South America at the beginning of the Cenozoic, whether descendants of earlier indigenous stocks or recent arrivals from elsewhere: marsupials, xenarthrans, condylarths, and various orders of "native" ungulates. Only the first two of these groups still survive. During the period of South American isolation, they were joined by members of the second stratum, caviomorph rodents and platyrrhine monkeys. The recent discovery of a fossil rodent in the Tinguiririca fauna (37-31 Mya) of the central Chilean Andes places the origin of the caviomorphs in South America at or before the Eocene-Oligocene boundary, and provides morphological evidence for an African origin of the group (Wyss et al., 1993). The oldest known platyrrhine, *Branisella*, is from deposits of early Deseadan age (late Oligocene, *c.* 27 Mya - MacFadden et al., 1985). It is likely that stratum II taxa arrived in South America by waif dispersal across the South Atlantic, perhaps facilitated by the emergence of oceanic island groups (Savage, 1993).

The third stratum of South American mammals consists of a large number of families of Holarctic origin which dispersed southwards mainly between the Pliocene and the Recent. At the same time, many South American taxa spread north into Central and North America. This event, often termed the Great American Biotic Interchange, has been the subject of much research and debate in recent years (e.g. papers in Stehli and Webb, 1985; Marshall, 1988; Webb, 1991). The first documented dispersals in this phase (the "heralds" of Webb, 1985) occurred slightly earlier, in the late Miocene, when members of two genera of ground sloths (*Pliometanastes*, a megalonychid, and *Thinobadistes*, a mylodontid) crossed the water gap northwards to reach what is now the southern United States, and the northern procyonid *Cyonasua* spread across to southern South America. One hypothesis that has been advanced to explain such pre-landbridge dispersals is the transport of segments of biotas on drifting fragments of the North American landmass ("terranes") that became accreted to northwestern South America (Hendrickson, 1986). Another hypothesis, which accounts for the two-way movement, invokes the presence of a Central American island arc between the two continents, washed by a southward-

flowing current on the Pacific side and a northward-flowing one on the Atlantic side (Duque-Caro, 1990). Most terrestrial taxa, however, dispersed once the isthmus of Panama had emerged in the Pliocene. The new arrivals in South America belonged to the orders Carnivora (with five families: cats, dogs, mustelids, raccoons, bears), Proboscidea (elephant-like gomphotheres), Artiodactyla (deer, camelids, peccaries), Perissodactyla (horses, tapirs), Primates (human beings), Rodentia (squirrels, kangaroo rats, pocket gophers), Lagomorpha (rabbits) and Insectivora (shrews). Two of these families, the gomphotheres and the horses, subsequently became extinct in the Americas. The kangaroo rats, pocket gophers and shrews are known in Recent South American faunas only from the northwestern corner of the continent (Marshall, 1988).

Although it is now generally accepted that the Neotropical Sigmodontinae had their proximal origin in North America (*pace* Hershkovitz, 1993), there is still no consensus on the question of whether they form part of the third stratum or whether they arrived in South America at some earlier time. Muroid rodents were present in the Palaearctic region during the Eocene, some 40 Mya, from where they spread southwards and eastwards to colonize Africa, Australia and the Americas (Catzeflis et al., 1992). Just which lineage gave rise to the New World rats and mice is still contested, as summarized by Carleton and Musser (1984), but fossil taxa attributable to the group are known from the Miocene of North America. The earliest known sigmodontine fossils in South America, however, are from Argentinian deposits of Montehermosan land mammal age (late Pliocene, c. 3.5 Mya), probably just before the final emergence of the Panamanian isthmus linking North and South America. The two species, *Bolomys bonapartei*, an akodontine, and *Auliscomys formosus*, a phyllotine, are advanced, pastoral forms allocated to extant genera (Reig, 1978). Four more species (two akodontines and two phyllotines) appear in the Chapadmalalan of Argentina, some 2.7 Mya, corresponding to the early stages of the Interchange proper.

In order to account for the great diversity within the Sigmodontinae in the Neotropics, some authors postulate a Tertiary, possibly early Miocene, dispersal of their ancestors to South America, by rafting either from North America (Hershkovitz, 1966b; Reig, 1980, 1981, 1984), or even from Africa (Hershkovitz, 1972, 1993). They argue that the advanced, "pastoral" morphology of the first known fossils of this group in South America implies that more primitive "sylvan" forms, similar to extant genera such as *Rhipidomys* and *Thomasomys*, must have existed there for a long time previously; they simply have not been sampled, possibly because forest environments are less likely to

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provide suitable conditions for fossilization to occur. By comparing geographical patterns of species diversity among the tribes of Sigmodontinae, Reig (1984) calculated that the sylvan Oryzomyini (including the thomasomyine genera) differentiated mainly in the northern Andes of Colombia and Ecuador, whereas the Akodontini and Phyllotini, regarded as offshoots of a basic oryzomyine stock, had their main area of differentiation much further south, in the puna zone of the Andes between southern Peru and northern Argentina. Consequently, careful sifting of Miocene sediments in the north-west of the continent might reveal fossil oryzomyines from which the rest of the sigmodontine radiation could be derived.

A different scenario has been proposed by other authors, such as Patterson and Pascual (1968), whereby the first sigmodontine rodents arrived in South America along with, or only just before, the remainder of the stratum III (landbridge) immigrants. Through rapid diversification, these pioneers then gave rise to the whole range of Neotropical genera. Neither this hypothesis nor the preceding one accounts for the existence of North American fossils attributed to or allied with Neotropical genera, which pre-date the Panama landbridge. *Abelmoschomys*, from the late Miocene (*c.* 9 Mya) of Florida, is claimed to be the earliest member of the "Neotropical" sigmodontine group and to support a hypothesis of descent from middle Miocene *Copemys*, regarded by many as the ancestor also of the Peromyscini (Baskin, 1986). Other "Neotropical" sigmodontine fossils from North America prior to the Great American Interchange include *Bensonomys* (questionably attributed to the extant phyllotine genus *Calomys* by Baskin, 1978), *Prosigmodon*, *Symmetrodontomys* and possibly *Oryzomys* (Baskin, 1986). Thus, if these finds have been correctly interpreted, either the early sigmodontines had diversified into both sylvan and pastoral forms in North America before migrating south in the Pliocene, or these fossil taxa resulted from earlier differentiation in South America and subsequent redispersal northwards. Using DNA-DNA hybridization data, Catzeflis et al. (1993) suggested that the *Sigmodon* lineage evolved early (*c.* 10 Mya) in North America, the Akodontini and Phyllotini arose more recently, and the oryzomyines possibly diversified first in Middle America in intermediate times. Mitochondrial cytochrome-b data points to a divergence time of roughly 6.6 Mya for oryzomyine genera (Patton & Silva, 1995).

Webb (1991) was of a similar opinion: "The roots of a sigmodontine radiation ... are evident in the late Miocene and Pliocene records of Florida, Arizona and Mexico. Although the fossil evidence is far from complete, it shows that phyllotine, sigmodontine, akodontine and oryzomyine genera had originated in southern North America before the

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interchange ... Subsequent diversification in a wide range of habitats could readily account for the 47 genera presently living in South America" (Webb, 1991: 277). As for the ecological problems associated with the southward dispersal of both forest-dwelling and pastoral rodents across the landbridge, he offers a two-phase ecogeographic model. During an initial interglacial, humid phase, rain forest would have dominated the isthmus allowing dispersal of sylvan forms; during a more arid, glacial phase, open-country biomes would have favoured pastoral forms. He invokes acidic conditions in rain forest soils to account for the lack of fossil remains of early forest-dwelling immigrants. Nevertheless, this hypothesis does not satisfactorily explain the pre-landbridge dates of the first known sigmodontine fossils in southern South America. The question of the origin of the Sigmodontinae in South America thus remains far from settled.

Thus the ancestors of present-day *Rhipidomys* probably reached the South American land mass in what is now northwestern Colombia, either by island-hopping or rafting from the southern peninsula of North America while the Central American seaway was still in existence, or by crossing overland once the Panama landbridge was complete at the Pliocene-Pleistocene boundary. On their arrival, their access to much of the continent was blocked by high mountain chains running from north to south parallel to the western coastline. An indication that many early Sigmodontinae must soon have occupied the highlands is that the greatest diversity of most tribal-level groups is found in the Andean region (Reig, 1984).

Present-day distributions of plants and animals are influenced by both contemporary and historical ecological conditions. Tropical South American ecosystems were greatly affected by global temperature fluctuations during the late Tertiary and Quaternary periods, as revealed by analyses of fossil marine microfauna, pollen from lake sediments, glacial geomorphology, sedimentology and other evidence (Ab'Sáber, 1982; Van der Hammen, 1985; Bigarella & Ferreira, 1985; Schubert, 1988; Bush et al., 1990; Absy et al., 1991; Clapperton, 1993b). The effects of these fluctuations were not uniform: during glacial periods, changes in circulation patterns brought greater humidity to a few areas but aridity to most of the continent, thus inducing horizontal vegetational shifts; temperature depression at higher altitudes was greater than in the lowlands, causing not only a vertical displacement but also a compression of vegetation zones due to the steeper temperature gradient. At the last glacial maximum, sand deserts may have covered the broad Orinoco plains (*llanos*) of Venezuela and Colombia and the plains and pampas of Bolivia and Argentina, while most of Brazil and the Caribbean coast were occupied by

thorn scrub (*caatinga*) and savanna (*cerrado*). Only the foothills of the Andes, western Amazonia, parts of the Guiana highlands and southeastern Brazil would have retained any continuous forest (Clapperton, 1993a).

On the basis of present-day patterns of diversity and reconstructions of past environments, many attempts have been made to identify "refugia" - isolated areas of forest that "protected" a sylvan fauna during arid phases and in which local conditions fostered speciation events (see especially papers in Prance, 1982, and Whitmore & Prance, 1987). Although some local predictions of the refuge hypothesis have been overturned (e.g., Bush et al, 1990) and much criticism has been levelled at it (Connor, 1986; Salo, 1987), it is indisputable that forest biotas must have been restricted to much smaller land areas during arid phases. Extreme fragmentation of forests may also have led to population crashes ("bottlenecks"), resulting in differentiation uncorrelated with environmental factors, as in Atlantic Forest *Drosophila* and certain lizards (Val, 1988). One element which has received perhaps less attention than it deserves is the probable persistence of gallery forests across drier, open formations, as occurs today in the cerrados of Brazil (Redford & Fonseca, 1986; Meave et al., 1991). These more mesic strips would have allowed certain sections of the earlier forest fauna to remain *in situ*, as well as serving as dispersal corridors between forest blocks.

The full complexity of past environmental change will begin to be revealed only after much more basic research has been done throughout the tropics, but it is safe to postulate that during colder periods, when altitudinal vegetation zones were lower than today, montane forests would have occupied more extensive and continuous areas on the lower slopes of the Andes and Guiana Highlands (Haffer, 1987). Mammals adapted to life in such forests could then have dispersed across what are now inhospitable barriers, but when more mesic conditions returned and the cool forests retreated upwards, the once continuous populations became fragmented and isolated in separate highland areas. A similar mechanism was proposed by Adams (1977) to explain the presence of butterflies isolated in narrow altitude bands in the Sierra Nevada de Santa Marta, northern Colombia. Such a scenario may also account for the current distribution of certain *Rhipidomys* taxa in the highlands of northern South America.

2.4 - *The position of* Rhipidomys *within the Sigmodontinae*

The sixty or so genera of Sigmodontinae fall into a number of more or less discrete groups, some of which have long been recognized informally. In the early

nineteenth century most Neotropical mice were placed in the genus *Mus* and, later, in *Hesperomys* Waterhouse, 1839, the scope of which came to correspond in general terms to that of the subfamily as understood today. Gradually the more distinctive portions of this assemblage were segregated into subgenera, which by the end of the century had been accorded full generic status (Thomas, 1896a). Certain groupings of genera came to be recognized informally but as yet there was no systematic attempt to order all the genera in such a way.

A group recognized early this century was that containing genera like *Rhipidomys* and *Thomasomys*, forms with relatively undifferentiated craniodental characteristics which probably lie near the base of the sigmodontine radiation. Thomas (1906) first delimited the group when he used the differences in palate length noted by Bangs (1900) to distinguish short-palate *Rhipidomys* and *Thomasomys* on the one hand from long-palate *Oryzomys* on the other. In particular, he removed all long-palate, arboreal species from *Rhipidomys* into *Oecomys*, a new subgenus of *Oryzomys*. Other short-palate genera - *Phaenomys*, *Delomys*, *Inomys*, *Aepeomys* and *Wilfredomys* - were later added to the thomasomyine group; these were named for divergent forms otherwise allocated to *Thomasomys*. With the exception of *Phaenomys*, these genera were usually dismissed into synonymy by later authors (e.g., Osgood, 1933; Ellerman, 1941; Vorontsov, 1959; Cabrera, 1961; Hershkovitz, 1962; Pine, 1980; and Reig, 1980), until recent attempts to codify diversity in the group brought most of them new recognition (e.g., Musser & Carleton, 1993; Voss, 1993).

In 1932 Tate organized his series of taxonomic histories of South and Central American cricetid genera around a number of loosely defined groupings, including oryzomine *[sic]* genera, akodont genera, cotton rats, "fish-eating" rats, and an unnamed phyllotine group; genera containing larger, rat-like species were left unaffiliated (Tate, 1932). However, he did not develop Thomas's (1906) work but treated both long- and short-palate forms as "oryzomine". The tribal status of such groupings was first formalized by Vorontsov (1959), who placed them directly in the Cricetinae together with North American and Old World cricetids, without recognizing any supra-tribal affinity between Neotropical taxa. The sigmodontine tribes he named were (with original spellings) the Oryzomyini, Akodontini, Phyllotiini, Reithrodonini, Sigmodonini and Ichthyomyini. Like Tate before him, Vorontsov did not separate the thomasomyines from the oryzomyines.

Hershkovitz (1962, 1966a) arranged the Neotropical mice into a sylvan division

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(thomasomyines and oryzomyines) and a pastoral one (akodonts, phyllotines, sigmodonts, ichthyomyines, oxymycterines and scapteromyines). He did not accord the groups formal tribal status because he considered the Sigmodontini as a whole to be a tribe within the Cricetinae. Taking data on penile morphology into account, he revised his earlier (1944, 1955, 1960) position and separated the thomasomyine genera from *Peromyscus* and its northern allies, although he retained the tylomyines *Nyctomys* and *Otonyctomys* within the thomasomyines; he did, however, admit that "some of the characters shared by the members of this group may be phenetic rather than phyletic" (Hershkovitz, 1966a:125, footnote). His evolutionary scenario placed pentalophodont, sylvan cricetines (i.e., "primitive" thomasomyines) at the base of the sigmodontine radiation. While one main branch led from these directly to the oryzomyine stock, another lineage developed tetralophodonty (reduction/loss of the mesolophostyle) and crossed into the pastoral domain as the akodont stock. From this lineage arose the ichthyomyine, phyllotine and sigmodont groups (Hershkovitz, 1962).

Opinion on the validity of a thomasomyine group has varied since then. Some authors (e.g., Gardner & Patton, 1976; Eisenberg, 1989) have followed Hershkovitz in recognizing its distinctiveness. Steadman and Ray (1982) were the first to use the tribal name Thomasomyini, under which they placed *Thomasomys*, *Rhipidomys* and *Megaoryzomys* (an extinct Galapagoan rat); later the same year Cerqueira (1982) used it for the more conventional set of *Thomasomys*, *Rhipidomys*, *Phaenomys* and *Delomys*. Other scholars (e.g., Reig, 1980, 1984; Patterson, 1992) preferred Vorontsov's (1959) arrangement and included these genera within the Oryzomyini. Contrary to Vorontsov, Reig (1980, 1984) placed his tribes within the Neotropical subfamily Sigmodontinae.

Voss (1993) pointed out that the "thomasomyines" were united only by shared plesiomorphic character states and therefore did not constitute a monophyletic assemblage. In a preliminary analysis of 18 mainly craniodental characters in the type species of *Thomasomys* and *Oryzomys* and the two species of *Delomys* (with various North American taxa as outgroups), he showed that *Thomasomys cinereus* consistently exhibited the primitive state. This result does not support an hypothesis of a thomasomyine clade containing *Thomasomys* and *Delomys* and excluding *Oryzomys*. Instead, the thomasomyines may well comprise several independent basal offshoots of the sigmodontine stock.

Steppan (1995) investigated the relationships of the tribe Phyllotini within the Sigmodontinae by means of a phylogenetic analysis involving many non-phyllotine species

of Sigmodontinae, with outgroup taxa from the Nearctic and the Old World. The resulting trees (his figures 19, 20 and 21) agree in broad terms with Hershkovitz's (1962) hypothesis of sigmodontine radiation outlined above. There are two main branches, one composed of the Oryzomyini and the other including the akodontines, phyllotines and certain other taxa. The Ichthyomyini form a small, monophyletic group near the base of the second branch. The thomasomyines included in the study (*Chilomys instans*, *Rhipidomys latimanus*, *Thomasomys aureus*, *T. baeops* and *T. rhoadsi*) are also basal but do not emerge as a monophyletic group. In particular, in some of the most parsimonious trees *Chilomys* is the sister group to the Oryzomyini but in others it is not, and *Thomasomys rhoadsi* is generally separated from its congeners while *Rhipidomys latimanus* is associated with them. *Wiedomys* also appears to be relatively plesiomorphic.

Use of the name Thomasomyini should therefore be avoided because it would imply monophyly for these genera, while their inclusion in the Oryzomyini would belie their postulated basal position within the Sigmodontinae. The expression "plesiomorphic Neotropical muroids" (Voss, 1993: 25) describes the group well, but the less cumbersome and more familiar term "thomasomyine group" could be retained informally. The genera included provisionally by Voss (1993) were *Abrawayaomys*, *Aepeomys*, *Chilomys*, *Delomys*, *Phaenomys*, *Rhagomys*, *Rhipidomys*, *Thomasomys* (including *Erioryzomys* and *Inomys*), and *Wilfredomys*. The list includes all the living short-palate forms that have been attributed to the thomasomyine group in the past (without the non-sigmodontines *Nyctomys* and *Otonyctomys*) plus three long-palate genera, *Abrawayaomys*, *Chilomys* and *Rhagomys*, that are too plesiomorphic in other respects to belong to the Oryzomyini (*sensu* Voss & Carleton, 1993). The extinct Recent genus *Megaoryzomys* should probably be included, and Steppan's (1995) analysis would seem to indicate that *Wiedomys* belongs here too, even though Reig (1980) placed it in a separate tribe, the Wiedomyini, together with the fossil genus *Cholomys*.

Most of the thomasomyine genera are small, containing only one or two species; only *Thomasomys* with 25 species (Musser & Carleton, 1993; a full revision may split it into several genera) and *Rhipidomys* with 18 (revised herein) are more speciose. Most are also restricted in range: *Thomasomys*, *Aepeomys* and *Chilomys* are confined to the Andean chains, *Megaoryzomys* was endemic to the Galápagos Islands, and all but one of the remaining genera occur only in the South American Atlantic forests and adjacent regions. Of all the group, only *Rhipidomys* has a broader distribution, ranging from eastern

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Panamá across the whole of forested tropical South America to southeastern Brazil and northern Argentina.

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CHAPTER 3 - MATERIAL EXAMINED AND DATA COLLECTED

3.1 - Collections and specimens

This study is based on the examination of *Rhipidomys* specimens from the twenty-nine collections listed in Table 3.1. Institutions judged likely to have holdings of *Rhipidomys*, according to information on geographical coverage given in world lists of mammalogy collections (Choate & Genoways, 1975; Genoways & Schlitter, 1981), were sent a questionnaire requesting details of their *Rhipidomys* material, if any. A version in Spanish was sent to museums in Hispanic America. Brazilian museums were not included in the survey since I had access to the required information through personal contacts. To 61 questionnaires sent, 34 replies were received, 22 of which reported holdings of the genus. Information received later from other sources showed that a few other collections also possessed relevant specimens.

Specimens in the collections of the Natural History Museum, London (BMNH) formed the nucleus of my study. In addition, I made personal visits to collections in the United States (AMNH, CM, FMNH, MCZ, USNM) and Brazil (IBAMA/MG, MNRJ, MPEG, MZUSP, UFMG, UFPB), most of which also sent specimens on loan. The other institutions listed in Table 3.1 lent material for my use, with the exception of UZM, where Dr R. S. Voss examined and measured the type series of *R. mastacalis* for me, and BZM and NMW, where a paratype of *R. leucodactylus* Tschudi and the holotype of *R. leucodactylus* Wagner, respectively, were examined and photographed by Drs A. Langguth and M. de Vivo. Photographs and descriptions of three specimens collected after my visit to Rio de Janeiro were supplied by L. Geise.

A total of 1734 specimens of *Rhipidomys* was examined personally. Most consisted of a round study skin and cleaned skull and mandible, with associated collector's data. A small number of the skins were on flat cards, and occasionally either the skin or the skull was absent. In a few the postcranial skeleton was also available. Relatively few specimens were preserved in ethanol; in most of these the skull had been extracted and cleaned and sometimes the skin had also been removed and made up separately, leaving only the carcass in fluid. *Rhipidomys* specimens examined are listed under each species or subspecies in chapter 7. Specimens of other genera used for comparison belong mainly to the collections of the BMNH, with some also from the AMNH, FMNH and MNRJ; since a large proportion of the BMNH collection of Neotropical muroids was examined during the course of this study, it would be impractical to list the specimens individually.

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AMNH	American Museum of Natural History, New York
BMNH	Natural History Museum, London
BZM	Berlin Zoologisches Museum
CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
IBAMA/MG	Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis, Superintendência Estadual de Minas Gerais, Belo Horizonte
KU	Kansas University Museum of Natural History, Lawrence
LSUMZ	Louisiana State University Museum of Zoology, Baton Rouge
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MHNG	Musée d'Histoire Naturelle de Genève
MHNLS	Museo de Historia Natural La Salle, Caracas
MHNN	Muséum d'Histoire Naturelle, Neuchâtel
MNHN	Muséum National d'Histoire Naturelle, Paris
MNLP	Museo Nacional de Historia Natural, La Paz
MNRJ	Museu Nacional, Rio de Janeiro
MPEG	Museu Paraense Emílio Goeldi, Belém
MSUMZ	Michigan State University Museum of Zoology, East Lansing
MUSM	Museo de Historia Natural, Universidad Mayor de San Marcos, Lima
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
MZUSP	Museu de Zoologia da Universidade de São Paulo
NHR	Naturhistoriska Riksmuseet, Stockholm
NMW	Naturhistorisches Museum Wien
OMNH	Oklahoma Museum of Natural History, Norman
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
UFMG	Universidade Federal de Minas Gerais, Belo Horizonte
UFPB	Universidade Federal da Paraíba, João Pessoa
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Washington, D.C.
UZM	Universitets Zoologisk Museum, Copenhagen

3.2 - Data sets

a) Non-metric characters

Because few of the available samples of *Rhipidomys* populations consisted of anything but skins and skulls, it was not feasible to extend the study to include additional character sets from post-cranial skeleton or viscera. A thorough examination of such material would have taken considerable time but was likely to contribute little to an

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understanding of intra-generic relationships because of the unrepresentative distribution of material available; therefore these character sets were not investigated in depth.

Skins were examined and compared for external characters of size, proportion, colour, texture etc. Pelage colour was not codified using Ridgway's or other colour standards: not only was colour variation generally too subtle for this, but the speckled appearance of "agouti" pelage like that of *Rhipidomys* is notoriously difficult to match accurately to an area of uniform colour as given in such reference works. In addition, specimens had been prepared using different methods and preserved in a variety of museum environments for periods ranging from a century and a half to just a few weeks before they were examined. How much or how little the specific conditions had affected pelage colour in each case was unknown. In the absence of freshly captured material for each taxon, therefore, it was inadvisable to attempt to provide very precise colour descriptions. However, where specimens had been collected and preserved under the same conditions for roughly the same length of time, colour comparisons among individuals were more feasible.

Skulls and teeth were also examined and compared among specimens for non-metric characters that might aid in distinguishing taxa. Evidently, ontogenetic variation also had to be recognized. Depending on the size of the structures involved, skulls were examined either with the naked eye or with a lens or stereo-microscope under low power; molar characters of course required the use of a stereo-microscope.

b) Dental age classes

For the purposes of morphometric analysis, it was necessary to sort the specimens into age groups. The molars in *Rhipidomys* are bunodont and once fully erupted do not continue to grow, unlike the truly hypsodont cheek teeth found in some pastoral rodents. From the moment of eruption in a weaned animal, the molar crowns are progressively worn down through attrition with foodstuffs, grit and the occluding teeth until eventually all occlusal relief is obliterated. The crown may be eroded away completely in old animals. Since cheektooth wear is evidently a cumulative process over time, the degree of wear must be correlated, however imperfectly, with the age of the animal.

Unfortunately, the factors affecting the rate of molar wear are not necessarily constant from one individual, species or locality to another. Tooth enamel may vary in hardness or resilience as a result of the metabolic availability of certain substances. Wear will be affected by the amount of abrasive matter in the diet; this may originate from the

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plant or animal tissues themselves or from grit acquired along with the food. Coarse grasses, for instance, are more abrasive than soft fruits, and ground-dwelling animals inhabiting sandy areas might be expected to show faster tooth wear than those on peaty soils. In the case of *Rhipidomys* species, which are mainly arboreal in their habits, the presence of extraneous grit in the diet may well be less significant than in more terrestrial animals, but the abrasive quality of the plant matter eaten is likely to vary over space and time. Thus animals of the same age in different localities or at different seasons of the year may show varying degrees of tooth wear.

Other characters often used as age indicators include suture closure, reproductive status and eye-lens weight. Of these, the last is not suited for use with museum collections of skins and skulls, and suture closure yields little information once the animal reaches adulthood, although it may serve as a check on age determined by other methods. Reproductive status is not always apparent from the material itself or from collector's notes, and the onset of sexual maturity is so conditioned by numerous internal and external factors that it is a poor indicator of absolute age. Therefore, although imperfect, occlusal molar wear is the most convenient indicator of age to use with skin-and-skull museum samples and may be assumed to provide a fair degree of comparability within age classes across populations.

Molar eruption and degree of occlusal wear were used to construct a series of dental age classes (DAC), from 0 (juvenile) to 5 (old adult). Since the aim was not to describe ontogenetic development but rather to form a basis for comparison of adult measurements, juvenile stages of development did not need to be distinguished in detail; thus all animals with incompletely erupted or unworn molars were included in class 0. The remaining classes were based mainly upon wear to the upper second molar (M2) and can be characterized as follows:

Class 0   M3 not completely erupted and/or unworn.

Class 1   Enamel surfaces of M2 slightly worn; dentine visible on lingual cusps but generally not along lophs and mure.

Class 2   Dentine visible along most lophs but not in central portion of mure.

Class 3   Dentine confluent between all cusps.

Class 4   Dentine broadly confluent; main crown features still distinguishable; labial cusps reduced in height.

Class 5   M2 worn down to single dentine basin without internal enamel elements; no cusp relief.

In practice, when specimens were examined and allocated to age groups, intermediate classes (e.g., DAC 2.5) were also recognized for those individuals with a degree of tooth wear lying between the categories listed above. However, such precision proved unnecessary in the subsequent analyses, except in rare cases (specified below in the description of the analyses) when certain intermediate classes were amalgamated with the class immediately above rather than the one below in order to provide groups of roughly equal size for statistical treatment.

c) Morphometric data

The skin measurements recorded were those provided by the collector on the specimen tag or in associated documentation (field notes, or specimen record cards). Since in most cases there was no way of knowing exactly how the measurements were taken, they were accepted merely as an indication of the size of the animal when caught and were not used in multivariate analyses. In view of this, where the collector gave total length instead of head-and-body length, the latter was found simply by subtracting the tail length from the value given, even though the sum of head-and-body and tail lengths is not normally precisely the same as total length owing to distortions induced by positioning the animal for measuring.

Although it was not always made explicit on the label whether hind foot length was measured in the European way, excluding the claws (s.u.), or in the American, including the claws (c.u.), in most cases the system used could be inferred from the nationality of the collector or from other material collected by him. It was also found that measurements taken with calipers or ruler of the dry foot (provided the digits were fully extended) generally corresponded closely to the collectors' measurements, and could therefore be employed with some confidence to determine the system used in doubtful cases and to supply the measurements where they were missing or questionable. In small rodents like *Rhipidomys* in which the claws are kept sharp and do not vary greatly with wear, it was found more convenient to measure the hind foot with the claw, since this provided a more precise end-point. Claw length varies with specimen size, adding approximately 2 mm to foot length s.u. in the largest species and 1-1.5 mm in smaller ones.

Skulls and teeth were measured to the nearest 0.01 mm with electronic calipers connected directly to a personal computer using Incal software (version 1.50, Office of Information Resource Management, The Smithsonian Institution, Washington, D.C.).

Thirty measurements were taken on each *Rhipidomys* specimen. On the basis of an assessment of measurement error (see Chapter 4), certain of these variables were subsequently excluded from further analyses. All the skin, skull and tooth measurements recorded are listed below, together with abbreviations and explanations.

Skin measurements (provided by collector)

HB   Head & Body Length

TL   Tail Length

HFcu   Hind Foot Length c.u.

HFsu   Hind Foot Length s.u.

Ecrn   Ear (from Crown)

Ench   Ear (from Notch)

W   Weight

Craniodental measurements (Fig. 3.1)

ONL   Occipito-Nasal Length (the greatest length of the skull in *Rhipidomys* - measured from the supraoccipital to the tips of the nasals)

CIL   Condylo-Incisive Length (from the occipital condyles to the anterior margin of the incisive alveolus; measured parallel with the sagittal plane of the skull, excluding the gnathic process of the premaxillary)

PL   Palatal Length (from the anterior margin of the incisive alveolus to the posterior edge of the bony palate in the midline, including any medial postpalatal process)

PPL   Post-Palatal Length (from the posterior endpoint of the previous measurement to the anterior/ventral margin of the foramen magnum)

MRC   Molar Row - Crown Length (from the anterior face of the first upper molar to the posterior face of the third, at crown height; this and the next two measurements were taken on the left side whenever possible)

MRA   Molar Row - Alveolar Length (from the anterior margin of the alveolus of the first upper molar to the posterior margin of that of the third)

M1B   1st Molar Breadth (maximum breadth across the centre of the first upper molar, i.e. across the protocone and paracone, at crown height)

PBL   Palatal Bridge Length (from the posterior margin of the left incisive foramen to the anterior margin of the mesopterygoid fossa, lateral to any medial postpalatal process)

TFL   Temporal Fossa Length (maximum internal length of the left orbitotemporal fossa,
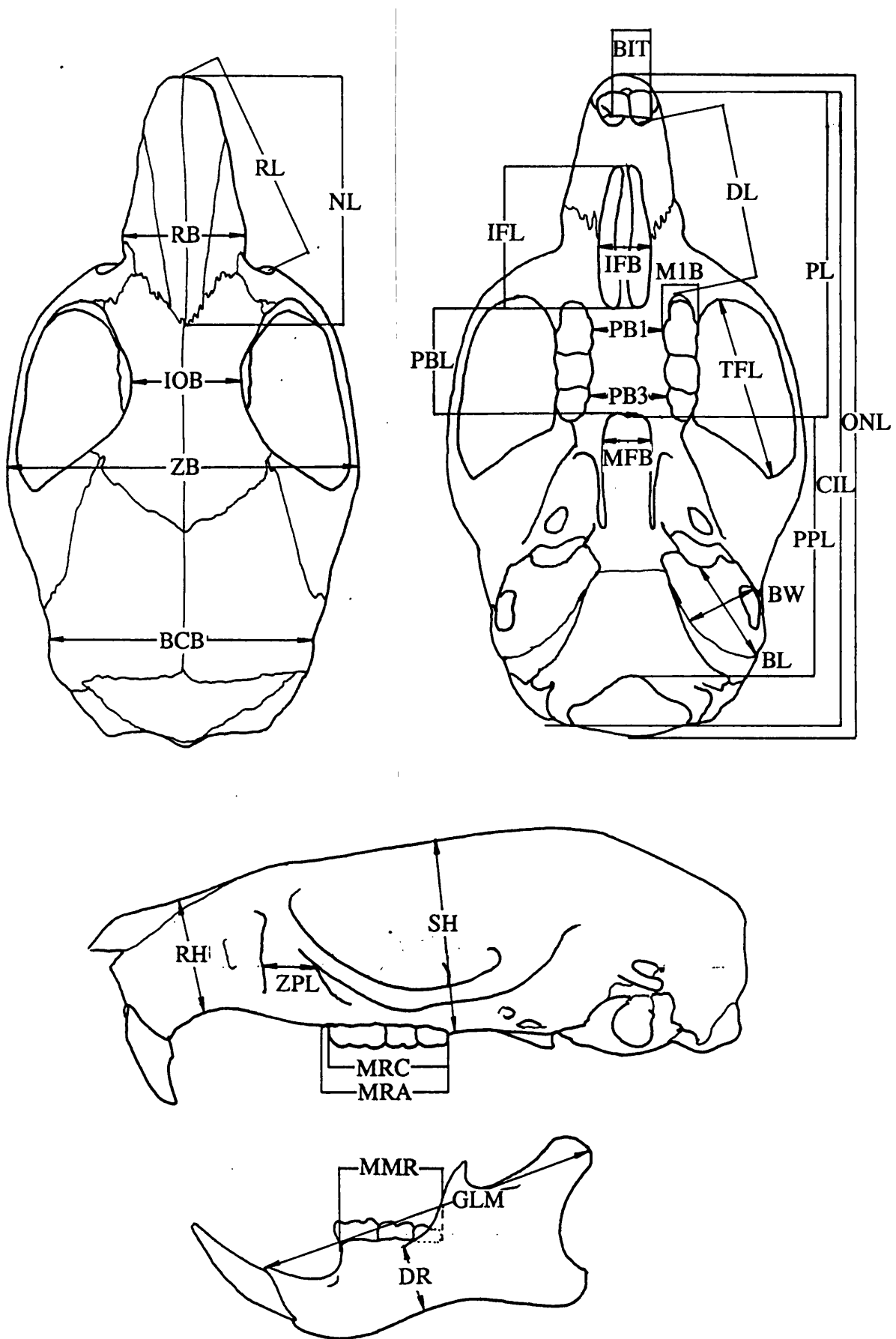
Fig. 3.1 - Measurements taken on *Rhipidomys* skulls.

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taken in ventral view, between the zygomatic plate and the squamosal root of the zygomatic arch)

DL   Diastema Length (between the alveoli of the upper left incisor and first molar, not taken parallel with the sagittal plane of the skull)

IFL   Incisive Foramen Length (maximum internal length of the left incisive foramen)

IFB   Incisive Foramen Breadth (maximum internal breadth across both foramina)

PB1   Palatal Breadth at M1 (minimum transverse distance between the alveoli of the first molars)

PB3   Palatal Breadth at M3 (minimum transverse distance between the alveoli of the third molars)

MFB   Mesopterygoid Fossa Breadth (internal breadth of the fossa half-way between its anterior margin and the basioccipital-basisphenoid suture)

BIT   Breadth across Incisor Tips (taken across both upper incisors just above the rounded wear zone)

BW   Bullar Width (maximum "width" of the left ectotympanic, taken with one jaw of the calipers lodged against the ventro-lateral face of the tegmen tympani and the other on the diagonally opposite, medial-posterior side of the ectotympanic)

BL   Bullar Length (maximum length of the left ectotympanic, excluding the bullar tube)

BCB   Braincase Breadth (taken across the hamular processes of the squamosals)

SH   Skull Height (minimum height taken immediately behind the third molars)

RH   Rostral Height (minimum height above the diastema)

RB   Rostral Breadth (maximum breadth across the nasolacrimal capsules)

RL   Rostral Length (maximum diagonal measurement between the anterior tip of the right nasal and the postero-lateral internal margin of the right zygomatic notch)

NL   Nasal Length (maximum length of the right nasal)

ZPL   Zygomatic Plate Length (measurement taken parallel with the longitudinal axis of the skull at mid-height on the zygomatic plate)

IOB   Interorbital Breadth (least breadth between the orbits/temporal fossae)

ZB   Zygomatic Breadth (greatest breadth across the zygomatic arches; not taken if these appeared deformed from the cleaning and drying process)

GLM   Greatest Length of Mandible (left dentary, from the rear edge of the condylar process to the most anterior point on the upper margin of the incisive alveolus that is visible from the labial side)

M1 MR ~~Lower~~ Mandibular Molar Row - alveolar length (in practice taken from the front face of the exposed anterior root of the first lower left molar to the posterior face of the third molar)

DR Depth of Ramus (on the left dentary, least distance/from the trough separating the molar row and the coronoid process to the ventral margin of the dentary ~~vertically below it~~)

The craniodental data collected as described above were transferred to dBASE III Plus files and combined with museum acronym, specimen number, sex, dental age class, provenance, skin data and provisional taxonomic identification to form the primary computer database. Specimens were allocated to provisional taxonomic groups ("populations") on the basis of observed characters and locality of origin. Such operational groups were later amalgamated when appropriate into species according to the results of analyses.

CHAPTER 4 - NUMERICAL METHODS AND PREPARATORY ANALYSES

4.1 - Overview

Given the amount of cranial variation present in *Rhipidomys* but the paucity of discrete characters that could be used to discriminate between species, numerical methods were used in an attempt to elucidate species differences and to aid in allocating individuals and populations to such morphological species. Although morphometric analysis can be a valuable tool in systematic studies there are certain caveats that must be addressed as regards the quality of the data used. Therefore, a number of preparatory procedures were undertaken as described in the following sections in order to (a) assess the reliability of the measurements taken, (b) gauge to what extent ontogenetic variation and sexual dimorphism must be taken into account in specimen comparisons, and (c) render the data more amenable to analysis by imputing missing values.

Where the emphasis of the analysis was on individual variables, as in the preparatory studies mentioned above, univariate methods such as analysis of variance and simple regression were appropriate. Multivariate procedures were used in the main part of the analysis, where the interest lay in assessing the relationship between individuals or groups of specimens. Principal components analysis was preferred for exploratory purposes because no *a priori* structure had to be imposed on the data. Discriminant analysis and test statistics such as Hotelling's T^2 were employed to assess the separateness of taxa and to allocate specimens to established groups.

Raw data were converted to natural logarithms for most purposes of analysis. A logarithmic scale reflects allometric relations better than an untransformed scale, because measurement intervals are then seen in proportion to the reference value (e.g. the sample mean) rather than as absolute quantities. For instance, when transformed to logarithms a 3 mm difference between specimens in a variable with a mean of 30 mm becomes equal to a 0.5 mm difference in a variable with a mean of 5 mm. Similarly, variances become directly comparable no matter how large the variable mean.

This work was carried out using the statistical package Genstat 5, releases 1.3 and later 3.1, developed at the Rothamsted Experimental Station (Genstat 5 Committee, 1987; Numerical Algorithms Group, 1993), running on the University of Cambridge Computing Service mainframe computer.

4.2 - Preparatory procedures

a) Measurement error analysis

Measurement error, or the difference between the measured value d and the true distance δ, is a phenomenon rarely touched upon in morphometric studies but which deserves attention. Repeatability is central to scientific method, and in many experimental procedures it is normal practice to make repeated determinations of a quantity in order to provide a more precise estimate of its real value. Ideally, therefore, each measurement on a specimen should be taken several times and an average calculated for use in analyses, but because of the time this would consume large series are usually measured only once.

Nevertheless, it was considered important to carry out a study of measurement error on a sample of *Rhipidomys* skulls to determine the reliability of the craniodental dimensions measured and, if necessary, to eliminate dimensions with high error terms from subsequent analyses. Not all measurements were felt to be equally reliable because of the varying precision with which the calipers could be placed on their end-points. External or internal measurements of robust structures, such as occipito-nasal length or incisive foramen length, could be taken with relative confidence, but error was introduced when one or even both jaws of the calipers had to be placed by eye. This was the case where one end-point was internal and the other external (e.g. post-palatal length, rostral length) and more especially where one or both end-points were poorly defined (e.g. bullar dimensions, especially bullar length, and alveolar measurements such as molar row alveolar or the two palatal breadths).

To analyse measurement error, the method described by Bailey and Byrnes (1990) and Lougheed et al. (1991) was used. In this method, a sample of specimens is measured a number of times, and for each craniodental dimension the variance due to differences between the repeated measurements is assessed as a percentage of the total variance present in the sample. To see how the level of variability among sample members might affect this percent measurement error, two sets of skulls were used for the study (see Appendix I for listing). The first consisted of 25 adult specimens of *Rhipidomys* sp. collected at Brasília, Brazil, over a short period, and judged to be a fairly homogeneous sample; the second group was composed of 19 larger specimens collected at widely differing times and places but all attributed at the time of analysis to the species *R. couesi*, although later it was concluded that they were not all conspecific. Each specimen

in both sets was measured three times, non-consecutively, without knowledge of previous measurement values. Although of course I was aware of my purpose in remeasuring, I aimed to be neither more nor less careful than usual with the precision of the measuring technique. Because the groups included some damaged specimens, the sample size was smaller for certain variables (Table 4.1).

For each group, the raw data from the three sessions were combined into a single data set for an analysis of variance of each variable. In this type of ANOVA, the individual specimens were regarded as "treatments", each with three values corresponding to the three replicated measurements. The total estimated sample variance was partitioned into a component due to variation among the three values for the same specimen (within-specimen variance, or s^2_{within}) and an estimate of real differences between specimens (among-specimen variance, or s^2_{among}). Percent measurement error was then the within-specimen variance expressed as a percentage of the total variance: %ME $= 100 \times s^2_{within} / (s^2_{within} + s^2_{among})$ (Bailey & Byrnes, 1990). The coefficient of variation among specimens was also calculated: $CV_{among} = 100 \times \sqrt{s^2_{among}} /$ grand mean, where the grand mean is the sample mean for the variable over all specimens and all three sessions (Table 4.1).

Because future analyses would be performed mainly on data transformed to natural logarithms and the purpose of determining percent measurement error was to identify variables to be eliminated from such analyses, %ME was also computed using log-transformed data. The transformation had little effect on the results obtained; these were very close to the values for %ME computed from raw data and are therefore not given here.

In the "Brasília" data set, percent measurement error varied from 0.21% (~~condylo-~~ occipito- ~~incisive~~ nasal length) to 34.06% (bullar length), similar to the range of variation found by Lougheed et al. (1991) for sparrow skeletal measurements, but with a greater proportion of values in excess of 10% (nine of the 30 variables). For the "R. couesi" data set %ME was generally smaller, ranging from 0.01% to 24.39% with only two values above 10%. The difference in the results may be due to the contrasting characteristics of the two groups: not only was the first set composed of smaller specimens than the second (compare the grand mean columns in Table 4.1), but it was also more homogeneous, with a lower among-specimen coefficient of variation for all the variables except MRA. Both properties imply smaller overall variance in the "Brasília" group, as shown in the table, with the consequence that measurement errors similar in absolute size become relatively greater when expressed as a percentage of total variance. A further possibility is that it

Vari-able	Set 1 - "Brasília"				Set 2 - "R. couesi"			
	n	Grand mean (mm)	Total variance (mm²)	ME (%)	CV_{among} (%)	n	Grand mean (mm)	Total variance (mm²)	ME (%)	CV_{among} (%)
ONL	23	33.36	1.1657	0.21	3.23	13	37.85	4.5108	0.01	5.61
CIL	24	30.33	1.2639	0.26	3.70	15	35.10	4.7209	0.12	6.19
PL	25	15.45	0.3299	0.60	3.71	19	18.00	1.1338	0.37	5.90
PPL	25	12.59	0.4361	0.81	5.23	14	14.46	1.4516	0.23	8.32
MRC	21	5.12	0.0349	2.58	3.60	17	5.98	0.0479	0.82	3.65
MRA	24	5.45	0.0560	10.55	4.10	19	6.30	0.0660	5.25	3.97
M1B	25	1.39	0.0021	20.98	2.94	19	1.64	0.0033	13.98	3.26
PBL	25	4.99	0.0731	2.51	5.35	19	6.15	0.2150	1.10	7.49
TFL	25	10.02	0.1579	3.44	3.90	19	11.23	0.3526	0.18	5.29
DL	25	8.23	0.1656	6.13	4.79	19	9.80	0.5636	1.11	7.62
IFL	25	6.80	0.1759	0.59	6.15	19	7.80	0.2914	0.54	6.90
IFB	25	2.90	0.0163	26.51	3.78	19	3.22	0.0526	2.48	7.03
PB1	23	3.06	0.0309	23.22	5.02	19	3.46	0.0780	4.54	7.88
PB3	23	3.37	0.0415	14.97	5.58	18	3.79	0.0562	7.28	6.02
MFB	24	2.28	0.0526	7.09	9.71	18	2.60	0.0859	8.50	10.80
BIT	21	2.14	0.0136	14.74	5.02	19	2.47	0.0850	3.35	11.62
BW	25	4.33	0.0248	25.58	3.14	19	4.65	0.0526	5.46	4.80
BL	24	4.13	0.0269	34.06	3.23	19	4.36	0.0516	24.38	4.53
BCB	24	12.99	0.0882	5.17	2.23	16	14.16	0.3429	1.48	4.10
SH	25	9.61	0.1369	1.24	3.83	19	10.57	0.3258	4.95	5.26
RH	23	6.17	0.0811	2.11	4.57	19	7.28	0.3985	0.65	8.65
RB	25	6.42	0.0819	3.14	4.39	19	7.49	0.4238	0.12	8.69
RL	23	10.06	0.3135	1.20	5.53	19	11.62	0.7375	1.10	7.35
NL	23	11.39	0.4042	3.63	5.48	19	12.99	0.8103	2.91	6.83
ZPL	25	2.83	0.0176	15.86	4.30	19	3.39	0.1194	3.92	9.98
IOB	25	5.22	0.0599	1.03	4.67	19	5.97	0.2165	0.25	7.78
ZB	19	17.70	0.6268	0.63	4.46	12	19.95	1.6061	0.06	6.35
GLM	24	17.50	0.4439	2.19	3.77	19	20.11	1.0838	0.92	5.15
MMR	23	5.25	0.0336	6.12	3.38	19	6.26	0.0603	2.36	3.84
DR	24	3.76	0.0371	4.43	5.02	19	4.18	0.0664	2.36	6.09

was easier to place the calipers accurately on the more robust "*R. couesi*" skulls without risk of damage, resulting in smaller absolute errors. This is partly borne out by an examination of the absolute difference between the largest and smallest of the replicate measurements, averaged over specimens, for each variable in the two samples (Table 4.2). For many dimensions with well-defined end-points where the caliper jaws did not have to be positioned by eye (CIL, PL, M1B, PBL, IFL, BCB, IOB, GLM, MMR) the mean greatest difference was approximately the same in both samples, but for some

(ONL, MRC, TFL, RB, ZB), it was considerably smaller in the "R. couesi" set. Only with the two height dimensions (RH and especially SH) was the reverse true, possibly because the more roughly parallel conformation of the bone in these regions in larger skulls made it more difficult to determine where exactly to take the measurement. With the less well-defined variables no appreciable pattern of difference was apparent.

Table 4.2. Measurement error: greatest absolute difference in mm among three repeated measurements (largest minus smallest value) averaged over specimens, for two untransformed data sets.

Variable	"Brasília"	"R. couesi"	Variable	"Brasília"	"R. couesi"
ONL	0.08	0.04	BIT	0.07	0.09
CIL	0.09	0.10	BW	0.10	0.09
PL	0.07	0.10	BL	0.16	0.19
PPL	0.10	0.09	BCB	0.10	0.11
MRC	0.05	0.03	SH	0.06	0.17
MRA	0.12	0.09	RH	0.06	0.08
M1B	0.03	0.03	RB	0.08	0.04
PBL	0.07	0.08	RL	0.10	0.14
TFL	0.08	0.04	NL	0.21	0.27
DL	0.15	0.13	ZPL	0.08	0.11
IFL	0.05	0.05	IOB	0.04	0.03
IFB	0.10	0.05	ZB	0.10	0.05
PB1	0.14	0.10	GLM	0.17	0.17
PB3	0.14	0.11	MMR	0.07	0.08
MFB	0.10	0.13	DR	0.06	0.06

Although %ME varied in degree between the "Brasília" and "R. couesi" data sets, when the variables were ranked according to their %ME scores their order in the two samples was very similar: Kendall's tau statistic of rank correlation was $r = 0.632$, giving a probability $p \ll 0.01$ (n $= 30$) that such similarity was due to chance (Sokal & Rohlf, 1981, Appendix 2, Table XIV). Thus the largest values of %ME tended to occur with the same variables in each sample. Variable means were highly negatively rank-correlated with %ME ($r = -0.568$ for "Brasília" and -0.503 for "R. couesi", both n $=$ 30 and $p \ll 0.01$), indicating that smaller measurements were less reliable. There was also, of course, the expected negative correlation with the total variance [a trivial result, given

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that $\%ME = (1 / s^2_{total}) \times s^2_{within} \times 100]$.

In neither sample of raw data was %ME significantly correlated with the coefficient of variation among specimens ($\tau = -0.062$ and -0.136, n = 30, $p > 0.10$), but the correlation was significant and positive in each case when log-transformed data were used ($\tau = 0.384$, $p < 0.01$ for "Brasília"; $\tau = 0.315$, $0.05 > p > 0.01$ for "*R. couesi*"). The effect of transformation to logarithms was to decrease CV_{among} in absolute terms for all variables except those with the smallest means - M1B, MFB and BIT (for which it increased) - with the greatest relative decrease occurring among the larger variables. This apparent effect was, however, an artifact due to division by a logarithm (the grand mean) during the computation of the coefficient of variation, inflating the value of the coefficient as the logarithmic mean approached zero. Thus it was merely an indirect expression of the above-mentioned negative correlation of %ME with the absolute size of the variable.

To test whether %ME values reflected my own feelings as regards the reliability of the dimensions measured, I divided the 30 variables into two groups according to whether or not they were easily measured, with well-defined end-points. Sixteen variables (ONL, CIL, PL, MRC, M1B, PBL, TFL, IFL, BCB, SH, RH, RB, IOB, ZB, GLM, MMR) were considered "well-defined", while the remaining 14 were felt to be "poorly defined" to a greater or lesser extent. The %ME rank positions for the two variable groups were used as data values for a Mann-Whitney test, a non-parametric test for location difference of two sample means (Sokal & Rohlf, 1981, Appendix 2, Table XI). The resulting U statistics were 33:191 ($p < 0.002$) for the "Brasília" sample, and 41:183 ($0.002 < p < 0.01$) for the "*R. couesi*" sample, indicating that the "well-defined" variable group had a significantly lower mean rank for measurement error than the "poorly defined" group. However, since the two groups were also significantly different in a Mann-Whitney test on rankings of variable means by size (U = 52:172 and 53:171 for the "Brasília" and "*R. couesi*" samples; $0.002 < p < 0.01$), the larger-sized variables belonging mainly to the "well-defined" group, it is unclear whether the difference in %ME between the two groups of variables was due to size, ease of measuring or both.

The principal purpose of the measurement error study was to identify "unreliable" variables that could be eliminated in subsequent analyses, in the hope that by reducing such external sources of "noise" a better picture of the pattern of specimen relationships might be revealed. An additional advantage in removing some of the 30 craniodental variables was that the sample sizes required to obtain reliable multivariate parameter

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estimates would be reduced accordingly (Krzanowski, 1988). Five variables with over 5% ME in both data sets were therefore marked for elimination, i.e. MRA, M1B, PB3, MFB and BL. Although BW also scored highly it was felt that the bulla was too important a structure for neither of its measurements to be included in the data set. Apart from these, four other variables had measurement errors of over 10% in the "Brasília" data set: IFB, PB1, BIT and ZPL. The first two of these were the only remaining breadth dimensions of the base of the skull after elimination of PB3 and MFB, and the others were the sole representatives of the incisors and zygomatic plate; since these structures might be of taxonomic significance it was decided to retain them for the morphometric analyses.

b) Ontogenetic variation and sexual dimorphism

Given the small size of most samples of *Rhipidomys*, it would be desirable to group specimens of different sexes and age classes together in the analyses. It was important, therefore, to assess the morphometric effects of sex and age class within a population by means of an analysis of variance for each variable and a multivariate analysis of variance for the whole set of variables. Such a study would require a large series of conspecific individuals from a single population, i.e. collected from a restricted area over a relatively short period; furthermore, only individuals furnishing complete sets of measurements could be used. Two series of specimens satisfied these criteria: the *R. macconnelli* collected at Cerro Duida, Estado Bolívar, Venezuela, by G.H.H. Tate and the Olalla Brothers during the American Museum's Tyler-Duida expedition, between November 1928 and February 1929; and the *R. "cearanus"* from the vicinity of São Benedito, Ceará, Brazil, collected by the Brazilian National Plague Service between August 1952 and April 1954.

Despite their size (totals of 148 and 124 skulls, respectively), these series did not yield sufficiently large samples of undamaged specimens for all possible combinations of dental age class (DAC) and sex, with the consequence that DACs 0, 4 and 5 for *R. macconnelli* and DAC 5 for *R. "cearanus"* had to be omitted from the analysis. The smallest remaining age/sex groups contained 11 *macconnelli* and 6 *"cearanus"* specimens. In order to balance the experimental design, the other groups were reduced by random selection to 11 or 6 specimens accordingly; an analysis of variance was then performed on the log-transformed data for three external measurements (HB, TL and HFSU) and all craniodental variables (including those already identified as subject to large percent measurement errors) for each of the two series. This process was carried out three times

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using different random selections of specimens. Although the F-test used with the analysis of variance is fairly robust to deviations from the assumption of homoscedacity, the equality of group variances was tested by calculating the ratio of largest to smallest group variance (F_{max}, Sokal & Rohlf, 1981) for each variable and comparing it with tabulated 5% critical values (Rohlf & Sokal, 1981). The only variables with F_{max} values substantially and consistently above the accepted level of significance for all three random selections of specimens were TFL and PB1 in the *R. "cearanus"* data set. In each case the ratio was inflated by a particularly small variance in one age/sex group. Since there is no biological reason to suppose that such an occurrence might be due to anything more than a random sampling effect, and since in a large number of comparisons a few are likely to appear significant purely by chance, the assumption of homoscedacity was considered justified for all variables in both series of specimens.

Initial results of the analyses of variance indicated that for most variables in both series there was considerable variation associated with dental age class but no effect of sex (Table 4.3, left-hand half of table). Although an interaction between DAC and sex was sometimes apparent, the main effect of DAC was so strong ($p < 0.1\%$ in most cases) as to render the interaction irrelevant. Molar dimensions (MRC, MRA, M1B, MMR), however, were mostly independent of age class, and palatal breadth (PB1, PB3) and bulla size (BW, BL) were less strongly affected by it than the majority of other variables. In the *R. macconnelli* series, which lacked the extreme age classes (DAC 0 and 4) present in the other set, there was also little evidence of any age effect on tail and hind-foot lengths (TL, HFSU) or on most skull breadth measurements (IFB, MFB, BCB, RB, IOB).

When juvenile age classes (DAC 0 and 1) were dropped from the analysis, however, the significance of the main effects changed and the differences between the two series of specimens became more apparent (Table 4.3, right-hand half). In the adult classes (DAC 2, 3 and 4) of the *R. "cearanus"* series, the pattern of significance for age main effect was similar to that for the whole *R. macconnelli* series (DAC 1, 2 and 3); i.e. age was not a significant source of variation for molar and bullar dimensions or many skull breadth variables, but it was for head-and-body length (HB), most skull length and height measurements, zygomatic breadth and breadth of incisor tips (BIT). Examination of the standard errors of differences of means revealed that there were significant differences not only between dental age classes 2 and 4 but also between adjacent classes. Sex effects were also common: 14 of the 33 variables had significant main effects due to

Table 4.3. Analysis of variance due to dental age class (DAC), sex, and DAC/sex interaction in two series of specimens: summary of significant results ($p \leq 1\%$ and $1\% < p \leq 5\%$ for acceptance of H_0: no difference between groups) in three replications with different random selections of specimens. Left-hand half of table corresponds to whole series, right-hand half restricted to adults.

R. macconnelli all age groups (n^a=11; g^b=6; DAC=1,2,3)			R. "cearanus" all age groups (n=6; g=10^c; DAC=0,1,2,3,4)			Vari-able	R. macconnelli adults (n=11; g=4; DAC=2,3)			R. "cearanus" adults (n=6; g=6; DAC=2,3,4)		
DAC	Sex	Inter.	DAC	Sex	Inter.	able	DAC	Sex	Inter.	DAC	Sex	Inter.
1'11	—	—	111	_5	51_	HB	1_1	111	5_	111	111	—
—	—	—	111	_55	—	TL	—	—	5_	_55	551	—
—	—	—	111	_5	—	HF	—	—	—	—	151	—
111	—	555	111	—	_5	ONL	5_	—	155	515	555	—
111	—	—	111	—	_5	CIL	5_5	—	55_	111	511	—
111	—	—	111	—	_5	PL	—	—	555	111	_55	—
111	—	—	111	—	_5	PPL	111	5_5	_5	111	511	—
—	—	—	—	—	—	MRC	—	—	5_	—	—	—
—	—	5_	_5	—	—	MRA	—	—	15_	—	—	—
—	—	—	_15	—	—	M1B	—	—	—	—	—	—
—	—	—	111	—	—	PBL	—	—	—	_5	5_	—
111	—	—	111	—	51_	TFL	—	—	—	_5	—	—
111	—	—	111	_1	5_	DL	151	5_5	555	111	111	—
111	—	—	111	—	_5	IFL	—	—	—	551	_55	—
—	—	—	111	—	_5	IFB	—	—	—	—	_5	_15
—	—	—	115	—	—	PB1	—	—	—	5_	—	5_
—	—	—	515	—	—	PB3	—	—	—	51_	—	—
—	—	—	111	—	—	MFB	—	—	—	—	—	—
111	—	—	111	—	_5	BIT	—	—	—	111	—	—
—	—	—	55_	—	—	BW	—	—	—	—	—	—
51_	—	—	555	—	—	BL	—	—	—	—	—	—
_5	—	—	111	—	_15	BCB	—	—	—	—	511	—
111	—	—	111	—	—	SH	_5	—	—	515	—	—
111	—	—	111	—	—	RH	5_5	—	—	111	511	—
_55	—	—	111	—	—	RB	—	—	—	551	5_1	—
111	—	115	111	_5	55_	RL	5_	5_5	111	555	111	—
111	—	—	111	—	_5	NL	5_	—	5_	55_	555	—
111	—	_5	111	—	—	ZPL	—	—	_1	—	555	—
5_	—	—	111	—	—	IOB	—	—	—	5_5	_5	—
111	—	—	111	—	55_	ZB	551	—	_5	111	555	—
111	—	—	111	—	_5	GLM	—	—	—	111	555	—
—	—	—	—	—	—	MMR	—	—	—	—	—	—
111	5_	—	111	—	55_	DR	—	—	—	555	—	—

^{a} n = number of specimens per group.

^{b} g = number of DAC/sex groups included in analysis.

^{c} Groups with DAC=0 excluded from analysis for MRC, MRA, PB3 and MMR; therefore g = 8.

^{d} Entries in each column correspond to percentage significance levels attained in each of three replications: "1" - significant at $p \leq 1\%$; "5" - significant at $1\% < p \leq 5\%$; "_" - not significant at $p = 5\%$.

sex in all three replications, and in six more they were present in one or two replications. The variables included head-and-body, tail and hind-foot lengths and most longitudinal skull measurements, nearly all of which also showed a significant effect of age class. In all cases males averaged larger than females, and with an almost total absence of age/sex interaction effects there was no evidence for differential growth rates between sexes.

When just two dental age classes (2 and 3) were analysed in R. macconnelli, only three variables showed significant age effects in all three randomized replications: post-palatal length (PPL), diastema length (DL) and zygomatic breadth (ZB); in three other variables age was significant in two of the three replications. Sex had a significant effect in only head-and-body length and three other variables. However, there is reason to suspect the validity of the R. macconnelli results as they stand. Mean measurements for dental age class 2 females were often larger than those of DAC 3 females (by more than one standard error of difference of means) and similar to those of DAC 3 males, whereas most DAC 2 male measurements were substantially smaller. Although in this particular sample there may have been environmental or other causes for the younger female age cohort to be larger than the older, this clearly cannot be a normal occurrence. On the assumption that DAC 2 females should be no larger on average than DAC 3 females, the analysis results must be biased to an unknown extent, with a reduction in the main age class effect (which is based on the combined data of both sexes) and an increase in the age/sex interaction effect. This is borne out by the fact that whereas DAC/sex interactions were almost totally absent in the R. "cearanus" adults, in the R. macconnelli adult set they were present in one or more replications of thirteen variables.

The results of a multivariate analysis of variance involving all 33 variables showed little evidence of any overall effect, except in the case of the whole R. macconnelli set (DAC 1,2,3) for which the age class effect was significant (Table 4.4). No analysis was performed on the whole R. "cearanus" set because variables involving the complete molar row were not defined for DAC 0.

Two general conclusions can be drawn from the results of these analyses of variance. Firstly, they show that sexual dimorphism and ontogenetic variation are not constant in the genus: both in the whole samples and in the adult subsets (DAC 2 and above) their effects were much more apparent in the R. "cearanus" sample than in the R. macconnelli. The latter results may have been affected by the anomalously large DAC 2 females, but this fact may indicate that females in this species grow rapidly from age class 1 to 2 and then remain at a more or less constant size from class 2 to 3, whereas males

Table 4.4. Multivariate analysis of variance due to dental age class (DAC), sex, and DAC/sex interaction in two series of specimens: summary of significant results ($p \leq 1\%$ and $1\% < p \leq 5\%$ for acceptance of H_0: no difference between groups) for approximate chi-squared and F-tests in three replications with different random selections of specimens.

Data Set	Approx. Test	Dental Age Class	Sex	DAC/sex Interaction
R. macconnelli all age groups (n^a=11; g^b=6; DAC=1,2,3)	χ^2	1 1 1	1 _ _	_ _ _
	F	1 5 5	5 _ _	_ _ _
R. macconnelli adults (n=11; g=4; DAC=2,3)	χ^2	5 _ _	_ _ _	_ 5 _
	F	_ _ _	_ _ _	_ _ _
R. "cearanus" adults[c] (n=6; g=6; DAC=2,3,4)	χ^2	_ _ _	_ _ _	_ _ _
	F	_ _ _	_ _ _	_ _ _

[a] n = number of specimens per group.

[b] g = number of DAC/sex groups included in analysis.

[c] No analysis was performed on all age groups for this series because certain variables were not defined for DAC 0.

[d] Entries in each column correspond to percentage significance levels attained in each of three replications: "1" - significant at $p \leq 1\%$; "5" - significant at $1\% < p \leq 5\%$; "_" - not significant at $p = 5\%$.

grow more steadily between age classes 1 and 3. In *R. "cearanus"*, however, growth rates in the two sexes are apparently similar, males always being slightly larger than females. The lack of agreement between the two samples makes it difficult to apply these results to other species of *Rhipidomys*. A conservative approach for determining whether or not individuals of differing age or sex can be pooled for analysis would be to take the *R. "cearanus"* sample as the model and assume that there will be some variation due to age class and sex in some variables.

The second conclusion is that growth patterns and sexual dimorphism vary between measurements, which may be grouped according to the patterns observed. Of the three external measurements analysed, head-and-body length increases relatively more during adulthood than does tail length, while hind-foot length remains stable. For all three, males

may be larger than females on the evidence of the *R. "cearanus"* sample, although the questionable data of *R. macconnelli* have the females significantly larger for head-and-body length. Among craniodental measurements, molar dimensions remain stable over the age range and between the sexes. The same is true, amongst adults at least, for bullar length and width, mesoptyerygoid fossa breadth and, less clearly, palatal bridge dimensions. Longitudinal dimensions of the skull, rostral height and zygomatic breadth are the most likely to show age class and sex effects in adult specimens. Skull height, breadth across incisor tips and depth of mandibular ramus are more affected by age than sex, and the reverse is true of zygomatic plate length.

It is unfortunate that several of the variables that are apparently most independent of age class and sex, and therefore most potentially useful for inter-taxon comparisons, are subject to high measurement errors. These include the alveolar length of the upper molar row (MRA) and the breadth of the first molar (M1B) among molar measurements, both bullar dimensions (BW, BL), mesopterygoid fossa breadth (MFB) and both palatal widths (PB1, PB3). It is, of course, possible that the greater variance associated with variables subject to high measurement error makes it less likely that the group means will be significantly different. In the selection of variables for subsequent analysis, a compromise must therefore be sought between usefulness and reliability.

On the basis of the results obtained in the studies of measurement error and sexual and ontogenetic variation, three different selections were made from the 30 craniodental variables originally measured. The smallest consisted of just four variables - MRC, PBL, TFL and IOB - which had relatively small percent measurement errors and showed little evidence of variation due to sex or age amongst adults of either *Rhipidomys macconnelli* or *"cearanus"*. It is noteworthy that all four are situated in the central section of the skull and are thus less influenced by the ontogenetic growth that continues in the rostral and basicranial regions after sexual maturity. The second subset, of 8 variables, consisted of these four plus PL, BCB, SH and RB. Here, the aim was to cover other important dimensions of the skull while keeping percent measurement error and adult age/sex variation as low as possible. Seven more variables - PB1, MFB, BW, NL, ZPL, MMR, DR - were added to these eight to form the third subset, expanding the number of cranial structures included. Most of these extra variables had either larger percent measurement errors or some adult variation due to sex or age, but they did not include the most extreme cases.

Several of the subsequent analyses were run four times, using in turn the subsets

of 4, 8 and 15 variables and the whole set of 30, in order to compare the results obtained with each. In practice, four variables were generally sufficient to demonstrate overall size differences between sets of specimens, although the distinction was usually clearer with eight or fifteen. Contrary to expectations, in most cases little additional information was gained by using all 30 variables; the "noise" of individual variation often hid any further population-level distinctions in the data which it had been hoped that analysis of so many measurements might reveal.

c) Imputation of missing values

Missing values are one of the main problems encountered in the analysis of morphometric data derived from museum specimens, many of which are incomplete or damaged to a greater or lesser extent. Many computer algorithms reject incomplete data outright while others deal with missing items in unsatisfactory ways, either by inserting the sample mean or by ignoring the entire record containing the missing value. In many taxonomic studies, the number of specimens available to represent a particular population may well be limited; therefore the relative loss of information caused by the removal of even one record can be considerable and should be avoided where possible. Since most morphometric variables are correlated with each other, often to a high degree, the replacement of a missing value with the sample mean in specimens that lie towards the extremes of the size range can seriously distort the relations between variables and lead to aberrant results. A more acceptable approach is for the variables affected simply to be dropped from the analysis, especially when they are highly correlated with others, but this is really only practicable when very few of the variables measured have any missing values.

In order to retain as much information as possible while keeping distortion of variable relationships to a minimum, a file was formed of log-transformed adult (DAC 2-5) craniometric data, excluding specimens with more than five missing values, in which missing values could be imputed to complete the data set whenever feasible. Imputation was carried out in the following manner. First, specimen records were ordered into provisional taxonomic groups ("populations"), and data distributions for each group were examined for multimodality, which might indicate that the group was composite and should be subdivided. Each population containing missing values was then dealt with separately. Missing values for a particular variable were replaced only when they occurred in 25% or fewer of the records in the group. Correlations between variables were then

determined using the data available for the group, and the variable in question was regressed on the variable with which it was found to be most highly correlated (variables otherwise eliminated on the basis of measurement error analysis were included for this purpose). The resulting regression equation was used to calculate replacement values for the missing data. The suitability of these values was tested in bivariate scatter plots of the variable against other highly correlated variables; if the imputed values lay consistently outside the otherwise elliptical scatters, they were rejected, a new regression was carried out on the next most correlated variable, and the new imputed values were tested in the same way. In some cases, especially where the variable was not highly correlated with any other or the sample size was small, this procedure proved unsatisfactory; the variable mean was then used as a replacement value provided that the specimen did not lie towards the extremes of the ranges of the other variables. Where missing values could not be replaced on account of small sample size within the population, either the specimen or the variable with missing values was excluded from the analysis, depending on the circumstances.

4.3 - Exploratory analyses

Principal components analysis (PCA) was employed as an exploratory technique to search for structure in the data. This procedure treats the data as a homogeneous set of observations and does not deal specifically with variation within or between groups defined *a priori*. Its results can, however, indicate where any groupings in the data may lie. The latent vectors (eigenvectors) of the variance-covariance matrix are used in turn to weight linear combinations of the original variables to form new variables - the principal components; the first of these accounts for as large a proportion as possible of the original variability of the data, with subsequent components representing successively smaller amounts. Thus a large percentage of the variability is concentrated into the first few dimensions. The number of components formed is equal to the number of original variables (if the data matrix is of full rank), but for the practical purpose of detecting taxonomic variation only the first few components contain useful information that is not smothered by individual variation or measurement error. Scores for the specimens are calculated for each of the components of interest; they can then be plotted on graphs or used as input into other procedures. Multivariate normality of the data is not assumed so long as no significance tests are required.

The purpose of using PCA in this study was to investigate the differences between

specimens rather than the relative importance of the variables. In order to prevent variables with larger variances from dominating the analysis and masking possibly important contributions from other variables, the data were standardized to have zero means and unit standard deviations for each variable (Neff & Marcus, 1980). As a result of this operation covariances were transformed into correlations, and the latent roots used in calculating the principal components were therefore extracted from the correlation matrix of the variables. It must be remembered that the latent vector coefficients found in PCA are specific to the set of specimens included in the analysis and will vary somewhat from one sample to another drawn from the same population (Neff & Marcus, 1980). Thus one should not draw detailed inferences from a PCA to apply to the population as a whole.

For morphometric data the first latent vector loadings are often of the same sign and similar magnitude; their combination can then be seen as representing a general size factor. Since the components are calculated to be uncorrelated with each other, the remaining ones may be interpreted as shape factors. The influence of allometric growth may, however, remain in the specimen scores and mask genuine differences between taxa. Thorpe (1976) suggests that to eliminate the influence of size on shape when using PCA, the principal components should be extracted from the matrix resulting from pooling the within-group covariance (or correlation) matrices. This is unsatisfactory for three reasons. First, the advantage of PCA is that no groups need to be established in the data *a priori* and the analysis can be used to investigate the possible existence of such groups. Calculation of within-group covariance matrices would require the prior imposition of such structure, resulting in circular argument. In addition, the method assumes the equality of these matrices, an assumption which may be reasonable when dealing with geographic races of a single species but which may not be met should the groups not be closely related. Lastly, the groups for analysis in the present study are often too small for reliable separate matrices to be calculated, so that the only option is to extract the principal components from the data pooled irrespective of any grouping. In practice, the influence of allometric growth was reduced by excluding juveniles and old adults from the analyses and concentrating on those variables that showed least ontogenetic and sexual variation amongst adults.

Principal components analysis was performed on the *Rhipidomys "cearanus"* dataset, first without any age restriction and then on adults (DAC 2, 3 and 4) alone. The performance of the analysis in revealing patterns of variation was compared using 4, 8,

15 and 30 variables. Specimen scores were plotted on single and bi-component diagrams and identified by sex and dental age class. On each of the first 5 components and the residuals, t-tests were carried out to compare the mean scores for males and females, and also for each pair of adult age classes.

In the four analyses that included both juveniles and adults, the first latent vector was made up of large, roughly equal coefficients for all variables (excepting molar lengths, palatal breadth and bullar width), forming a general size component. As expected, juveniles lay towards one extreme and older adults towards the other, but there was considerable overlap especially among adults (DAC 2 to 4). The other principal components involved combinations of particular variables; the second component in each case, for example, had a large loading of molar row length. But in no case was there any apparent association with DAC or sex, except for the fifth component in the 8-variable analysis, for which females tended to have negative scores and males positive ones. The main contribution to this component was provided by braincase breadth, for which the analysis of variance (see section 4.2) had already indicated some sexual dimorphism in this population. Thus apart from the juvenile/adult size difference revealed in the first component (which accounted for 58-70% of the total variance of the sample), most of the remaining variation was "noise" due to individual differences between specimens, not attributable to age or sex. In the 4 and 8 variable cases at least, this result was to be expected given the fact that the variables used were selected so as to reduce the effects of age and sex among adult specimens.

When the analyses were restricted to adults only, certain age and sex differences became more apparent, having previously been swamped by the large size variation associated with the presence of juveniles. The first component usually provided some sorting of specimens by age and sex, opposing males and older individuals to females and younger ones (Table 4.5a), although there was always much overlap. The coefficients of the first latent vector were all of the same sign and, except in the analysis with 30 variables, of similar value, thus reflecting general skull size (males and older specimens being larger).

Few tests on other components proved significant (Table 4.5b). The second principal component on 4 variables and the third on 15 variables both differentiated specimens in DAC 3 (lower scores) from those in DAC 4 (higher scores); in each case the main loadings were for IOB (positive, together with BW in the 15 variable case) and MRC (negative); in the larger analysis several other variables were also involved.

Table 4.5 Principal components analysis of *Rhipidomys "cearanus"* adults
using standardized, log-transformed data: t-test results on
differences in scores according to sex and dental age class along the
principal component axes (Prob. = probability of no difference in means).

a) Results of t-tests on first principal components:

No. vari-ables used	Sex (53 d.f.)		DAC 2-DAC 3 (39 d.f.)		DAC 2-DAC 4 (25 d.f.)		DAC 3-DAC 4 (40 d.f.)	
	t	Prob.	t	Prob.	t	Prob.	t	Prob.
4	-2.434*	1.8%	-1.236	22.4%	-2.615	1.5%	-1.667	10.3%
8	2.887	0.6%	1.216	23.1%	3.208	0.4%	2.540	1.5%
15	2.616	1.2%	1.205	23.6%	3.253	0.3%	2.577	1.4%
30	2.803	0.7%	1.477	14.8%	3.739	0.1%	3.071	0.4%

* Evidence in data of unequal variances for males and females; test may be inappropriate.

b) Other t-test results significant at 5%:

No. variables used in analysis	Component	Test	d.f.	t	Prob.
4	PC2	DAC 3-DAC 4	40	-2.306	2.6%
15	PC2	Sex	53	2.248	2.9%
15	PC3	DAC 3-DAC 4	40	-2.185	3.5%
15	PC4	DAC 2-DAC 3	39	-2.347	2.4%
30	PC4	DAC 2-DAC 3	39	-2.357	2.4%

DAC 2 and DAC 3 specimen scores were also significantly different on the fourth component in both the 15 and 30 variable analyses, yet the only obvious feature held in common by the two eigenvectors was a large negative coefficient for BW. The only component apart from the first to show a significant difference between the sexes was the second in the 15 variable analysis, with females averaging higher scores on MFB, MMR and MRC and lower on ZPL and PBL than males. It is worth noting that the 8 variable analysis was most successful in concentrating variation into the first component, with 61.6% of the total, against 54.9% for 4 variables, 50.5% for 15 and 55.1% for 30. All

tests on residuals were far from significant.

The results from the *Rhipidomys "cearanus"* data set raise two important points regarding the use of PCA with other populations. First, they demonstrate that this technique will reveal variation due to sex and age class, particularly size differences. Care must therefore be taken when interpreting PCA results to distinguish such variation from that due to taxonomic differences, especially in the first principal component. Secondly, although the power of the technique was greater with eight variables rather than four, it did not increase dramatically when more than eight variables were analysed. This confirms the premise that the variables in the smaller sets contained most of the relevant information, whereas those excluded contained mainly "noise" due to individual differences. Since PCA requires the sample size to be greater than the number of variables used, this result shows that it is reasonable to reduce the number of variables to allow the analysis of smaller samples than would otherwise be possible.

In order to reduce age-based size variation within populations, old adult specimens (DAC 4.5 - 5), which tend to be considerably larger than other adults, were excluded from further analyses. These were usually based on the set of 15 variables, or sometimes eight when fewer specimens were included. Specimens for which missing values could not be replaced for any one of these variables had to be omitted.

With adult occipito-nasal length varying from 24.7 mm in the smallest *Rhipidomys wetzeli* to 44.81 mm in the largest *R. leucodactylus*, size and size-related allometric factors would have dominated any numerical analysis that embraced the whole genus, giving no clearer answers than could be gained by visual examination. Instead, morphometric methods were used principally to help elucidate taxonomic differences among those groups of specimens that were otherwise difficult to sort on the basis of external and cranial morphology.

4.4 - Discrimination of taxa

Discriminant analysis is an eigenanalysis technique for groups of specimens defined *a priori*, in which functions of the original variates are found that maximize between-group variance relative to within-group variance. It includes two conceptually different techniques (Huberty, 1994). In Descriptive Discriminant Analysis (DDA), the functions that describe group separation or difference are the outcome of a given grouping variable. In Predictive Discriminant Analysis (PDA), however, specimens are allocated to groups on the basis of existing discriminant functions; i.e. the functions are given and

the grouping variable is the outcome. The groups formed may be represented graphically in the reduced number of dimensions provided by canonical variates space. In this study DDA was used to compare populations for which sufficiently large samples were available, and problem specimens were then allocated by PDA techniques. Single-variate and bivariate plots were produced to summarize group relationships. Discriminant analysis (and especially the associated tests) requires multivariate normality and equality of group covariance matrices. Because of the difficulties of testing for these requirements, especially with unequal sample sizes, they were assumed to be met and therefore statistical results are conditional upon the truth of this assumption.

The efficiency of a set of discriminant functions may be tested by using the functions to reallocate each specimen to the group with the nearest multivariate mean vector (centroid), and then calculating the "hit rate" - the proportion of specimens reassigned to their original group. The functions are likely to perform too well when reallocating the same specimens that were used to construct the functions in the first place. To prevent the bias inherent in such an internal testing procedure, two sets of specimens with known group membership should ideally be used, one to form the functions (the training set) and the other for calculating the hit rate (the testing set). When there are too few specimens to split the samples in this way, as in this study, a good approximation to the true performance of the discriminant functions can be achieved by the Leave-One-Out method (Lachenbruch, 1975). In this method, similar in principle to jackknife procedures but without the averaging of pseudo-estimators, one of the N specimens in the sample is omitted, the functions are calculated from the remaining N-1 units and the excluded specimen is allocated to the nearest group. This is repeated N times, with a different specimen omitted each time. The proportion of excluded units correctly classified is used as a hit rate estimator. Such methods tend to be fairly free of distribution assumptions (Neff & Marcus, 1980). When N is sufficiently large, the number of correct allocations or hits o can be tested against the null hypothesis that o is no greater than the number expected by chance e [where $e = \Sigma(n^2/N)$, and n is the number of specimens in each group in turn], by using the standard normal statistic $z = (o - e)/\sqrt{[e(N-e)/N]}$ (Huberty, 1994).

The use of discriminant analysis was limited by the size of the available samples. To achieve reasonable precision in an external (e.g., leave-one-out) analysis, Huberty (1994) recommends that the number of specimens comprising each group should be at least three times the number of variables used. But discrimination between groups is more

powerful when the number of variables is increased, provided that these variables all contribute more than just "noise" (as shown by significant variance ratios in univariate analyses of variance). Therefore, groups of fifteen or preferably more specimens are needed for a reasonably powerful and precise analysis. There were not many natural groups of this size in the total sample available, so where necessary the results of principal components analysis were used to combine morphologically similar specimens from neighbouring locations in order to increase group sizes. Of course, specimens from smaller sets could be included just for allocation without contributing to the analysis proper.

In practice, discriminant analysis was not used to a great extent, partly because of the constraints imposed by sample sizes, and partly because the technique of itself cannot distinguish between species differences and geographical variation within a species. Any two sufficiently large samples from different localities are likely to prove distinct in some way. In an attempt to overcome this drawback, the significance of between-sample differences was tested with univariate Student's t-tests (for which the database without replacement of missing values was used), and the multivariate Hotelling's T-squared test. Again, with large samples the tests were so sensitive as to suggest that nearly all pairs of populations were significantly different. If this were taken to indicate species status for each one, the number of species in *Rhipidomys* would be greatly inflated. Because they contributed little to the taxonomic assessment of the genus, the results of such analyses and tests will not be discussed.

CHAPTER 5 - DELIMITATION OF THE GENUS

As mentioned in chapter 2, *Rhipidomys* belongs to the thomasomyine group, an informal assemblage of genera which retain many character states considered plesiomorphic for the Sigmodontinae. Other putative members of the group are *Abrawayaomys*, *Aepeomys*, *Chilomys*, *Delomys*, *Phaenomys*, *Rhagomys*, *Thomasomys*, *Wiedomys* and *Wilfredomys*. These taxa correspond approximately to the thomasomyine genera of Hershkovitz (1962, 1966a), which he regarded as a separate group, but most were placed within the Oryzomyini by Vorontsov (1959) and Reig (1980, 1984) on the basis of their pentalophodont molar morphology. Voss and Carleton (1993) provided the first phylogenetic diagnosis of the Oryzomyini, in accordance with which all these genera are excluded from that tribe.

It is therefore pertinent to concentrate on comparisons of *Rhipidomys* with the other plesiomorphic genera (especially *Thomasomys*, certain species of which bear some resemblance to *Rhipidomys*), and with representatives of the Oryzomyini *sensu stricto*. As defined by Voss and Carleton (1993) this tribe contains terrestrial, palustrine and arboreal rodents. Apart from its type genus (which is diverse and currently unrevised) the most appropriate choice amongst these for comparison is the arboreal genus *Oecomys*, which is sympatric with *Rhipidomys* over much of its range. Comparisons will also be made with the Central American tylomyine *Nyctomys* owing to its superficial resemblance to *Rhipidomys*. To construct or test a phylogenetic hypothesis involving all these genera is beyond the scope of the present study. Instead, my purpose here is to examine the characters that best distinguish and delimit *Rhipidomys* within the Sigmodontinae. In the following chapter it will be seen that the aberrant characters of *R. macconnelli* point to a probable basal position for this species within *Rhipidomys*: while it shares certain derived features with the remainder of the genus it also has many character states that are plesiomorphic for the Sigmodontinae or doubtfully polarized in common with species currently included in *Thomasomys*. Such points need to be discussed not only in connection with intra-generic relationships and distinctions, as in Chapter 6, but also in a broader comparative context involving the thomasomyine group and the Sigmodontinae in general. Therefore, the discussion of characters below includes many for which *R. macconnelli* differs from the remainder of the genus, as indicated where appropriate.

5.1 External morphology

Pelage. In a genus that occurs in habitats ranging from lowland rain forests to upper montane forests at over 3000 m, it is to be expected that pelage characteristics will vary accordingly. Lowland and lower montane forms of *Rhipidomys* have short coats (mid-dorsal body hairs typically about 7 or 8 mm in length) that are moderately fine to medium-coarse in texture but not as coarse as in *Sigmodon*, for instance, and never spinous as in *Neacomys* or *Abrawayaomys*. Adult pelage is usually sleek, but rather woolly fur somewhat resembling that of juveniles is retained ventrally in many adults of *R. leucodactylus* and certain other species. At higher altitudes (above 1500-2000 m) the pelage tends to be finer and longer (8-12 mm on mid-dorsum, 6-9 mm mid-venter, guard hairs 2-4 mm longer), but not to the extremes found in certain *Thomasomys* species or phyllotines.

In the majority of *Rhipidomys* species, dorsal colour ranges from a fairly bright reddish-orange to a duller greyish-brown agouti. The basal 60-70% of each body hair is medium to dark slate, above which lies a broad, orange to straw-coloured subterminal band, followed by a narrow, dark apical band. Guard hairs vary from reddish brown to black. *R. macconnelli* has longer, almost black hair bases with narrow subterminal bands, giving a darker chocolate-brown appearance. In species with more intense phaeomelanin pigmentation, the apical band and guard hairs take on a reddish tinge and contrast less strongly with the orange subterminal band, producing a more uniform, brighter red appearance with less dark flecking. In others, the subterminal band is paler and less saturated and the guard hairs relatively darker, resulting in a greyer and more conspicuously agouti overall impression. The shoulders and rump may be rather more intensely pigmented than the middle dorsum, and the flanks are often a little paler than the back.

On the ventral surface - from chin to perineum, on the inner face of the limbs, and laterally on the upper lip - the hairs are whitish-tipped over slate-grey bases that vary from zero to 70% or more of the hair length. In lowland forms the grey bases are rarely noticeable, being pale and short or more often absent, particularly along the midline of the lower thorax and abdomen, and on the throat and upper lip. A specimen with an otherwise pure white venter may sometimes have a "pectoral spot" - a small area with dark slate bases on the upper thorax. In certain species the ventral colour is more a pale, drab yellow rather than white or cream, and in others the hair tips at the "pectoral spot"

may be tinged with orange. Species from higher altitudes with longer pelage consistently have dark hair bases ventrally as well as dorsally; except in *R. macconnelli*, they remain concealed by the white tips unless the fur is ruffled. In some specimens the "white" tips may be tinted throughout with orange; in these the normally distinct dividing line between dorsal and ventral pelage becomes blurred.

Pelage colour and texture distinguish *Rhipidomys* from most other Sigmodontinae. Many of the large species currently attributed to *Thomasomys* (*T. apeco, T. aureus, T. auricularis, T. popayanus, T. princeps*) are also reddish-orange agouti dorsally, but they have longer hairs with darker bases and shorter yet more intensely pigmented orange bands than *Rhipidomys*. The majority of *Thomasomys* species, however, are as dark as *R. macconnelli* or even darker. Ventrally their cream or light brown hair tips are either absent or so short that they do not conceal the grey bases but instead contribute to an overall silvery-grey or beige-grey ventral appearance; they do not have a distinct dorsal-ventral dividing line. *Chilomys* has dark grey-brown dorsal and grey ventral pelage which is velvety in texture. The rarely captured *Phaenomys* is a much brighter orange than any *Rhipidomys*, with a creamy-white venter; it also lacks the white patch on the upper lip. In contrast, most Oryzomyini are less brightly coloured than *Rhipidomys*, with a more apparent agouti pattern. Other taxa have distinctive colour patterns of their own: e.g., the dorsal stripe in *Delomys* or the reddish nose and rump in *Wiedomys* and *Wilfredomys*. Coloration similar to that found in *Rhipidomys* is, however, shared by a number of taxa, notably *Thomasomys notatus* and most species of *Oecomys*.

Tail. The tail in *Rhipidomys* ranges from roughly equal to head-and-body length to over one-and-a-half times as long. It is covered with small, imbricated scales, the exposed parts of which are squarish in shape, arranged in annuli along the shaft. Adult tails have 9-18 scales per 10 mm (measured longitudinally at mid-shaft). Scale colour varies between individuals from pale to dark brown and is uniform both around and along the shaft (save for a slightly paler area towards the base on the ventral surface in many specimens); *R. macconnelli*, however, resembles many *Thomasomys* in having a tail that is dorsoventrally bicolour along most of its length. The tail shaft is clothed in rather short, stiff hairs, three of which emerge from under the posterior edge of each scale. They are rarely long enough to obscure the scales over the proximal part of the tail, but they lengthen on the distal third and at the tip form a distinct terminal tuft or pencil, varying from about 5 mm up to 40 mm or more in length. This character is sufficient to

distinguish all *Rhipidomys* from most other Sigmodontinae. The few other genera that have tufted tails, such as *Scapteromys* and *Ichthyomys*, are easily differentiated by other external features, such as tail length, ear size, relative length of digits and claw shape. The non-sigmodontine *Nyctomys*, which resembles *Rhipidomys* in several other characters as well as its tail pencil, can be distinguished by its brighter colour and the fact that the whole tail shaft is clothed in long hairs. Some species of *Rhipidomys*, particularly lowland, small-bodied forms, have rather short and sparse tail pencils which approach the condition found in certain species of *Thomasomys* and *Oecomys*, although the overlap between the genera is minimal (except for *T. notatus*). The colour of the tail hairs varies somewhat but is usually a dull, medium-dark, reddish brown, sometimes rather darker towards the tail tip. The hairs are not banded.

Hind foot. All *Rhipidomys* species excepting *R. macconnelli* have a short, broad foot suited to their arboreal habits, distinguishing them from all other Sigmodontinae except *Oecomys*. The metatarsals are relatively short compared with the digits: the longest digit is roughly two-thirds the length of the metatarsals. The ratio of hind foot length (including claw) to head-and-body length was calculated for all adult (DAC $\geq$ 2) *Rhipidomys* specimens for which skin measurements were available; dry measurements of the foot were taken and used where the stated values seemed dubious, and a correction of 0.02 was added to the ratio in cases where it had to be calculated from HFsu. The mean of the ratios for all specimens except *R. macconnelli* was 0.209 (s.d. = 0.021; n = 574). For the less arboreal *R. macconnelli*, which has a narrower, longer foot, the mean was 0.243 (s.d. = 0.014; n = 199). Hershkovitz (1960) found means of 0.209 and 0.193 for small samples of arboreal *Oecomys bicolor* and *Oe. superans*, and 0.237 and 0.214 for series of terrestrial *Oryzomys alfaroi* and *Or. laticeps*. Thus most *Rhipidomys* appear to have feet of a similar size to *Oecomys*, whereas the results for *R. macconnelli* lie closer to the proportions found in *Oryzomys*.

The hind foot in *Rhipidomys* has the basic mammalian complement of six plantar pads (Brown & Yalden, 1973) - four interdigital at the bases of the digits, and a medial thenar and lateral hypothenar at metatarsal level. In a more elongated, cursorial foot the pads are small and narrow; the thenar is located some distance behind the hypothenar, and one or both may be reduced or even absent. In the broad-footed *Rhipidomys*, however, all the pads are well developed, covering a large part of the ventral surface of the foot.

The distal end of the thenar lies beside or only just behind the proximal part of the hypothenar, the distal end of which in turn lies close to the fourth interdigital pad. *R. macconnelli* has all six plantar pads but they are a little smaller and more separate than in the other species.

The first and fifth digits in *Rhipidomys* are longer than in most other Sigmodontinae: the claw of digit I (hallux) reaches the end of the first phalanx of digit II, and the claw of digit V extends as far (or, in *R. macconnelli* particularly, very nearly as far) as the base of the claw on digit IV. The middle three digits are subequal in length. The fifth digit is held at an angle to the others and appears to be at least partially opposable to them (see Fig. 1.1). Webbing between the digits is minimal. The claws are short, sharp and tightly curved, in contrast to the less recurved, blunter claws of terrestrial muroids. Ungual vibrissae rooted at their bases extend beyond their tips; these tufts are denser than in many other genera, but often not as dense as in many *Thomasomys*, for example.

Body fur extends down the limb as far as or even slightly beyond the heel (except in *R. macconnelli*), leaving the remainder of the sole naked and the dorsal surface of the foot covered with very short, stiff hairs. While the digits and both sides of the foot are generally pale or golden, the metatarsals are covered medially by a darker patch, distinctly outlined or not, which is often broader at the base of the digits and may extend onto the proximal phalanges. Similar foot patches are found occasionally in other scansorial taxa, such as some *Oecomys* and *Thomasomys*, but not as consistently as in *Rhipidomys*.

Eyes, ears and nose. Rhipidomys has very large and protruding eyes (Fig. 1.1), perhaps important for a nocturnal, scansorial animal in improving both light capture and stereoscopic perception in a three-dimensional habitat. The membranous ear pinnae, which vary from light to very dark brown, are of medium size and are thinly furred on the external surface. The infranarial portion of the rhinarium is expanded into a pair of disc-shaped flaps partly covering the nares.

Vibrissae. Mystacial, genal, superciliary, submental, interramal and ulnar carpal vibrissae (Brown, 1971; Brown and Yalden, 1973) are found in *Rhipidomys*. The prominent mystacial vibrissae, etymologically the basis for the genus name (Greek *rhipidos*, fan, *mus*, mouse), are noticeably long (up to 70 mm, a little less in *R. macconnelli*), and when

appressed to the head extend back far beyond the ears. In most cases they are very dark, but they may occasionally be paler or even white. Collectors have noted that they are very mobile (e.g., I. R. Bishop, field catalogue of Xavantina-Roncador expedition, Brazil, 1968, regarding specimen M 249, *R. emiliae*, BMNH 81.374). The mystacial pads in which they are rooted are particularly thick in *Rhipidomys*, a condition also found in the Ichthyomyini, another group with well-developed mystacial vibrissae (Voss, 1988).

The genal and superciliary groups of vibrissae (on the cheek and above the eye, respectively) are sparse, with only one to three long, dark hairs in each. The submental vibrissae consist of an indeterminate series of short, stiff, white hairs along the lower lip, which are difficult to distinguish from normal cover hairs. The interramal group (not present in all specimens), on the midline between the mandibular rami, and the ulnar carpal group on the inner face of the forelimb consist of one or two stiff, unpigmented hairs which stand out at a different angle from the normal pelage.

Mammae. Three pairs of mammae are clearly visible in lactating female *Rhipidomys*, in inguinal, abdominal and postaxial positions (terminology from Voss and Carleton, 1993). Occasional specimens (e.g. FMNH 63783) have bare areolar patches corresponding in position to the thoracic mammae of other taxa, but with no sign of an actual teat. I was unable to determine the cause of these bare patches. A survey of the skins of *Thomasomys*, *Oryzomys*, *Oecomys* and two dozen other Neotropical muroid species revealed that a majority (including all the *Oryzomys* and *Oecomys* species examined) had a mammary count of eight. Other taxa with only six mammae were the species of *Thomasomys*, *Delomys dorsalis* (some populations have eight; Voss, 1993), *Aepeomys vulcani*, *Rhagomys rufescens* (probably: mammae are countable on only one of the two extant skins, which has not been ideally prepared), and *Ichthyomys stolzmanni* (as all other ichthyomyines; Voss, 1988). One female of *Neacomys spinosus* appeared to have only six mammae, while two others had eight. (Steppan [1995: 51], based on the literature, attributed six mammae to *Neacomys*.) Wied-Neuwied (1826: 421) reported six mammae for *Wiedomys*. Higher numbers of mammae were found in *Sigmodon hispidus* (five pairs) and *Calomys murillus* (five or six pairs). The non-sigmodontine *Nyctomys sumichrasti* had only two pairs of mammae (inguinal and abdominal). Thus a mammary count of six as found in *Rhipidomys* appears to be relatively uncommon amongst Neotropical muroids.
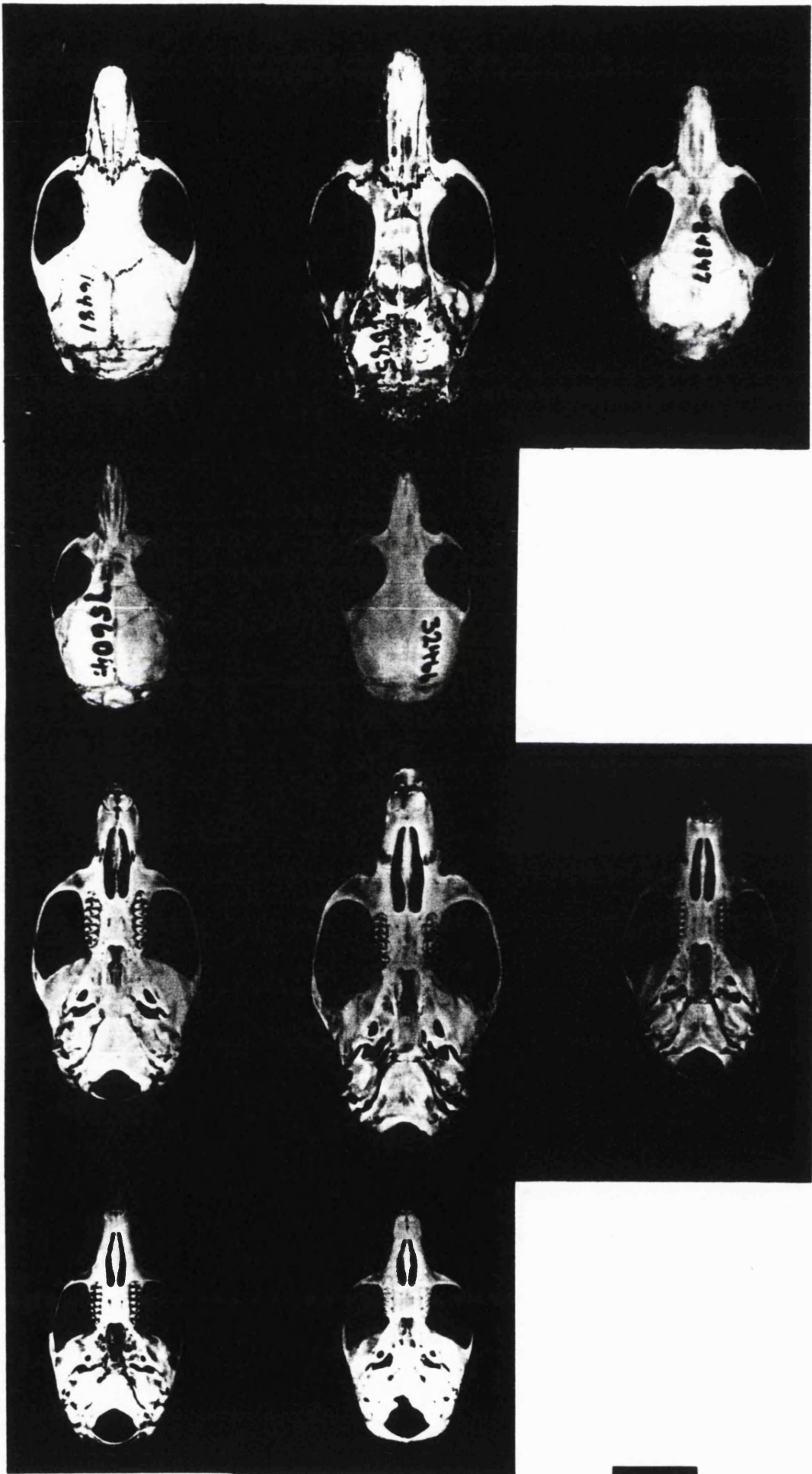
Fig. 5.1. Representative *Rhipidomys* skulls. Details on following page.
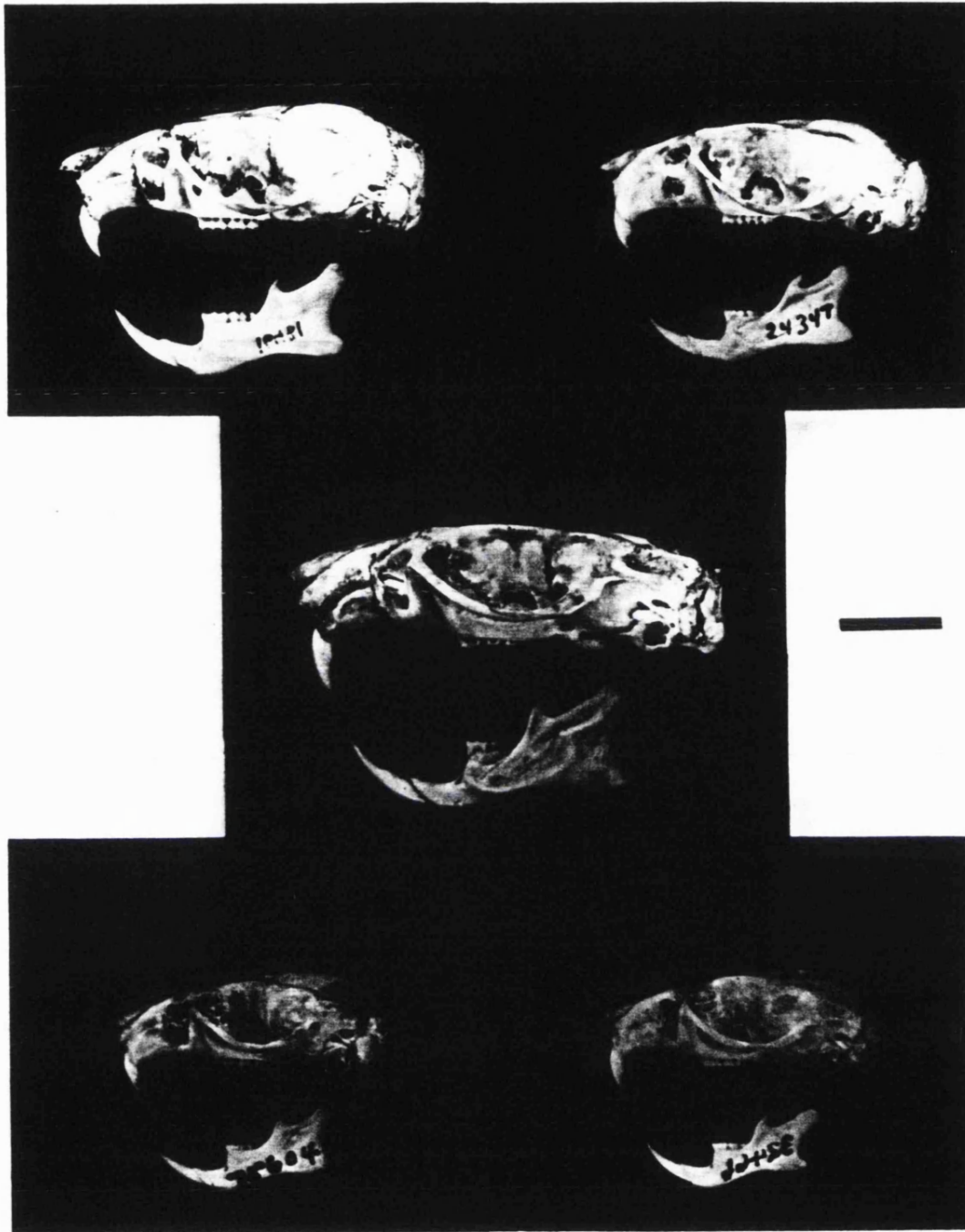
Fig. 5.1 (previous page). Representative *Rhipidomys* skulls, dorsal and ventral views (X 1.5). Left to right, first and third rows: *R. ochrogaster* (holotype, AMNH 16481), *R. couesi* (holotype, AMNH 5956/4685), *R. latimanus venezuelae* (AMNH 24347); second and fourth rows: *R. macconnelli* (AMNH 75604), *R. caucensis* (holotype, AMNH 32466). The bar represents 1 cm.

Fig. 5.2 (above). Representative *Rhipidomys* skulls, lateral view (X 1.5). Specimens as in Fig. 5.1. Top left: *R. ochrogaster* (reversed); top right: *R. latimanus venezuelae*; centre: *R. couesi*; bottom left: *R. macconnelli*; bottom right: *R. caucensis* ∧.The bar represents 1 cm.
                 ∧
      (reversed)

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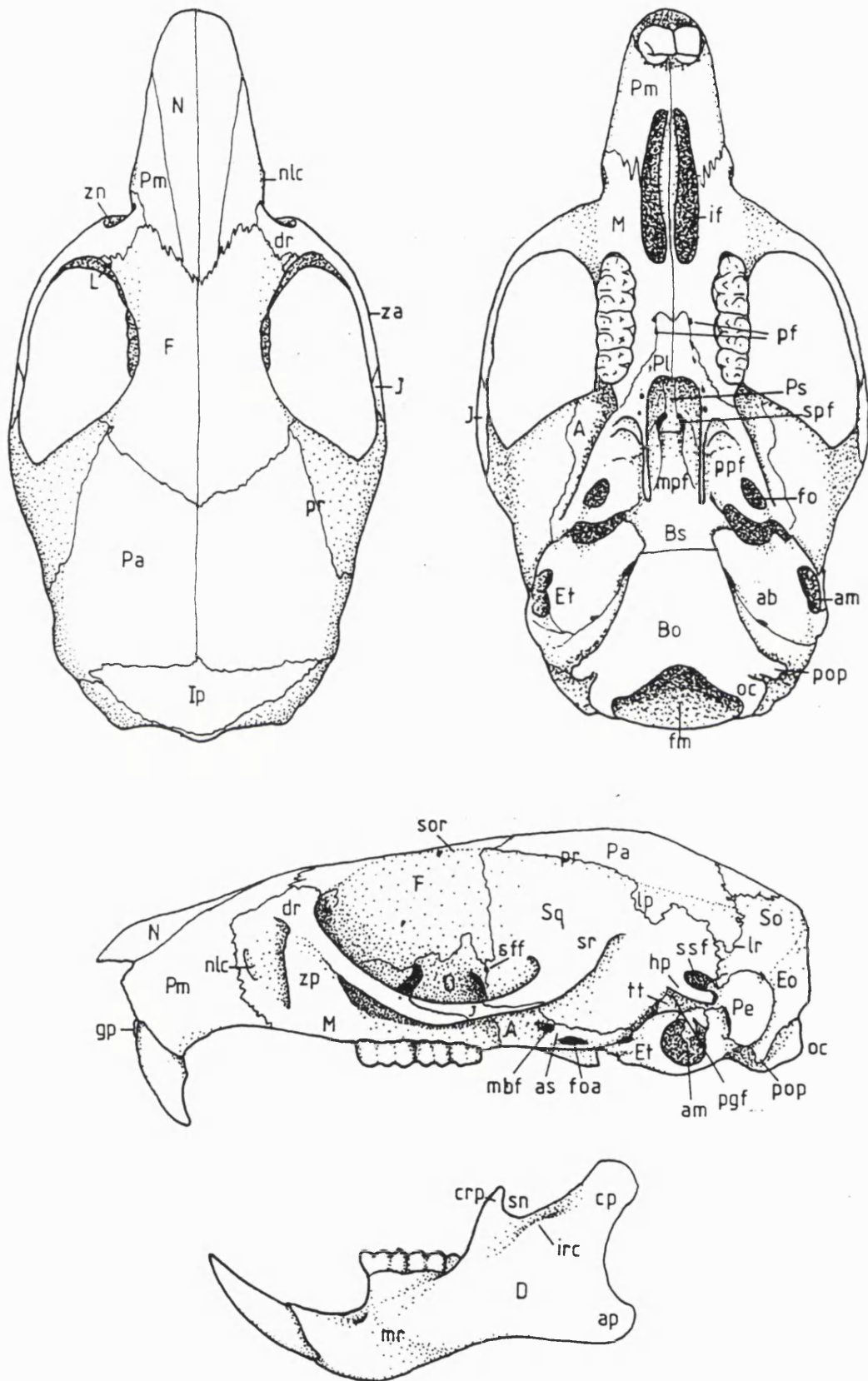
Fig. 5.3. Bones and structures of a *Rhipidomys* skull and mandible (*R. ochrogaster*, holotype, AMNH 16481). Key on the next page.

5.2   Cranial characters

Representative *Rhipidomys* skulls are illustrated in Figures 5.1 and 5.2. Cranial structures are identified in Figure 5.3.

Rostrum. The *Rhipidomys* rostrum is short, rather deep and blunt, lengthening relative to overall skull size in older specimens. In dorsal view it tapers gradually from the naso-lacrimal capsules to the anterior end of the nasals, but in lateral view the shallowest point is usually some distance behind the incisors. Although the nasals and premaxillaries project a little beyond the anterior face of the incisors, they are usually separated by a notch and do not form a tube as in *Delomys* (see Voss, 1993). A small gnathic process projects forwards from between the incisor alveoli. The nasolacrimal capsules are situated on the sides of the rostrum just in front of the zygomatic plate and closer to it than is the norm in *Thomasomys*. They are not usually greatly expanded. The height and angle of their posterodorsal opening varies considerably in both *Rhipidomys* and *Thomasomys*.

Fig. 5.3 (continued). Key: *Bones (capital initial):* **A** alisphenoid, **Bo** basioccipital, **Bs** basisphenoid, **D** dentary, **Et** ectotympanic, **Eo** exoccipital, **F** frontal, **Ip** interparietal, **J** jugal, **L** lacrimal, **M** maxillary, **N** nasal, **O** orbitosphenoid, **Pl** palatine, **Pa** parietal, **Pe** periotic, **Pm** premaxillary, **Ps** presphenoid, **So** supraoccipital, **Sq** squamosal. *Structures and foramina:* **ab** auditory bulla, **am** auditory meatus, **ap** angular process, **as** alisphenoid strut, **cp** condylar process, **crp** coronoid process, **dr** dorsal (maxillary) root of zygomatic arch, **fm** foramen magnum, **fo** foramen ovale, **foa** foramen ovale accessorium, **gp** gnathic process, **hp** hamular process of squamosal, **if** incisive foramen, **irc** lower incisor root capsule, **Ip** lateral process of parietal, **lr** lambdoid ridge, **mbf** masticatory-buccinator foramen, **mpf** mesopterygoid fossa, **mr** masseteric ridge, **nlc** nasolacrimal capsule, **oc** occipital condyle, **pf** palatal foramina, **pgf** postglenoid foramen, **pop** paraoccipital process, **ppf** parapterygoid fossa, **pr** parietal ridge, **sff** sphenofrontal foramen, **sn** sigmoid notch, **sor** supraorbital ridge (or ledge), **spf** sphenopalatine fissures, **sr** squamosal root of zygomatic arch, **ssf** subsquamosal fenestra, **tt** tegmen tympani, **za** zygomatic arch, **zn** zygomatic notch, **zp** zygomatic plate.

Zygomatic notch and plate. In many Sigmodontinae the zygomatic plate has a free antero-dorsal edge which projects forwards from its dorsal root, delimiting a more or less distinct notch adjacent to the rostrum which is visible from above. At one extreme (e.g., in *Holochilus*) the projecting spine extends well forward beside the nasolacrimal capsule, and the notch becomes an almost enclosed space. The opposite occurs in *Ichthyomys*, in which the anterior edge of the plate is retracted posteriorly below its dorsal root and no notch is formed. *Rhipidomys* is intermediate in that only an extremely shallow notch is visible dorsally; the anterior edge of the plate is tall and stands roughly vertical, curving back very slightly at the top to the dorsal root. It never leans backwards so obliquely as, for example, in *Aepeomys lugens*. Similarly small zygomatic notches are found in many other members of the thomasomyine group, although *Delomys* resembles most Oryzomyini in having a more conspicuous notch; many *Oecomys*, on the other hand, have a small notch like *Rhipidomys*.

Interorbital region. The interorbit in *Rhipidomys* is moderately broad and never so constricted as in *Phaenomys* or *Nesoryzomys*, for instance. Dorsally it is flat or it may have a slight medial depression, which in some specimens extends to the tip of the rostrum. The dorsal edges are squared or more usually marked with slight supraorbital ledges or ridges. These begin just behind the dorsal processes of the lacrimals and diverge posterolaterally in straight or gently curved lines across the frontals above the posterior part of the orbit, to merge with the parietal ridges on the braincase. Because of these ledges, the narrowest part of the interorbit is located well forward. In contrast, in the "hourglass-shaped" interorbit found in most *Thomasomys*, the interorbital edges are rounded rather than squared or ridged, and the narrowest point is more central. Certain *Thomasomys* and members of the *Rhipidomys fulviventer* group display intermediate conditions in which slight ridges begin more medially on top of the frontals, the distance between the ridges at this point being narrower than the least interorbital breadth; nevertheless, the squared edge over the posterior part of the orbit will usually be better developed in the *Rhipidomys*. Both main patterns are widespread in the Sigmodontinae; the majority of oryzomyines have more or less well-developed ridges, as also do *Phaenomys* and *Wiedomys*, whereas the rounded interorbit is found in *Delomys* and *Chilomys*. Much heavier supraorbital ridges occur in *Nyctomys*.

Braincase shape. The braincase in *Rhipidomys* is large relative to overall skull length and

oval in dorsal view, with a domed profile in smaller species which becomes flattish in adult specimens of larger species. *Thomasomys* braincases (with the exception of the very largest species) are shorter and more globular in comparison. On each side of the *Rhipidomys* braincase, a usually delicate parietal ridge or beading extends from the supraorbital ledge along the parietal-squamosal suture to a point dorsal to the squamosal zygomatic root. There it inflects posteromedially across the parietal bone towards the corner of the interparietal, where it joins the lambdoidal crest running down the exoccipital-squamosal suture. In smaller specimens with more domed crania the ridge runs along almost the widest part of the braincase, but as skull size increases the relative braincase size decreases, so that in the largest the ridges come to occupy a less lateral position on the dorsal surface. Such ridges are present in most sigmodontine skulls, but in those with very rounded interorbits and braincases (e.g., many *Thomasomys*) they may be difficult to trace.

Interparietal. In *Rhipidomys* the interparietal is broad, its outer corners reaching the parietal ridges. It is rather narrower in *Wiedomys, Aepeomys* and some *Oryzomys*, and very much narrower in most akodontine genera. It is also long, its greatest length (in the sagittal plane) usually exceeding 40% of its width, more than in most species of *Thomasomys, Delomys, Aepeomys, Wiedomys* and the majority of the Oryzomyini.

Lateral process of the parietal. Where the parietal ridge leaves the parietal-squamosal suture to run across the posterior part of the parietal bone, it marks off the lateral process of the parietal, which projects into the squamosal. In *Rhipidomys* (excepting *R. macconnelli*) this process is large and typically almost rectangular in shape; although it may become a little shallower posteriorly, its rear edge always makes contact with the occipital. In most oryzomyines the process is also rectangular, sometimes more so than in *Rhipidomys*. In many *Thomasomys*, however, the lateral process is more much triangular in shape, being deeper in its anterior portion and narrowing rearwards as the parietal-squamosal suture runs back up towards the parietal ridge. In *R. macconnelli* this character shows considerable variation; whereas many resemble *Thomasomys*, a few specimens have the typical *Rhipidomys* form, while in many others the suture returns dorsally to the parietal ridge well before it reaches the lambdoidal crest, leaving a small, isolated lateral process with no contact with the occipital. This pattern is also found in specimens of *Wiedomys* and *Wilfredomys*, some akodontines and most phyllotines. In

Nyctomys the suture does not deviate at all from the parietal ridge and therefore the lateral process is not formed; with the broad interparietal extending to or beyond the parietal ridge in this genus, the parietal bone does not contact the occipital at all.

Posterior region of the squamosal. The topography and proportions of the region of the squamosal that lies between the root of the zygomatic arch, the lateral process of the parietal, and the subsquamosal fenestra provides some distinction between *Rhipidomys* and *Thomasomys*. In *Rhipidomys* this area is rather long and high. Given the relatively large braincase and small auditory bullae of the genus, the dorsal margin of the subsquamosal fenestra lies less than half-way up the skull, or more precisely the distance (projected onto a sagittal plane) between the ventral surface of the bulla and the dorsal margin of the subsquamosal fenestra is less than, or rarely equal to, the distance from the latter point to the mid-point of the parietal-interparietal suture. In *Thomasomys*, however, the dorsal margin of the subsquamosal fenestra lies relatively higher on the skull, being closer to the parietal-interparietal suture than to the ventral surface of the bulla, and rarely equidistant between the two.

The zygomatic arch in *Rhipidomys* joins the braincase at an oblique angle to the longitudinal axis of the skull; the rearmost extension of its squamosal root ends a little below the lateral process of the parietal, and well anterior to and above the hamular process of the squamosal. In *Thomasomys* the zygomatic arch joins the braincase more perpendicularly; its posterior root ends close to (and often no higher than) the origin of the hamular process, and it may be prolonged posteriorly in a ridge confluent with the dorsal margin of the subsquamosal fenestra. *Delomys* and *Wilfredomys oenax* follow the pattern found in *Thomasomys*, whereas *Phaenomys* and *Oecomys* resemble *Rhipidomys*, sometimes with the zygomatic root located even higher on the squamosal.

Auditory bullae. The bullae in *Rhipidomys* are relatively small for the size of skull and not inflated as in *Wiedomys*, *Wilfredomys*, or especially the tylomyine *Otonyctomys*. On the medial side a narrow wedge of periotic is visible between the ectotympanic and basioccipital; in many specimens it extends anteriorly to form the dorsolateral wall of the carotid canal. The ectotympanic ring surrounding the auditory meatus is incomplete, a gap remaining in the dorsal margin adjacent to the postglenoid foramen. The bony eustachian tubes extend anteromedially from the bullae at a rather larger angle to the longitudinal axis of the skull (i.e., more transversely) than in many other genera; they open at or just

anterior to the basioccipital-basisphenoid suture.

Bullar suspension. The anterior squamosal suspension of the bulla in *Rhipidomys* is formed by the tegmen tympani, an outgrowth of the periotic, where it overlaps the posterior suspensory process of the squamosal (terminology from Voss, 1993). In many specimens the tegmen tympani expands dorsally, occluding a large part of the postglenoid foramen and often much of the subsquamosal fenestra too. In the Oryzomyini the contact between the tegmen tympani and the squamosal has been lost, although in some species of *Oecomys* there may be secondary overlap which does not involve a distinct posterior suspensory process (Voss & Carleton, 1993). This region of the squamosal thus serves to distinguish *Rhipidomys* from *Oecomys*.

Carotid circulation. Two carotid circulatory patterns are found in *Rhipidomys*:

1) Skulls of the *R. fulviventer* group (excluding *R. caucensis*; see chapter 6) display the following suite of character states: a large stapedial foramen in the petrotympanic fissure on the ventroposteromedial side of the auditory bulla; a groove across the posterolateral corner of the parapterygoid fossa to the foramen ovale; a groove across the internal surface of the squamosal and alisphenoid (visible by transmitted light); this groove leads to an opening within the orbit generally termed the sphenofrontal foramen, although in these species it is located on the suture between the alisphenoid and orbitosphenoid and rarely involves the frontal bone. This complex corresponds to the primitive muroid circulatory pattern, whereby the facial circulation is supplied by the stapedial artery, the supraorbital ramus of which follows the internal groove mentioned above and exits the braincase via the sphenofrontal foramen (Bugge, 1970; Voss, 1988, p. 297: "pattern 1").

2) The remaining species of *Rhipidomys* exhibit a derived pattern characterized by a minute stapedial foramen and the absence of the other structures mentioned above. The stapedial artery supplies only the middle ear while the facial circulation is provided by a branch of the carotid originating within the braincase (Voss, 1988, p. 298: "pattern 3"). The derived pattern seems to have arisen several times within the Sigmodontinae: both primitive and derived conditions co-occur within different tribes (Ichthyomyini - Voss, 1988; Oryzomyini - Voss and Carleton, 1993) and even within genera (*Rhipidomys, Oecomys, Thomasomys* and *Sigmodon*), and the derived pattern is also found in *Rhagomys* and *Reithrodon*.

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Alisphenoid strut. The alisphenoid strut is consistently present in all species of *Rhipidomys*, separating the buccinator-masticatory foramen from the foramen ovale accessorium. Of the 1700 *Rhipidomys* specimens examined, only one (IBAMA/MG 107, *R. mastacalis*, Serra da Canastra, MG, Brazil) lacked a strut on both sides; its braincase was also rather more inflated than usual, but otherwise the skull had all the normal characteristics of the genus. Absence of an alisphenoid strut is considered a synapomorphy for the Oryzomyini (Voss and Carleton, 1993) but I have found it to be present in several (but not all) species of *Oecomys*. Most species of *Thomasomys* have a strut, but it is absent in at least some individuals and populations of *T. cinnameus*, *T. ischyrus* and *T. niveipes*, as well as *Aepeomys lugens* and *Wilfredomys oenax*.

Sphenopalatine fissures. The roof of the mesopterygoid fossa is formed by the basisphenoid and presphenoid. It may be entire, or these bones may be flanked by narrow slits or large vacuities. In *Rhipidomys* these fissures are usually absent, or there may be short, narrow openings beside or near the suture between the two bones. Large sphenopalatine fissures are present in several (but not all) Oryzomyini, in *Wiedomys*, *Wilfredomys*, akodontines and phyllotines; in *Delomys* and *Phaenomys* they are usually small; in *Thomasomys* they vary from absent to large.

Palate. Palate length was the character that led Thomas (1906) to separate *Oecomys* from *Rhipidomys* and to align it with *Oryzomys*, and it was used again by Hershkovitz (1962, 1966a) to distinguish his oryzomyine and thomasomyine groups. In *Rhipidomys* (and most of the other plesiomorphic genera) the palatal bridge is short: the incisive foramina extend close to or beyond a line connecting the anterior roots of the first molars, and the mesopterygoid fossa reaches between the third molars. The rear edge of the palatal bridge, forming the anterior margin of the mesopterygoid fossa, is broadly concave or nearly rectangular and often has a posteriorly projecting medial process. In such a conformation the bony connections from the palate to the pterygoids are narrow, tightly squeezed between the third molars and the fossa, and bear small, simple foramina. In contrast, *Oryzomys* and its allies have a longer palatal bridge, since the mesopterygoid fossa does not reach the level of the third molars; the anterior margin of the fossa often tapers to a point on the mid-line, although in some *Oecomys* it approaches the shape found in *Rhipidomys*; and the bony ridges between the third molars and the fossa are

broader and bear posterolateral pits, depressions in the bone into which several foramina open. Although certain *Oecomys* species may be convergent with *Rhipidomys* in many ways, they may usually be distinguished by the presence of these pits.

Mandible. The *Rhipidomys* mandibular ramus is average in size and proportions, being neither as slender as in *Aepeomys* nor as robust as in *Holochilus*. The coronoid process is small and falciform, and the angular is generally short and blunt. Relative to the occlusal plane of the lower molars, the condyloid process rises somewhat higher than the coronoid and in most cases extends posteriorly approximately as far as does the angular, and sometimes a little farther. The lower masseteric crest is moderately well developed, especially in older individuals; its juncture with the less pronounced upper masseteric crest lies below the anterior part of the first molar. The root capsule of the lower incisor is situated immediately below the front of the sigmoid notch, just behind the coronoid process; the capsule ranges in size from a slight bulge, through a distinct shelf parallel with the sigmoid notch, to a prominent, elongated knob.

5.3   Dental characters

Incisors. The upper incisors in *Rhipidomys* are slightly opisthodont relative to the molar occlusal plane, never proodont as in *Aepeomys* or especially *Chilomys*, or even orthodont as in certain *Thomasomys*. They do not have conspicuous grooves, but fine striations may sometimes be seen in reflected light down their bright orange anterior face. Their cross-section is oval with a single axis of symmetry, the anterior face being broader and less curved than the posterior. The incisor tips wear regularly without forming a deep notch between the two teeth.

The lower incisors are paler and more slender than the upper pair. Their moderate angle of procumbency is reflected in the overall proportions of the mandible.

Molars: form. The occlusal structure of *Rhipidomys* molars is illustrated in Figure 5.4. *Rhipidomys* is described as a pentalophodont genus, in common with most of the other plesiomorphic sigmodontine genera and the majority of the Oryzomyini. The term refers to the five transverse lophs typical of their cheek teeth, best appreciated in the upper second molar: the anteroloph, paraloph, mesoloph, metaloph and posteroloph (terminology for occlusal features from Reig, 1977). In other genera the mesoloph has

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Procingulum
anteromedian style
anteromedian flexus
anterolingual conule

anterior mure
protoloph
protostyle
protoflexus
PROTOCONE
paraloph
median mure
enterostyle
enteroloph
hypoflexus
HYPOCONE
metaloph

Procingulum
anterolabial conule
anteroflexus
anteroloph
parastyle

paraflexus
PARACONE
paralophule
oblique paralophule
mesoflexus
mesostyle
mesoloph
metalophule
metaflexus
METACONE
oblique metalophule
posteroflexus
posteroloph

LINGUAL   LABIAL

Procingulid
anterolingual conulid
anteroflexid
anterolophid
metastylid

metaflexid
METACONID
metalophulid
mesoflexid
mesostylid
mesolophid
entoflexid
entolophulid
ENTOCONID
posteroflexid
posterolophid

Procingulid
anterolabial conulid
anteromedian flexid
transverse lophid
protolophid
protostylid

protoflexid
PROTOCONID
metalophid
median murid
ectolophid
ectostylid
hypoflexid
HYPOCONID
entolophid
posterolabial flexid

Fig. 5.4 - Occlusal structures of typical *Rhipidomys* molars. *Above:* upper left molar row; *below:* lower right molar row. Homologous elements in the second and third molars are not labelled. Terminology from Reig (1977).

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been lost, resulting in a tetralophodont condition. *Rhipidomys* molars are also brachydont or low-crowned with closed roots, so that after eruption they cease to grow and become increasingly eroded with use. In contrast, grazing rodents such as phyllotines have high-crowned or hypsodont molars with open roots that allow continuous growth as the occlusal surface is ground away. An associated feature is that *Rhipidomys* molars are initially crested or bi-level (terms from Hershkovitz, 1962, 1967), with four main cusps standing above the occlusal plane. Very soon they become terraced with use, as the lingual cusps in the upper molars and the labial cuspids in the lower are worn down to a flat surface, while the cusps on the opposite side of the tooth remain prominent. Eventually, in very old individuals, all the occlusal enamel architecture is eroded down to a level rim surrounding a single dentine basin.

The characters discussed below will serve to distinguish the molars of *Rhipidomys* from those of most other taxa. It should be noted that there is considerable individual variation in the degree of development of many secondary occlusal features, such as enteroloph, protoloph, ectolophid and paralophules, and in the smoothness or crenulation of enamel elements. In most cases such variation seems to be uncorrelated with geographical or taxonomic units.

Relative lengths of molars. As in most muroids, the first molar in both maxillary and mandibular dentitions is expanded anteriorly by an enlarged procingulum, providing two additional cusps in the upper (M1) and one or two in the lower (m1). The second molars remain close to the primitive condition, but in the third molars, particularly in the upper dentition, the posterior half of the tooth is considerably reduced. Typically, M2 is 70-75% the length of M1, and M3 is 75-80% the length of M2 (measurements taken along the central axis of the teeth), although M3 does vary somewhat in relative size. Reduction in the length of m3 is less severe. In absolute terms, the crown length of the upper molar row in the *Rhipidomys* specimens examined ranged from 3.5 mm in a specimen of *R. wetzeli* (USNM 387918) to 7.2 mm in one *R. leucodactylus* (FMNH 24811). The ratio of M1 breadth to molar row length lay mostly between 0.27 and 0.29, with extremes of 0.24 and 0.32.

Procingulum. The anteromedian flexus of M1 is usually well defined and divides the procingulum into two conules. Although the anterolingual conule tends to be slightly smaller than the anterolabial, it is never so reduced that it affects the oblong outline of

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M1, as occurs in *Phaenomys* and especially *Nyctomys*. The conules are similar in shape to the main cusps on the same side of the tooth, although often slightly smaller. On the anterior face of the procingulum, the anteromedian flexus may sometimes split into two branches around an anteromedian style.

In the lower dentition, the procingulid forms a pair of conulids usually separated by a well-defined anteromedian flexid. Sometimes, even in unworn teeth but especially after wear, this flexid can be reduced to a mere groove on the anterior procingular surface and a small median fossetid (which is soon obliterated) on the occlusal side; in such cases, careful examination of this rearward-facing occlusal surface usually reveals a double medial band of enamel flanked by two areas of exposed dentine, indicating the presence of two conulids closely appressed together. Unlike their counterparts in the upper dentition, the anterolingual and anterolabial conulids do not duplicate the shape of the main cusps but rise like a twin prow at the front of the tooth, their exposed dentine surfaces facing rearwards along its major axis.

Cusps. The four main cusps in the primitive sigmodontine upper molar are the protocone and hypocone on the lingual side and the paracone and metacone on the labial. In *Rhipidomys* these are all roughly equal in size on M1 and M2. On M3 the protocone and paracone are often slightly smaller than in the previous teeth, whereas the posterior pair of cusps is severely reduced; the metacone particularly is often indistinguishable as a raised cusp even when the tooth is unworn. The occlusal surfaces of all lingual cusps soon wear to a common flat plane; these cusps in plan view are shaped as equilateral triangles with a rounded lingual apex, separated by triangular hypoflexi and interdental notches. In comparison, the cusps in *Delomys* and many species of *Thomasomys* are elongated lingually with a less triangular outline, and the hypoflexi are narrower and more slit-like; in many *Oryzomys* and some *Oecomys* the cusp outline is more rounded with a less pronounced lingual apex. *Rhagomys* has separate, raised lingual cusps.

The labial cusps in *Rhipidomys* are "sugarloaf" shaped: blunt, rounded cones with a flatter posterolingual face where the edges of the enamel wear back to expose the dentine. Thus they do not share a common plane of occlusal wear with each other or with the lingual cusps, at least not until a very advanced stage of erosion. These cusps are roughly as long as they are broad, unlike those of *Thomasomys aureus* and its allies, which are smaller and distinctly compressed laterally.

Similar considerations apply to the main cusps of the lower molars. Here it is the

labial cusps - the protoconid and hypoconid - that are triangular prisms that wear quickly to a common occlusal plane, whereas the lingual cusps - the metaconid and entoconid - are conical with their exposed dentine facing anterolabially. The entoconid of m2 and especially the metaconid of m3 tend to be smaller than the cusp in front, while the m3 entoconid is either very small indeed or more usually absent altogether as a separate raised element. With the reduction of its lingual structures, m3 becomes much narrower in its posterior half although it is often not appreciably shorter than m2. The loss of the m3 entoconid is common in *Oryzomys, Oecomys, Delomys* and *Thomasomys*, but a large entoconid is retained on m3 in *Phaenomys*.

Mesoloph and mesolophid. The upper molars in *Rhipidomys* always have a fully developed, separate mesoloph running from the mure to the ~~lingual~~ labial side of the tooth, where it merges with the mesostyle. Its juncture with the median mure, separate from that of the paraloph, is not greatly expanded to form a mesocone such as is found in *Wilfredomys oenax*. The mesoloph is separated from the paraloph and paracone by a persistent mesoflexus (or, more properly, mesofossetus, since it is blocked at the margin of the tooth by a cingular ridge from paracone to mesostyle), which reaches the median mure opposite the hypoflexus. The mesofossetus may be crossed and thus subdivided by an oblique paralophule linking the mesostyle or distal end of the mesoloph with the posteromedial base of the paracone. In a few specimens, especially in *R. caucensis*, this lophule may parallel the mesoloph, giving the appearance of a double mesoloph. In the modified occlusal structure of M3 the mesoloph can still be distinguished in most cases, although it may be distorted, truncated or bifurcated.

In *Thomasomys aureus* and several other species currently placed in that genus, the mesoloph loses its identity as it coalesces with the paracone and/or the above-mentioned oblique paralophule. Together they form a median loph (Reig, 1977), which curves from the mure anterolabially to the paracone and from the paracone posterolabially to the mesostyle; the proximal section may be absent, and after little wear the median loph becomes a mere marginal expansion of the paracone. Coalescence of the mesoloph with the paracone in *Rhipidomys* occurs only after considerable wear (Dental Age Class 4, at least).

The mesolophid in the lower dentition of *Rhipidomys* is as prominent (at least in m1 and m2) as its counterpart in the upper, running from the murid to the mesostylid on the lingual margin of the tooth. In m3, however, the much greater reduction of the lingual

cusps compared with the labial ones means that the median murid is displaced lingually, foreshortening the mesoloph; in extreme cases the murid coalesces with the mesostyle, and the mesoloph is non-existent.

Reduction or replacement of the mesolophid in many *Thomasomys* species occurs in an analogous fashion to the process described above with regard to the mesoloph, with the capture of the mesolophid by the entolophid/entoconid. In *Wiedomys* the process is complete and the mesolophid is absent.

Flexi and flexids. The principal labial folds in the upper molars - the paraflexus and metaflexus - delimit the paracone and metacone respectively by curving around their anterior and medial margins. In so doing they generally describe a quarter of a circle or a fraction more, ending at the posteromedial corner of the cusp where they are blocked by the paraloph or metaloph. This terminal part of the flexus is often slightly expanded or even bifurcated, with one short branch extending posteriorly and another penetrating lingually into the protocone or hypocone. In some individuals only the latter branch is present, and the resulting interpenetration of the labial folds and the hypoflexus approaches the layout found in *Delomys*, interpreted by Voss (1993) as incipient lophodonty.

Cingular elements on the labial edge of the tooth obstruct the mouths of these flexi, transforming them after little or no wear into fosseti, as described above with regard to the mesoflexus. In labial view the molars of *Rhipidomys* differ from those of *Delomys* and most *Thomasomys* in that the cusps and styles are linked by these marginal ridges, which block off the deep valleys corresponding to the flexi.

Similar developments have occurred in the lower molars, where the principal lingual folds are the mesoflexid and posteroflexid. These penetrate behind the metaconid and entoconid respectively, curving around them as far as the metalophid and entolophid. Since the lower molar lingual cusps are smaller relative to the size of the tooth than the upper labial cusps, these flexids often take a less curved, more oblique path than the paraflexus and metaflexus. As in the upper molars, the internal end of the flexids is often expanded or bifurcated, and the opposite extremity is obstructed by cingular elements; this is particularly apparent in m3, where the lingual cingular ridge includes the rudimentary entoconid.

Styles and stylids. In addition to the mesostyle already mentioned, the upper molars in

Rhipidomys have two other labial styles: a parastyle at the tip of the anteroloph, in close contact with the paracone (and with the anterolabial conule in M1), and a posterostyle at the tip of the posteroloph, merging with the metacone (indistinguishable in M3). On the lingual side of the tooth there is an enterostyle in the hypoflexus, rarely with an enteroloph connecting it to the middle of the anterior margin of the hypocone. In the protoflexus of M1 there is a protostyle, often with a complete or partial loph extending to the anterior mure; usually in M2 and less frequently in M3 a distinct anterolingual cingulum is isolated on the face of the protocone by a slit-like protoflexus. The presence of these lingual styles means that the flexi are roofed and do not extend vertically from crown to root.

On the lingual side all three lower molars have a mesostylid and posterostylid at the tips of their respective lophs, closely associated with the neighbouring cusps. In m3 the posterolophid is well developed, despite the reduction of the entoconid. A metastylid is present in m1, connecting the metaconid with the anterolingual conulid at the end of a generally rather weak anterolophid, but it is absent in m2 and m3, where the metalophid and metaconid form the anterolingual margin of the tooth. The labial stylids are more prominent than the lingual styles in the upper dentition and similarly form a floor to their flexids. All three teeth have a large ectostylid, sometimes with a medially-oriented ectolophid. The protostylid in m1 forms a pronounced ridge from anterolabial conulid to protoconid; its equivalent in m2 and m3, the anterolabial cingulid, is conspicuous even in those individuals that lack an anterolingual cingulum on upper M2 and M3.

5.4   Postcranial skeleton and soft anatomy

Owing to a shortage of suitable material for reliable inter- and intrageneric comparisons, I did not investigate these areas systematically or in detail. The following points are based on very small samples and on information from the literature.

Ribs and vertebrae. Twelve pairs of ribs (five pairs of which floating) were found in two specimens (*R. mastacalis*, MNRJ 5393, Santa Teresa, Espírito Santo, Brazil; and *R. macrurus*, AMNH 134523, Anápolis, Goiás, Brazil) and 13 pairs (six floating) in one individual (*Rhipidomys* sp., AMNH 134521, Maracaju, Mato Grosso do Sul, Brazil). The first rib in each case articulated with the transverse processes of the 7th cervical and 1st thoracic vertebrae, while the 6th cervical (and also the 5th in MNRJ 5393) buttressed the

7th. The 2nd thoracic vertebra, and to a lesser extent the 3rd, had an enlarged neural spine. Each specimen had 7 cervical, 19 thoracicolumbar and 4 sacral vertebrae; the second and third specimens had complete caudal skeletons with 37 and 41 vertebrae respectively. Steppan (1995: Table 5) conducted a survey of vertebral counts in 179 species (153 Sigmodontinae) and found that a complement of 13 thoracic (rib-bearing) and 6 lumbar vertebrae was the most widespread condition, occurring in most akodontines and many ichthyomyines, phyllotines and thomasomyines. The Oryzomyini, however, were characterized by having 12 thoracic and 7 lumbar vertebrae, a condition also found in *Wiedomys*. Among the 23 *Rhipidomys* specimens he examined, counts of both 13+6 and 12+7 occurred in roughly equal proportions; unfortunately, the samples of each species were too small to show whether or not the differing counts might cross taxonomic boundaries. The number of caudal vertebrae in *Rhipidomys* ranged from 35 to 42, similar to that in *Thomasomys* (35-43) and *Wiedomys* (39) and rather greater than in *Delomys* (*c.* 30); most oryzomyines had 27-35, a few reaching 39 or 40.

Gall bladder. Voss (1991: table 4) investigated the occurrence of a gall bladder in 354 specimens representing 90 species in 47 genera and subgenera of Sigmodontinae. Amongst these were samples from five species of *Rhipidomys* (two specimens of *R. "couesi"* [= *Rhipidomys* sp.] from Chijchipani, Bolivia; three *R. fulviventer* from Buena Vista, Venezuela; one *R. leucodactylus* from Huanhuachayo, Peru; ten *R. macconnelli* from Cerro Roraima, Venezuela; and eight *R. "mastacalis"* [= *R. nitela*] from San Ignacio Yuruaní, Venezuela). In all 24 of these specimens the gall bladder was absent. In contrast, it was present in all the other thomasomyines dissected (40 specimens in total from *Aepeomys lugens, Chilomys instans, Delomys dorsalis* and eight species of *Thomasomys*), whereas it was consistently absent in all 30 oryzomyine species investigated. The only other taxa in which the gall bladder was found to be absent were *Akodon cursor* (but not congeneric species), *Lenoxus apicalis* and the species of *Ichthyomys*. Such a pattern of presence and absence constitutes strong, albeit not conclusive evidence for the unity and distinctness of *Rhipidomys* as a genus vis-à-vis *Thomasomys* and the other plesiomorphic genera.

Glans penis and baculum. Hooper and Musser (1964) described and illustrated the phallic morphology of one specimen of *Rhipidomys "mastacalis"* (in fact *R. macrurus*, AM-CA 2655, now AMNH 202655, from Anápolis, Goiás, Brazil). They concluded that with its

three-pronged baculum it evidently belonged to the main Neotropical complex-penis group, and was morphologically closest to the two other thomasomyines examined, *Thomasomys aureus* and *T. laniger*.

5.5   Phylogenetic analyses

Voss (1993) compared *Delomys* with the type species of *Thomasomys* and *Oryzomys* over the following 18 morphological characters: ungual tufts (claw vibrissae), plantar pads, mammae, rostral tube, zygomatic notch, interorbital shape, palate length, sphenopalatine vacuities, alisphenoid strut, carotid circulation, tegmen tympani, capsular process of lower incisor alveolus, incisor size and angle, molar design (lophodonty), anteromedian flexus, ectolophid, number of ribs, gall bladder. By means of outgroup comparisons he determined hypothetical primitive states for the Sigmodontinae for all but two of these. *Thomasomys cinereus* exhibited the primitive state for all 16 polarized characters, whereas *Oryzomys palustris* had derived states for 14 of them. Of the five apomorphies of *Delomys*, two were exclusive, one occurred in only one of its two species, and the other two were states that had arisen several times among Neotropical rodents, including *Oryzomys palustris*. There was thus no conclusive evidence for a close relationship between any of the three taxa.

Although these characters were originally selected to distinguish *Delomys* from the other two taxa (hence the inclusion of unusual characters for which *Delomys* is apomorphic, such as "rostral tube"), they also serve to show how plesiomorphic *Rhipidomys* is in most of these aspects. Derived states occur in only four characters: convergent interorbit, reduced stapedial circulation, twelve ribs and absence of gall bladder. Both primitive and derived states of carotid circulation and rib number are found within *Rhipidomys*; for the former character the distribution of states follows species groups, whereas this is not clear for the latter (see discussion above). These four derived states also occur in *Oryzomys palustris* but not in *Thomasomys cinereus* or *Delomys*. The apomorphies exhibited by *Rhipidomys* also appear in other genera within the Sigmodontinae: for example, many phyllotines have a convergent interorbit; the stapedial circulation is reduced in *Ichthyomys* (Voss, 1988: 298); vertebral counts were discussed above; and a gall bladder is absent in *Ichthyomys* and *Lenoxus* (Voss, 1991, table 4). In view of such a distribution and given the wholly plesiomorphic states exhibited by

Thomasomys cinereus, these characters provide little evidence for the common ancestry of *Rhipidomys* with *Oryzomys*, *Delomys* or *Thomasomys* to the exclusion of the others.

In Steppan's (1995) phylogenetic analysis of 29 species of Sigmodontinae plus 11 outgroup taxa, mentioned previously, *Rhipidomys* was represented by *R. latimanus*. Of the 34 characters for which *R. latimanus* was coded, the only ones that clearly separated this species from the three *Thomasomys* (*aureus, baeops* and *rhoadsi*) were the presence of a distinct supraorbital shelf, the absence of a gall bladder and the lack of a supertrochlear foramen in the humerus (the last character state was unique amongst the Sigmodontinae surveyed). Consequently, in the resulting cladogram *R. latimanus* was placed as the sister taxon to *T. aureus* and *T. baeops* in a basal branch of the Sigmodontinae clade. Had more of the characters discussed above been included, however, such a close association might not have occurred.

CHAPTER 6 - DIVERSITY WITHIN *RHIPIDOMYS*

6.1 Primary division of the genus

Although superficial examination reveals that there is considerable morphological diversity within *Rhipidomys*, very few characters have discrete states that differ consistently between populations. As a result, species boundaries must often be based on continuously varying characters such as size, shape and colour. With little apparent sympatry in the genus to aid in defining species, the assessment of what constitutes a taxonomically important character as against mere geographical variation is bound to be subjective to a large degree. In addition, there is much variation that appears to occur sporadically at an individual level, but which is difficult to evaluate with the small available samples. The shortage of consistent characters and the uncertain polarities and possible homoplasy in those that exist preclude a rigorous phylogenetic analysis of species relationships within the genus.

The two carotid circulatory patterns described in the previous chapter are an exception in that they discriminate with 100% consistency between different populations of *Rhipidomys*. Taxa displaying the primitive pattern include *R. fulviventer* and its allies; they are restricted to the montane forests of the Andes, Venezuelan coastal range and Guiana Highlands. Of course, joint possession of a plesiomorphic character state does not imply that all members of the group form a monophyletic entity, although that may be the case. Of the species which show the derived carotid morphology, *R. caucensis* shares most other characteristics with the *R. fulviventer* group and for practical purposes will be included in the same section in the following discussion and in the taxonomic synthesis of chapter 7. *R. macconnelli* possesses a number of highly distinctive external features and will be treated as a separate section of the genus; it occurs only on the Guiana shield *tepuyes* or table mountains. The remaining species make up the largest and most diverse division, referred to here for convenience as the *R. leucodactylus* section after the type species of the genus. They are found mainly at lower elevations from eastern Panama and Trinidad to northern Argentina and southeastern Brazil.

The distribution of certain other character states is at least partly congruent with the carotid circulation patterns. Details of these and other characters serving to distinguish between the three main sections of the genus follow.

Cranial. Skulls in the *R. fulviventer* group (including *R. caucensis*) have a broader and

more rounded appearance than similarly sized skulls with the derived circulation. Their supraorbital ridges are less pronounced, giving a more hourglass-shaped interorbital region with less angular edges, and the extensions of the ridges onto the parietals are weaker and tend to curve around the braincase rather than cut straight across it. The exoccipital breadth of the braincase appears greater; quantification, however, is not feasible because skull conformation and individual variation in suture position makes it difficult to select suitable homologous endpoints for measurement.

Dental. The first upper molar in the *R. fulviventer* group generally lacks a protoloph and protostyle, whereas the latter at least is commonly present in other taxa of the genus. *R. macconnelli* teeth are distinguished by the lack of a transverse lophid in the procingulid of m1 (see Fig. 5.4), a condition rarely found in other *Rhipidomys* taxa.

External. Rhipidomys macconnelli differs from the other sections of the genus and resembles certain *Thomasomys* species in a suite of external characteristics correlated with its more terrestrial habits. Its dorsal pelage is a dark chocolate brown, seldom as bright orange-brown as many members of the *R. fulviventer* section and never yellowish agouti as in many of the *R. leucodactylus* group. Ventrally the cream or pale brown hair tips are too short to obscure their long, dark slate bases, which are evident even when the fur is not ruffled. The tail in *R. macconnelli* is bicoloured - paler underneath from the base almost to the tip; some individuals in other species (especially in the *R. fulviventer* group) may have a lighter area ventrally near the base of the tail, but most of the shaft is one colour. *R. macconnelli* has a longer, narrower hind foot, less specialized for climbing; whereas the digits are similar in length to those of other *Rhipidomys* species of its size, the metatarsals are much longer. Its heels and wrists are bare, in contrast with the remaining species, in which they are well furred, and the dark foot patch is indistinct and poorly delimited. It shares dark ear pinnae with taxa in the *R. fulviventer* group. In the latter group, the ears are on average darker than the dorsal fur; in the *R. leucodactylus* group the ears are generally similar in tone to, or even rather lighter than, the dorsal pelage.

The juvenile pelage of *R. fulviventer* group species (excluding that of *R. ochrogaster*, which is unknown) differs from that of other young *Rhipidomys*. Whereas the latter have a grey, rather woolly coat resembling that found in many juvenile small mammals, pelage in the young of the *R. fulviventer* group is a little less brightly pigmented than that of adults but similar to it in texture.

Pelage length and ventral colour may help distinguish between sections of the genus but they are not fully diagnostic. Members of the *R. fulviventer* group and *R. macconnelli* have long, soft fur, which is associated with long, slate-coloured hair bases on the ventral surface as well as the dorsal. This character reflects environmental conditions at the higher altitudes occupied by these animals and is therefore also found in the few other *Rhipidomys* that occur in similar habitats (e.g., certain populations of *R. nitela*). Some, but not all, specimens of the *R. fulviventer* group and *R. macconnelli* display an orange wash over the whole ventral surface through pigmentation of the otherwise white or creamy hair tips; hence the specific epithets *fulviventer* and *ochrogaster*, both meaning "tawny belly". Against the darker background colour of *R. macconnelli* the impression given by the orange wash is more a pale brown. In specimens with such pigmentation the lateral dividing line between dorsal and ventral pelage becomes blurred. Orange hair tips on the ventral surface may occasionally be found in the *Rhipidomys leucodactylus* section, but they are nearly always restricted to certain parts of the venter and are not generalized.

6.2   The Rhipidomys fulviventer *section*

Of the *Rhipidomys* specimens examined, those qualifying for inclusion in this group on the basis of their primitive carotid circulation pattern were first sorted by size and geographical origin into "populations". The very smallest specimens (the "wetzeli" size class) represented three populations from the highlands of southern and eastern Venezuela: Cerro Neblina, Cerro Duida, and NE Bolívar state (Km 125 and Churi-tepui). Small forms ("elatturus" size class) came from the Venezuelan coastal range (states of Sucre and Monagas) and the Eastern Cordillera (Páramo de Tamá on the Venezuelan-Colombian border), while medium-sized specimens ("fulviventer") were found in the Eastern Cordillera in Cundinamarca, Colombia. Moderately large specimens ("venustus") occurred in two populations in Venezuela (in the coastal range near Caracas, and the Mérida/Trujillo Andes) and three in Colombia (the Serranía de la Macarena, an isolated tableland close to the eastern Andean foothills; southern Huila, Central Cordillera; and Cauca, Western Cordillera). By far the largest specimens ("ochrogaster") were from the upper Inambari region of southeastern Peru.

Morphometric methods were used to address two main questions: 1. Does morphometric evidence reinforce the carotid circulation criterion for group membership;

and 2. Is there a morphometric basis for recognizing separate species within the group? To address the first question, principal components analysis (PCA) was used to compare members of the *R. fulviventer* group with similarly sized adult specimens of the *R. leucodactylus* group, particularly those occurring in the same general area. The condition of similar size was intended to reduce as far as practicable the predominance of size differences in the analyses. Size differences between taxa within the genus are accompanied by allometric changes in the *Rhipidomys* bauplan comparable to those associated with age; such shape changes between size classes are easily observed and measured but would be difficult to segregate in an analysis from age-related changes, given the small population samples available.

Fig. 6.1 - *Rhipidomys* "ochrogaster" and "leucodactylus" from Inka region, Peru: plot of scores on the first two principal component axes.

The first analysis included the specimens in the "ochrogaster" size class together with members of the *R. leucodactylus* group also from Inka region, SE Peru. A plot of

specimen scores on the first two component axes provided complete separation of the two groups (Fig. 6.1; 8-variable analysis). While the first component indicated negative general size, the second contrasted rostral breadth (large positive loading) with molar row length, braincase breadth and interorbital breadth (large negative loadings). The "ochrogaster" specimens therefore had a combination of narrower rostrum, broader cranium and/or larger molars than the others for a given skull size.
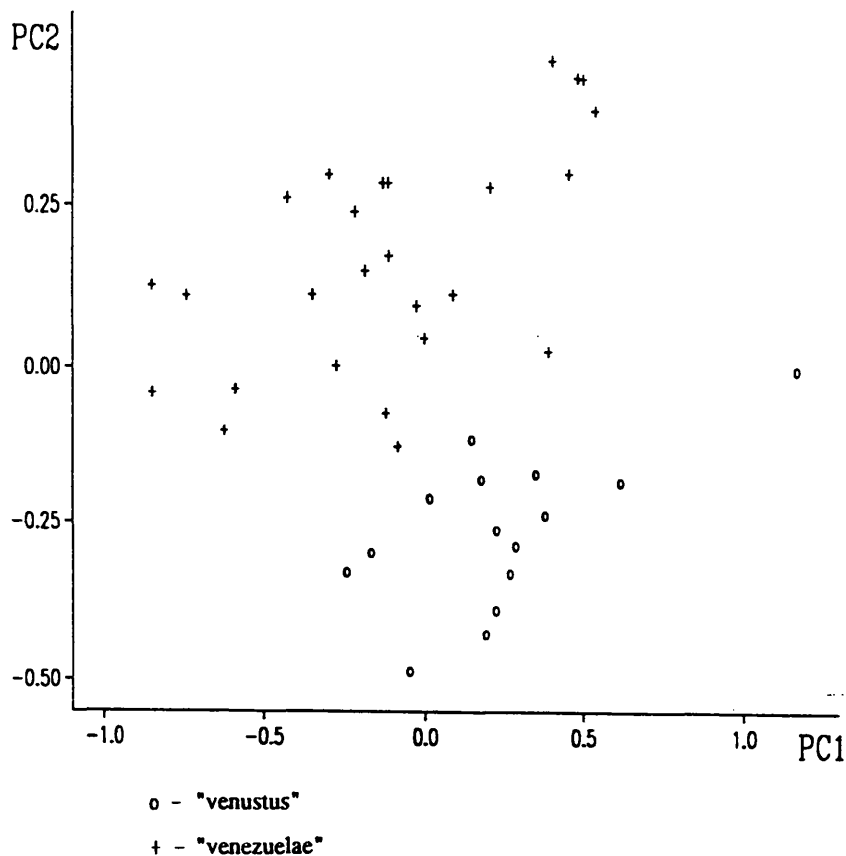
Fig. 6.2 - *Rhipidomys* "venustus" and "venezuelae" from N and NW Venezuela: plot of scores on the first two principal component axes.

Next, populations of *R. fulviventer* in the "venustus" size class from Venezuela (Mérida Andes and northern coastal range) were analysed together with specimens provisionally identified as "venezuelae" from approximately the same areas. In order to prevent the variation from the numerically far larger "venezuelae" set from dominating that originating from the "venustus" specimens, two analyses (based on 15 variables) were performed on the "venustus" material, the first together with the "venezuelae" from

Mérida and the northern coastal states (Falcón to the Federal District), and the second with the series of "venezuelae" from Río Tocuyo. In the first case, a plot of specimen scores for PC2 against PC1 showed two adjacent, roughly parallel clusters with no actual overlap (Fig. 6.2). The axis of separation between the two species was almost parallel to the second component axis, with "venustus" scoring lower on PC2; only two "venustus" scores overlapped the range of the "venezuelae" scores on this component. The corresponding latent vector, which accounted for 18% of the total variation, revealed large positive loadings for PBL, IOB, ZPL and MMR, and large negative ones for BCB, PB1, NL, BW and SH (lists in decreasing order). In the second analysis, most of the separation between the taxa was again expressed in the second component, this time corresponding to over 22% of the total variation; only one "venustus" and one "venezuelae" overlapped in this dimension. In this analysis, the second latent vector had large positive loadings for MRC, MMR, PBL, ZPL and IOB, and moderately large negative loadings for SH, MFB, PB1 and BCB; the scores for "venezuelae" specimens were mostly positive and those for "venustus" all negative.

Thus the results of the two analyses are in good agreement. In comparison with "venezuelae" of the same general size, the "venustus" specimens may be expected to have a broader and deeper braincase, a broad rather than long palate, a narrower interorbit and zygomatic plate, smaller molars, and perhaps longer nasals and broader auditory bullae. The differences between the two species can be appreciated visually, particularly in the broader, more rounded braincase of "venustus" compared with the flatter, longer one of "venezuelae", the narrower interorbit of "venustus", and the short, broad nasals of "venezuelae".

While morphometric analysis showed a clear distinction between members of the R. fulviventer group and "venezuelae" in Venezuela, the picture was less clear with regard to comparisons with specimens provisionally assigned to "latimanus" in Colombia. Specimens of the R. fulviventer group in the "fulviventer" and "venustus" size classes from Cundinamarca, La Macarena, Huila and Cauca were included in a PCA together with specimens of "latimanus" collected on the slopes of the Western Cordillera and upper Cauca valley (Cauca and Valle departments), middle Magdalena valley (Boyacá and Cundinamarca), and the upper Magdalena valley at Pitalito and San Adolfo (Huila). The analysis of 15 variables produced a first "size" component (51% of total variation) with coefficients that were all negative; although most were of similar magnitude the contribution of bullar width was virtually nil and those of PB1 and ZPL were reduced.

As expected, the *R. fulviventer* populations were spread along this axis, with "fulviventer" ranking high (i.e., small) and the "venustus" from Cauca low (large). The remaining specimens lay between these extremes, except for the two "latimanus" from Pitalito which grouped with the "fulviventer". On the second component axis, the specimens from Pitalito and San Adolfo grouped with the "fulviventer" and "venustus" populations, while the other "latimanus" formed a slightly separate cluster towards the positive end of the scale. The variable coefficients forming the second latent vector were large and positive for IOB and large and negative for BW and ZPL. The other components did not help to resolve the overlap any further.

The results were similar when the analysis was expanded to include the "venustus"

circles - R. fulviventer ("venustus" and "fulviventer" size classes)

crosses - R. latimanus (excluding Huila specimens)

asterisks - R. latimanus, Huila specimens
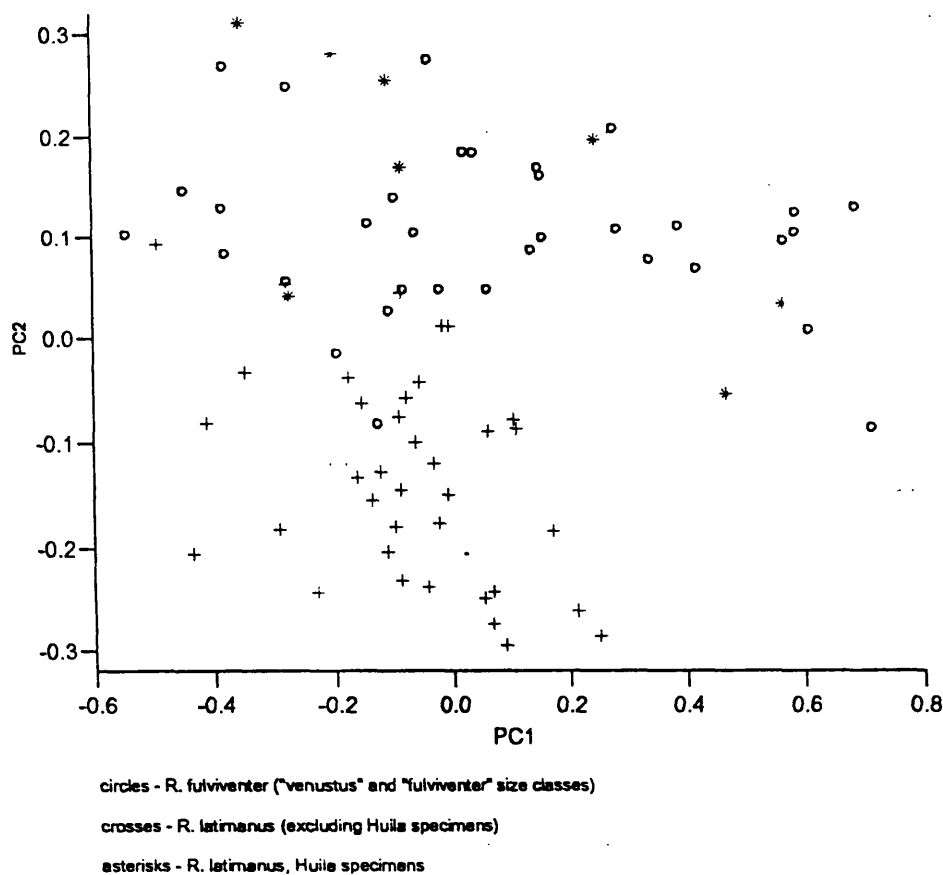
Fig. 6.3 - *Rhipidomys fulviventer* ("fulviventer" and "venustus" size classes, from Colombia and Mérida, Venezuela) and *R. latimanus* (from Ecuador and Colombia): plot of scores on the first two principal component axes.

sample from Mérida and the "latimanus" samples from Antioquia (Colombia) and Ecuador. Again, the second component provided the best segregation, but the "latimanus" specimens from Pitalito and especially San Adolfo remained within the R. fulviventer group cluster (Fig. 6.3). This time, most scores for "latimanus" were negative whereas most scores for specimens of the R. fulviventer group were positive. The second latent vector had large positive loadings for BW and BCB and large negative ones for IOB and PBL, and accounted for 13% of total variation. The results of the two analyses indicated that the R. fulviventer group (and the "latimanus" specimens from San Adolfo and Pitalito) might have larger bullae, narrower interorbit and perhaps broader zygomatic plate and braincase and shorter palate than the remaining "latimanus". Thus in comparison with both "venezuelae" and "latimanus", the R. fulviventer group is characterized by its broader braincase, larger bullae, shorter palate and narrower interorbit.

The anomalous position of the Pitalito and especially the San Adolfo specimens is congruent with the fact that in appearance they resemble "fulviventer" and "venustus" respectively, with their larger bullae, broader braincases and narrower interorbit, with less pronounced supraorbital ridges than other "latimanus". They also have grey-based ventral pelage. However, their derived carotid circulation pattern, shorter tail pencil, shorter pelage, paler ears and the low altitude of their collecting localities (1350-1400 m) are not in keeping with the R. fulviventer group. Perhaps their peculiar skull morphology is due to their rather isolated, cul-de-sac position near the head of the long, narrow Magdalena valley, along which gene flow to and from other populations of "latimanus" must be tenuous.

A PCA was also performed on adult specimens of the small "wetzeli" size class of the primitive carotid circulation group together with similarly sized adult specimens with a derived carotid circulatory pattern, provisionally identified as R. caucensis. These originated from high altitudes in the Colombian departments of Huila (junction of Central and Eastern Cordilleras), Antioquia and Cauca (both Western Cordillera). Only 10 "wetzeli" and 7 R. caucensis qualified for inclusion in the analysis, the results of which must therefore be interpreted with caution owing to the small sample size. In the 15-variable PCA, specimens of R. caucensis showed a broad spread on all components, whereas the "wetzeli" grouping was much more compact on components 1-3. On the first component, scores for five of the seven R. caucensis specimens were negative (larger skull size) whereas those for all but one "wetzeli" were positive (smaller), especially for the Bolívar specimens. In a plot of scores on the first two components (Fig. 6.4), which
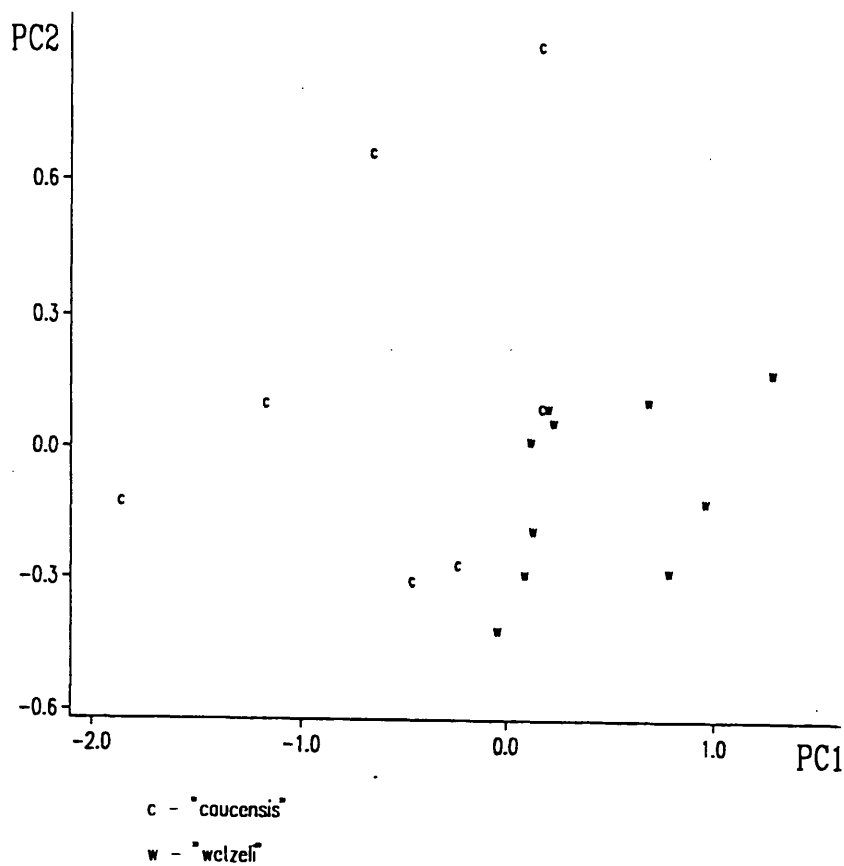
Fig. 6.4 - *Rhipidomys* "wetzeli" and "caucensis" from Venezuela and Colombia: plot of scores on the first two principal component axes.

together expressed nearly 75% of the sample variation, the Cauca specimens lay close to the "wetzeli" cluster, while the other four *R. caucensis* lay some distance away in a line roughly parallel to the main axis of the cluster. None of the other components provided any separation congruent with the population distribution. One noteworthy result was the very close correspondence in scores on components 1 to 5 between the "wetzeli" specimen from Cerro Duida (USNM 406111) and a *R. caucensis* from Cauca (AMNH 32572). Thus in skull morphometrics "wetzeli" and *R. caucensis* specimens appear to be very similar, despite their differing carotid circulatory patterns. In external measurements, however, the longer tail of "wetzeli" helps to distinguish between the two forms (adult tail length in "wetzeli": mean 134.9 mm, s.d. 7.6, range 120-148 mm, $n = 14$; in *R. caucensis*: mean 122.4 mm, s.d. 9.9, range 106-133 mm, $n = 7$; Student's $t = 3.222$, significant at $p = 0.01$).

Another PCA was performed on *R. caucensis* and "latimanus" specimens from regions where the two forms occur in near sympatry: Cauca, Antioquia and Huila departments, Colombia. The first component (general size, accounting for 63% of total variation) was the most efficient at segregating the taxa, but the relatively large *R. caucensis* specimen from Huila (FMNH 71736) and the two small "latimanus" from nearby Pitalito had similar scores on this axis. In a plot of PC2 against PC1, the Huila *R. caucensis* specimen was roughly equidistant between other *R. caucensis* and the "latimanus" from San Adolfo, Huila; the latter were distinguished on the second axis from the other "latimanus" in the analysis on account of their narrower interorbit and larger bullae. A plot of PC5 against PC1, however, placed the *R. caucensis* individual firmly with the *R. caucensis* from Antioquia in a group some distance from the Cauca material; the fifth component stressed principally the greater depth of the mandibular ramus in the former group compared with the latter.

The working division of the *R. fulviventer* group into the size classes discussed above is intended only as a rough guide and is based on the mean general skin/skull dimensions for each population. Although the size range of the individuals in a population of one class may to some extent overlap the range found in the next larger or smaller class, the available data suggest that there is no sympatry of different size classes, such as might be indicated by bimodality in specimen size within one "population". Specimen AMNH 14737 (holotype of *Oryzomys tenuicauda* J. A. Allen, from Sucre state, Venezuela), which is the size of a small "wetzeli", might appear to be an exception; its molar row length, however, a relatively invariant character within a population, is greater than that of any "wetzeli" and matches that of the surrounding population of the "elatturus" size class, to which it can be assigned as a statistical outlier. Therefore, without any sympatry to indicate the existence of separate gene pools, some or all of these geographically separate populations may be considered potentially conspecific. The enormous size difference between "wetzeli" and "ochrogaster" (adult "wetzeli" head-and-body length ranges from 92 to 112 mm, $n = 14$; "ochrogaster" HB = 154 to 176 mm, $n = 4$) makes it most unlikely that these extreme groups should belong together in the same species. But the apparently random alternation of rather small ("elatturus"), medium ("fulviventer") and moderately large ("venustus") size classes along the Andean chain from eastern Venezuela to southern Colombia is suggestive of locally differentiating populations belonging to a single species or superspecies.

To answer the question of how many species might be recognized within the *R.*

PC2

0.1

0.0

-0.1

-0.2

-0.8   -0.4   0.0   0.4   0.8 PC1

Es – ˈelatturusˈ (Sucre)   Vl – ˈvenustusˈ (La Macarena)
El – ˈelatturusˈ (Tamá)   Vm – ˈvenustusˈ (Mérida)
F – ˈfulviventerˈ (Cundinamarca) Vs – ˈvenustusˈ (Cauca)
O – ˈochrogasterˈ (SE Peru)   Wb – ˈwetzeliˈ (Bolívar)
Vc – ˈvenustusˈ (Caracas)   Wd – ˈwetzeliˈ (Co. Duida)
Vh – ˈvenustusˈ (Huila)   Wn – ˈwetzeliˈ (Co. Neblina)
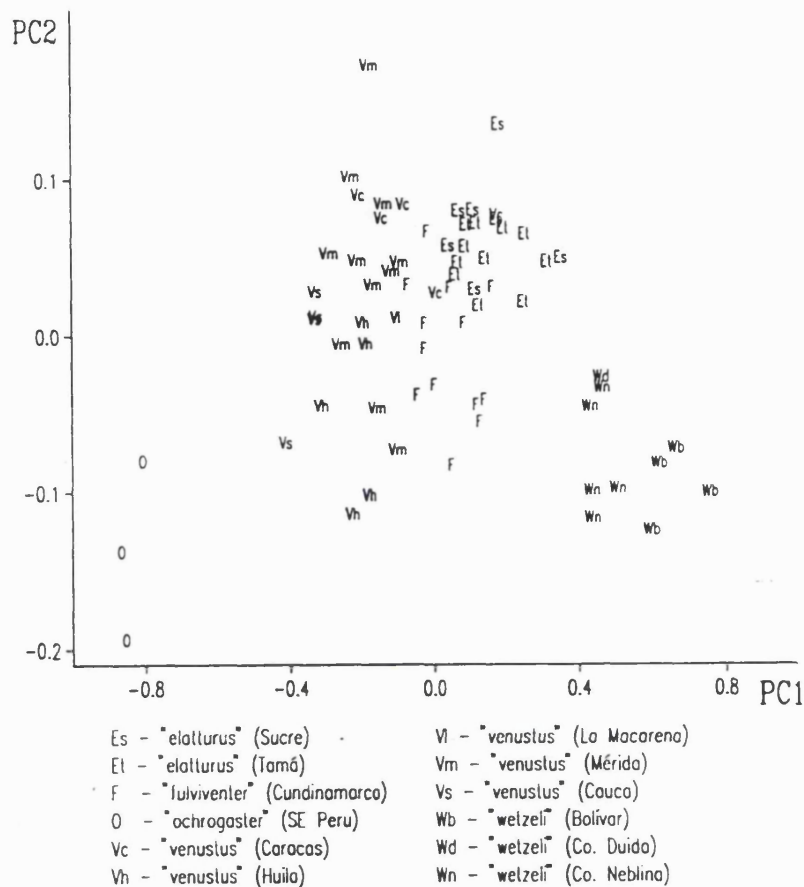
Fig. 6.5 - The *Rhipidomys fulviventer* group: plot of scores on the first two component axes (8-variable analysis).

fulviventer group, principal components analyses were performed that included all specimens with the primitive carotid circulation pattern, using the 8-variable and 15-variable data sets. Similar results were obtained from both. Three main clusters were apparent in a plot of scores on the first two component axes (Fig. 6.5; 8-variable set). With coefficients that were all negative and very similar in value, the first component (PC1) may be interpreted as a general size factor. Cluster separation was essentially along this first axis. The smallest and most isolated cluster consisted of the three "ochrogaster", arranged at the negative (large-size) end of the axis. At the opposite end were all ten "wetzeli", in a distinct but not so distantly isolated group. The remaining specimens formed a large array in the middle, with those in the "venustus", "fulviventer" and "elatturus" size classes occupying slightly overlapping sub-areas. Of these, nearly all the "venustus", particularly the Cauca population, were more negative on PC1 (i.e., larger)

99

than the others. The mean size difference between "fulviventer" and "elatturus" was much smaller, as reflected by their considerable overlap on PC1, but the "elatturus" were partially sorted from the "fulviventer" along PC2. In fact, in the 8-variable analysis, PC2 provided partial sorting of all Venezuelan populations (two of "elatturus" and two of "venustus") from the Colombian (the "fulviventer" and three of "venustus"). The corresponding second latent vector consisted mainly of a contrast between IOB (negative) and TFL and PL (positive); most Venezuelan specimens scored higher than most Colombian, indicating a narrower interorbit relative to skull length for the former. In the second vector for the 15-variable analysis, MFB and NL (negative) contrasted with BW, PB1 and IOB; this time "elatturus" scored low, indicating a relatively broad mesopterygoid fossa and long rostrum compared with narrow bulla, palate and interorbit. The remaining components did not offer any further grounds for sorting populations. Similar results were obtained from a PCA in which "ochrogaster" and "wetzeli" were excluded.

The fact that "venustus", "fulviventer" and "elatturus" lie in adjacent regions within the same cluster on PC1 merely reflects their provisional identification on the basis of size, whereas the separation on PC2 is at best partial and can be attributed to geographical variation. Thus PCA provides no compelling evidence in favour of species-level taxonomic separation of these populations. Without prior identification based on size and origin there would be no reason to divide the cluster in such a way. In the absence of any sympatry, these populations may be considered to form a single morphospecies. Given their differences in size and other characters and their circumscribed ranges (see species accounts in chapter 7), the populations may be regarded as subspecies with the following names: R. fulviventer tenuicauda (J. A. Allen, 1899) for the Sucre/Monagas population; R. f. venustus Thomas, 1900, for the specimens from the Mérida/Trujillo Andes; R. f. elatturus Osgood, 1914, for those from Páramo de Tamá; R. f. fulviventer Thomas, 1896, for the population in Cundinamarca; and R. f. similis J. A. Allen, 1912, for the Western Cordillera form in Cauca; the populations in the Caracas region (R. f. ssp. 1), La Macarena (R. f. ssp. 2) and southern Huila (R. f. ssp. 3) will be formally named in a forthcoming publication (Tribe, in prep.).

In contrast, the largest and smallest members of the primitive carotid circulation group are morphometrically separate from the central complex and may be given species status as R. ochrogaster and R. wetzeli, respectively, at least until such time as any newly-discovered intermediate populations should force a reassessment of their position.

Lastly, despite its morphometric proximity to *R. wetzeli*, *R. caucensis* deserves recognition as a separate species on the basis of its derived carotid circulatory pattern. It is included in the *R. fulviventer* group here on account of its similarity in most other characters. One might speculate either that *R. caucensis* acquired a derived circulatory pattern independently of other *Rhipidomys*, or that this species is an offshoot from near the base of the derived lineage, which had its origin in a *wetzeli*-like ancestor.

The scenario of temperature depression and aridity during glacial maxima, as outlined in chapter 2, may account for the present-day disjunct distribution of the component taxa in the *R. fulviventer* section. With its closest relatives restricted to the cloud forests of the northern Andes and the Venezuelan coastal range, the ancestors of *Rhipidomys wetzeli* are likely to have spread from there to the Guiana Highlands when a cooler climate allowed montane-type forests to thrive at lower elevations. This dispersal must have taken place around the ends of the sand desert occupying the Orinoco plains, either from the region of southeastern Colombia via gallery forests across the savannas that covered northwestern Amazonia, or by a northeastern route by way of forests in the Orinoco delta area. The disappearance of such an ecological bridge subsequently allowed a small endemic fauna of mammals to evolve in isolation in the Guiana Highlands. Eisenberg and Redford (1979) claimed there were 14 endemic species but did not identify them. Applying perhaps more rigorous criteria as regards the limits of the region, Gardner (1989) mentioned only the following endemic taxa, two of which he described as new: the genus *Podoxymys*, a rodent, with its single species *P. roraimae*; the species *Marmosa tyleriana* (marsupial), *Vampyrops aurarius* (bat), *Rhipidomys macconnelli*, *Rhipidomys wetzeli* and possibly *Neusticomys venezuelae* (rodents), and the subspecies *Didelphis albiventris imperfecta* and *Marmosops impavidus neblina* (marsupials).

The geologically ancient Guiana Highlands are greatly eroded and dissected, with the result that they are covered by a complex mosaic of vegetation types (Huber, 1986). Forests lying at suitable altitudes for *R. wetzeli* (specimens have been taken at 1800-2000 m on Neblina, 1400 m on Duida, 1032 m at Km 125, and c. 1500 m on Churi-tepui) are now scattered discontinuously over numerous isolated massifs, many still poorly known. This has led to some local differentiation in the species: although the available samples of adult individuals are very small, specimens from eastern Bolívar state (Km 125 and Churi-tepui) average slightly smaller than those 500 km or more to the southwest in Territorio Federal Amazonas (Mount Neblina, the type locality, and Mount Duida). Information on habitats at Duida (Cabecera del Caño Culebra) and Km 125 indicates

moist, dense, high evergreen forest that was undisturbed at the time of collecting; all *R. wetzeli* specimens were captured on fallen logs only a few feet above ground level, and they accounted for only 0.6% and 1.3% of the mammals taken at these two localities, respectively (Handley 1976; treated as "*R. fulviventer*"). Had traps been set higher in the canopy, perhaps more *R. wetzeli* would have been captured.

Separated by the llanos from *R. wetzeli*, *R. fulviventer* occupies the Andes and coastal mountains from southern Colombia to northeastern Venezuela. Given the relatively high altitudes at which it is found (mostly above 2000 m, but only 1000-1800 m in Sucre/Monagas), the variation between its populations may similarly be attributed to a scenario of regional isolation, as suitable habitat, once continuous at lower altitudes, retreated upwards with the warming of the climate. In the extreme northeast of the species range, the small-bodied *R. f. tenuicauda* forms a discrete, isolated unit in the highlands of Sucre and Monagas around Cerro Turumiquire and Caripe. Over 200 km of land below 1000 m (much of it below 100 m) separates this region from the central coastal range, where the next subspecies in the chain, *R. f.* ssp. 1, is a form of the "venustus" size class. This population has been found only in a small area in the mountains near Caracas and is apparently unknown from the adjoining Aragua highlands.

From here it is a distance of 200-300 km west-southwest, across the lowland Yaracuy forests and the dry hills of Lara state, to the Mérida-Trujillo Andes, where the next suitable habitat is found. Here, the moderately large *R. f. venustus* until historical times had a potentially more extensive range than the previous two subspecies, but deforestation has occurred on a large scale. In 1966 the Smithsonian Venezuelan Project (SVP) collecting locality at Hacienda Misisí was in perhaps the last remaining block of primary cloud forest in the state of Trujillo (Handley, 1976). Some forests remain in the state of Mérida, but they are increasingly disturbed. How far to the southwest this population extends is unknown, but it is most unlikely to descend into the hot, dry valleys between San Cristóbal (Venezuela) and Cúcuta (Colombia).

These valleys separate the Mérida Andes from the Páramo de Tamá, a high, eastwardly projecting spur of the Eastern Cordillera, where the smaller *R. f. elatturus* occurs. A single individual collected at Cachirí (CM 3192), at the same latitude but about 100 km away on the western side of the Cordillera, is morphologically similar to these and probably belongs to the same population. Whether there is continuity between this population and *R. f. fulviventer* in the Colombian department of Cundinamarca, 300 km to the south, is unknown. The clear morphological differences between the two

populations, as documented above, indicate that they should be treated as separate forms, but sampling from the intervening area is required to confirm their status.

Only some 30 km of lowland separates the probable range of *R. f. fulviventer* in the Eastern Cordillera of Cundinamarca from the Serranía de la Macarena, an isolated tableland in the eastern plains which is geologically similar to the tepuyes of Venezuela. The single specimen known from there (AMNH 142140) is of the "venustus" size class and distinct from the form in the high Cordillera, and is thus placed in a subspecies of its own (*R. f.* ssp. 2). The Eastern Cordillera is unlikely to provide continuously suitable habitat for *R. fulviventer* throughout the 300-400 km from Cundinamarca southwestwards to its junction with the Central Cordillera, although isolated populations may yet be found in the higher parts. The next known population is the unnamed form (*R. f.* ssp. 3) collected from the mountains at the head of the Magdalena Valley in southern Huila; its range may prove to extend considerably further north along the Central Cordillera, and possibly south into the department of Nariño. Finally, isolated in the Western Cordillera by the Cauca-Patía valley, *R. f. similis* consists of the largest specimens of the "venustus" size class, collected only in the departments of Cauca and Valle. Whether *R. fulviventer* occurs in other parts of the Western Cordillera is not known; it did not appear in the collections made by Hershkovitz further north at Páramo Frontino (Antioquia department), where he did find *R. caucensis*, a species sympatric with *R. fulviventer* in Cauca and Huila.

Throughout its range, *R. fulviventer* is found in evergreen, humid forests at moderately high altitudes, including cloud forests that occur a little below the tree line. It does not enter areas of true páramo vegetation, although it may venture into the forest-páramo ecotone (Aagard, 1982; Montenegro-Díaz et al., 1991). SVP specimens from the Mérida-Trujillo Andes and northern coastal range (*n* = 52) were collected in cloud forests (55%), evergreen forests (40%), and orchards (5%); most (68%) were found in trees and vines, a few (5%) in houses, and the remainder under bushes, on rock ledges and in a log (Handley, 1976; all identified as *"R. venustus"*). Near Mérida, Aagard (1982) found the species to be predominantly arboreal, with 80% of captures in trees; it was more likely to come down to the ground in the wetter forests at higher altitudes.

In the eastern coastal range in the Venezuelan states of Sucre and Monagas, the vegetation zones and their characteristic faunas lie at substantially lower altitudes than further west (Chapman, 1925). *R. f. tenuicauda* was taken here at only about 950 m (3100 ft) at El Latal, an area of coffee and cacao plantations among the northern foothills

of Mt Turumiquire, and at 1700 m (5600 ft) at Carapas, to the east of the peak in an area of subtropical forest and coffee groves (Tate, 1931). At San Agustín, near Caripe (Monagas), specimens were taken between 1160 and 1340 m (Handley, 1976). The other Venezuelan subspecies were trapped at altitudes between 2095 and 3160 m. Some specimens collected by Salomón Briceño Gabaldón and sons in the Mérida region in the 1890s and 1900s have lower elevations written on their labels, but the Briceños' estimates of altitudes outside the city were often patently inaccurate and the reliability of these labels is therefore doubtful.

In Colombia, most specimens of *R. fulviventer* have been caught in mountain forests above 2000 m, with certain exceptions. One from La Aguadita in Cundinamarca, on the western slopes of the Eastern Cordillera (BMNH 15.1.3.3) was taken at 1800 m. The altitude at which the specimen from the Serranía de la Macarena was collected (by James Dillon in 1942) is of interest: the skin label has "1140" without indication of feet or metres, whereas the skull has "300 m". An altitude of 1140 m would be very low for a member of the *R. fulviventer* group (only one record from Sucre is lower), but 1140 ft (347 m) would be not only extraordinary but also below the altitude of the bridge of land connecting La Macarena to the Cordillera. It would thus beg the question of why no other *R. fulviventer* specimens have ever been collected in lowland forests along the foot of the Cordillera or elsewhere, and would render an hypothesis of regional isolation untenable. I prefer, therefore, to assume the height of "1140" was in metres and to doubt the validity of the data associated with the skull.

In southern Huila, at Río Aguas Claras, near San Adolfo, one specimen of *R. fulviventer* ssp. 3 (FMNH 71712) was caught at 1600 m. Since this is just 200 m above the point where the lowland species *R. latimanus* was found, it indicates the parapatric nature of the distribution of these two species: they may be found in close proximity but they apparently do not occupy the same altitudinal zones. *R. caucensis*, however, is found in true sympatry with *R. fulviventer* in southern Huila and Cauca departments. In Cauca (Western Cordillera), *R. fulviventer similis* was collected at 2400 m on the eastern side of Cerro Munchique, but at elevations as low as 1220 and 1830 m (4000 and 6000 ft) at Cocal, on the western slopes of the cordillera. *R. caucensis* was found at similar altitudes: on Cerro Munchique at 2537 m (8325 ft) and at Cocal at 1830 m. Surprisingly, *R. latimanus* was taken at between 1500 and 2000 m near Munchique (Sabanetas, Charguayaco), at 1220 m at Cocal, and at 1800 m further north at Peñas Blancas in the department of Valle. The overlap between *R. latimanus* and the two highland species,

however, is not as great as it might seem. The climate of the western slopes is much colder and more humid than at equivalent elevations on the eastern slope, and the cloud forest extends down to lower levels (Michael Alberico, personal communication). Thus each species occurs at higher altitudes on the eastern slope than on the western; if each versant is taken separately there is no overlap, except for the co-occurrence of *R. f. similis* and *R. latimanus* at 1220 m at Cocal. There is a possibility that this remarkably low altitude for a *R. fulviventer* is an error: certain upper montane birds from the same collection labelled as having been taken at that altitude were in fact stated by Leo Miller, the collector, to have been caught on the trail some distance above the settlement (Chapman, 1917: 31, footnote 2). Perhaps the same is true for *R. f. similis*.

In some parts of its range, *Rhipidomys fulviventer* is apparently rather scarce. It represented only a small proportion (less than 4%) of the total number of mammals collected by the SVP at San Agustín (Monagas), Pico Avila (near Caracas), and Tabay (Mérida), but 13% at Buena Vista (Páramo de Tamá) and 17% at Hacienda Misisí (Trujillo). In Aagard's study close to Tabay, however, *R. f. venustus* made up nearly 10% of the total number of non-flying small mammals captured in forest and páramo locations, or nearly 15% if only forest mammals were counted; wet-season abundance per 1000 trap-nights was 1.5-1.6 in forest areas, as against 0.8 for the SVP collection from the same locality (Aagard, 1982). Similarly, in a capture/mark/recapture study of non-volant small mammals at Reserva Biológica Carpanta, Cundinamarca, Colombia, *R. f. fulviventer* (reported as *R. latimanus*) represented 16% of all individuals taken - an abundance of 2.9 first captures per 1000 trap-nights (López-Arévalo et al., 1993). The variation between these figures may be due to genuine differences in abundance or to a lack of true comparability between studies, each of which has a different emphasis in trapping effort; for example, only Aagard (1982) specified the proportion of traps set above ground (50%, except in páramo), and most SVP collections also included bats.

Although montane forests are found in the Andes of Ecuador and Peru, representatives of the *Rhipidomys fulviventer* group have never been captured in them, despite intensive collecting efforts especially in Ecuador. (Specimens from northern Peru at the Field Museum, reported as *R. fulviventer* by Osgood, 1914b, proved on examination to belong to *Thomasomys notatus*.) A similar discontinuity has been noted in the distribution patterns of birds: Haffer (1986) observed that the avifauna of SW Colombia had little in common with that of W Ecuador or NW Peru.

Only in the Carabaya mountains of extreme SE Peru, nearly 2000 km from

southern Colombia, does the next member of the group occur. H. H. Keays, who collected *R. ochrogaster* here, provides a brief environmental note on its type locality, "Inca Mines" on the Río Inambari: "Our camp is situated in the loop of the Inambary River. The country is very broken, with deep narrow cañons, and is covered with a dense undergrowth of shrubs and vines, with here or there a palmetto or a cedar rising above the surrounding vegetation" (quoted by J. A. Allen, 1900: 219). He gives the altitude as 6000 feet (1830 m); the specimen labels, however, have 6800 feet (2070 m) for the holotype and 4000 feet (1220 m) for the paratype. The only other known specimens are two at the BMNH from "Santo Domingo", presumed to be the same place (Stephens & Traylor, 1983). With its isolated and apparently highly restricted range, the relationship of this much larger species to the rest of the group is difficult to interpret.

6.3 The Rhipidomys macconnelli *section*

Rhipidomys macconnelli is a ubiquitous mouse on the isolated summits of the sandstone *tepuyes* or table mountains of the Guiana Highlands where it inhabits the rocky, often treeless scrubland. It has also been found in the evergreen forests surrounding the mountains, where it occurs principally on the ground and on cliffs at elevations as low as 750 m (Handley, 1976). In his field notes for the Lee Garnett Day Expedition to Roraima in 1927-28, which belong to the Department of Mammalogy library at the American Museum of Natural History, G. H. H. Tate makes the following comments regarding *Rhipidomys macconnelli*:

> "It proved to be the only moderately common mammal that occurs [on Roraima]. [...] this animal, but for its brush-tipped tail, might well be a Thomasomys. Its grey color and long, lax pelage as well as its decidedly terrestrial habits point to that genus. [...] Here in Rondon Woods [6900 feet] it runs deep beneath the rocks and fallen trees and is none too easily captured. It is apparently as secretive as any of the dark colored forest Oryzomys. Again, though, when I trapped out among the bowlders [sic] of the burned hill-side I caught it as much as I used to take Thomasomys baeops in Ecuador" (p. 137).
> "During my stay [at Summit Camp, 8600 feet,] I took between 25 and 30 specimens of the mouse. It occurs amongst the vegetation on the sides of the 'morros' or rocky hillocks that surround the 'amphitheatre' described by Mrs. Clementi. Most frequently, its runways are beneath overhanging rock ledges which are to some extent protected from the excessive humidity of the mountain top, also a few specimens were taken among the sphagnum of the Bonettia swamps. It appears to be very much restricted to the basin close to the 'ledge' by which the

only communication with the outer world can occur. This however may be due to the distribution of the brush vegetation.

"By far the greater part of the interior of the table mountain is bare rock, only a small percentage of it, such as the Great Central Rift and the inclines of the inner Morros like Six Blocks and Cairn Hill, being suitable for and supporting bush. Had I been able to work traplines so far from camp I feel assured that I should have taken both it and the next species [*Podoxymys*]" (p. 155).

The major features distinguishing *Rhipidomys macconnelli* from the other sections of the genus were outlined in chapter 5 and in section 6.1 above, and greater detail is given in the taxonomic synthesis of chapter 7. The conflicting evidence offered by its *Thomasomys*-like external characters and *Rhipidomys*-like cranial morphology led to great uncertainty as regards its generic allocation. Originally described as a *Rhipidomys* by De Winton in 1900, it was seen by Thomas (1906) to be an aberrant form, which he eventually transferred to *Thomasomys* without explanation (Thomas, 1917). This arrangement was accepted for the next forty years, until Hershkovitz summarily transferred it back to its original genus in 1959. The fact that neither Thomas nor Hershkovitz gave details of the reasoning behind his decision indicates perhaps that neither felt that his arguments were conclusive, given the evidence supporting both positions. My view that *macconnelli* should remain as a separate branch within the *Rhipidomys* radiation is based on a belief, perhaps erroneous, that external features are more likely to be environmentally conditioned than are cranial characters. The discovery by Voss (1991) that *R. macconnelli* lacks a gall bladder, in common with other *Rhipidomys* but in contrast with the other thomasomyine species examined, lends support to this position. However, a firm allocation to genus will depend on the accumulation of evidence from other systems, especially molecular, for a wide selection of the species currently included in these genera and in suitable outgroups.

The distinctiveness of *R. macconnelli* was confirmed in a 15-variable principal components analysis on 96 adult specimens provisionally attributed to *R. macconnelli* and *R. nitela* from the states of Bolívar (Venezuela) and Roraima (Brazil). The first latent vector had variable loadings that were all negative, although with some divergence in magnitude. This vector may be interpreted as representing mainly size with a certain shape component, but the fact that it accounted for only 31% of the total variance indicates that in this sample the variation in shape represented by the other components was more important than any variation in size. There was no separation of taxa along the first component axis, but t-tests revealed highly significant ($p < 0.01$) differences in
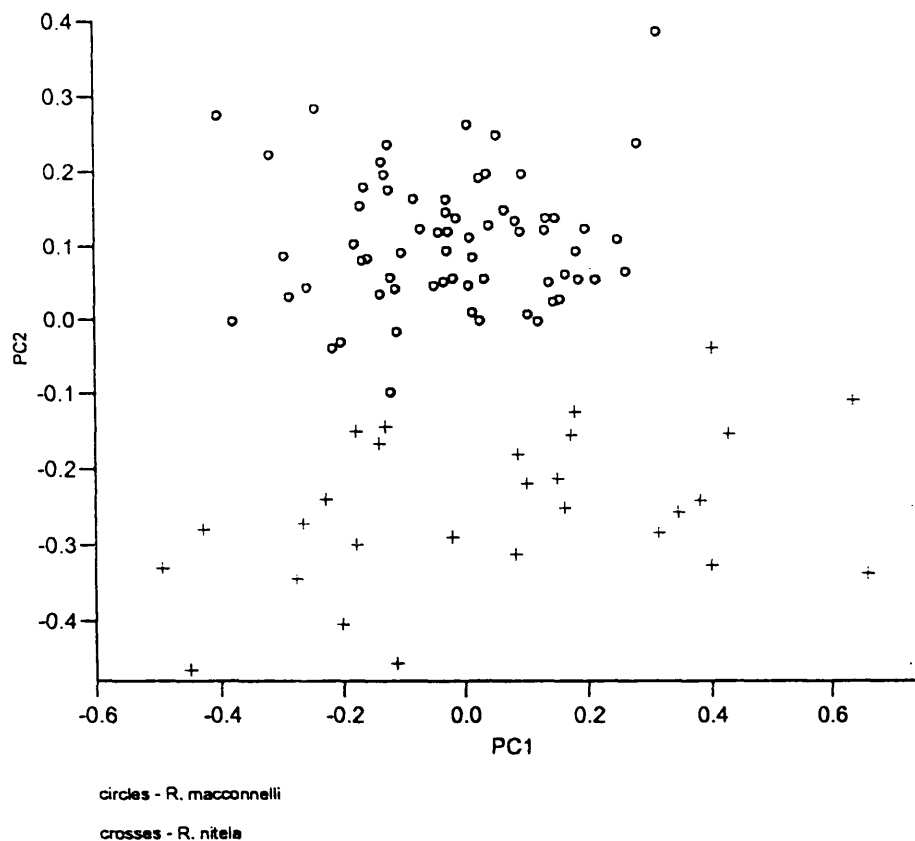
Fig. 6.6 - *Rhipidomys macconnelli* and *R. nitela* from Bolívar (Venezuela) and Roraima (Brazil): plot of scores on the first two principal component axes.

specimen scores between dental age classes 2 and 3 and between classes 2 and 4 (but not between classes 3 and 4 or between the sexes), suggesting that ontogenetic growth was still occurring amongst young adults. In contrast, component 2 provided almost perfect separation between *R. macconnelli* (mostly positive scores) and *R. nitela* (negative scores), as can be appreciated in a plot of scores on the first two component axes (Fig. 6.6). The second component, accounting for 22% of total sample variation, consisted essentially of a contrast of molar row length (upper and lower) plus bullar width and nasal length, against a combination of orbito-temporal fossa length, rostral breadth, palatal bridge length and skull height. *R. macconnelli* might therefore be expected to have larger molars and bullae, a longer and slimmer rostrum, and a shorter interorbital region than *R. nitela*, predictions which are borne out by examination.

Distinctions within *R. macconnelli* are less clearcut. It seems likely that suitable

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habitat is not continuous throughout the species' range and that populations are therefore fragmented to a certain extent. This is reflected in the slight variation in colour between specimens from the four collecting areas from which samples were examined (Mounts Neblina, Duida and Roraima, and northeastern Bolívar state, including Auyán-tepui): Duida specimens are often a little redder and Neblina specimens slightly more olive than the others. Variation also occurs with altitude, dorsal colour often appearing darker and more saturate at higher elevations. Tate (1939) based his subspecies *R. m. subnubis* on a paler specimen originating from the lower slopes of Auyán-tepui at a little over 1000 m, but such variation appears to be stochastic and clinal, precluding taxonomic categorization. In addition, with glossy pelage such as that of *R. macconnelli* it is difficult to assess and compare individuals for the colour factors of hue, saturation and brilliance (Itten, 1973) because they are greatly affected by the quality and especially the angle of the incident light.

A 15-variable PCA was performed on specimens coded for locality and altitude of origin in order to investigate morphometric variation within the species. The first latent vector again represented general size plus a small shape component (variable loadings all negative, but some rather larger than others), accounting for a relatively small proportion (37%) of the total sample variance. The second vector represented a contrast of upper and lower molar lengths (highly positive loadings) against palatal, rostral, interorbital and mesopterygoid fossa breadths (negative loadings). The results of t-tests showed that there were significant differences in the mean scores for DAC 2 and the mean scores for DAC 3 and DAC 4 on both PC1 and PC2, indicating that ontogenetic changes in size and shape occurred between DAC 2 and DAC 3 stages. PC1 scores also showed that Mount Duida specimens were on average slightly larger than the others, although there was considerable overlap, while PC2 showed a partial distinction between specimens from Roraima (higher scores) and those from Neblina (lower scores), with Duida and Bolívar specimens spanning most of the range of both groups.

To test correlations of PC scores with altitude, collection localities were grouped into altitude classes by rounding each altitude to the nearest 100 metres; Spearman's rank correlation was then calculated between the altitude and mean PC scores for each class. Scores for both PC2 and PC3 were significantly correlated with altitude ($p < 0.01$ and $p < 0.05$ respectively, with 22 degrees of freedom), but when the sample was restricted to just Duida specimens significant correlations were found for PC1 and PC2 scores with altitude ($p = 0.001$ and $p < 0.01$, respectively, with 8 d.f.). Correlations with PC1 and

PC2 may, however, be just a reflection of the age-related differences in scores described above, because the two highest altitude classes consisted predominantly of DAC 2 specimens whereas the two lowest altitude classes had more DAC 3 and DAC 4 members. The correlation between PC3 scores (for the whole sample) and altitude cannot be explained thus; since the third latent vector was composed principally of a contrast between length dimensions and breadth dimensions, it indicates that the sampled specimens from higher altitudes tend to be rather shorter and broader than those from lower elevations.

While it is clear that some morphometric differences have evolved between geographically isolated populations of *R. macconnelli*, they are apparently small and do not warrant taxonomic recognition. With regard to altitude of origin, there is no morphometric support for anything other than minor clinal variation.

6.4 The Rhipidomys leucodactylus section

The *R. leucodactylus* group differs somewhat from the preceding sections in the colour and texture of its pelage. Dorsally these animals vary in colour from bright reddish-brown with inconspicuous dark brown guard hairs through yellowish brown strongly flecked with black to a drab grey-brown agouti. The ventral pelage is generally short and often white or off-white to the base, at least on the throat and along the mid-line of the abdomen. When grey hair bases are present ventrally they are rarely conspicuous. Fulvous patches occur in some species but are usually not as intense as in the *R. fulviventer* group and rarely extend beyond the upper thorax or occasionally the inguinal region. In texture the fur may be fine or relatively coarse, and either sleek or slightly woolly. Young individuals have greyer, woollier pelage than adults. Moult patterns sporadically observed in museum specimens suggest that the adult coat appears first on the flanks and sides of the head, spreading thence to the crown, mid-back, upper limbs and venter; juvenile pelage persists longest on the rump and lower limbs and across the shoulders. Ears and tail are generally no darker than the dorsal pelage and often paler, and the tail is not dorso-ventrally bicoloured (except possibly near its root), unlike that of *R. macconnelli*. Hind feet average broader than in either of the preceding sections of the genus.

All members of the *R. leucodactylus* group have a derived carotid circulatory

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pattern, as demonstrated by the minute size of the stapedial foramen in the auditory bulla, the lack of an internal, translucent groove crossing the squamosal and alisphenoid from the bullar region to the orbit, and the lack of a sphenofrontal foramen in the orbit. The edges of the interorbital region are more pronounced than in the R. *fulviventer* group, particularly in adult specimens, and usually form slight ledges or ridges. The braincase tends to be more elongated than in the other sections and in many cases becomes flatter and more angular with age.

Karyotypes. Information on the karyotypes of *Rhipidomys* is sparse but growing steadily (Table 6.1) and is important in distinguishing morphologically similar species. So far, karyological information has become available only for certain members of the R. *leucodactylus* group, and for convenience will be examined here as a whole before the contents of this group are discussed in more detail.

The first published data were for a specimen of R. *latimanus* (USNM 507264) from Peñas Blancas, Valle, Colombia, which had a diploid number (2n) of 44 and a fundamental number (FN) of 48, with both X and Y chromosomes acrocentric (Gardner and Patton, 1976). Similarly, a specimen of R. *leucodactylus* (UFPB 1259) from the Brazilian state of Rondônia in the western Amazon basin also proved to have 2n = 44 and FN = 48 (Zanchin et al., 1992a). Three male and two female R. *leucodactylus* (field numbers J.L.P. 15426, 15683, 15704, 15724 and 15923), collected by J. L. Patton and colleagues along the river Juruá in western Amazonia, had 2n = 44 but only two small pairs of biarmed autosomes, the remainder being uniarmed (J.L. Patton, *in litt.*), equivalent to a fundamental number of 46.

Karyotyped specimens representing other Brazilian species have mostly had the same diploid number (44) but the number of biarmed autosomes has varied considerably. A young *Rhipidomys* sp. (UFPB 345) from southern Espírito Santo state was found to have a fundamental number of 50 (Zanchin et al., 1992a), while a female R. *macrurus* (FMNH 128325) from the Federal District (Granja do Ipê in the Brasília National Park) had a fundamental number of 48, differing from the pattern of the previous specimen in only one pair of autosomes (Svartman and Almeida, 1993). A male karyotype from nearby Águas Emendadas (collection number not published, presumably belonging to the University of Brasília collection) differed from the female's only in that a pericentric inversion in one autosome resulted in FN = 49; the same heterozygosity was found in a female *Rhipidomys* cf. *macrurus* from Casa Grande in São Paulo state (no specimen

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identification given), which also had a slightly different X chromosome morphology (Svartman and Almeida, 1993). A specimen from Mocambinho, in the São Francisco valley in northern Minas Gerais state, had FN = 51 (L. Pessoa, *in litt.*).

A much larger number of biarmed chromosomes resulting in a very different fundamental number - FN = 74 - was apparent in the karyotypes of specimens from Lagoa Santa (the type locality of *R. mastacalis*) and southern Bahia (MNRJ 30033 and UFPB 425, respectively; Zanchin et al., 1992a). These authors also found that a specimen of *R. "cearanus"* (UFPB 947) from Pernambuco, northeastern Brazil, had a similarly high fundamental number, although an exact count was apparently not possible. Interestingly, fundamental numbers of both 50 and 74 have also been found in *Rhipidomys* specimens from Rio de Janeiro state, the first from the foothills of the Órgãos mountains (Garrafão, municipality of Magé: field nos. ORG 32, female, and ORG 40, male) and the second from only 100 km away on the coastal plain (Fazenda União, municipality of Casimiro de Abreu: field no. FU 19, female; all three specimens in the collection of the Department of Ecology, Universidade Federal do Rio de Janeiro - L. Geise, *in litt.*).

Chromosome number and morphology is an important taxonomic tool but must be interpreted with caution. Similar counts can occur in species well differentiated on skin and skull criteria: both *R. latimanus* and *R. leucodactylus* may have $2n = 44$, FN = 48, but they are easily distinguished on the basis of macroscopic characters. Conversely, it is quite possible for slightly different karyotypes to coexist within the same population, so some variation in diploid or fundamental numbers does not necessarily imply the existence of separate species. The occurrence of a heteromorphic pair of autosomes in the specimens from Águas Emendadas, Casa Grande and Mocambinho indicates that fundamental numbers of 48, 49 and 50 must be found in *Rhipidomys* sp. at the first two of these localities and 50, 51 and 52 at the last. One might also conjecture that the single pericentric inversion required to equate the Espírito Santo karyotype with that of Brasília and Casa Grande may exist polymorphically throughout southeastern Brazil. Conversely, the *R. mastacalis* karyotype is much more distinct, requiring pericentric inversions in 14 chromosome pairs to derive its fundamental number of 74 from the Brasília arrangement (Svartman & Almeida, 1993). Given its near-sympatry in Rio de Janeiro state with specimens showing FN = 50, it seems unlikely that the two forms can be conspecific. The significance of these chromosomal differences will become apparent later in the discussion of the *Rhipidomys* taxa of eastern Brazil.

Table 6.1 Summary of karyotype data on Rhipidomys

Species	2n	FN	Locality (with gazetteer reference)	Source
R. latimanus	44	48	Colombia, Valle, Peñas Blancas (156)	Gardner & Patton, 1976
R. leucodactylus	44	48	Brazil, Rondônia, Rio Jamari (22)	Zanchin et al., 1992a
	44	46	Brazil, Amazonas, Rio Juruá (26)	J.L. Patton, in litt.
R. macrurus	44	48	Brazil, Distrito Federal, Granja do Ipê (107)	Svartman & Almeida, 1993
	44	49	Brazil, Distrito Federal, Águas Emendadas (108)	Svartman & Almeida, 1993
cf. macrurus	44	49	Brazil, São Paulo, Casa Grande (83)	Svartman & Almeida, 1993
	44	50	Brazil, Espírito Santo, Monte Verde (77)	Zanchin et al., 1992a
	44	50	Brazil, Rio de Janeiro, Garrafão (80)	L. Geise, in litt.
	44	51	Brazil, Minas Gerais, Mocambinho (104)	L. Pessoa, in litt.
R. mastacalis	44	74	Brazil, Minas Gerais, Lagoa Santa (97)	Zanchin et al., 1992a
	44	74	Brazil, Rio de Janeiro, Casimiro de Abreu (78)	L. Geise, in litt.
R. "mastacalis"	44	74	Brazil, Bahia, Fazenda Unacau (75)	Zanchin et al., 1992a
R. "cearanus"	44	high	Brazil, Pernambuco, Serra dos Cavalos (59)	Zanchin et al., 1992a
R. nitela	48	71?	Venezuela, Bolívar, San Ignacio (322)	R.S. Voss, personal communication
R. cf. nitela	50	?	Brazil, Manaus (29)	Silva, 1994

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Whereas a diploid number of 44 occurs in at least four *Rhipidomys* species (*latimanus*, *leucodactylus*, *mastacalis* and *macrurus*, three specimens of *R. nitela* from San Ignacio, southeastern Venezuela (male RSV 1067 [field number], females USNM 448625 and AMNH 257274) were found to have a diploid number of 48 and a fundamental number of approximately 71 (R.S. Voss, personal communication). In addition, a diploid number of 50 was discovered in a *nitela*-like specimen from Manaus, Brazil (Silva, 1994). Such higher diploid numbers may prove to be a distinctive feature of this group, but karyotypes of many more taxa are needed before a clear pattern can emerge. However, the high fundamental number found in the Venezuelan specimens is similar to that obtained from *R. mastacalis* and *R. "cearanus"* in Brazil. Karyotypic investigation of geographically intermediate *Rhipidomys* specimens from eastern Amazonia might shed some light on any possible relationship between these forms.

Large-bodied species.

Owing to a lack of discrete characters that might readily distinguish between the several taxa belonging to the *R. leucodactylus* group, adult body size and molar row length were used to provide an initial sorting of populations. Large-bodied forms, i.e. those with adult head-and-body length generally greater than 150 mm and molar row longer than 5.5 mm, are known from the lower valleys and foothills west of the Andes in Ecuador and northern Peru and east of the Andes between Venezuela and northern Argentina, from the foothills of the Guiana highlands, from Trinidad and the adjacent Venezuelan coast, from *terra firme* ("dry land", i.e. non-flooded) forests in Amazonia, and from the hills of eastern Paraguay and adjacent Mato Grosso do Sul state in Brazil.

The majority of the roughly 300 large-bodied specimens examined were from separate localities or belonged to very small series, so that individual and local variation were difficult to distinguish from taxonomically significant differences. Specimens were grouped into "populations" according to congruent morphology and geographical proximity, but several isolated individuals could not be thus grouped, and many were too damaged to be included in the morphometric analyses. The material available included four series of moderate size: a) Hacienda Buena Vista, Río Chinchao, Huánuco, Peru ($n = 27$, including many juveniles, collected by E. Heller, August-September 1922, FMNH, MCZ and MNRJ); b) Hacienda Cadena, Marcapata,

Inka region (Cuzco), Peru (n = 13, collected by C. Kalinowski, 1949-1951, FMNH); c) Chijchipani, La Paz, Bolivia (n = 19, several of which without skulls, collected by Le Pont and Ruedas, 1986, AMNH); and d) Maracaju, Mato Grosso do Sul, Brazil (n = 28 but only 12 skins, collected by the Rockefeller Institute International Health Division, June-August 1927, AMNH and MNRJ). Once juveniles, old adults and damaged specimens had been discounted, however, the number of skulls suitable for morphometric analysis was only 9 for Río Chinchao, 9 for Marcapata, 7 for Chijchipani and 20 for Maracaju.

At first sight the specimens presented a confusing degree of variation in a number of characters, particularly pelage length and texture, ventral colour, hairiness of tail, length of tail pencil, overall size, hind-foot length, skull size and molar row length; this variation was not adequately covered by the thirteen nominal species-group taxa so far described for this group. Within this array a number of basic morphological "varieties" were heuristically distinguished, each associated with one or more populations and often also with an existing nominal taxon, although no taxonomic or phylogenetic content was intended at this stage. Other specimens were allocated to secondary "varieties" usually similar to or intermediate between the basic forms. The morphological relations between these varieties could then be investigated by means of direct examination and morphometric analysis.

The basic forms provisionally established were as follows (measurement ranges are approximate and, except for molar row length, refer only to adult specimens; the hind-foot length given includes the claw, which adds 1.5-2.0 mm to the length without claw):

a) "couesi" from Trinidad: moderate to very large in size, head-and-body length 150-210 mm; upper molar row mostly 5.8-6.1 mm; hind foot 29-32 mm; tail moderately haired with medium-length pencil, not very bushy; ventral colour pale, sometimes with inconspicuous grey hair bases; skull long, robust, rather narrow, with well developed supraorbital, parietal and occipital ridges. Includes the holotype of *Tylomys couesi* Allen & Chapman. Associated secondary forms from the nearby Venezuelan states of Sucre (with the holotype of *cumananus*) and Nueva Esparta (Margarita island), and possibly the Andean foothills in Barinas (Venezuela) and Cundinamarca/Meta (Colombia).

b) "goodfellowi" from the eastern foothills and lowlands of Ecuador: large to very large, head-and-body length 170-205 mm; upper molar row mostly 6.2-6.6 mm;

hind foot 33-36 mm; tail well haired with long pencil; ventral pelage white or cream with grey hair bases often apparent, and sometimes a fulvous pectoral wash; skull large, rather broad, with well developed supraorbital ridges. The holotype of *R. goodfellowi* is in fact rather smaller than the measurements given above but agrees well in other respects. Associated secondary forms from peripheral parts of Amazonia in Brazil, Peru, Colombia and Venezuela, and the Guianan coastal plain, including the holotypes of *sclateri, bovallii* and *aratayae*.

c) "leucodactylus" from the eastern Andean valleys of central Peru: large to very large, head-and-body length 165-210 mm; upper molar row mostly 6.6-7.0 mm; hind foot 34-38 mm; tail well haired with long, bushy pencil; ventral pelage white or yellowish, often with inconspicuous grey bases, and rather coarse or woolly in texture; skull large, robust and broad, with well developed supraorbital, parietal and occipital ridges. Includes the holotypes of *leucodactylus, lucullus* and *rex*. Associated secondary forms from the western Andean valleys, foothills and coastal plain of Ecuador and northwestern Peru (including the holotype of *equatoris*).

d) "modicus" from the eastern Andean valleys of northern and central Peru (potentially sympatric with "leucodactylus" in parts at least of its range): moderate size, head-and-body length 130-165 mm; upper molar row mostly 5.3-5.7 mm; hind foot 28-30 mm; tail shaft with short hairs and short to moderate pencil; ventral pelage white to roots or with grey bases that may or may not be apparent; skull moderate in size, rather slender, with squared supraorbital edges and rather pointed rostrum. Includes the holotype of *modicus*.

e) "cuzco" from the Madre de Dios drainage in the Peruvian region of Inka (formerly the departments of Cuzco and Madre de Dios): large to very large, head-and-body length 160-205 mm; upper molar row mostly 6.0-6.5 mm; hind foot mostly 33-35 mm; tail shaft hairs short with moderate pencil; ventral pelage white or cream, often with inconspicuous grey bases and sometimes a fulvous pectoral wash; skull large, fairly broad, with moderately well developed supraorbital ridges. No existing type specimens included. Secondary forms from the Urubamba valley area (also in Inka region) and the Ucayali valley (southern Loreto), which on geographical grounds suggest possible relationships with "leucodactylus" and "goodfellowi", respectively.

f) "austrinus" from the eastern Andean foothills and valleys between Santa Cruz de la Sierra (Bolivia) and Jujuy (Argentina): moderate size, head-and-body length 135-165 mm; upper molar row mostly 5.5-6.0 mm; hind foot 28-33 mm; tail shaft

with short hairs and short to moderate pencil; ventral pelage creamy over often apparent grey bases, soft; skull moderate in size with fairly well developed supraorbital ridges and narrower interorbit than the forms listed above. Includes the holotypes of *austrinus* and *collinus*. Secondary forms from Pitiguaya (1700 m) and Chijchipani (850 m), both in the upper Beni drainage in La Paz department. A single specimen from the *yungas* (tropical valleys) near Cochabamba, Bolivia, resembles "austrinus" in many ways but is considerably larger and has a much longer molar row; it might be more closely allied to "cuzco" or even "goodfellowi".

g) "maracaju" from the Maracaju hills of Mato Grosso do Sul, Brazil: moderate to large, head-and-body length 145-175 mm; upper molar row mostly 5.4-5.8 mm; hind foot 31-33 mm; tail moderately well haired with short to moderate pencil; ventral pelage creamy with inconspicuous grey bases; skull moderate in size with fairly well developed supraorbital ridges. No existing type material included. Associated form from nearby eastern Paraguay.

Thus "modicus", "austrinus" and "maracaju" are substantially smaller than the others in both head-and-body length and molar row length. Of the larger forms, "couesi" and to a lesser extent "cuzco" have toothrows of intermediate length; those with the largest molars, "leucodactylus" and "goodfellowi", also have the hairiest tails.

Principal components analysis was used to explore the occurrence of morphometric differences between the main forms and the proximity to them of the secondary forms. PCA was first applied to all the 125 qualifying adult skulls. The first component, representing general size, accounted for 71% of total variation and provided a rough ordination of the populations but with considerable overlap between them. On account of the large range of variation included, other components were difficult to interpret and no clear groupings were apparent. Therefore, several separate analyses were subsequently performed, each using fewer populations, in such a way that as far as possible each form, main or secondary, was included with each other in at least one PCA. As a result, all the main forms were found to differ from each other morphometrically, although seldom was there complete separation on any single component without some degree of overlap.

In a PCA of 40 specimens belonging to the forms with largest teeth and hairiest tails ("leucodactylus" and "goodfellowi" and their associated secondary populations), the first component represented negative skull size and accounted for only 54% of the total variation in the sample, providing no separation between populations. The second
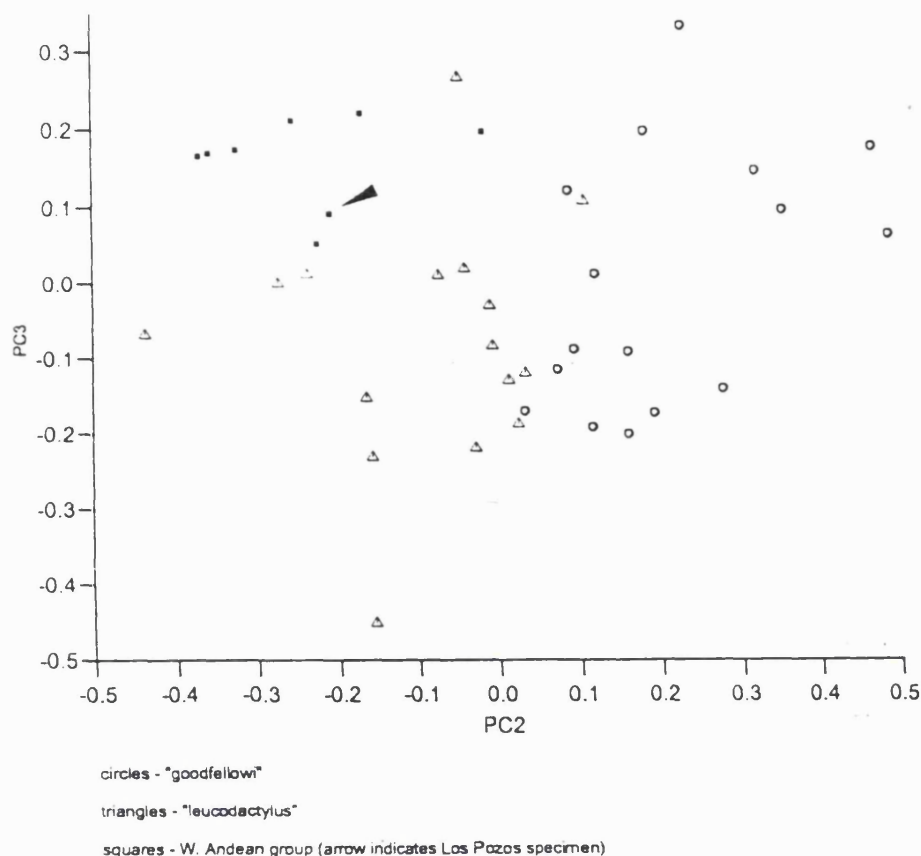
Fig. 6.7 - *Rhipidomys* "goodfellowi", "leucodactylus" and western Andean specimens: plot of scores on the second and third principal component axes.

component (13% of the sample variation) sorted "goodfellowi" and associated specimens from the remainder with little overlap, suggesting that they had smaller molars and narrower zygomatic plate and bullae relative to interorbital breadth and palatal bridge length. A plot of scores for the first two components placed the two groups in adjacent, non-overlapping areas. The third component (7.5% of total variation) partly distinguished eastern Andean "leucodactylus" from the western Andean specimens, with "goodfellowi" mixed throughout; vector loadings suggested that "leucodactylus" had a broader palate and mesopterygoid fossa in relation to zygomatic plate length and interorbital breadth. In a plot of PC3 scores against PC2 scores (Fig. 6.7), three contiguous areas could be distinguished: one for "goodfellowi", one for "leucodactylus" and one for the western Andean (W Ecuador and NW Peru) group, with one "leucodactylus" specimen falling into each of the other

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areas. The three isolated Amazonian specimens that qualified for analysis (from Rio Jamari, Rondônia, Brazil; Tamatamá, T. F. Amazonas, Venezuela; Rio Jari, Pará, Brazil) grouped with "goodfellowi", as expected on geographical grounds. It was also noteworthy that the small specimen from Los Pozos, on the dry coastal plain of southwestern Ecuador, lay well within the western cluster in this plot in which skull size was ignored. The three known individuals from this locality (two of which are excluded from morphometric analyses) resemble members of the western group externally and cranially except in their small size; this result confirms their affinity with this group.

When "couesi" and "cuzco" specimens were added to the analysis the picture

circles - "goodfellowi"   crosses - "couesi"

triangles - "leucodactylus"   asterisks - "cuzco"

squares - W. Andean group

Fig. 6.8 - *Rhipidomys* "couesi", "cuzco", "goodfellowi", "leucodactylus" and W Andean specimens: plot of scores on the first two principal component axes.

became more complex. Component 1 (accounting for 56.5% of the total sample variation) again represented essentially negative skull size but included rather lower contributions from BW, ZPL and IOB. On this axis the scores for "leucodactylus", "goodfellowi" and western Andean individuals were predominantly negative and those for "couesi" and "cuzco" mainly positive, but there was considerable overlap. A plot of PC2 against PC1 partly resolved the overlaps (Fig. 6.8): the groups formed four contiguous, obliquely oriented clusters roughly parallel to each other, with "couesi" scoring highest on both axes, followed by "cuzco", then "goodfellowi" plus the western Andean group together, and "leucodactylus" averaging the lowest scores on both axes. Most of the remaining overlaps were due to the spreading of the third group into adjacent clusters. The latent vector corresponding to PC2 (8.7% of total variation) had large negative loadings for toothrow lengths and palatal and mesopterygoid fossa breadths and large positive loadings for zygomatic plate length, interorbital breadth, nasal length and rostral breadth. Other components also provided some separation congruent with group boundaries. Scores on PC3 (7.6% of total variation) completely segregated "goodfellowi" (negative) from the western Andean group (positive), while the remaining specimens occupied the middle ground and overlapped with both; the latent vector had high positive loadings for ZPL, BW and molar dimensions. On PC5 (4.7% of total variation), which stressed interorbital and braincase breadths against nasal length and palatal breadth, 17 of the 18 "cuzco" specimens had positive scores whereas 11 of the 13 "couesi" had negative ones, reflecting the generally broader skulls of the former and longer skulls of the latter. Overall, this analysis showed that for the samples available the main groups did differ morphometrically but not without some ambiguities. The western Andean specimens were associated with "leucodactylus" in most plots, and one or both of these groups often clustered with "goodfellowi". The other main groups, "couesi" and "cuzco", were found together in some plots but apart in others.

In an analysis of those forms that occur wholly or partly in Peru, i.e., the same groups as above but with "modicus" replacing "couesi", scores on the first three components sorted the specimens into contiguous regions with relatively little overlap between the main groups (Fig. 6.9). The first component (64% of total variation) again expressed negative overall size (although with slightly reduced contributions from PB1, BW, ZPL AND IOB), while the second latent vector (7.6% of total variation) was composed mainly of positive loadings for interorbital breath (plus
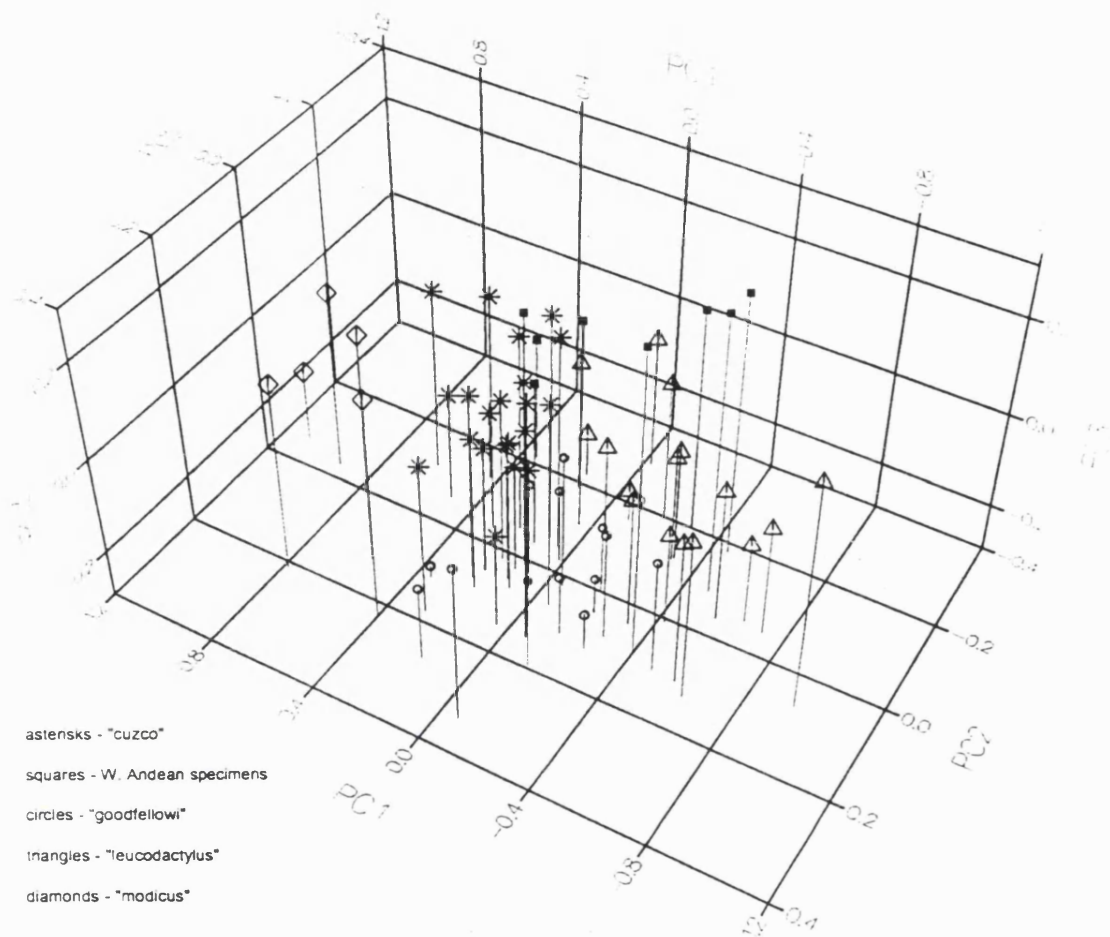
Fig. 6.9 - Large-bodied forms of *Rhipidomys* occurring wholly or partly in Peru: plot of scores on the first three principal component axes.

rostral breadth and skull height) and negative ones for molar row lengths (plus bullar width and zygomatic plate length). PC3 (6.9% of variation) represented a contrast between BW, ZPL and IOB (positive loadings) versus PBl and MFB (negative).

Most of the separation between "modicus" and "cuzco" and between these and the remainder occurred along the first component axis, with "modicus" relatively isolated at the small end of the scale. Thus "modicus" skulls were clearly the smallest overall, with "cuzco" intermediate in size but partly overlapping with the remainder. The two specimens from the Urubamba drainage were closer to "modicus" than to other "cuzco" on the first axis because these, the only ones out of the 17 specimens examined from that area to qualify for inclusion in the analysis, happened to be among

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the smallest adults in that sample; the second component axis shows their greater
affinity with "cuzco".

Among the larger specimens, "goodfellowi" was segregated from
"leucodactylus" and the western Andean sample mainly on a combination of PC2 and
PC3. Thus the difference between "leucodactylus" and "goodfellowi" was less of size
than of shape, with "goodfellowi" having on average smaller molars, bullae and
zygomatic plate but perhaps a relatively broader interorbit than "leucodactylus". Most
western Andean specimens fell close to the latter group, although the smallest were
separated from "cuzco" only along PC2.

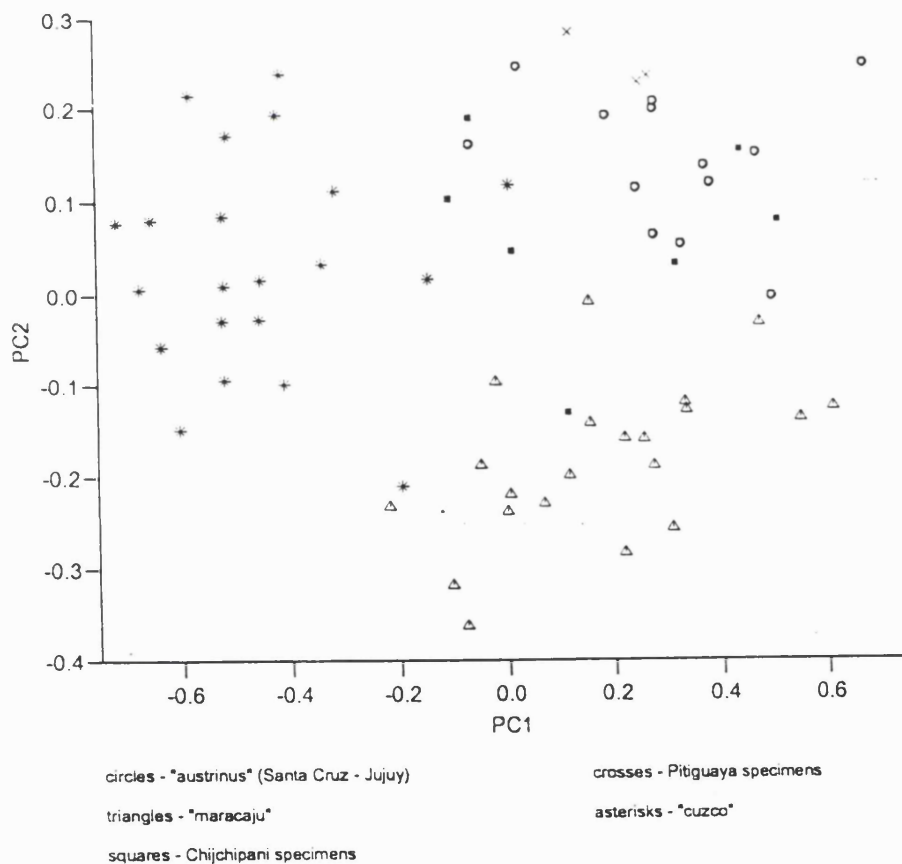PCA was next used to investigate samples from the area extending from SE

Fig. 6.10 - Large-bodied *Rhipidomys* from SE Peru to N Argentina: plot of scores on
the first two principal component axes.

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Peru and Bolivia to N Argentina and SW Brazil, i.e. the groups "cuzco", "austrinus" and "maracaju" with their associated secondary forms. The first component (60% of total variation) had a latent vector with roughly equal negative loadings for most variables, but small contributions from PB1 and MFB and virtually nil from BW. This component served to separate the "cuzco" skulls (larger) from the remainder (smaller), with just one "maracaju" and one Urubamba specimen overlapping. The second component (11.8 % of total sample variation; with large positive loadings from BW, MRC and MMR and large negative loadings from PB1 and MFB) separated "austrinus" and its secondary forms (higher scores) from "maracaju" plus the specimen from Paraguay (lower scores), with an overlap of only one on each side (Fig. 6.10). This PCA thus supports separation of the three main groups included: "cuzco" is larger than the rest, whereas "maracaju" is distinguished from "austrinus" by its relatively broad palate and mesopterygoid fossa and small bullae.

To confirm the relative positions of "austrinus" and "maracaju", the PCA was rerun without "cuzco" and its associated specimens. The first latent vector, now corresponding to only 41% of total variation, consisted of variable loadings all of the same sign (negative) but of differing magnitudes: the smaller skull dimensions generally had small loadings. This axis provided no sorting at all of populations, but it did sort specimens by DAC (t-tests on PC1 scores for DAC 2 vs DAC 3, and DAC 2 vs DAC 4: $p < 0.001$, d.f. = 35 and 29 respectively). Component 2 (18.7% of total variation) separated "maracaju" (plus the Paraguayan specimen) at the negative end from all Bolivian material at the positive, with a single specimen overlapping on either side; the corresponding latent vector had large positive loadings for MMR, MRC, BW and PBL, and large negative ones for PB1 and MFB. This reiterates the findings from the previous PCA, in which "maracaju" was seen to have small bullae but broad palate and mesopterygoid fossa in comparison with "austrinus".

Although analysable samples were small, specimens from Pitiguaya (elevation 1700 m) appeared in this PCA to differ somewhat from those from nearby Chijchipani (850 m), particularly on the third component. On this axis, "austrinus" specimens all had positive scores, and Chijchipani specimens were all negative, whereas the three Pitiguaya individuals included in the analysis were intermediate. The corresponding latent vector (11.3% of total variation) had high positive loadings for ZPL, BW and NL and a large negative loading for IOB, implying that Chijchipani specimens might have relatively narrow zygomatic plate, small bulla, short rostrum and broad interorbit

in comparison with "austrinus". Visual examination of the specimens shows a notable difference in the shape of the supraorbital ridges. In the Chijchipani specimens they are heavy and converge to a point well forward in the interorbital region, giving a highly angular impression; in contrast, "austrinus" and the Pitiguaya specimens have a more hourglass-shaped interorbit with ridges that become conspicuous only in older specimens and converge towards the centre of the region. Externally, the few adult skins available for comparison suggest that Pitiguaya specimens have longer, darker pelage and a longer hind foot than those from Chijchipani. The Pitiguaya sample thus resembles "austrinus" from southern Bolivia more than it does its geographically closer neighbours, and this is partly reflected by its intermediate position in the principal component plots. It is possible, therefore, that the Pitiguaya specimens are representatives of "austrinus" in northern Bolivia, whereas those from Chijchipani belong to a separate taxon.

Morphometric analyses thus confirm the distinctness of the basic forms from each other and suggest the possible addition of two more, one from the western Andean valleys of Ecuador and NW Peru and the other from Chijchipani, Bolivia. Unfortunately, however, the absence of good samples from intermediate areas means that the relationships between many of these forms cannot properly be assessed. There are three areas where two morphologically distinct forms are found in close proximity, if not in true sympatry: a) Meta, Colombia, where the specimen from Serranía de la Macarena (probably a "goodfellowi") is considerably larger than those from Villavicencio and Susumuco (which are possibly related to "couesi"); b) the eastern Andean valleys of central Peru, where "modicus" and "leucodactylus" have been found close together at Chinchavito (former department of Huánuco) and in the Chanchamayo valley (Junín, both now in Región Andrés Avelino Cáceres); and c) the case discussed above of specimens from Pitiguaya (probably related to "austrinus") and Chijchipani (probably a separate form) in La Paz department, Bolivia. Such occurrences suggest that different species are involved, but exactly how many depends at present on the subjective assessment of morphological and morphometric differences, viewed in the light of knowledge of habitat distributions. I propose the following arrangement of the large-bodied *Rhipidomys* taxa as an hypothesis for future testing through the accumulation and analysis of further data (i.e., new material from intermediate localities, and data from as yet little explored systems, such as karyotypes and DNA-DNA hybridization). Full descriptions of these species may be found in

Chapter 7.

1) *Rhipidomys couesi*, occurring in Trinidad and the Venezuelan states of Nueva Esparta and Sucre, and possibly extending along the wooded edge of the llanos on the south-, southeast- and east-facing slopes of the Venezuelan coastal range, Mérida Andes and Eastern Cordillera of Colombia as far south as Meta. Specimens from the island of Trinidad are on average larger than those from the mainland and may warrant recognition as a distinct geographical race; the same may apply also to the Margarita population. Specimens from the southernmost part of the range differ somewhat in having rather more slender skulls. Subfossil material from Tobago originally identified as *"R. leucodactylus"* (Eshelman & Morgan, 1985) may well belong in *R. couesi*, a possibility apparently not considered by those authors. The fossilized teeth and skull fragments from the Dutch island of Bonaire, identified by Hooijer (1959: 18-20 and pl. III, figs. 8-10) as *"Thomasomys* spec.*"* (from comparison with *"Thomasomys" [= Delomys] dorsalis*) appear from his description and illustrations to be more similar to *Rhipidomys*, especially *R. couesi*, than to any extant *Thomasomys* or *Delomys* and may represent a closely related taxon, now extinct.

2) *Rhipidomys leucodactylus*, including the provisional forms "leucodactylus", "goodfellowi" and "cuzco" as well as the specimens from west of the Andes in Ecuador and NW Peru. Reasons for including these forms together in one taxon are discussed below. As understood here, this species occurs in the lowland rainforests of the Guianas and the Amazon and upper Orinoco basins, in the adjacent foothills and valleys of the Andes from Meta in Colombia to southeastern Peru up to altitudes of 2000 m, and along the western Andean slopes and valleys of NW Peru and Ecuador. It may also prove to occur farther north in the humid Chocó region of western Colombia, although no specimens have yet been reported from there. Superficial examination of a very large, poorly prepared specimen from the Maracaibo lowlands of Venezuela (MHNLS 554) suggests that a related population may exist in the forests there. The southern limit of the species range is apparently the *yungas* of Cochabamba, Bolivia; the single known specimen from there agrees in size with *R. leucodactylus* far more than it does with the neighbouring *R. austrinus* (see below).

3) *Rhipidomys modicus*, from the eastern Andean valleys and foothills of northern and central Peru. This medium-sized species is probably sympatric with the much larger *R. leucodactylus* in at least part of its range.

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4) *Rhipidomys* sp. 1, known from Chijchipani, La Paz, Bolivia, at 850 m, but apparently replaced at higher altitudes in this region by the following taxon. It may prove to be related to the *R. leucodactylus* populations of southeastern Peru (i.e., the "cuzco" form), but is regarded here as a separate taxon on account of its distinctive morphology. If it is related, the distribution pattern in this region would resemble that of southeastern Brazil (see below, in the last section of this chapter), where a more southerly species extends its range northwards at higher elevations than those occupied by a more northerly species.

5) *Rhipidomys austrinus*, extending from La Paz (Pitiguaya, at 1700 m) along the eastern flanks of the Andes southwards to Jujuy and Salta, Argentina. A certain amount of geographical variation is present within this species: specimens from Pitiguaya are rather darker than those to the south, and Argentinian specimens may prove to be rather larger than Bolivian ones, although samples examined are too small to be sure.

6) *Rhipidomys* sp. 2, from the hills of Maracaju, Mato Grosso do Sul, Brazil, and adjacent Paraguay. Although similar in some respects to *R. austrinus*, this form is distinct morphologically and isolated from that taxon by the Chaco of Bolivia and Paraguay.

Although there are obvious differences in size and coloration between specimens from, for example, western Ecuador and SE Peru, these diverse forms have been subsumed here under *R. leucodactylus* because of a lack of evidence for clear separation between them at species or subspecies level. Geographically and morphologically intermediate specimens show that characters such as hind foot length and hairiness of tail cannot easily be divided into discrete states; for instance, the large, hairy-tailed specimens of eastern Ecuador grade into the smaller, shorter-pencilled form of the Madre de Dios through material collected at San Jerónimo in southern Loreto. In eastern Ecuador alone, where the most common ventral coloration is creamy white hair tips over pale to mid-grey bases, there are specimens without any grey (like many Madre de Dios individuals), others with conspicuous dark grey bases (like the holotypes of *bovallii* and *sclateri* from Guyana) and yet others that are greyish yellow (as in central Peru), together with intermediate shades. At most other localities, too, the degree of grey in the ventral pelage varies from one individual to another. In view of the fact that potentially suitable habitat links the areas in which they have been found, the superficially distinct forms of "leucodactylus",

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"goodfellowi", "cuzco" and W Ecuador/NW Peru are best regarded at present as geographical variants within a single species. Although the analyses of craniodental data have supported certain general groupings within this overall assemblage, results are not clear-cut and so are consistent with this approach. Whether these apparently distinct forms merely represent different points on the same morphological gradients, whether they are subspecies separated by hybrid zones, or whether they are true species are questions that can only be resolved through further collecting, especially in intermediate areas, and investigation of other data sets such as karyotypes and DNA sequences.

Although *Rhipidomys leucodactylus* has not been captured in the eastern valleys of northern Peru, its presence on the western side of the Cordillera suggests a hypothesis of gene flow through the Huancabamba depression in the not too distant past. The sample from Canchaque, altitude 1230 m, overlooking the Sechura desert of northwestern Peru, closely resembles individuals from Río Chinchao in central Peru and Napo in eastern Ecuador. A little farther north, specimens from SW Ecuador are slightly smaller, especially those from Los Pozos in the dry coastal forests of El Oro, but size increases again farther north still in the more humid conditions of Santo Domingo de los Colorados, Pichincha.

The Amazon-Orinoco forests extend to the eastern foothills of the Andes as far north as the Serranía de la Macarena in Meta, Colombia. Beyond that point the northern savannas or *llanos* approach the mountains, and piedmont forest continues only in a narrow band along the foothills. Here, *R. leucodactylus* is apparently replaced by *R. couesi*, whose range extends northeastwards to Trinidad. This species has been reported from most parts of this island, including lowland cacao plantations and the north coast range, and also from the more mesic parts of the rather arid Isla Margarita and the coastal region of NE Venezuela. In the Reserva Forestal de Ticoporo, on the lower slopes of the Mérida Andes in Barinas state, it inhabits an area of dense rainforest with many lianas and epiphytes, where it is considered scarce (Ochoa et al., 1988). Specimens caught by the SVP in Sucre, Nueva Esparta and Barinas states, Venezuela, were taken mainly in evergreen forest or plantations and in one case inside a house (Handley, 1976).

Medium and small-bodied species.

Medium-sized and small *Rhipidomys* are found in the valleys and foothills of the northern Andean systems as far south as northern Peru, in extreme eastern Panama, in the Guiana Highlands, in the Amazon and Atlantic coast rainforests, and in mesic enclaves and gallery forests within the drier and/or more open vegetation formations of Brazil and Venezuela. As with the large-bodied taxa, the specimens available were grouped provisionally on the basis of external and craniodental morphology and analysed morphometrically using PCA. A single analysis of all the material was not appropriate because there were too many individuals involving too much variation for any clear patterns to emerge; therefore several analyses were performed using subsets of the specimens.

a) Northwestern South America.

Preliminary examination suggested that two main forms were present in the northern Andean area and adjacent lowlands: a brightly coloured, small-eared form with medium to dark feet, tail and ears inhabiting the western slopes of Ecuador ("latimanus"), and a rather less intensely pigmented form with large ears and pale extremities from the Mérida region of Venezuela ("venezuelae"). The dorsal pelage of "latimanus" specimens is orange-brown, moderately flecked with dark brown or black guard hairs; ventrally their pelage is white, sometimes with short, inconspicuous grey hair bases. They have a moderately long tail pencil and a rather slender foot with a dark, narrow foot patch. The skull is slender with straight supraorbital ledges converging well forwards and a braincase that is not greatly flattened. Specimens from the Cauca valley of southwestern Colombia are very similar, although sometimes slightly paler. In contrast, specimens of "venezuelae" have less saturate, reddish-brown dorsal pelage; their sparser and browner guard hairs mean that the fur is softer and less obviously agouti. Their ventral pelage is white to the roots, grey bases to the hairs being absent or confined to a small patch on the upper thorax. The tail pencil is short, and the more robust foot has a faint foot patch that varies from narrow to moderately broad. The skull is more robust, with a heavier rostrum and flatter braincase than "latimanus" specimens of similar age. Samples from the northern coastal range and parts of Falcón state are similar to the Mérida population, or sometimes rather brighter in colour.

Examination of specimens from other parts of Colombia and Venezuela (and from easternmost Panama and northernmost Andean Peru) revealed a more complex pattern of

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variation in the region than was initially apparent. In the middle Magdalena valley (western Cundinamarca and Boyacá departments) dorsal colour is similar to that of "latimanus", with more obvious dark flecking especially in older specimens. In Antioquia department (in the Cauca valley and the foothills of the northern ends of the Western and Central Cordilleras), the Serranía de Perijá (on the Venezuelan-Colombian border west of Lake Maracaibo), the Sierra Nevada de Santa Marta (near the Caribbean coast of Colombia) and parts of northern Venezuela many specimens are more intensely red-brown, whereas those from eastern Panama and northern Peru are bright orange-brown with less dark flecking. A darker, more olive-brown tinge is found in southern Huila department, Colombia, at the head of the Magdalena valley. Samples from Río Tocuyo (Lara state), Montalbán (Carabobo) and Capatárida (Falcón) in Venezuela, and from El Orinoco (César department) and Miraflores (Valle) in Colombia are much less intensely pigmented, giving a rather yellowish-brown, more strongly agouti effect more typical of drier habitats. The occurrence of grey-based ventral fur is most common in Huila and Perijá, less common in the remainder of Colombia and Ecuador, and very infrequent elsewhere except at above 2000 m in Mérida. Tail pencils are short in Venezuela, northern Colombia (Santa Marta and Perijá) and Huila, and longer elsewhere. The slender foot of Ecuador becomes steadily more robust with stubbier digits as one moves farther north and east through Colombia (although the Miraflores specimen and some from Cundinamarca have small feet); the Peruvian population also has stout feet. Ears are largest in Venezuela, especially Mérida, and smallest in Cundinamarca and Miraflores. Skulls from Perijá are elongated and smooth, resembling "latimanus", while those from Santa Marta and N Peru are more robust like "venezuelae"; in central Colombia and Panama they are intermediate, whereas in the Venezuelan coastal range skulls can be more massive even than those from Mérida. These patterns of variation forced a reappraisal of the initial dichotomous arrangement of the group, suggesting a more complex picture.

The material from Huila department, Colombia, is somewhat anomalous in that it bears some resemblance to R. *fulviventer* not only in its longer, slightly olive dorsal pelage and often conspicuous grey bases to its ventral hairs, but also in its long nasals, narrow interorbit and more rounded braincase. Nevertheless, the coarser texture of its pelage, its short tail pencil, narrow, well-defined foot patch, derived stapedial circulation, non-fenestrated parapterygoid fossae and poorly developed lower incisor root capsule point to a closer relationship with the "latimanus-venezuelae" group. An

individual collected at Bonda, near the seaward foot of the Sierra Nevada de Santa Marta, differs so greatly from other specimens from the area in its small size, greyish pelage, short and broad hind foot, small molars, short rostrum and relatively broad interorbit that it probably does not belong with this group; it will be discussed later in relation to *Rhipidomys nitela*.

A principal components analysis of all this material proved difficult to interpret in detail because of the number and variety of specimens included. However, in a plot of scores on the first two components, the single resulting cluster was very roughly divided into an upper left-hand part composed mainly of northeastern specimens (i.e., from Venezuela and northern Colombia), and a lower right-hand part comprising mostly southwestern specimens (from Panama and central Colombia to N Peru). The first latent vector loadings indicated mainly negative size, whereas the second contrasted molar row and palatal bridge length (positive loadings) with braincase breadth, interorbital breadth and skull height (negative). The plot thus indicated that the northeastern group tended to be larger overall than the southwestern, with relatively larger molars and/or a narrower and flatter braincase. The third component provided a different contrast: the Huila sample scored very low compared with nearly all other specimens. The corresponding latent vector had high positive loadings for interorbital breadth and molar length and large negative ones for temporal fossa length and braincase breadth; thus Huila specimens might be expected to have a narrower interorbit and broader braincase for a given skull/molar size. Huila specimens were similarly distinguished in other analyses in which they were included, as mentioned in the discussion regarding *R. fulviventer* (see Fig. 6.3).

A second PCA (using 15 variables) was restricted to specimens from central and northern Colombia, eastern Panama and Mérida. This time a plot of scores on the first two components resulted in three contiguous, elongated clusters with relatively little overlap (Fig. 6.11). The group with lowest scores on both axes corresponded to the Mérida sample, the one with highest scores to Antioquia plus Cundinamarca and Panama, while the intermediate group was formed of Santa Marta and Perijá specimens. The points for the small Bonda and El Orinoco individuals were peripheral to the main clusters, the former lying closer to the axis of the highest group and the latter to that of the central group. The first latent vector, which accounted for 43% of total sample variation, represented negative general size (but with virtually no contribution from palatal breadth and little from mesopterygoid breadth and nasal length); the second (15% of total variation) contrasted these three variables plus braincase breadth and height (positive

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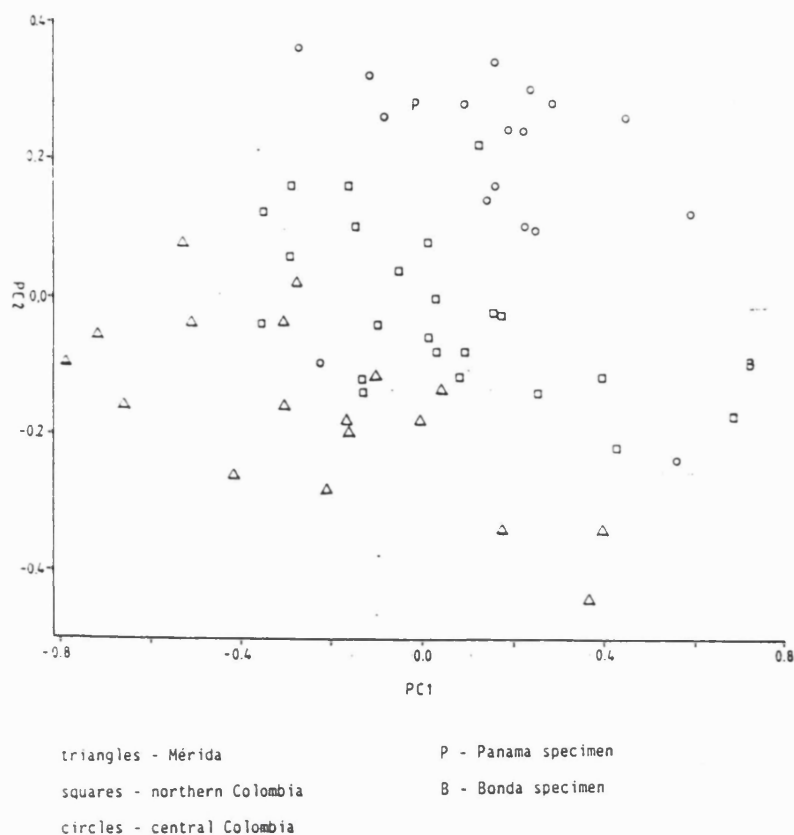
Fig. 6.11 - Medium-sized *Rhipidomys* specimens from central and northern Colombia, eastern Panama and Mérida (Venezuela): plot of scores on the first two principal component axes.

loadings) with molar lengths, palatal bridge length and zygomatic plate length (negative loadings). With so many variables involved, morphological interpretation of the plot is difficult but it is compatible with the contrast in overall size, braincase shape and molar length indicated in the previous analysis. These results suggest, however, that the Santa Marta-Perijá material is somewhat intermediate between the Venezuelan and southwestern groups. Its relation to the Venezuelan material was examined next.

When all the Venezuelan and north Colombian specimens were analysed together, no patterns at all emerged from the distribution of specimens on the first three component axes; only the fourth and fifth components (accounting for 7.2% and 6.6% of total variation, respectively) provided any segregation of samples from different areas. The fourth component separated the Falcón, Mérida and most Lara specimens from all but one of those from Perijá, while Santa Marta individuals were scattered in both parts; the latent

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vector loadings suggested the Perijá specimens had larger MFB, BCB and DR and smaller PBL, TFL and ZPL. Component 5 provided some distinction between the Mérida and Falcón samples, the former having larger ZPL, PB1 and IOB and smaller PBL, NL and PL than the latter. Compared with the separation achieved in the previous analysis, however, these results show little morphometric pattern of significance and suggest that the Santa Marta-Perijá samples are not easily distinguished from the Venezuelan material.

In view of the variation in skin and skull characters revealed during examination and the results of the morphometric analyses, the medium-sized specimens collected between northern Peru and northern Venezuela (excluding the Bonda specimen) appear to belong to a single, variable species, within which three subspecies may be recognized: *Rhipidomys latimanus latimanus* for the southwestern group (including *pictor, cocalensis, mollissimus, quindianus, microtis* and *scandens*), occurring from northern Peru to central Colombia and eastern Panama; *R. l. venezuelae* for the northeastern group, ranging from Santa Marta in northern Colombia along the Perijá and Mérida ranges to the northern coastal region of Venezuela; and *R. latimanus* ssp. for the apparently isolated and morphometrically distinct sample from Huila, Colombia.

Rhipidomys latimanus specimens were compared visually and morphometrically with representatives of other congeneric taxa. The results are discussed in the appropriate places.

In the llanos of central Venezuela a different form of *Rhipidomys* appears to occur. Unfortunately only one skin and one immature skull have been examined, but this form is regarded as distinct from *R. latimanus venezuelae* by workers who have studied both forms in the field (Eisenberg et al., 1979; O'Connell, 1982, 1989; August, 1984). In addition, the length of its molar row (5.1 mm) exceeds that of all known specimens of *R. nitela* but is considerably less than that of all known *R. couesi*, the other lowland species whose ranges adjoin the llanos. It therefore seems to represent a separate species and is provisionally treated in the taxonomic synthesis of chapter 7 as *Rhipidomys* sp. 3.

b) The Guiana Highlands and Amazon Basin

Members of the *Rhipidomys leucodactylus* group with small bodies and small molars have been found in the forests and savannas of eastern Venezuela and the Guianas and in the northern, central, eastern and southeastern parts of the Amazon rainforest; in addition, isolated specimens have been collected on the island of Little

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Tobago, northeast of Trinidad, and at Bonda near the northern foot of the Sierra Nevada de Santa Marta, northern Colombia. The oldest available species name within this assemblage is *R. nitela* Thomas, 1901. Diploid numbers of 48 and 50 have been discovered in these specimens, in contrast to the $2n = 44$ found in all other *Rhipidomys* karyotypes investigated (see Table 6.1). These small forms are distinct from the rather larger *R. latimanus* of the northern Andean region and also from the medium-sized species of central and eastern Brazil.

The qualifying specimens of this assemblage were analysed in a PCA together with some small-bodied individuals with larger molars from the cerrado (savanna) of Brasília and Minas Gerais, some larger specimens with small molars from the region of Belém (Pará), provisionally identified as "emiliae", and some larger individuals collected together with *R. nitela* in the Serra do Roncador, northeastern Mato Grosso. Other analyses (to be discussed later in relation to eastern Brazilian taxa) suggested that the larger Roncador specimens could be included in "emiliae". Just eight variables were used in this PCA so as to exclude fewer damaged specimens. The first component represented negative general size, accounting for 73% of total sample variation, whereas the second latent vector contrasted molar row length (large positive loading) especially with braincase breadth (moderate negative loading), covering roughly 8% of total variation.

In a plot of specimen scores on the first two component axes (Fig. 6.12), the four members of the cerrado sample formed a very separate cluster from the remainder: with their combination of small size but large molars they are morphologically distinct from the *R. nitela* group. The "emiliae" specimens occupied the large-size end of the general cluster, adjacent mainly to the sample from the Yuruán valley of eastern Venezuela ("yuruanus") and many of the Amazonian specimens from the lower Rio Tapajós. The three "emiliae" from Roncador (arrowed crosses in the figure) were separated from the single *R. nitela* from the same area (arrowed triangle) on the first component axis, but not on the second. No other components provided any clustering that could be easily interpreted in relation to sample morphology or origin. Thus in this analysis, "emiliae" is differentiated from the *R. nitela* group mainly by its larger size; however, because of the sympatry between the larger "emiliae" and smaller *R. nitela* at Roncador, the two taxa must be regarded as separate species.

The extent to which the *R. nitela* group differs morphometrically from other *Rhipidomys* taxa was investigated in a number of PCAs, the first of which included the specimens of *R. caucensis*. To reduce the obvious body-size difference between the
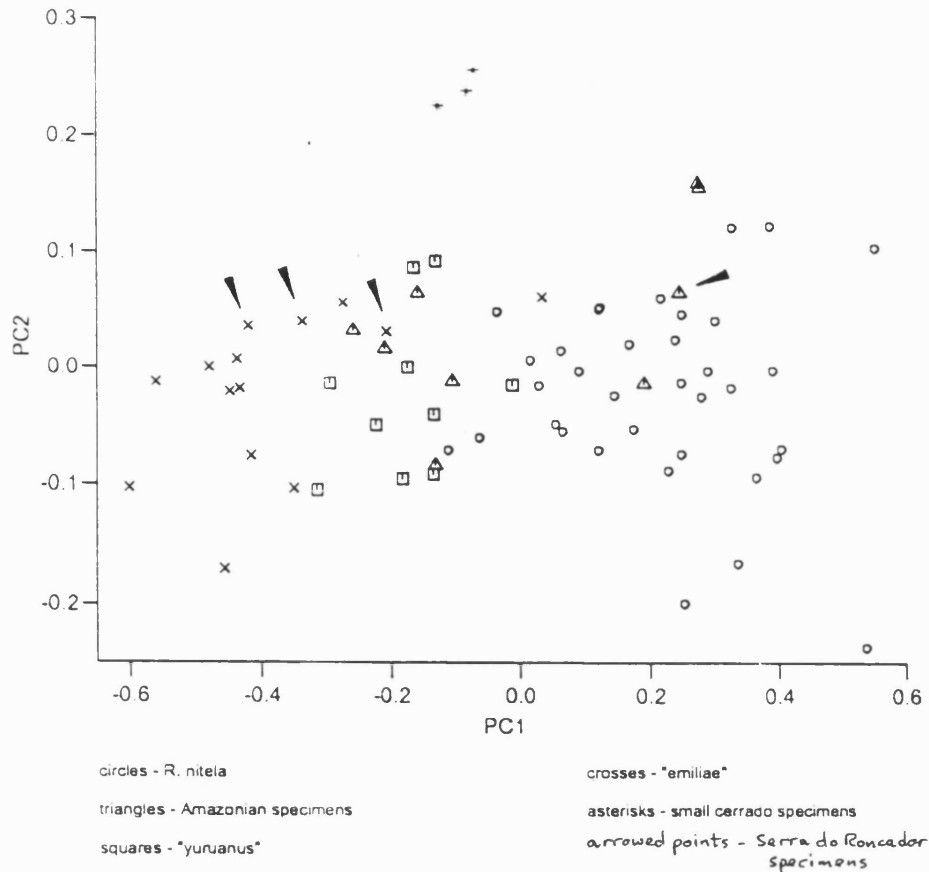
Fig. 6.12 - *Rhipidomys nitela* and *R. emiliae*: plot of scores on the first two principal component axes (8-variable analysis).

groups, the largest *R. nitela* specimens, i.e. the "yuruanus" sample, were omitted. The resulting first component accounted for 52% of total variation and represented negative general size, as usual, but with negligible or greatly reduced contributions from PB1, MFB and BW. Some overlap occurred on this axis between the largest *R. caucensis* (FMNH 71736, from Huila, Colombia) and the smallest *R. nitela* (the "milleri" sample from the Potaro Highlands, Guyana, particularly AMNH 36337). The overlap was resolved in a plot of scores on the first two component axes (Fig. 6.13), in which *R. nitela* formed an elongated cluster with low co-ordinates on one or both axes whereas *R. caucensis* scored higher. The smallest "milleri" specimens lay within the general *R. nitela* cluster but not far from the three *R. caucensis* specimens from Cauca. The *R. nitela* specimen from Bonda, northern Colombia, was situated centrally within the *R. nitela* cluster and no resemblance to *R. caucensis* was indicated. Component 2

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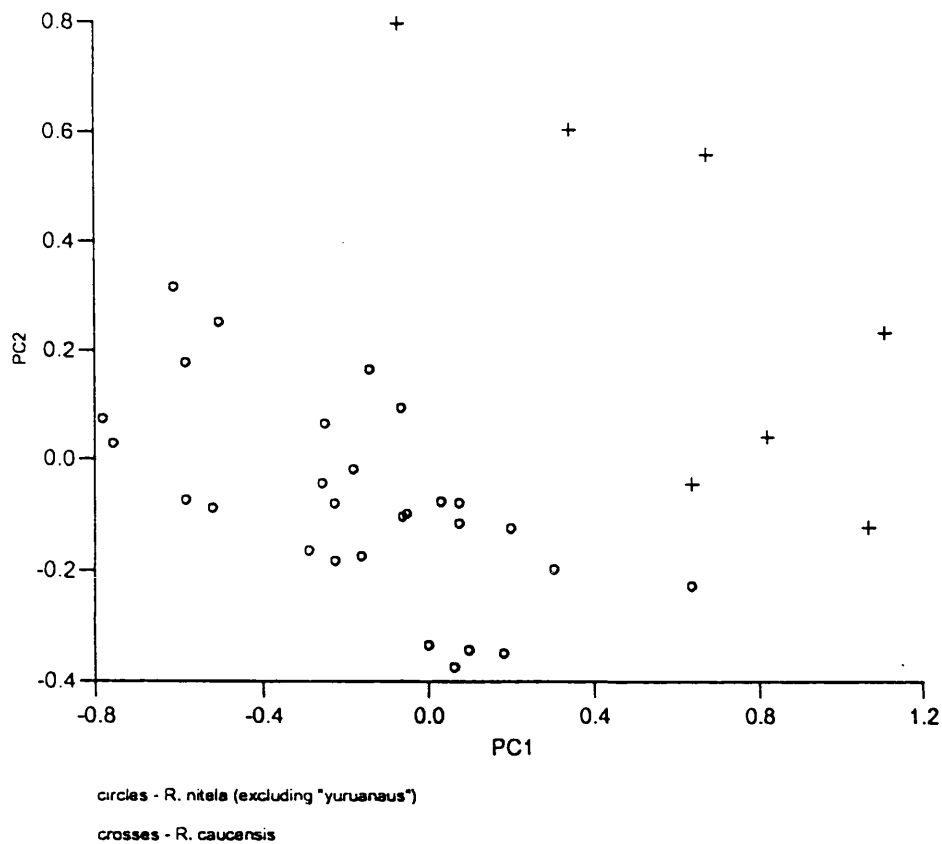
Fig. 6.13 - *Rhipidomys nitela* and *R. caucensis*: plot of scores on the first two principal component axes.

loadings were principally for BW, PB1, DR and BCB (positive) and IOB (negative), in decreasing order of importance. In addition to being larger overall in most cases, *R. nitela* might therefore be expected to have relatively smaller bullae, narrower palate and braincase, shallower mandible and broader interorbit than *R. caucensis*. These traits should be most evident in the Tapajós specimens, which occupied the lower margin of the *R. nitela* cluster.

The distinctness of *R. nitela* from both *R. couesi* and *R. latimanus venezuelae* was shown in a PCA of specimens from northern Venezuela and Trinidad. *R. nitela* was represented by the specimens from north of the Guiana Highlands ("yuruanus" from the Yuruán valley and "fervidus" from the lower Caura valley) and those from Bonda (Colombia) and Little Tobago; *R. couesi* by material from Trinidad and NE Venezuela; and *R. l. venezuelae* by the samples from Falcón to the Federal

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circles - R. nitela (northern specimens)

triangles - R. venezuelae (northern Venezuela)

crosses - R. couesi (Trinidad and Sucre)
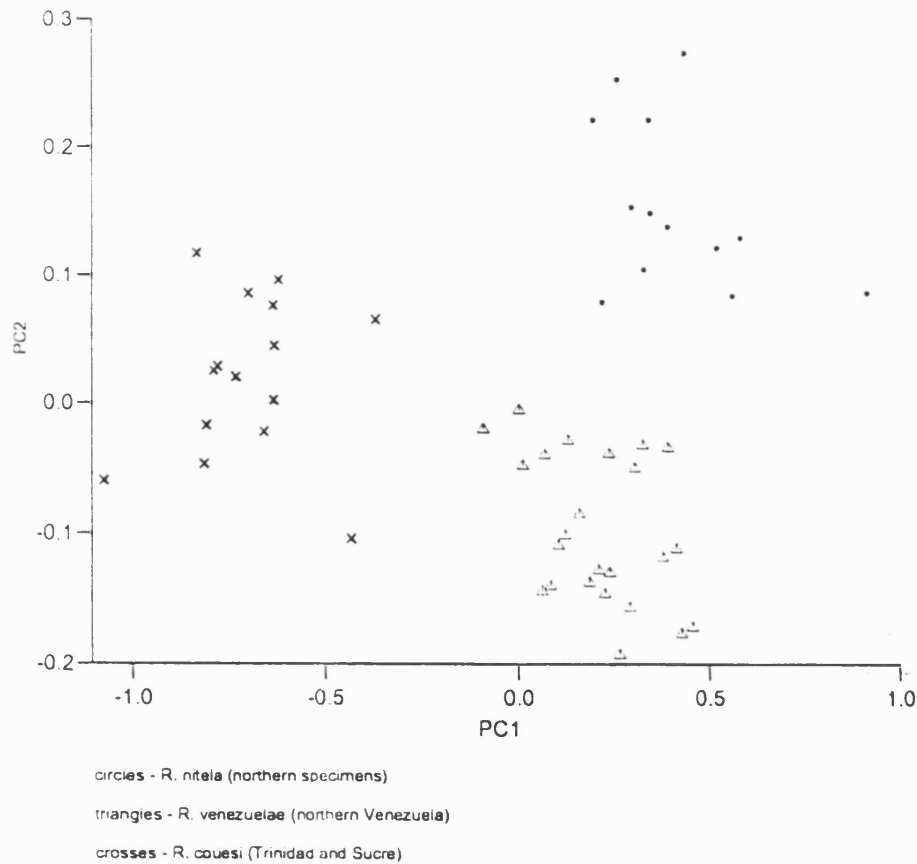
Fig. 6.14 - *Rhipidomys nitela, R. venezuelae* and *R. couesi*, from northern Venezuela and Trinidad and Tobago: plot of scores on the first two principal component axes.

District (but only half of the available specimens from Río Tocuyo were included so as not to overload the analysis in this direction). In a plot of scores on the first two component axes, the three taxa formed completely separate clusters (Fig. 6.14). *R. nitela* was distinguished from *R. couesi* mainly along the first axis and from *R. l. venezuelae* mainly on the second. The first component expressed general (negative) size and corresponded to 80% of total sample variation, reflecting the great size difference between the largest *R. couesi* and the smallest *R. nitela*. The second latent vector (nearly 5% of total variation) was composed especially of large positive loadings for IOB and PB1 and large negative loadings for BW, MMR and MRC: compared with *R. l. venezuelae*, *R. nitela* has a combination of relatively broader interorbit and palate and smaller bullae and molars. A PCA of Venezuelan *R. nitela* together with all samples of *R. l. venezuelae* and without *R. couesi* produced a second component

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with similar loadings to the one above. Scores on this axis plotted against those on PC1 separated *R. nitela* (higher scores on both components) from *R. l. venezuelae* (lower scores), with a similar interpretation to that given above.
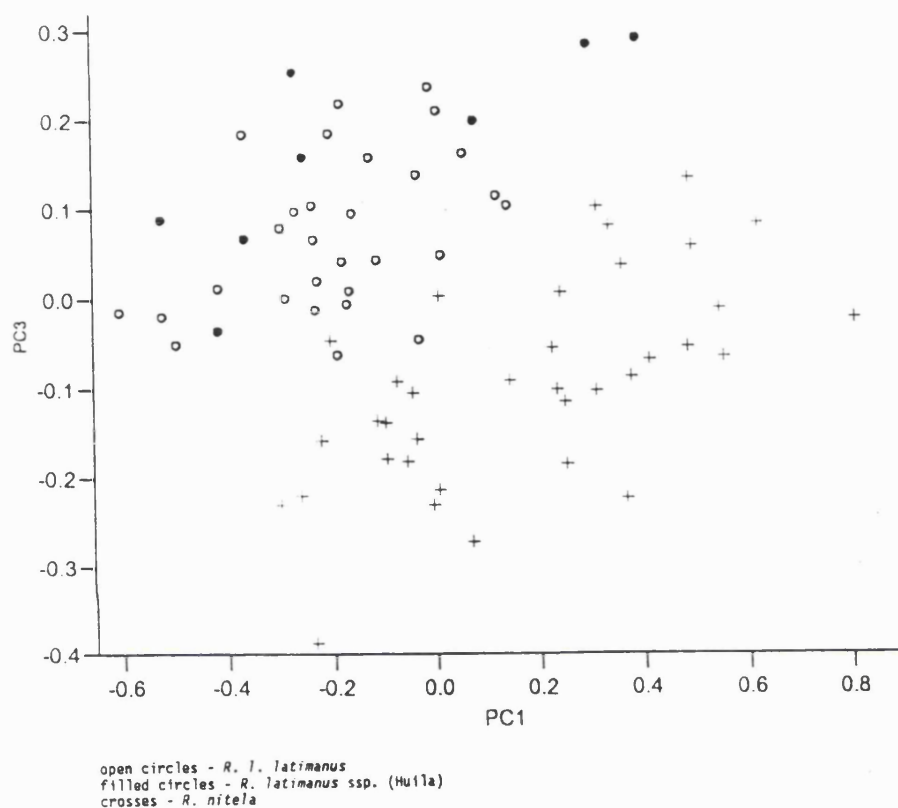
Fig. 6.15 - *Rhipidomys nitela, R. latimanus latimanus* and *R. latimanus* ssp. (Huila): plot of scores on the first and third principal component axes.

Rhipidomys nitela was then compared with *R. l. latimanus* and *R. latimanus* ssp. (Huila). A dozen specimens of *R. nitela* from Suriname and San Ignacio, Venezuela, were omitted to reduce crowding of points in the plots. The first component (46% of total variation) corresponded to negative general size, with rather lower contributions from PB1, BW and IOB. The second component (10.7% of total variation) pointed to the afore-mentioned difference between the two subspecies of *R. latimanus*, the Huila specimens scoring higher on this axis than the remainder, but revealed no patterns regarding *R. nitela*. The latent vector had high positive loadings for BW and BCB and a large negative loading for IOB. Reasonable separation between

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the two species was achieved in a plot of scores on the first and third component axes, in which they formed contiguous elliptical clusters, average *R. nitela* scores being higher on PC1 and lower on PC3 (Fig. 6.15). With large positive loadings for dental dimensions and nasal length and large negative ones for rostral breadth, palatal bridge length and interorbital breadth, the third component (9.8% of total variation) emphasized the smaller teeth and short, broad rostrum of *R. nitela* compared with *R. latimanus*.

The specimen from Bonda, northern Colombia, was collected at a distance of over 1000 km from the nearest known *R. nitela* locality in the Caura valley of central Venezuela, beyond the barriers of the Andes and the llanos, or 1500 km from Little Tobago along the Caribbean coast. Nevertheless, in the results of PCAs this individual

circles - R.latimanus (Antioquia)

diamonds - R. nitela (Guiana Highlands)

squares - R.l.venezuelae (Santa Marta)

inverted triangle - Bonda specimen

(Large symbols indicate group centroids)
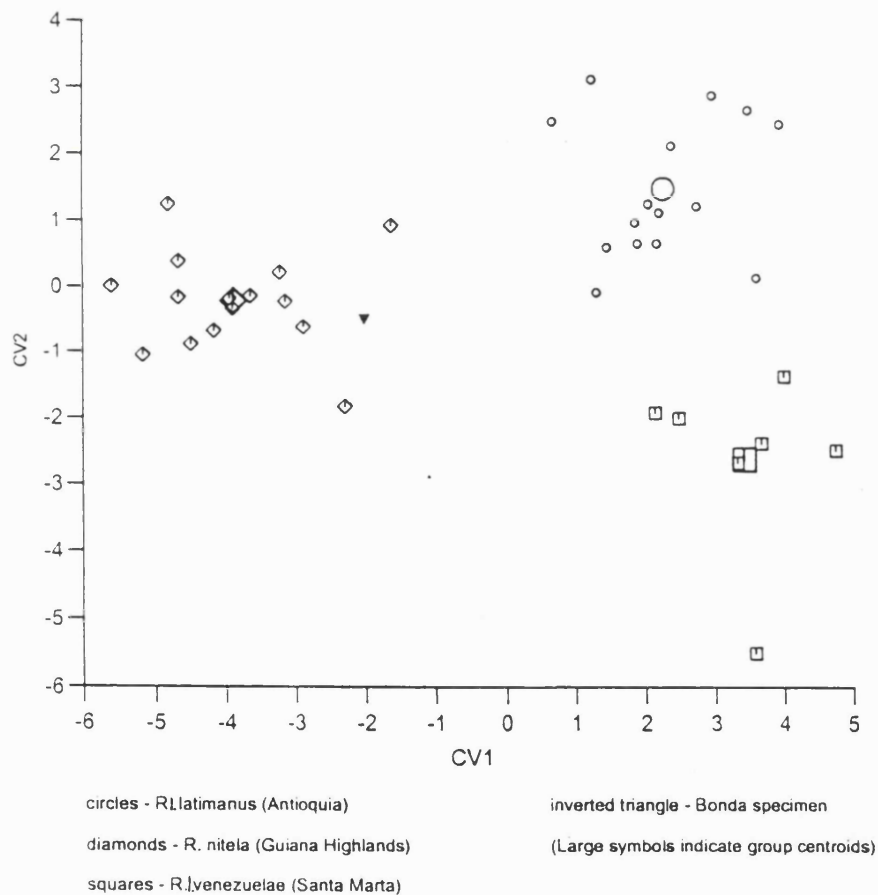
Fig. 6.16 - Clustering of *Rhipidomys latimanus* (central and northern Colombia) and *R. nitela* (Guiana Highlands) in canonical variate space, with allocation of the specimen from Bonda.

consistently lay close to other *R. nitela* specimens, particularly the one from Little Tobago (the holotype of *tobagi*). To confirm its identification as *R. nitela*, a predictive discriminant analysis (PDA - Huberty, 1994) was carried out, using the only 7 available specimens of *R. l. venezuelae* from nearby in the Sierra Nevada de Santa Marta, Colombia, 15 specimens from the nearest known population of *R. l. latimanus* in Antioquia, Colombia, and 15 *R. nitela* from western Guyana, eastern Venezuela and Little Tobago. The Bonda specimen was not included in the calculation of the discriminant functions but on the basis of these was allocated to the group with the nearest centroid. All specimens and group centroids were plotted on the resulting canonical variate axes (Fig. 6.16). The specimen from Bonda clearly belonged with the *R. nitela* group rather than either of the others, and was close enough to the group centroid for one not to suspect that it might belong instead to an unknown group not included in this analysis. The conclusion must be that a population of *R. nitela* exists in northern Colombia, which raises the possibility that other as yet undiscovered populations may occur along the northern coast of the continent. It is curious that the isolated specimens from Bonda, Little Tobago and Sinnamary (near the coast in French Guiana) were apparently discovered almost by accident: the two Little Tobago individuals may have drowned in a fresh-water tank (Goodwin, 1961), and those from Bonda and Sinnamary were shot in bat roosts, presumably when the collector intended to take bats (L. Roguin and R. S. Voss, personal communications). At the last locality, *R. nitela* had not been captured previously despite two years of trapping effort. The species is likely, therefore, to have been overlooked at many localities where it occurs.

Lastly, *Rhipidomys nitela* was shown in a PCA to be morphometrically distinct from material collected in the Serra da Ibiapaba (Ceará, Brazil), provisionally referred to as "cearanus". A plot of specimen scores on the first two component axes (Fig. 6.17) showed a diagonal separation between *R. nitela* (mostly positive scores on PC1) and "cearanus" (mostly negative on PC1) with little overlap. The first component represented negative general size and PC2 contrasted molar lengths (positive loadings) with mesopterygoid fossa breadth (negative loading). The larger specimens from north and south of the Guiana Highlands were closer to "cearanus" than other *R. nitela*; nearly all the "fervidus" and "yuruanus" points lay close to the dividing line, as did half of the points for Amazonian specimens, the rest lying well within the main *R. nitela* cluster. This reflected the arrangement seen earlier in relation to the "emiliae" sample (Fig. 6.12): the "fervidus/yuruanus" specimens, and to a certain extent those from the

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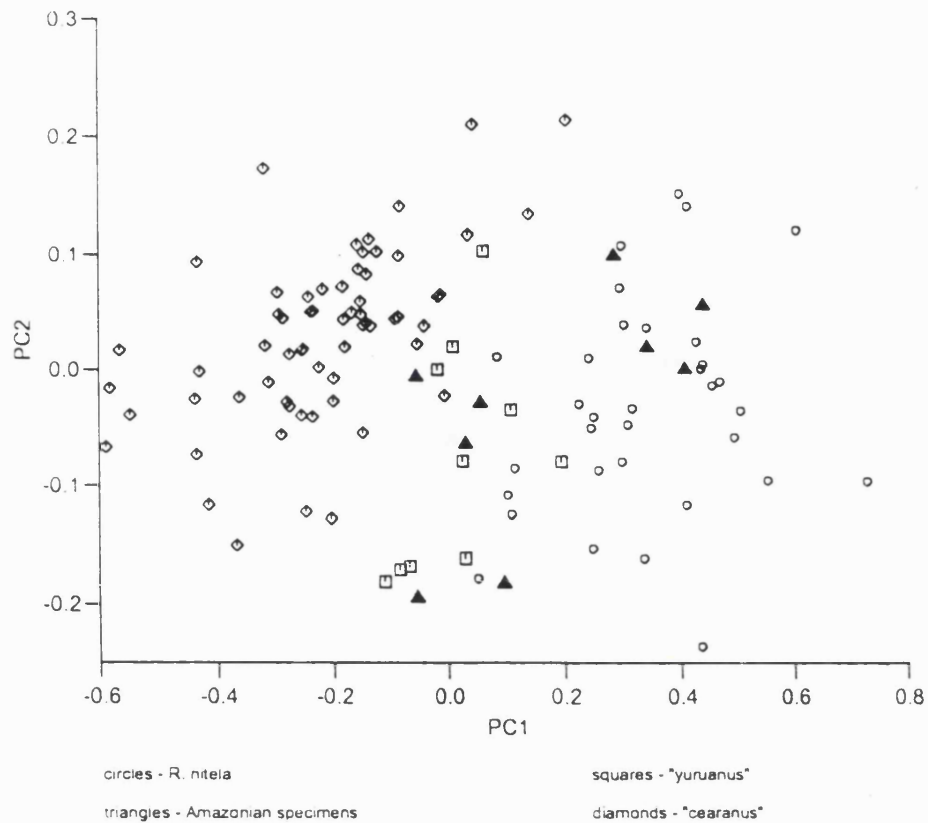**Fig. 6.17** - *Rhipidomys nitela* and "cearanus": plot of scores on the first two principal component axes.

Tapajós, were shown to be intermediate in size between "emiliae" and the Guiana Highland samples of *R. nitela*. This raises the possibility that these larger forms might belong with "emiliae" rather than with *R. nitela*. The Tapajós specimens, particularly, have a relatively narrow occipital region like "emiliae", and they are geographically intermediate between Belém and the Guiana Highlands. However, in their smaller overall size, narrower hind foot and shorter toes they resemble other *R. nitela*. Thus on the basis of the external and cranial morphology of existing samples, it is extremely difficult to allocate these specimens to one group or the other with any degree of certainty. For want of more compelling evidence to the contrary, they are best left in *R. nitela* for the present. More and better samples need to be collected systematically from the whole region and other forms of data must be stored, including karyotypes, which may well prove important in distinguishing *R. nitela* from its neighbours.

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Relations between the populations included within *Rhipidomys nitela* are also difficult to elucidate. As in the cases of *R. leucodactylus* and *R. latimanus* there is considerable geographical variation within the species, but samples are too scattered to determine whether it is clinal or discrete, and therefore whether or not division into subspecies would be justified. The difference in skull size between the small "milleri" specimens (from the eastern end of the main highland massif in Guyana) and the much larger "yuruanus" and Tapajós specimens, for instance, is difficult to reconcile in a single, undivided taxon; yet the "milleri" are morphometrically close to the type series and Suriname sample, which in turn intergrade with material from the Gran Sabana (SE Bolívar state), the larger specimens of which approach "yuruanus" in size. Pelage colour varies with habitat, from dull, greyish brown agouti in savanna regions (Kanuku Mountains and Suriname), to brighter reddish or orange brown in lowland rainforests both north and south of the highlands; the most intensely pigmented specimen of all those examined is the holotype of *fervidus* from the lower Caura valley. Ventrally the hairs frequently have pale grey bases in specimens from the highlands and foothills; in lowland forms they are white to the base. The darkness and distinctness of the hind foot patch and the colour of ears and tail vary without any obvious pattern.

Except in overall size, cranial differences between samples are slight. The edges of the interorbit are usually squared or slightly ledged, in most cases diverging from a point well forward; sometimes the divergence starts further back, giving a narrower, more rounded appearance to the region (as in the holotype of *nitela*, but not the paratypes). The ledges are heavier and slightly raised in specimens from the Manaus area of the Amazon basin and in "yuruanus" and "fervidus". The rostrum is usually short and rather broad, but it is more slender and pointed in the specimens from Little Tobago and Bonda. The "yuruanus", "fervidus" and Bonda specimens also have more elongate skulls than the typical form, with a slightly more evident zygomatic notch and longer, flatter braincase. Tapajós specimens have a narrower braincase and palate and relatively broader interorbit. The molars of "milleri" average smaller (mean = 4.25, range = 3.80-4.54, s.d. = 0.21, n = 11), and those of Tapajós specimens larger (mean = 4.77, range = 4.59-4.94, s.d. = 0.12, n = 10) than the remainder, but overlap is great except between these extreme samples.

The "fervidus/yuruanus" form thus differs somewhat from highland *R. nitela* in size, coloration and skull shape. With its range apparently circumscribed between the edge of the highlands and the llanos and Orinoco delta, it has the attributes required of

a subspecies. In contrast, the specimens from Little Tobago and Bonda are not clearly distinguished morphometrically from the highland form, although both have a more pointed rostrum, the Bonda individual has an elongated braincase, and the Little Tobago specimen has small yet conspicuous sphenopalatine vacuities (absent or very rudimentary in all other specimens). But without larger samples to indicate the extent of individual variation, it seems inadvisable to allocate them to their own subspecies. Similar considerations apply to the few specimens examined from Amapá (one skin only), the Serra do Roncador and the Manaus area, although karyotype information suggests that the latter at least, with a diploid number of 50 (Silva, 1994), may deserve more formal recognition. The larger sample from the lower Rio Tapajós is characterized by an elongated skull with narrow braincase. However, neither is it clearly distinguished morphologically or morphometrically from other samples of *R. nitela*, particularly the "fervidus/yuruanus" group, nor can its relations with the other Amazonian (Manaus and Roncador) populations be resolved without larger samples of these. Finally, although the "milleri" sample appears distinctive in its small size and especially its small molars, there is substantial overlap with specimens from other areas. Thus only the northern lowland form appears at present to be diagnosable as a separate subspecies. If it were formally recognized as such, however, it would leave the nominotypical subspecies containing an assemblage of forms united only through lacking the qualities that defined the "fervidus/yuruanus" taxon, and therefore undiagnosable. So despite the considerable variation included within *Rhipidomys nitela* as understood here, formal recognition of subspecies would at present be inappropriate.

Neighbouring *Rhipidomys nitela* to the east is the "emiliae" population from the region of Belém (Pará, Brazil). At first sight the eight specimens in the USNM collections (some of which may have been kept in captivity) appeared to represent two rather different forms: one with dark greyish brown dorsal pelage and a recurved rostrum, and the other with brighter orange-brown agouti pelage and a straighter rostrum. Certain specimens from Belém in other collections, however, proved intermediate in colour and/or curvature of rostrum, so it appears that they all belong to a single, variable population. The measurements taken did not distinguish between the two kinds, and they were treated as one in subsequent analyses. Also allocated to "emiliae" was a specimen from near Turiaçu (state of Maranhão), some 300 km E of Belém, which consistently clustered with the Belém specimens in principal component plots.

As mentioned previously, *R. nitela* is sympatric with a larger form of

Rhipidomys in the Serra do Roncador, northeastern Mato Grosso state. The identity of the larger specimens was investigated in a PCA which included "emiliae" from Pará (1200 km to the N), "macrurus" from Goiás (300-600 km to the E and SE), "maracaju" from Mato Grosso do Sul (1100 km to the S), and *R. austrinus* from southern Bolivia and northern Argentina (1400-1800 km to the SW). In a plot of scores on the first two components, "maracaju" and *R. austrinus* were distinguished from the rest mainly on the first component axis (negative size), whereas a combination of the two axes served to separate "macrurus" from "emiliae" plus the Roncador specimens. The latent vector loadings for the second component suggested that, for a given overall skull size, "emiliae" and Roncador should have smaller molars and bullae and a longer and broader interorbit than "macrurus". A similar combination of variable loadings distinguished "emiliae" and the Roncador sample from "macrurus" in other analyses in which they were included. It is reasonable, therefore, to identify the larger specimens from Roncador with "emiliae".

The "emiliae" sample was next compared with specimens from further east in the state of Ceará. These consisted of a large series from São Benedito ("cearanus") and samples from Crato and Pacoti. As usual, the first component (accounting for 48% of total variation) represented negative general size, but with reduced contributions from PBL, MFB and IOB; the Crato and Pacoti samples coincided with the largest "cearanus" on this axis, while most "emiliae" fell in the middle of the "cearanus" cluster. The second component (15% of variation) sorted most "emiliae" from the other groups; this latent vector consisted mainly of large positive loadings for IOB, TFL and PBL and large negative ones for MMR, MRC, ZPL and BW. Thus "emiliae" were distinguished once again by their small molars and bullae and their long, broad interorbit. Distinct from their neighbours on all sides, these specimens deserve recognition as the species *Rhipidomys emiliae* J. A. Allen.

c) Eastern Brazil.

Brazil possesses a wide diversity of vegetation types, from the dense rainforests of Amazonia to the open pampa grasslands of the extreme south (Fig. 6.18). The predominant domain in central Brazil is *cerrado*, a term that embraces a variety of savanna-type landscapes that occupy most of the central plateau region and interdigitate in a complex way with other types of vegetation; the cerrado is crossed by gallery forests accompanying the rivers and streams. Much of the semi-arid northeast is covered by various forms of *caatinga* or thornscrub; rainfall is irregular and nearly all rivers are

Fig. 6.18 - Main natural vegetation types of Brazil. Highly simplified from Fundação Instituto Brasileiro de Geografia e Estatística (1993). Areas of transitional vegetation and enclaves not shown.

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intermittent. The Atlantic rainforest that once grew along the whole eastern coast has now been almost totally cleared for agriculture, except in certain mountainous areas, especially towards the south; inland of the coastal ranges the forest becomes semi-deciduous and eventually deciduous. Large areas of transitional vegetation types exist between and within the principal domains but for the sake of simplicity have been omitted from the map.

Small mammals from a number of localities in eastern Brazil are well represented in the collections of the Museu Nacional, Rio de Janeiro. Between 1937 and 1945 the Brazilian Yellow Fever Research Service (Serviço de Estudos e Pesquisas sobre a Febre Amarela - SEPSFA, a joint undertaking of the Brazilian Ministry of Education and Health and the Rockefeller Foundation International Health Division) made collections at several points between southern Mato Grosso (Maracaju) and southern Bahia (Ilhéus). Numerically even more important were the mammals collected between 1952 and 1955 in northeastern Brazil by the National Plague Service (Serviço Nacional da Peste - SNP) - 44,000 were taken in five states from Piauí to Alagoas (Freitas, 1957) and many thousands more in Sergipe and Bahia.

In the *caatinga* region of the northeast, *Rhipidomys* was found in isolated mesic forests known locally as *brejos* (a term that in other parts of Brazil refers to swampland) situated mainly on the north and east-facing slopes of the massifs, where the prevailing winds from the ocean deposit their moisture. Varying in size, structure and floristic composition, these enclaves may be much altered relicts of a former continuous forest belt linking the Amazon and Atlantic forest domains (Vanzolini, 1981). The large series of "cearanus" mentioned above was collected by the SNP in the vicinity of São Benedito, in the Serra da Ibiapaba in western Ceará state, very close to the type locality of *Rhipidomys cearanus*. Specimen labels give the local name *"rato sarapó"* (probably of Tupi origin) and indicate that they were found mainly in hollow trees in the forest. These mice are moderate in size with fairly long tails; they have reddish-brown, rather sleek dorsal pelage with little agouti effect, and white underparts.

In contrast, the samples from Pacoti (in the isolated Serra de Baturité in the north of the state) and Crato (in the Cariri *brejo* in the south) are larger overall, with hind feet that are longer (27-30 mm as against 26-28 mm) and noticeably broader, larger ears, and larger molars; they have duller, less reddish and more evidently agouti dorsal fur, and white ventral pelage which is somewhat woolly in texture. The Pacoti specimens were collected in sugar cane and coffee plantations. Those from Crato, known locally as *"ratos palmeira"* - palm rats, were mostly shot in plantations and palm trees; they

were originally misidentified in the field as *Holochilus* (and were listed as such by Freitas, 1957). These animals are unlikely to represent the same taxon as the "cearanus" sample. Three specimens of uncertain provenance but possibly from the Jequitinhonha valley in NE Minas Gerais (UFMG specimens Jequi XCI, XCVIII and C) resemble the Crato sample in their large feet and conspicuously agouti pelage, but are more greyish brown dorsally and have longer, darker tails and less robust skulls.

Most other *Rhipidomys* specimens collected in eastern Brazil are similar in external appearance to the "cearanus" sample. Adult body size varies more within samples than between them. Hind foot length is fairly constant at about 26-28 mm c.u., but in most specimens from the central plateau (Brasília and Anápolis) it is a couple of millimetres less. Dorsal colour shows a certain amount of variation between localities: the Caruaru sample from the Pernambuco plateau is mainly a deeper red; a small series of old adults from São Felipe (near Salvador, Bahia) is bright, intense orange; specimens from Brasília tend to be rather greyer; in the samples from Teresópolis (Rio de Janeiro state) and Ilhéus (southern Bahia) the dorsal pelage ranges from a dull, chocolate brown to a brighter reddish brown. Ventral pelage is always creamy white throughout or with barely noticeable pale grey bases to the hairs, particularly at the sides of the belly. The tail is usually moderately long with a short pencil.

Skulls are also difficult to tell apart. Most have a short, broad rostrum, a ledged (rather than ridged) interorbit, and a moderately broad, rounded braincase. The rostrum is longer and narrower in the putative Jequitinhonha sample, and perhaps shorter than usual in material from Brasília. Supraorbital ridges are better developed in the Crato and Pacoti samples and in older, larger skulls from elsewhere, particularly amongst the Caruaru, Jequié (S Bahia) and Ilhéus samples; in contrast, specimens from Brasília and the southeast tend to have more rounded interorbits with squared edges. The molar row length of the Crato and Pacoti samples averages longer than that of the remainder, partly because the third upper molar is less reduced in size. Nevertheless, differences are slight and inconstant, even between the Crato-Pacoti samples and other specimens. When external and craniodental characters are taken together, only the Crato, Pacoti and Jequitinhonha specimens stand out, whereas the remaining specimens appear to form a relatively uniform grouping.

The presence in eastern Brazil of two very distinct karyotype groups (see references in Table 6.1), however, indicates that the latter assemblage must include at least two separate taxa. A fundamental number of 74 has been found in specimens from

central Minas Gerais (Lagoa Santa), the coastal plain of Rio de Janeiro (Fazenda União) and southern Bahia (Fazenda Unacau), and a high but unspecified FN is reported from the plateau of Pernambuco (Serra dos Cavalos). Specimens with FN in the range of 48-51 are known from the central plateau (Granja do Ipê and Águas Emendadas, near Brasília, Federal District), the São Francisco valley near the Minas Gerais-Bahia border (Mocambinho), and the coastal mountains and foothills in the states of São Paulo (Casa Grande), Rio de Janeiro (Garrafão) and Espírito Santo (Hotel Fazenda Monte Verde). The karyotyped specimens from Serra dos Cavalos, Unacau and Lagoa Santa were unfortunately not in the required age range to be included in morphometric analyses; however, the ones from Serra dos Cavalos are very similar in all respects to the large sample from nearby Caruaru, while those from Fazenda Unacau fit in well with the series from around Ilhéus, a few kilometres away. I was unable to examine the specimens from Fazenda União, Garrafão and Águas Emendadas directly, but I was provided with photographs of the first two (courtesy Lena Geise).

Although there are very few localities in eastern Brazil from which specimens of *Rhipidomys* have been karyotyped, the pattern of known distribution of the two morphs in the Atlantic forest region is partially congruent with the ranges of at least three pairs of "sibling" species of birds, mice and opossums. In each case one species is found mainly at higher altitudes in the mountain ranges parallel to the coast while the other occupies the coastal lowlands and the interior; at intermediate elevations the two may be sympatric (Fig. 6.19).

Although the antbird *Drymophila rubricollis* (Formicariidae) had long been relegated to the synonymy of *D. ferruginea*, Willis (1988) was able to discriminate between these forest-dwelling species on the basis of their songs as well as their plumage and proportions. Through personal observations in the field and examination of specimens preserved in museum collections he related their occurrence to details of habitat and elevation. *D. ferruginea* is found in mixed dicot and bamboo forest in the coastal lowlands from Bahia to Santa Catarina state, up to 850 metres or so on the coastal ranges (Serra do Mar, Serra dos Órgãos) and to over 1200 m on the Serra da Mantiqueira, thence spreading northwest across the interior plateau of São Paulo and Minas Gerais. *D. rubricollis* occurs from eastern Paraguay, Misiones (NE Argentina) and northern Rio Grande do Sul, across Paraná state to the higher levels of the coastal and interior ranges of SE Brazil, where it is found in dense bamboo stands. Willis found the birds to be sympatric at several points in São Paulo and Rio de Janeiro states. Thus *D. ferruginea*
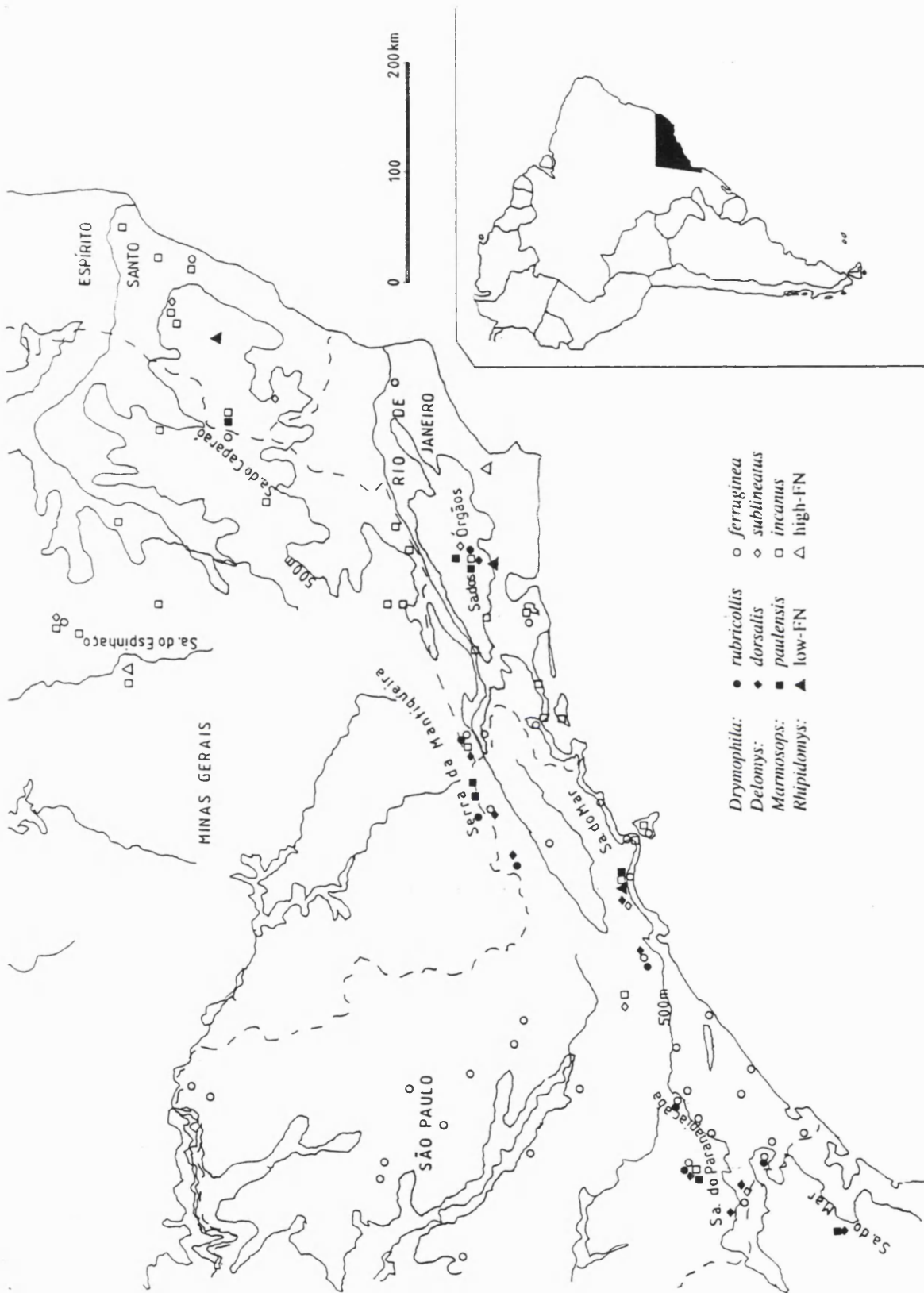
Fig. 6.19 - Distribution of four pairs of "sibling" species in SE Brazil. Data from Willis (1988), Voss (1993), Mustrangi (1995), Zanchin et al. (1992a) and Svartman & Almeida (1993). Positions of most *Drymophila ferruginea* points are approximate.

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is a more northern, interior and lowland species, whereas *D. rubricollis* has an essentially southern and upland distribution. The range of the latter species is remarkably similar to that of the Parana pine, *Araucaria angustifolia*, which is also widespread in the states of Santa Catarina and Paraná but restricted to the highest parts of the mountain ranges from São Paulo to Rio de Janeiro and Minas Gerais (Hueck, 1972, fig. 121).

In his revision of the sigmodontine rodent genus *Delomys*, Voss (1993) demonstrated that *Delomys sublineatus* and *D. dorsalis* could be distinguished on the basis of their colour and external morphology, although he was unable to find consistent differences in craniodental characters. The two species also differ in karyotype (Zanchin et al, 1992b). Whereas *D. sublineatus* has been found to occur along the coast from Espírito Santo to Santa Catarina and inland in Minas Gerais and São Paulo, *D. dorsalis* is distributed from Misiones and Rio Grande do Sul northeastwards to the mountain ranges of São Paulo and Rio de Janeiro, where it occurs mainly at higher elevations. There is some evidence to suggest that *D. sublineatus* can tolerate rather less humid conditions than *D. dorsalis*. As with *Drymophila*, the two species have been found in sympatry at a number of localities in these mountains.

With the aid of mitochondrial cytochrome b sequences, Mustrangi (1995) found that the opossum taxon generally regarded as *Marmosops incanus* was in fact a composite of two species, *M. incanus* and *M. paulensis*. This discovery led her to discern congruent differences in the animals' external and cranial morphology and to recognize a correspondence between their distribution pattern and that of the previous pairs of species. In this case, *M. incanus* is the form more widely distributed along the coast from Bahia to Paraná and in the semi-deciduous forests on the inland plateau of Minas Gerais. *M. paulensis* is restricted to the montane forests above 800 m on the coastal and interior ranges of the southeast, and once again there is sympatry at several localities in these mountains.

The *Marmosops* distribution pattern differs in two minor ways from that of *Drymophila* and *Delomys*. The montane species, *Marmosops paulensis*, has not been recorded from farther south than southern São Paulo, and thus appears to be endemic to the mountains of southeastern Brazil, whereas both *Drymophila rubricollis* and *Delomys dorsalis* have been found in Misiones and Rio Grande do Sul. Secondly, the lowland/interior species, *Marmosops incanus*, differs from

Drymophila ferruginea and *Delomys sublineatus* in that it is stated to occur in Minas Gerais as far inland as Mocambinho, in the São Francisco valley, while it has not been recorded from the inland plateau region of São Paulo. These differences may of course be due to inadequate sampling in these areas, but the Mocambinho record in particular is relevant to the case of the two *Rhipidomys* karyomorphs.

Having been collected on the coastal plain of Rio de Janeiro and southern Bahia as well as at Lagoa Santa on the Minas Gerais plateau, the high-FN form of *Rhipidomys* appears to be congruent with the more northerly, lowland/interior taxon in each of the previous species pairs. The low-FN morph is known from three localities in the coastal ranges of southeastern Brazil - Casa Grande, Garrafão and Monte Verde - and thus resembles the southern, higher-altitude forms. The similarity is striking but not perfect, because the altitude difference in the case of *Rhipidomys* is less clear-cut. Whereas in the other three genera the highland form was found nearly always at elevations above 800 m in the northern part of its range, the low-FN specimens from Garrafão were collected at an elevation of only 300 m, one third of the way up the escarpment. The exact altitude of Hotel Fazenda Monte Verde is not known but it may well be less than 800 m.

A series of *Rhipidomys* was collected in 1942-43 in virgin montane rainforest at the top of the escarpment at Fazenda Comari (also known as Fazenda Carlos Guinle) in Teresópolis, about 5 km north of Garrafão and 600 m higher. Several *Delomys dorsalis* were also collected there, while *D. sublineatus* was taken in drier secondary forest in the lee of the ridge at Fazenda Boa Fé, a locality where no *Rhipidomys* were found. *Drymophila rubricollis* and both *Marmosops* species have been recorded from Teresópolis, but Willis (1988) and Mustrangi (1995) do not give details of their exact provenance. It is tempting to surmise that the *Rhipidomys* specimens from Comari should belong to the same low-FN form as the two karyotyped individuals from Garrafão, given that the habitat in both areas is (or was) relatively undisturbed, wet montane forest. However, the relation between the two karyomorphs and their habitat is far from clear, and they may yet be found to occur sympatrically in the same forest, just as the two species of *Delomys* have been trapped within 5 m of the same spot at Boracéia, near Casa Grande (B. D. Patterson, pers. comm., *in* Voss, 1993). The same reasoning applies to the *Rhipidomys* specimens taken at Casa Grande and Boracéia, which need not all be conspecific with the karyotyped individual from there.

Although this general distributional hypothesis cannot determine which form will

be found at particular locations in the coastal mountains, it does allow predictions to be made outside the possible areas of sympatry. Thus the *Rhipidomys* specimens from Ilhéus and Jequié in southern Bahia are likely to belong to the high-FN form, as are specimens from localities that lie within the original limits of Atlantic forest in central Minas Gerais, like Lagoa Santa, the type locality of *R. mastacalis*. Since the low-FN form is not expected to occur there, the name *mastacalis* may reasonably be restricted to the high-FN karyomorph.

Beyond this point the hypothesis no longer holds. At Mocambinho, in the São Francisco valley some 550 km north of Lagoa Santa, the *Rhipidomys* and *Marmosops* data conflict: Mustrangi (1995) identifies the local species as *M. incanus*, the same as at Lagoa Santa (albeit without DNA data to confirm the identification), whereas the *Rhipidomys* specimen from Mocambinho has a karyotype with low FN. A similar (but not identical) karyotype occurs 400 km west of Mocambinho in the *Rhipidomys* population around Brasília. In none of the other three species pairs does either form occur there on the central Brazilian plateau. This raises the suspicion that the Brasília form, found in gallery forests in the cerrado, might represent a different taxon from the low-FN morph present in the montane forests of the coastal ranges 900 km to the southeast, from which it is separated by *R. mastacalis*. On the assumption that the Brasília taxon spreads over the central plateau as far as Crixás on its western edge, the name *Rhipidomys macrurus* is available for it. No names are available for the other known low-FN populations.

In addition to *mastacalis, macrurus* and *cearanus*, two other nominal taxa referrable to *Rhipidomys* have been described from the region. The holotype of *Mus maculipes* Pictet & Pictet was part of a collection sent to the Geneva Museum from Bahia without details of exact provenance. The specimen is not in good condition (the skin is overstuffed and the fur has become stuck down, the tail is broken, and much of the braincase is missing or poorly reconstructed), but it is definitely a *Rhipidomys*, and in the intact part of its skull it closely resembles the sample from Jequié, SE Bahia. The name *maculipes* may therefore be regarded as available for the high-FN morph from that area. The second holotype is that of *Hesperomys leucodactylus* Wagner, collected by Johann Natterer at Porto do Rio Paraná (now Igarapava), on the northern border of São Paulo state; from photographs of the skull (courtesy of Alfredo Langguth and Mario de Vivo) it was not possible to identify it beyond doubt as either *R.*

mastacalis or *R. macrurus*, but if the distribution of *Rhipidomys* in this area is congruent with that of *Drymophila*, *R. mastacalis* is the species expected. Wagner published his name in 1845, after *mastacalis*, before *macrurus* and in the same year as Tschudi's *leucodactylus*. It has not proved possible to establish priority between Tschudi's and Wagner's homonyms, but in view of the fact that *leucodactylus* Tschudi is the widely used and senior name for the type species of *Rhipidomys*, whereas to my knowledge *leucodactylus* Wagner has been mentioned in the literature only three times this century (Tate, 1932: 5, as a *Rhipidomys*; Moojen, 1952: 75, and Vieira, 1955: 419, as an *Hesperomys*), Wagner's name should be rejected as a junior homonym. As such, it would not take priority over *macrurus* if the two came to be regarded as synonyms.

In the hope that morphometric methods might reveal cranial differences between the two karyomorphs, a principal components analysis was performed first on the presumably low-FN "macrurus" from the central plateau (Brasília, Anápolis, Formosa and Nova Roma) and samples from SE Bahia (Ilhéus, Jequié and Três Braços) provisionally identified with the high-FN morph. No separation was evident on the first axis; the loadings on the corresponding latent vector, which corresponded to 41% of total sample variation, were all negative but not uniform in magnitude. In a plot of scores on the second and third component axes the "macrurus" and SE Bahia groups tended to cluster separately, albeit with some overlap on both sides (Fig. 6.20). In particular, both specimens from Nova Roma scored low on the second component and clustered with the Bahian group. The second latent vector (11.7% of total variation) had large positive loadings for molar row lengths plus MFB and BW and large negative ones for NL, ZPL and PBL, while the third (11.4%) contrasted palatal and bullar breadths (positive) with IOB, PBL and MMR (negative). The scores suggested that "macrurus" specimens should have some or all of the following features in comparison with the SE Bahian group: larger teeth and bullae, a relatively short, broad palate, broader mesopterygoid fossa, shorter nasals and a narrower interorbit. While the raw data do not show any significant difference in molar row length, the "macrurus" sample does have a narrower interorbit than the other group and a palatal bridge that is usually shorter than the molar row, whereas in Ilhéus and Jequié specimens the palatal bridge is often marginally longer than the teeth.

The "macrurus" specimens were next analysed together with the "cearanus" sample from the area of São Benedito, Ceará. The resulting principal components were somewhat

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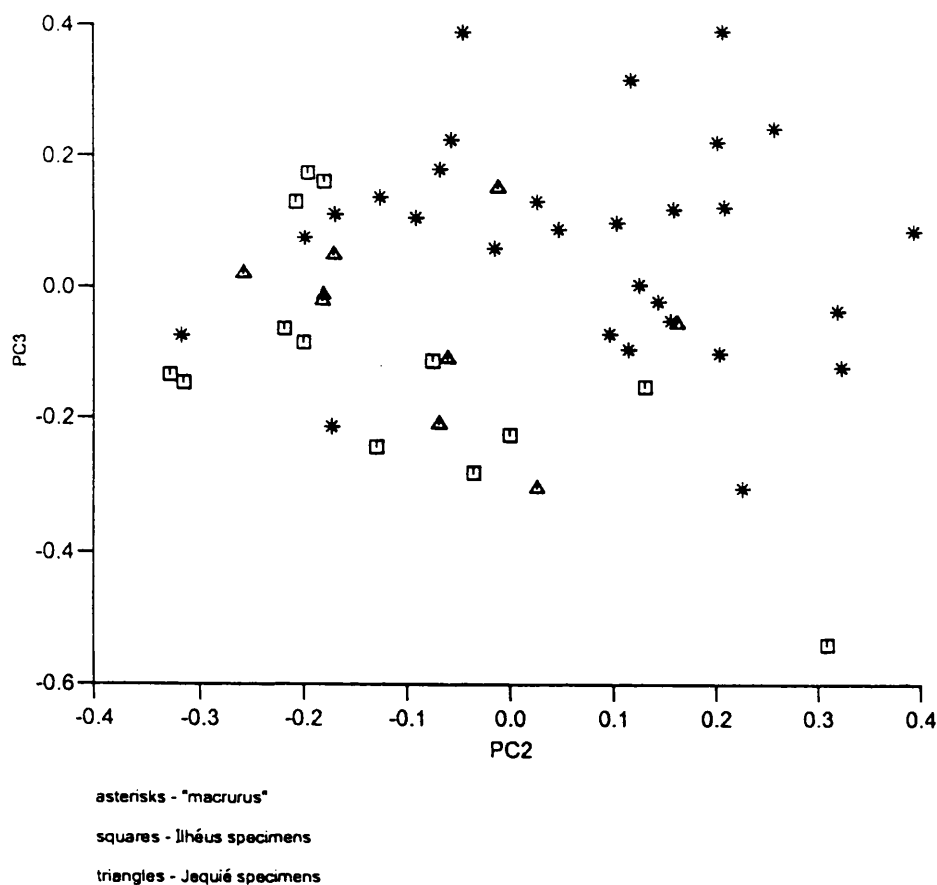
Fig. 6.20 - *Rhipidomys* from central and eastern Brazil - "macrurus", Ilhéus and Jequié samples: plot of scores on the second and third principal component axes.

similar to those in the previous analysis: the second latent vector (11.7% of total variation) had large loadings (this time negative) for molar row lengths and MFB and positive ones for ZPL and NL, while the third (8.1% of variation) contrasted PBL plus MMR (positive) with PB1 plus MFB and IOB (negative). In a plot of scores on the second and third component axes a certain separation between samples was evident, due mostly to component 2. The main "macrurus" cluster was distinguished from the "cearanus" specimens principally by some or all of the following: relatively larger molars, broader mesopterygoid fossa, narrower zygomatic plate (i.e., shorter on the longitudinal axis of the skull), and shorter nasals; there was also some suggestion of a shorter, broader palatal bridge. In this analysis most of the "misplaced" points were on just one side where a number of the "macrurus" specimens clustered with the "cearanus". Many of these specimens were in fact the same ones with rather smaller molars that lay away from the

rest of their sample in the previous plot, including the two from Nova Roma.

The following analysis included "macrurus" and the remaining samples from northeastern Brazil, i.e. those from Crato and Pacoti (Ceará), Caruaru (Pernambuco, including one specimen from Garanhuns) and the São Francisco valley (western Bahia and northern Minas Gerais). The first component (44% of total variation) represented negative general size, but with low contributions from PBL, PB1, MFB and IOB. On this axis the Crato, Pacoti and S. Francisco specimens scored lower (i.e., were larger) than the overall mean. On the second axis the Pacoti and S. Francisco samples (negative scores) were segregated from the Crato and most Caruaru specimens (positive scores), whereas the "macrurus" were spread throughout. Latent vector 2 (11.3% of total variation) had large positive loadings for MFB, PB1 and IOB and large negative ones for MRC, MMR and BW. On this component each dental age class had a significantly different mean score from each of the others ($p \leq 0.001$), DAC 2 scoring high and DAC 4 low, corresponding to the fact that both the Crato and the Caruaru samples contained a large proportion of older adults (DAC 4) while the Pacoti and S. Francisco samples contained none. The fact that the "macrurus" specimens were not significantly sorted by age class along this axis indicates that the variation expressed by this component was not merely ontogenetic but reflected genuine differences between the samples; the apparent age effect was thus merely due to the composition of the segregated samples.

The third component (10.2% of total variation) was concerned essentially with the relative shape of the palate and base of the skull, having large positive loadings for PBL and IOB and large negative ones for BW, MFB and PB1. Although confusing at first sight, a plot of scores on the second and third axes revealed three main groupings with a small amount of overlap (Fig. 6.21): a) Crato and "macrurus" together, with negative scores on PC3; b) Pacoti and São Francisco together, with scores that were negative on PC2 and around zero on PC3; and c) Caruaru alone, with positive scores on PC3 and positive or small negative scores on PC2. Most of the overlapping points were for "macrurus" specimens that scored higher than the majority on PC3 (but not all were the same individuals as were misplaced in the previous plots). Although the Pacoti and S. Francisco samples clustered together on the first three components, the fifth provided reasonable separation between them. The fifth latent vector (5.7% of total variation) had large positive loadings for IOB, MMR, MFB and MRC, and negative ones for ZPL, PBL and BW; the Pacoti (and most Caruaru) specimens scored higher than all but one of the São Francisco sample.
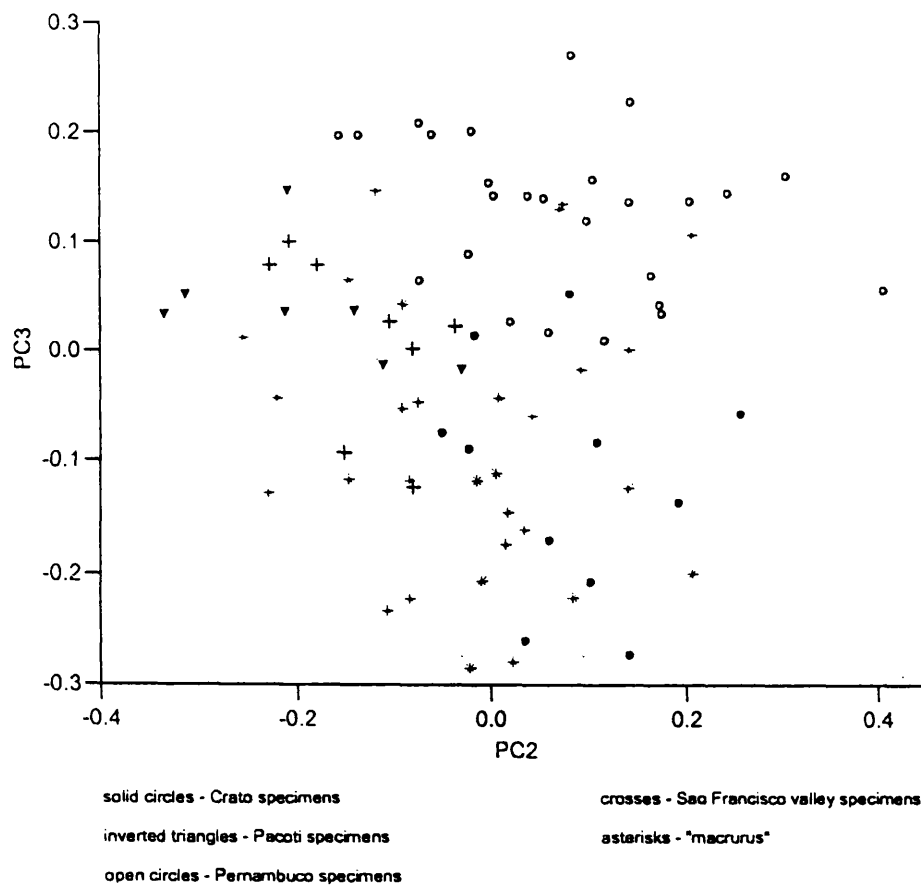
Fig. 6.21 - *Rhipidomys* from central and NE Brazil: plot of scores on the second and third principal component axes.

This analysis revealed that the five main samples were morphometrically slightly different from each other, although none of them was totally distinct from the rest. Despite their external resemblance, the Crato and Pacoti samples did not group together in any of the plots examined. Instead, the Crato and "macrurus" samples often clustered together on account of their broader palate and mesopterygoid fossa, although they are distinguished readily by external proportions, particularly hind-foot length. The Pacoti and São Francisco specimens were also frequently mixed together in the plots; they are a little more similar to each other in external appearance than the previous pair, but they are still separable.

The "macrurus" sample was finally compared in a PCA with material from SE Brazil. This included the nine analysable members of the Teresópolis series, seven specimens from elsewhere in the coastal plains and mountains (Casa Grande, Boracéia,

Ilha Grande, Monte Verde) and six from inland in Minas Gerais (Ibitipoca and Peti in semi-deciduous Atlantic forest; and São Roque de Minas, Pedrinópolis and Perdizes in forest patches and galleries within the cerrado). Although this material is likely to include both high-FN and low-FN specimens, no clear patterns were discernible either on single component axes or in bicomponent plots. In case the presence of "macrurus" might be preventing patterns amongst the southeastern specimens from emerging clearly in the first few components, the analysis was redone without "macrurus" and with the addition of the small-bodied "cerrado" sample (mentioned previously in connection with *Rhipidomys nitela*), three members of which were from Serra da Canastra, near São Roque de Minas. Only eight variables were used in order to exclude fewer damaged specimens, including one from Passos, about 60 km from São Roque de Minas but in an area originally covered by semi-deciduous forest. Again, the results were rather inconclusive. The four small "cerrado" specimens stayed fairly close together in all plots involving the first five components; likewise the other two individuals from São Roque de Minas often lay close to the two from Pedrinópolis and Perdizes, and the four from Boracéia and Casa Grande formed another moderately compact group. But the position of these three small clusters in relation to each other, to the Teresópolis specimens and to the remaining points was inconstant. The Passos specimen lay close to the small "cerrado" sample on components 1 to 3, but was widely separated from them on component 4 on account of its broader braincase and smaller molars. The Teresópolis series did not form a tight cluster but was widely scattered along all the axes; neither did it display a bimodal distribution, as might be expected if it were a composite of two taxa.

There is evidently a large amount of variation within the *Rhipidomys* specimens from SE Brazil but it is not easily related to the two-karyomorph hypothesis. Instead, in the available material it appears to be randomly distributed. The samples that have been collected are generally small and from scattered localities, with a large proportion of immature or damaged specimens, so it is to be hoped that more material, particularly karyotyped material, would allow the recognition of external and cranial characters diagnostic of the morphs. For the present, however, all that can be said is that in this area the low-FN form *may* be associated with a longer tail, smaller ears, a broader, more inflated braincase (and consequently more divergent supraorbital ledges), and larger bullae than the high-FN form - characters observed in the karyotyped individuals examined and in photographs of the Garrafão and Fazenda União specimens. With regard to the small-bodied specimens from the cerrado, the analysed sample is too small to show clearly their

relations with larger individuals from similar habitats. It is possible that a more representative sample from the area would show that size varied continuously from small to large. Unusually small specimens with molars of normal size are known from a number of *Rhipidomys* taxa (e.g., AMNH 30731 in the "yuruanus" group of *R. nitela*, or the type specimen of *R. fulviventer tenuicauda*). Provided they are similar in form, they are most parsimoniously regarded as statistically outlying members of the surrounding population. Since in the present case individual variation within the small amount of material available from the region makes it difficult to establish a basic form for comparison, creation of a new taxon for the small specimens is not yet warranted.

When analysed together with the samples from Bahia and northern Minas Gerais (Ilhéus, Jequié, São Francisco valley), the southeastern specimens clustered together on the second and fourth component axes in opposition to some or all of the other groups, albeit with some overlap. According to the loadings on the second and fourth latent vectors (11.1% and 8.8% of total variation, respectively), the southeastern grouping should have a combination of shorter palate and nasals and/or broader mesopterygoid fossa; the São Francisco material should have larger bullae, longer palatal bridge and/or narrow mesopterygoid fossa; and the Ilhéus and Jequié specimens should have longer nasals and/or smaller bullae. On component 3, however, the four specimens from *cerrado* habitat (from São Roque de Minas, Pedrinópolis and Perdizes) were separated from most other southeastern specimens and associated with those from the dry forests of the São Francisco valley in having larger bullae and perhaps a broader palate, and/or braincase than the others. The Ilhéus and Jequié samples generally grouped together except on component axis 5, which suggested the Jequié specimens had a broader braincase and mesopterygoid fossa, a shallower mandible and narrower zygomatic plate than those from Ilhéus. Finally, the single specimen from Santa Teresa, Espírito Santo state, grouped consistently with the Ilhéus sample and not with the Monte Verde specimen, suggesting that both karyomorphs are to be found in the hills of Espírito Santo.

The next analysis dealt with material from northern Minas Gerais, inland Bahia and Ceará, i.e. the samples from the São Francisco valley, Jequitinhonha, Jequié, Vitória da Conquista, Crato and Pacoti. The first latent vector (42% of total variation) represented negative general size, but with lower contributions from PBL and PB1 and virtually nil from MFB. On this axis the Jequié specimens were noticeably smaller on average than the other samples. The second component (13.2%) expressed a contrast between PBL plus MMR (large positive loadings) and MFB plus PB1 (very large negative
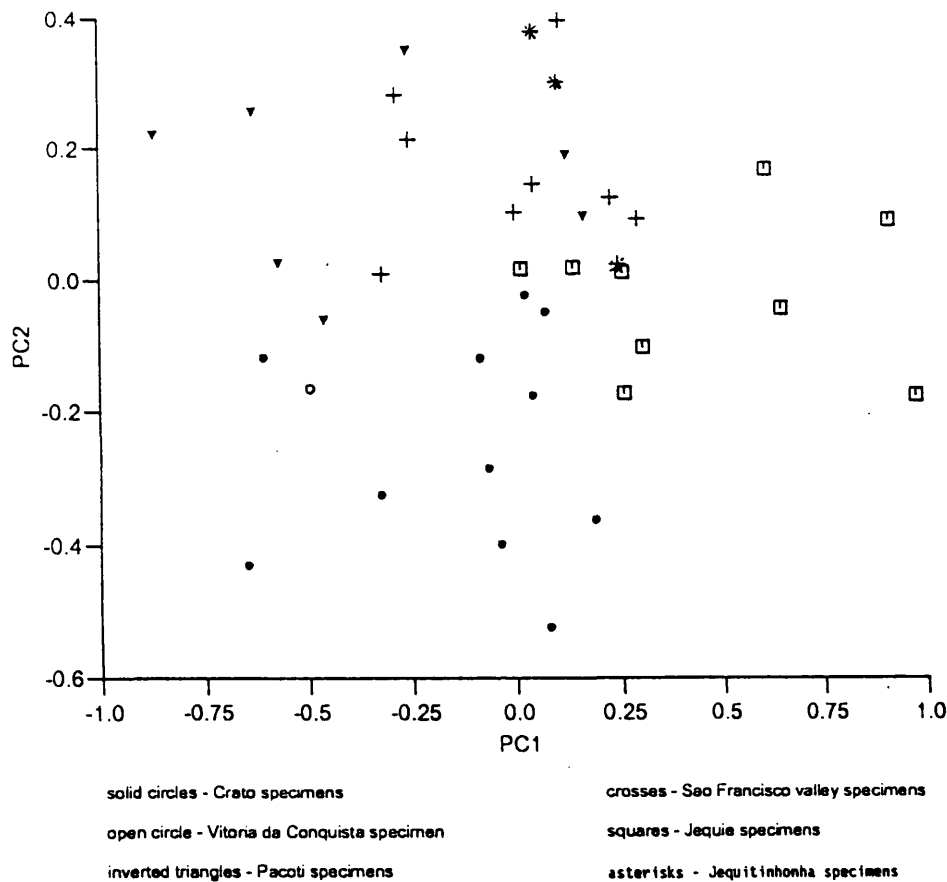
Fig. 6.22 - *Rhipidomys* samples from the interior of NE Brazil: plot of scores on the first two principal component axes.

loadings). In a plot of scores on the first two axes, three main areas were apparent (Fig. 6.22). With negative scores on PC2 the Crato sample was separated from most of the remainder owing to its large size, its broad, short palate and broad mesopterygoid fossa. The Jequié sample had medium scores on the second component and was confined to the positive side of the PC1 space. The São Francisco valley and Pacoti samples could not be separated on these axes, scoring mainly positive on PC2 (i.e., longer, narrower palatal region) and moderate to low on PC1 (medium to large size). The specimen from Vitória da Conquista was ambiguously placed near the boundary between the Crato and the Pacoti/São Francisco areas. The overlap between the São Francisco and Pacoti specimens was partly resolved on the fourth component axis, Pacoti scoring higher than S. Francisco with one specimen overlapping on each side; the corresponding latent vector (just 7.2% of total variation) stressed NL, BCB and PL (positive loadings) against DR, IOB and TFL

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(negative), suggesting that Pacoti specimens would have a longer rostrum and broader braincase in relation to the interorbital region, and/or a shallower mandible.

When the analysis was repeated with the Caruaru sample in place of the one from Jequié, the first component again represented overall skull size (negative, 45% of total variation) but with much lower contributions from basicranial structures. On this axis the Caruaru sample occupied a much larger size range than the remainder, which had mostly negative scores. Component 2 (14% of variation) split Caruaru plus Crato (mostly negative scores) from Pacoti and the Bahia/Minas Gerais material (positive scores), opposing MMR, MRC and BW (large positive loadings) to MFB, IOB and PB1 (large negative ones). On this component the mean scores for each age class differed significantly, reflecting not only the imbalance in age distribution between samples but also ontogenetic patterns within the Caruaru and Crato samples. Thus older members of these groups differed from the other samples more than younger ones did in their relatively broader mesopterygoid fossa, palatal bridge and interorbit compared with molar size. A combination of the first and third components was moderately successful at showing the difference between the Caruaru sample and the rest, the former scoring on average higher on both axes. The third latent vector (9% of total variation) stressed palatal bridge length and palatal length (positive loadings) against bullar and mesopterygoid fossa breadth (negative). Thus for a given overall size, a Caruaru skull would be expected to have longer, narrower ventral structures.

A similar distinction in palatal proportions between the Crato and Pacoti specimens was revealed in the analysis described previously in which *Rhipidomys emiliae* was compared with material from Ceará. Although the third component axis (10% of variation) provided no separation between "cearanus" on the one hand and the Pacoti and Crato specimens on the other, it did distinguish between the last two samples; the corresponding latent vector contrasted PBL and NL (positive) with MFB and PB1 (negative), indicating that Crato specimens had a relatively shorter and broader palate and broader mesopterygoid fossa than those from Pacoti. Some segregation from "cearanus" was apparent along the fifth component axis (4.5% of total variation), admittedly with some overlap. With large positive loadings for SH, NL and ZPL and a large negative loading especially for TFL, the vector suggests that the skulls from Pacoti and Crato were flatter and had shorter nasals and longer orbits than those from São Benedito.

The final PCA restricted to samples from eastern Brazil concerned the two large series from São Benedito ($n = 63$) and Caruaru ($n = 26$). Since these specimens were

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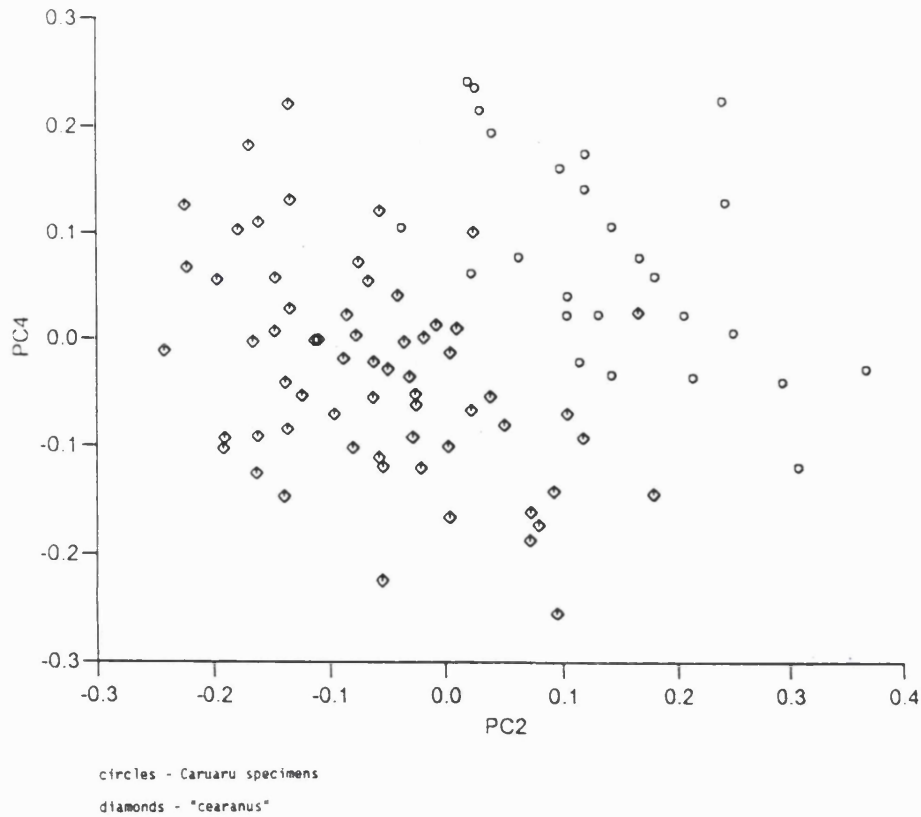
Fig. 6.23 - *Rhipidomys* "cearanus" and the Caruaru sample: plot of scores on the second and fourth principal component axes.

very similar in skull size, no separation between localities was reflected along the first axis. There was, however, a highly significant (p = 0.005) difference in mean score for males and females (males being larger) and between the mean score for dental age class 2 and that for older classes (DAC 2 *v.* DAC 3, p = 0.02; DAC 2 *v.* DAC 4, p = 0.001). A combination of the second and fourth components provided almost complete segregation of the two samples into contiguous clusters, the Caruaru specimens averaging higher scores on both axes (Fig. 6.23). The second latent vector (10.8% of total variation) was formed especially of large positive loadings for MMR, MRC and PBL and large negative ones for BW and ZPL, while the fourth (7.0% of variation) stressed PBL and PL (large positive loadings) and MRC, MMR, BW and PB1 (large negative ones). Thus the main contrast between the two samples was the longer, narrower palatal bridge and narrower bullae of the Caruaru specimens compared with those from São Benedito.

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I have dealt extensively with the principal components analyses of the material from eastern Brazil because the variation that exists in and between the various samples examined is subtle and difficult to assess visually. Numerous combinations of samples were subjected to PCA (more than there is space here to describe in detail); those variables that were most often found to be involved in distinguishing a particular sample in the various analyses in which it was included could then be verified directly in the skulls themselves. Only half a dozen variables were responsible for nearly all the main differences between the samples: PBL, PB1, MFB, BW, NL and MRC, which define the shape of the palatal bridge, the breadth of the mesopterygoid fossa, the relative size of the bullae, the length of the rostrum and the size of the molars.

The "macrurus" sample from Goiás and the Federal District was found to be characterized by a short rostrum, rather narrow interorbit, short and broad palate, broad mesopterygoid fossa and large bullae. Most specimens from southeastern Brazil were similar to this in rostrum, palate and bullae, particularly those from areas of cerrado in western Minas Gerais. A short, broad palate and large bullae were also found in the "cearanus" sample from western Ceará, which had a slightly longer rostrum and broader zygomatic plate than "macrurus". The material from Crato was similar to "macrurus" in cranial proportions, but on average was larger overall and had larger molars. In contrast to all these, the samples from Ilhéus, Jequié and Caruaru coincided in having a longer rostrum, broader interorbit, long and narrow palatal bridge (frequently longer than the toothrow) and small bullae; their molars were similar in size to those of "macrurus" and smaller than those of Crato specimens. Two samples were somewhat intermediate between these two contrasting groups. The Pacoti sample resembled the Crato material in its large overall size, molars and bullae, but it had a longer rostrum, broader interorbit, and narrower palate and mesopterygoid fossa in common with Caruaru. The specimens from the São Francisco valley were characterized by a very narrow mesopterygoid fossa, moderately large molars and bullae, long and narrow palatal bridge and broad zygomatic plate.

The two main groups conform moderately well to the two-karyomorph hypothesis for *Rhipidomys* in eastern Brazil. Thus the "macrurus" and "cearanus" samples correspond to the low-FN form and therefore may be allocated to *R. macrurus*, while the Ilhéus, Jequié and Caruaru samples would be high-FN and identified with *R. mastacalis*. The Crato and Pacoti samples are ambiguous in that they resemble each other and differ from the other specimens in external characters and molar size, yet

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contrast with each other and resemble the other groups in cranial morphometry. I believe that they are distinct enough from the remaining material to warrant recognition at species level (*Rhipidomys* sp. 4); the two populations may be regarded as subspecies. The São Francisco valley specimens share certain character states with each of these three species: in size, external appearance, large auditory bullae and broad zygomatic plate they resemble *R. macrurus*; their molars are rather larger, as in the Crato-Pacoti material; and their palate and mesopterygoid fossa is narrow like *R. mastacalis*. In view of the low-FN karyotype found in a specimen from Mocambinho, they are provisionally allocated to *R. macrurus*.

The above arrangement of the northeastern samples - from São Benedito, Crato, Pacoti and Caruaru - is plausible from a biogeographical perspective. The four localities lie in mesic forest patches separated from each other by semi-arid caatinga. The forests around Pacoti and Crato are completely isolated; the rivers in the region, unlike those of the cerrado farther to the southwest, are seasonal and do not support gallery forests that might link one forested area with another. Caruaru, however, lies towards the northern extreme of the Atlantic forest, now almost totally cleared for agriculture, but in historical times it was connected with the forests of coastal Bahia and the southeast. This continuity is reflected in the morphological resemblance of the sample from Caruaru with those from Ilhéus and Jequié. In contrast, the forests around São Benedito in the Serra da Ibiapaba lie close to the western edge of the caatinga. According to the vegetation map published by the IBGE (Fundação Instituto Brasileiro de Geografia e Estatística, 1993), these forests are linked at their northern end with transitional and seasonal forests in the neighbouring state of Piauí, which extend in a chain southwestwards and southwards to western Bahia, the São Francisco valley and the cerrado domain. This corridor may, therefore, account for the similarity between the population at São Benedito and that on the central plateau in Goiás and the Federal District.

The southeastern material examined is problematic in that it includes both karyomorphs, but individuals are not easily separated by skin and skull morphology or by morphometric techniques. From photographs, the Garrafão and Fazenda União specimens do appear to agree in form with *R. macrurus* and *R. mastacalis*, respectively, on the basis of bullar size, mesopterygoid fossa breadth and nasal length, but not palatal bridge proportions. Other, non-karyotyped individuals, however, are often intermediate in skull characters and cannot be identified with any certainty by these means. Where possible, specimens from this region have been allocated provisionally to

either *R. macrurus* or *R. mastacalis* on the basis of biogeographical hypothesis: the former is regarded as occurring in areas of cerrado, i.e., in northern and western Minas Gerais, as far south as São Roque de Minas and the Serra da Canastra National Park; and the latter in the areas covered (or formerly covered) by Atlantic forest, in southern and eastern Minas Gerais and the interior of São Paulo.

The situation as regards the coastal area of São Paulo and Rio de Janeiro is less easily resolved. First, the relationship between the low-FN form that occurs here and *R. macrurus* is unclear. According to the two-species hypothesis (a more southerly-high altitude taxon and a more northerly-low altitude one), their ranges would be disjunct because the area inland of the coastal mountains would be occupied by the more northerly species (i.e., *R. mastacalis*). In this case, the coastal range form might be regarded as distinct from *R. macrurus*: their karyological similarity does not necessarily imply that they belong to the same species - after all, *R. leucodactylus* also has a similar karyotype (Zanchin et al., 1992a). Secondly, the hypothesis also predicts possible sympatry of the northerly and southerly taxa at localities such as Casa Grande and Teresópolis. The fact that the low-FN (southerly/high altitude) form has been found at an elevation of only 300 m at Garrafão suggests that sympatry might even occur near sea-level where the coastal plain is very narrow or non-existent in such places as Ilha Grande and São Sebastião. On account of these uncertainties, the karyotyped specimens with low fundamental number from Casa Grande, Garrafão and Monte Verde are provisionally treated here as "cf. *R. macrurus*", while the non-karyotyped specimens from coastal São Paulo and Rio de Janeiro have been left unallocated.

In many respects the *Rhipidomys* of eastern Brazil resemble *R. latimanus* of the northern Andean region: they are approximately the same size in body, skull and molars and show a similar range of variation in skull characters. *R. latimanus*, however, is in general more brightly pigmented, whereas in eastern Brazil many specimens are more grey-brown in dorsal colour. Given the variation in skin, skull and chromosome morphology that can occur between local populations of *Rhipidomys* over relatively short distances, it is highly unlikely that any similarity observed between these taxa, isolated on opposite sides of the continent by the whole Amazon basin, should be due to anything more than parallel and independent evolution. Nonetheless, subsets of eastern Brazilian samples were compared with the subspecies of *R. latimanus* in a series of PCAs to investigate whether they were morphometrically distinct.

One such analysis comparing the sample of *R. macrurus* from Goiás and the

Federal District with *R. latimanus venezuelae* also included *R. emiliae*. The second component separated the latter sample (including the specimens from Serra do Roncador in Mato Grosso) from both the other groups, confirming the distinctness and internal coherence of *R. emiliae*. The loadings on the corresponding latent vector (accounting for 16.8% of total variation) suggested that this species had smaller molars, bullae and zygomatic plate and a broader interorbit than the others. As in many of these analyses, however, there was considerable overlap between *R. macrurus* and *R. l. venezuelae*. These taxa were separated most on the third component axis (8.4% of variation), which contrasted the longer rostrum and palate of *R. l. venezuelae* with the broader palate, mesopterygoid fossa and braincase of *R. macrurus*. When *R. macrurus* was analysed together with *R. l. latimanus* and the subspecies from Huila, Colombia, the Huila specimens proved to be morphometrically very similar indeed to *R. macrurus* in their broader braincase, narrower interorbit and larger bullae in comparison with the nominal subspecies. Overall, there was considerable overlap between the eastern Brazilian specimens and those from the northern Andes.

CHAPTER 7 - TAXONOMIC SYNTHESIS

Rhipidomys Tschudi

South American climbing mice, Ratos arborícolas, Ratas arborícolas

Etymology: Greek ριπίδος *rhipidos* fan, μûς *mus* mouse, referring to the animal's abundant, long, mobile whiskers.

Type species: *H[esperomys]. leucodactylus* Tschudi, 1845

Synonyms

Mus, sensu Lund, 1840a: 240 (part; not Linnaeus, 1758)

Rhipidomys Tschudi, 1845: 183, as subgenus of *Hesperomys*. Type species *H[esperomys]. leucodactylus* Tschudi, by indication (monotypy).

Hesperomys, sensu Wagner, 1845: 147 (part, not Waterhouse, 1839)

Calomys, sensu Giebel, 1859: 543, as subgenus of *Hesperomys* (part, not Waterhouse, 1837)

Holochilus, sensu Giebel, 1859: 543, as subgenus of *Hesperomys* (part, not Brandt, 1835)

Myoxomys Tomes, 1861: 284, as subgenus of *Hesperomys*; no type species designated; included species: *salvini* (a *Nyctomys*), *latimanus* (a *Rhipidomys*) and *bicolor* (an *Oecomys*)

Nyctomys, sensu Fitzinger, 1867: 88 (part; not de Saussure, 1860)

Cricetus (Rhipidomys): Thomas, 1888: 133 (new name combination)

Rhipidomys: Winge, 1888: 54 (raised to rank of genus)

Tylomys, sensu J. A. Allen & Chapman, 1893: 211 (not Peters, 1866)

Rhipodomys: J. A. Allen, 1899: 206 (incorrect subsequent spelling)

Oryzomys, sensu J. A. Allen, 1899: 211 (part; not Baird, 1858)

Œcomys, sensu J. A. Allen, 1916: 525 (part; not Thomas, 1906)

Thomasomys, sensu Tate, 1939: 194 (part, not Coues, 1884)

Rhipidomus: Hopkins, 1949: 470 (incorrect subsequent spelling)

Rhidomys: Vorontsov, 1959: 135 (incorrect subsequent spelling)

Phipidomys: Cabrera, 1961: 423 (incorrect subsequent spelling)

Rhipdomys: Saunders, 1975: 85 (incorrect subsequent spelling)

Rhipodmys: Saunders, 1975: 85 (incorrect subsequent spelling)

Rhyppidomis: Guitton et al., 1986: 233 (incorrect subsequent spelling)

Rhidpidomys: Stallings, 1988: 187 (incorrect subsequent spelling)

Ripidomys: Stallings, 1988: 190 (incorrect subsequent spelling)

Taxonomic notes

The name *Rhipidomys* was first published by Tschudi in December 1843 (Sherborn, 1922: cxxiv) in his article "Mammalium conspectus" (p. 252), as a subgenus of *Hesperomys* Waterhouse: "2. Subg. Rhipidomys. Wagn. in litt. 1844. Tsch.", below which he listed the only included species: "87. 1. *H. leucodactylus*. Tsch. Fauna peruan. cum fig." The reference was to his *Untersuchungen über die Fauna peruana*, published in parts between 1844 and 1846. But the part of the latter work in which he described *Hesperomys leucodactylus* appeared only in 1845 (Sherborn, 1922). Because the "Mammalium conspectus" contained no description or definition of the species, nor a reference to a *previously published* work, the species name as used therein is not available according to Article 12 of the International Code of Zoological Nomenclature (1985). Similarly, the subgeneric name as used in the "Mammalium conspectus" is not accompanied by a definition or description, nor by an *available* species-group name, and is therefore not available under the terms of the same article. On page 16 of the first part of the *Fauna peruana*, published in 1844, the names *Rhipidomys* and *H. leucodactylus* are again listed without definition, and are therefore not available according to Article 10(b) of the Code ("Interrupted publication"). They become available only from page 183 of the *Fauna peruana*, published in 1845. Here Tschudi first briefly defines the genus - "Subgenus RHIPIDOMYS. Wagn. Cauda corpore longior apice penicillata" (tail longer than body, with tufted tip) - and then defines and describes the species *H. leucodactylus* at length. The animal is figured in an engraving (Plate XIII, fig. 2; i.e., the left-hand rodent illustrated).

Revised diagnosis

A genus of arboreal-scansorial muroids within the Sigmodontinae (sensu Reig, 1984). Dorsal pelage reddish-brown, orange-brown or greyish-brown agouti; ventral fur white, cream or straw-coloured, either to base of hairs or with pale tips over grey bases; tail subequal to over 1.5 times head-and-body length, with distinct terminal pencil of hairs, the proximal half of the shaft not thickly haired; hind foot short and broad with pale sides and darker dorsal patch over the metatarsals; four interdigital and two metatarsal plantar pads; digit V of pes long, partially opposable to other digits, with claw reaching or very nearly reaching base of claw of digit IV; forefoot with greatly reduced

yet distinct pollex with nail; five palmar pads; claws on all feet short and strongly recurved, covered with pale claw vibrissae; mystacial vibrissae long, extending to well behind pinnae when appressed; six mammae. Skull with no or very slight zygomatic notch in dorsal view; anterior edge of zygomatic plate approximately vertical in lateral view; weak to moderate supraorbital ledges continued as parietal ridges; interparietal long and broad; lateral process of parietal present below parietal ridge; incisive foramina extending to level of anterior root of first molar; palate short and broad, with small venous foramina in place of posterolateral palatal pits; rear edge of palate straight or rounded or with medial process projecting into mesopterygoid fossa, the latter anteriorly broad, never pointed; sphenopalatine vacuities absent or very small; alisphenoid strut present; bullae small, with tegmen tympani overlapping posterior suspensory process of squamosal; zygomatic root on squamosal not confluent with upper margin of subsquamosal fenestra. Upper incisors ungrooved, slightly opisthodont; molars cuspidate, brachydont, pentalophodont with cusp(id)s opposite, not alternate; mesoloph(id)s distinct in M1-3 and m1-2 until advanced stage of wear; M1 with anterolingual conule not greatly reduced; labial cingulum isolating labial flexi from exterior in M1-3; lingual cingulid isolating lingual flexids from exterior in m1-3.

Description
External

Small to large muroid rodents (known adult head-and-body lengths from less than 90 mm to over 210 mm, weights from under 30 g to nearly 200 g).

Dorsal pelage brown agouti with slate-grey hair bases, often appearing rather uniform reddish-brown or orange-brown owing to intense orange (phaeomelanin) subterminal hair bands and dark red-brown hair tips and guard hairs, sometimes paler grey-brown where less intense phaeomelanin pigmentation leaves subterminal bands straw-coloured and hair tips and guard hairs without red admixture, rarely dark agouti with predominance of black (eumelanin) guard hairs and hair tips. Colour uniform dorsally from snout to rump, sometimes a little richer on crown of head and rump; flanks and sides of head often slightly paler. Body hairs dark to medium slate-grey on basal 60% to 70% of length, with subterminal (20% to 30%) orange band and usually dark tip; mid-dorsal length from 6 mm in small, lowland forms to 14 mm in large, upland forms. Guard hairs (unbanded) fairly conspicuous when dark, inconspicuous when reddish-brown; mid-dorsal length typically 3-5 mm greater than body hair. Texture moderately

fine to slightly coarse, never spiny or bristly; generally smooth and sleek, occasionally a little woolly. Transition to ventral pelage usually sharp.

Ventral pelage either white/cream/pale-straw to base or with pale to dark slate-grey bases ($\leq$ 60% of length); grey bases may occur only at the sides of the belly and in a patch in the upper pectoral region; grey bases usually only apparent when fur is ruffled, not affecting the overall impression of whiteness (except in *R. macconnelli*). Orange suffusion present in some species, either covering the whole venter or restricted to the pectoral and/or inguinal regions. Orange suffusion makes lateral transition line less distinct. Throat coloured as venter (more often without grey bases), as is a small area of the upper lip below the lowest row of mystacial vibrissae. Mid-ventral length of body hair from 3 mm in small, lowland forms to 9 mm in large, highland forms; guard hairs (white or grey-and-white) generally 2-4 mm longer. Texture fine to slightly coarse; generally smooth, occasionally a little woolly.

Forelimbs furred to wrist, with short hair cover on dorsal surface of manus and digits; colour as body flanks on dorso-lateral side, as venter on ventro-medial side. Manus broad, of moderate size. Five large, fleshy palmar pads (at bases of digits II, III-IV, and V, plus thenar and hypothenar). Digits III and IV longest, subequal, webbed together proximally; digits II and V subequal, with claws reaching the base of claws III and IV; digit I greatly reduced yet distinct, with nail. Claws II to V moderate in size, strongly curved, covered by tufts of pale, claw-length hairs.

Hindlimbs furred to ankle and sometimes over heel, with short hair cover on dorsal surface of pes and digits; colour mostly as body flanks, with zone of ventral pelage on medial surface of limb not reaching ankle. Dorsal surface of pes with dark patch over metatarsals, sometimes barely darker than the rest of the foot but usually distinctly marked, narrow proximally and broader distally, extending to base of digits or sometimes over first phalanges, rarely further; sides of foot and remainder of digits pale. Pes short and broad; mean length 20.9% of adult head-and-body length (standard deviation 2.1, n = 574, excluding *R. macconnelli*), rather longer in *R. macconnelli*; longest digit approximately two-thirds of length of metatarsals. Six large, fleshy plantar pads covering most of plantar surface (four interdigital at bases of digits I, II, III-IV, and V, plus thenar and hypothenar); distal end of thenar adjacent to or level with proximal end of hypothenar. Little interdigital webbing at base of toes. Digits II, III and IV subequal in length; digit V long, with claw tip reaching or nearly reaching base of claw IV; digit I with claw reaching to end of first phalanx of digit II; digit V partly opposable to the rest.

Claws moderate in size, strongly curved, overlain by tufts of pale hairs usually as long as or longer than claws.

Tail usually longer than head and body, occasionally subequal (observed range 93% to 180% of head-and-body length). Squarish scales arranged in annular pattern, each with three hairs emerging from under distal edge; scales uniformly light- to dark-brown, sometimes a little paler proximally on ventral surface (on whole ventral surface of tail in *R. macconnelli*); adult tails have 9-18 scales per 10 mm longitudinally. Hairs short over most of shaft (1-2 mm, rarely 3 mm), longer towards tail tip, uniform in length around shaft; terminal pencil short to very long (5 mm to 40 mm or more), usually 10 to 20 mm; hairs reddish-brown to dark-brown.

Ear pinnae neither very small nor especially large, membranous, pale brown to nearly black, very lightly furred on outer surface. Eyes large, black. Rhinarium naked, with conspicuous disc-shaped flaps in infranarial portion. Mystacial vibrissae long, up to 70 mm, extending well behind the pinnae even when the latter are folded back; dark in colour, occasionally with white tips. Other vibrissae (number on one side except for interramal): 1-3 genal, 1-3 superciliary, several submental, 0-2 interramal, 1-2 carpal.

Mammae six, in inguinal, abdominal and postaxial pairs (see Voss & Carleton, 1993, fig. 8, for nomenclature of mammary loci).

Cranial

Maximum (occipito-nasal) skull length ranging from 20% to 32% of head-and-body length. Skull with relatively large, broad braincase, short rostrum and narrow zygomatic arches; skull profile gently convex over nasals and frontals, more so on parietals and interparietal especially in younger specimens, flatter overall in older and larger specimens.

Rostrum shortish and fairly slender, but increasingly robust in larger, older specimens; nasals and dorsal process of premaxillaries extend posteriorly roughly to level of dorsal extensions of lacrimals, which project slightly into the orbit; incisive capsule rather small; gnathic process of premaxillaries projecting forward but not greatly prominent. Zygomatic notch not visible dorsally or very small; free antero-dorsal edge of zygomatic plate absent or extremely short and rounded; anterior margin of zygomatic plate straight and vertical in lateral view, or leaning very slightly backwards. Zygomatic arches slender to moderately robust, rarely dipping as low as horizontal plane across dorsal surface of molar alveolar mound; greatest zygomatic breadth usually across squamosal roots (across jugals only in old specimens); jugal present; maxillary and

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squamosal zygomatic processes not overlapping each other above and below jugal. Interorbital region moderately broad, flattish, sometimes with slight medial depression extending onto posterior half of nasals; interorbit usually waisted anteriorly, occasionally more hourglass-shaped; supraorbital margins square-edged or with slight but distinct ledges or ridges, straight or slightly concave, diverging posteriorly; in the anterior part of more rounded interorbits the ridges may run slightly medial to the supraorbital margin itself; postorbital processes absent, or barely incipient in very largest specimens.

Braincase broad and slightly domed, flatter in larger individuals and species. Supraorbital ridges prolonged as weak or moderate parietal ridges, which run along the parietal-squamosal suture to the broadest point of the parietals, where they inflect or curve postero-medially across the parietals to the lambdoidal crest at the juncture of parietal, interparietal and occipital. Lateral process of the parietal (region latero-ventral to the posterior parietal ridge) roughly rectangular or a little shallower posteriorly, but always extending as far as occipital suture (except sometimes in *R. macconnelli*). Interparietal long and wide, usually extending laterally to posterior ends of parietal ridges.

Incisive foramina long, extending at least to level of M1 anterior root, rarely shorter, narrow anteriorly and rather broader in the posterior two-thirds of their length. Palatal bridge short, roughly equal to or shorter than molar row, not deeply grooved or pitted; rear margin usually with small medial process projecting into mesopterygoid fossa; palatal foramina sometimes one pair (opposite M2 hypoflexus) but often multiple (up to 5 pairs), subequal in size and often in bilaterally asymmetrical arrangement; small posterolateral venous foramen (not large pit) on ridge of bone between M3 and mesopterygoid fossa.

Mesopterygoid fossa with anterior end rounded or biconvex, never pointed, extending to level of rear margin of M3 or even to M3 hypoflexus; anterior part of fossa often rather expanded laterally; posterior part with parallel sides; sphenopalatine vacuities in roof of fossa absent or present as short, narrow slits adjacent to the posterior presphenoid and/or anterior basisphenoid. Parapterygoid fossae triangular, shallow, never deeply excavated. Pterygoid processes project ventrally beyond plane connecting ventral surface of bullae and occlusal surface of molars. Alisphenoid strut present, usually robust.

Stapedial circulatory pattern either primitive (stapedial foramen large, supraorbital ramus of stapedial artery following groove across inner surface of alisphenoid to sphenofrontal foramen) or derived (stapedial foramen small, no alisphenoid groove or sphenofrontal foramen), according to species. Bullae small, with bony eustachian tube

opening at or just in front of basisphenoid-basioccipital suture; wedge-shaped portion of periotic visible medially between ectotympanic and basioccipital, sometimes forming dorso-posterior wall of carotid canal. Tegmen tympani of periotic broadly overlapping posterior suspensory process of squamosal (as defined by Voss, 1993) and often partly or almost totally obstructing the postglenoid foramen and even the subsquamosal fenestra. Hamular process of squamosal robust, usually straight and lying at shallow angle to horizontal. Paroccipital processes small, slender, hooked slightly towards the occipital condyle.

Mandible slender rather than robust. Condylar process broad and moderately long, rising higher than coronoid process above occlusal plane of molars. Coronoid process small, slender and usually only slightly hooked; sigmoid notch (between coronoid and condylar processes) shallow and open. Angular process variable, from short and broad to longer and narrow, sometimes extending farther in posterior direction (with reference to occlusal plane of molars) than condylar process. Incisive capsular process present generally as an elongated swelling, ridge or shelf below the sigmoid notch, rarely as a more distinct protuberance. Masseteric ridges distinct but not prominent.

Dentition

Upper incisors slightly to moderately opisthodont (between $10°$ and $30°$ from vertical, relative to molar occlusal plane), rather slender; bright orange anterior faces gently convex in section, not grooved; tips wearing evenly and not forming medial cleft. Lower incisors with paler yellow-orange anterior faces.

Upper and lower molars bunodont, terraced (terminology from Hershkovitz, 1967); labial cusps and lingual cuspids conical when unworn, lingual cusps and labial cuspids wearing quickly to triangular prisms with flat occlusal surfaces. Cusps/cuspids arranged in opposite pairs, not alternate. Lingual and labial flexi/flexids not or barely interpenetrating. Upper molars each with three roots (anterior, posterior and lingual); M1 sometimes with accessory internal-labial root. Lower molars each with two roots (anterior, posterior); m1 sometimes with accessory internal-lingual root.

Procingulum on M1 with anteromedian flexus (occlusal terminology from Reig, 1977) moderately to well developed, often remaining as enamel pit in well worn tooth; anteromedian style sometimes present on anterior face of procingulum, causing anteromedian flexus to branch around it; anterolingual and anterolabial conules subequal or former rather smaller than latter, both slightly smaller than main cusps. Loph from anterolingual conule meets anterior mure at point where it gives off anteroloph; loph from

anterolabial conule usually meets at same point, but sometimes connects to one or other of those two lophs. Procingulum continues labially round tooth as marginal ridge connecting anterolabial conule to parastyle; cingulum also present along labial side of M1-3 in the form of stylets or ridges linking parastyle, paracone, mesostyle, metacone and posteroloph, thus blocking or partly barring the external ends of all labial flexi.

Anteroloph present in M1-3, connecting with parastyle. Protostyle in M1-2 present in many species, but often lacking in M3; protostyle occasionally connected by weak lophule to anterior face of protocone in M1, and linked by cingular ridge across front of tooth to origin of anteroloph in M2. Enterostyle usually present in M1-3. Protocone and hypocone in M1-2 triangular with lingual apex rather sharp in unworn tooth, soon becoming rounder with wear; hypocone much reduced in M3. Paracone in M1-3 with paraloph oriented medially or slightly postero-medially from postero-medial corner of cusp to join posterior horn of protocone; oblique enamel crest or paralophule roughly perpendicular to paraloph often crossing latter at base of paracone, sometimes connecting with mesoloph or mesostyle at posterior end and rarely with anterior horn of protocone at the opposite end. Mesostyle well developed, usually associated with adjacent cingular stylets, and connected to strong mesoloph, which is confluent with anterior horn of hypocone. Extremely short section of median mure separating mesoflexus from hypoflexus, and linking the paraloph/protocone with the mesoloph/hypocone. Metacone in M1-2 similar to paracone, with metaloph oriented slightly postero-medially from postero-medial corner of cusp to join posterior horn of hypocone at origin of posteroloph; oblique crest (metalophule) sometimes crossing metaloph but rarely connecting to posteroloph and anterior horn of hypocone. Posteroloph coalescing distally with postero-lateral face of metacone, isolating posteroflexus as fossetus.

Third upper molar roughly three-quarters length of second. Anterior part of M3 mirroring that of M2 on a slightly smaller scale, but posterior part greatly reduced especially on labial side, giving tooth a rounded triangular shape. Hypocone small but recognisable (except in very worn tooth); metacone no more than a marginal elevation on postero-labial corner of unworn tooth, rarely persisting. Mesoloph usually present, often oriented postero-labially, but internal topography of post-paracone region of M3 variable and often difficult to interpret owing to differential reduction, coalescence or reorientation of lophs and lophules.

First lower molar with slight to deep anteromedian flexid; if slight, groove on anterior surface is sometimes erased after little wear, but enamel fossetid always remains

in middle of procingulid. Anterolingual and anterolabial conulids subequal, considerably smaller than main cuspids; their respective lophids often join immediately behind the fossetid to form one or even two transverse lophids anterior and parallel to anterolophid, especially in larger specimens. Cingular ridge that connects anterolingual conulid to metastylid in m1 and other cingular elements that link lingual stylids and cuspids in m1-3 block or partly bar the external ends of all lingual flexids (cf. labial cingulum in upper molars).

Anterolophid present in m1, usually but not always reaching metastylid at margin of tooth; metalophid linking metaconid anteriorly (or antero-labially) with anterolophid. In m2-3 separate anterolophid absent. Protolophid/protostylid present in m1-3, set off by deep transverse groove on anterolabial face of protoconid, occasionally reduced on m3. Ectostylid usually present on floor of hypoflexid in m1-3, sometimes with ectolophid. Mesolophid connecting posterior horn of protoconid with mesostylid in m1-3; long and straight in m1-2, much shorter in m3 because of lateral compression of posterior half of tooth which mainly affects structures on lingual side. Entoconid in m1-2 subequal to metaconid, but greatly reduced in m3 and seldom surviving slight wear. Entolophid in m1-3 (very short in m3) linking antero-medial corner of entoconid to anterior horn of hypoconid. Very short section of median murid running longitudinally or slightly postero-labially, linking protoconid/mesolophid to hypoconid/entolophid, and separating entoflexid from hypoflexid. Entoflexid reduced to tiny fossetid in m3, occasionally completely absent. Posterolophid well developed in m1-3, in m3 preventing tooth from being substantially shorter than m2. Distinct fold occasionally present on posterolabial face of m1-3 (especially m3), herein termed posterolabial flexid.

Postcranial skeleton

Nineteen thoracicolumbar vertebrae, of which 12 or 13 thoracic (rib-bearing); 35-42 caudal vertebrae (data from Steppan, 1995). Tuberculum of first rib articulates with transverse processes of seventh cervical and first thoracic vertebrae; second thoracic vertebra with very long neural spine. Entepicondylar foramen of humerus absent.

Soft anatomy

Viscera not examined for this study. Voss (1991, table 4) reported absence of gall bladder in all five species of *Rhipidomys* he dissected. Carleton (1973) found one *Rhipidomys* specimen to have a unilocular-hemiglandular stomach, in common with the majority of "South American cricetines" examined. Hooper and Musser (1964) described one *Rhipidomys* phallus.

Distribution

Tropical South America from its northern coast to northern Argentina and southeastern Brazil at approximately 24° S, including eastern Panama, Trinidad and Tobago, and coastal islands in Venezuela and Brazil. Within this area, the genus occurs in forests of most types, especially lowland and montane evergreen forests, including gallery forest and other mesic enclaves in savanna and xeric scrub, but also certain seasonally dry forests. It is absent from the puna and páramo zones of the high Andes, and also apparently from the Pantanal region of SW Brazil.

Subdivisions

Character state distributions suggest that *Rhipidomys* may be divided into three parts: A. the *R. fulviventer* section, B. The *R. macconnelli* section, and C. the *R. leucodactylus* section. The order of species accounts below follows these subdivisions.

Section A. The *Rhipidomys fulviventer* section.

Rhipidomys fulviventer Thomas

Etymology: Latin *fulvus* tawny, *venter* belly

Synonyms: See under subspecies.

Revised diagnosis

Small to medium-sized *Rhipidomys* specimens with long, soft pelage; ventral fur grey-based; ears darker than dorsal pelage; juvenile pelage similar to that of adults but less bright. Weakly developed supraorbital ridges; carotid circulatory pattern primitive, i.e., with large stapedial foramen, internal groove across squamosal and alisphenoid, which leads to sphenofrontal foramen lying on alisphenoid-orbitosphenoid suture (frontal rarely involved). First upper molar lacking protoloph and protostyle.

Description

Pelage long, soft and sleek. Dorsal colour varying from bright chestnut brown to mid-brown with olive tinge; hair bases dark slate. Ventral hairs with white, cream or pale orange tips over long (50-65% of hair length) dark grey bases; grey bases often absent on throat. Tail longer than head-and-body and usually medium to dark in colour, with

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rather lighter area near base on ventral surface; scales small; tail pencil usually dense and moderately long. Hind foot narrow; dark patch often indistinctly delineated. Juvenile pelage similar to adult, but a little darker and duller.

Skull with broad, rounded braincase; highest point of skull generally on parietals rather than frontals (except in oldest specimens). Supraorbital ridges almost absent in smallest specimens, giving very rounded, "hourglass-shaped" interorbit; ridges a little more pronounced in larger specimens, usually converging on top of anterior part of interorbital region with the narrowest point of interorbit displaced forward of centre. Nasals often tapering posteriorly to a point or to a blunt end, usually a little behind the rearmost point of the premaxillaries. Parietal ridges poorly developed in most cases, tending to curve round braincase rather than inflecting sharply at anterior end of lateral process of parietal. Occipital bone broad. Incisive foramina generally narrow and parallel-sided, sometimes a little more expanded in posterior half, extending at least to level of anterior roots of first molars. 2-4 pairs of palatal foramina, the largest usually in the palatine bone. Medial spine of palate (projecting into mesopterygoid fossa) often very small or absent, resulting in straight or slightly concave (rather than biconcave) rear edge of palate. Sphenopalatine vacuities usually small, sometimes closed. Parapterygoid fossae often fenestrated (medial unossified zone). Bullae with rather transverse (rather than oblique) anterior face, lateral to the bony eustachian tubes. Carotid circulation pattern primitive: i.e., stapedial foramen (on ectotympanic suture) large; internal groove across squamosal and alisphenoid, leading to sphenofrontal foramen; this foramen lies on alisphenoid-orbitosphenoid suture a little below the frontal, which is rarely involved in its formation. Mandible with prominent incisor root capsule forming small knob in many specimens. Molars follow standard *Rhipidomys* pattern, but first upper molar very rarely has protostyle/protoloph.

Distribution

Mid to high elevation forests in the Colombian and Venezuelan Andes and the Venezuelan coastal range (Fig. 7.1).

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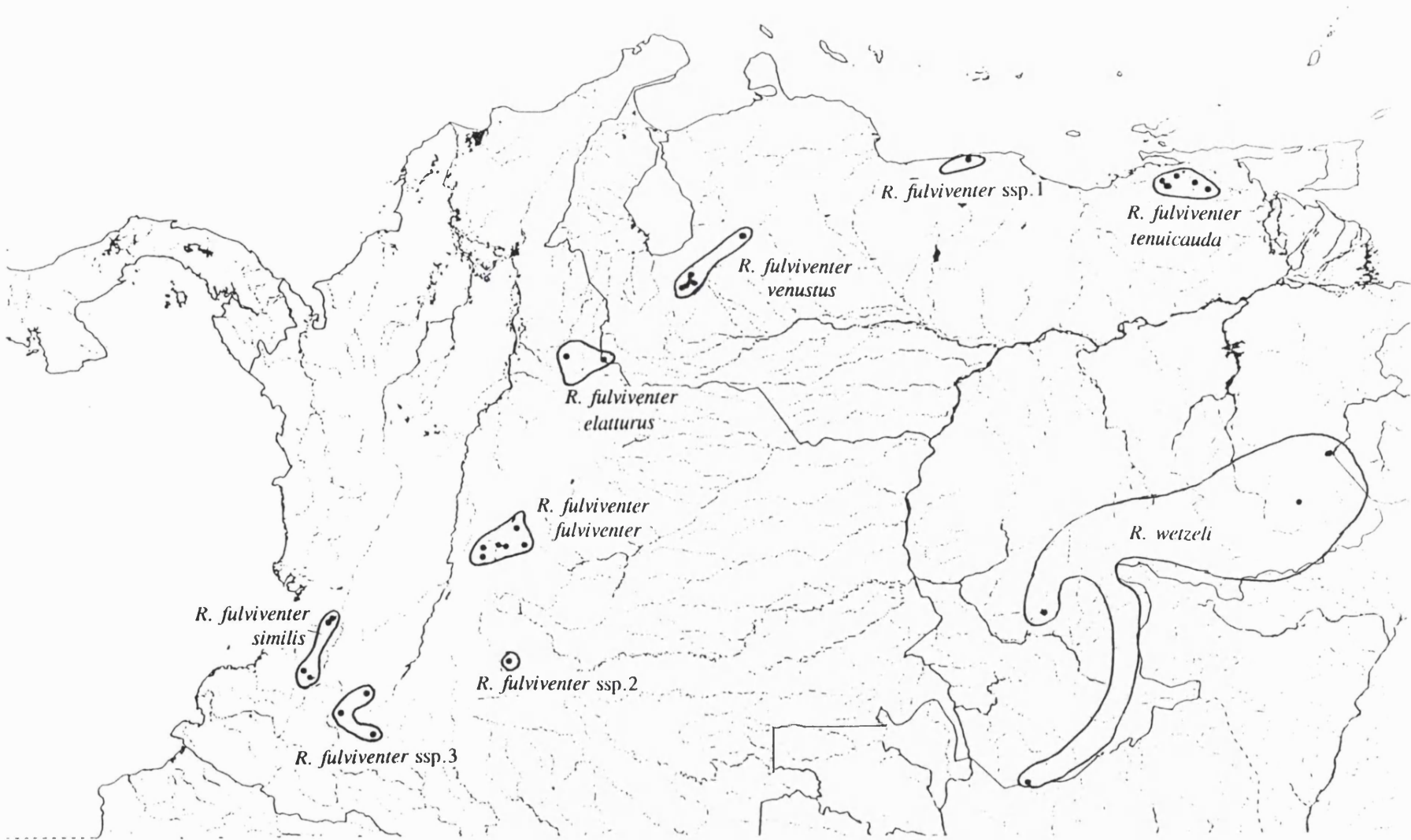
Fig. 7.1 - Distribution of *Rhipidomys fulviventer* and *R. wetzeli.*

R. fulviventer ssp.1

R. fulviventer
tenuicauda

R. fulviventer
venustus

R. fulviventer
elatturus

R. fulviventer
fulviventer

R. wetzeli

R. fulviventer
similis

R. fulviventer ssp.2

R. fulviventer ssp.3

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Subspecies: Eight (in geographical order from northeast to southwest):

Rhipidomys fulviventer tenuicauda (J. A. Allen)

Etymology: Latin *tenuis* thin, *cauda* tail

Synonyms

Oryzomys tenuicauda J. A. Allen, 1899: 211. Type locality "Los Palmales, [Sucre,] Venezuela"

[Rhipidomys] tenuicauda: Tate, 1939: 195 (name combination)

Phipidomys [sic] *mastacalis tenuicauda*: Cabrera, 1961: 423 (name combination)

Rhipidomys venustus, sensu Furman, 1972a: 27 (not Thomas, 1900). Also Johnson, 1972: 12 (part); Tipton & Machado-Allison, 1972: 28 (part); Handley, 1976: 50 (part).

Rhipidomys sp.: Goff & Brennan, 1977: 1090 (specimen from San Agustín, Monagas, Venezuela)

Rhipidomys fulviventer: Musser & Williams, 1985: 4 (part; first published referral to this species)

Holotype: AMNH 14737, adult male, skin and skull; "trapped in forest" at "Los Palmales, [Sucre,] Venezuela" on 5 December 1898, by F. W. Urich.

Description

Small-bodied representative of the species from northeastern Venezuela. The holotype is even smaller in body and skull measurements than other adults of this subspecies, but its molars are close in size to the sample mean. Dorsal pelage often bright orange-brown agouti, sometimes more chestnut brown; length (guard/body hairs) 10/8 to 14/10 mm. Ventral pelage with cream hair tips on mid to dark grey bases; length (guard/body hairs) 8/6 mm. Hind feet small and narrow. Skull with rounded interorbital region with slight supraorbital ridges. Lateral process of parietal narrowing posteriorly. 1-2 pairs of palatal foramina, the largest situated in the maxillary. Parapterygoid fossae sometimes fenestrated. Sphenopalatine fissures variable, from long and moderately broad to short and narrow or absent.

Distribution

Northeastern Venezuela, in the mountains in the states of Sucre and Monagas (Fig. 7.1).

Ecological notes

Habitat: premontane humid forest (Holdridge classification), coffee and cacao plantations (Tate, 1931; Handley, 1976) above 900 m. Reproduction: Two females had 4 embryos and one had 5 in June-July (USNM). Parasites: see Furman (1972a), Johnson (1972), Tipton & Machado-Allison (1972). Guerrero (1985) listed the ectoparasites recorded from all species of Venezuelan *Rhipidomys*.

Material examined[1]

VENEZUELA: **Monagas**, San Agustín, 5 km NW Caripe, 1160-1340 m *(311)* (USNM 409921, ~25 to ~34); **Sucre**, Los Palmales *(308)* (AMNH 14737 - holotype of *tenuicauda*); El Latal, 3100 ft *(307)* (AMNH 69901); Carapas, 5600 ft *(307)* (AMNH 69902, ~04, ~05); Cerro Turumiquire, 6000 ft *(310)* (FMNH 38060). Total: 17.

Rhipidomys fulviventer ssp. 1

Synonym

Rhipidomys venustus, *sensu* Machado-Allison & Barrera, 1972: 8 (part, not Thomas, 1900). Also Furman, 1972a: 12 (part); Johnson, 1972: 19 (part); Tipton & Machado-Allison, 1972: 60 (part); Herrin & Yunker, 1975: 112; Handley, 1976: 50 (part).

Description

Medium to large specimens from the northern coastal range of Venezuela. Dorsal pelage rather less bright than *R. f. venustus*; length (guard/body hairs) 12/9 to 14/10 mm. Hind foot patch fairly well defined. All specimens examined have an accessory sphenofrontal foramen situated high in the alisphenoid or even in the lower part of the frontosquamosal suture, fed by a branch of the supraorbital stapedial artery. Medial spine on posterior edge of palate often present. Small sphenopalatine fissures occasionally present. Parapterygoid fossae usually not fenestrated.

Distribution

Northern coastal range of Venezuela in the Distrito Federal and Estado Miranda;

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[1] To save space in lists of material examined, a tilde (~) may be used to abbreviate a museum number where the first part of the number is the same as the previous one; a sequence of consecutive numbers is indicated by the word "to". Numbers in italics are locality reference numbers used in the maps and gazetteer.

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known only from the vicinity of Hotel Humboldt on Pico Ávila, on the ridge above Caracas. May possibly occur also farther west in the higher parts of Aragua state.

Ecological notes

Habitat: Lower montane humid forest (Holdridge classification, Handley, 1976), above 2000 m. Reproduction: One female had a single embryo in September (USNM). Parasites: see Furman (1972a), Herrin & Yunker (1975), Johnson (1972), Machado-Allison & Barrera (1972), Tipton & Machado-Allison (1972).

Material examined

VENEZUELA: **Distrito Federal/Miranda**, Pico Ávila, 2095-2223 m *(295)* (USNM 371236, ~39 to ~44, ~46, 372525). **Total: 9.**

Rhipidomys fulviventer venustus Thomas

Etymology: Latin *venustus* charming, attractive

Synonyms

Rhipidomys venustus Thomas, 1900a: 152. Type locality "Las Vegas del Chama", Mérida, Venezuela, "alt. 1400 m".

Rhipidomys latimanus venustus: Cabrera, 1961: 420 (name combination)

Rhipidomys latimanus, *sensu* Corbet & Hill, 1980: 145 (part; not *Hesperomys latimanus* Tomes, 1860)

Holotype: BMNH 99.12.1.1, adult female, skin and skull; collected at "Las Vegas del Chama", Mérida, Venezuela, on 14 July 1896, by S. Briceño.

Description

Large-bodied specimens from the Mérida-Trujillo Andes of Venezuela. Dorsal colour bright chestnut brown; pelage length (guard/body hairs) 14/9 to 16/11 mm. Tail sometimes reddish rather than dark. Hind foot patch dark and well defined. Supraorbital ridges slightly more pronounced than in other forms of the species. Parapterygoid fossae often fenestrated.

Distribution

The Mérida-Trujillo Andes of Venezuela (Fig. 7.1). Current range probably highly restricted on account of widespread deforestation (Handley, 1976).

Ecological notes

Habitat: lower montane humid forest and montane rain forest (Holdridge

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classification, Handley, 1976), and coffee plantations, mostly above 2000 m. Elevations of Briceño's capture localities near Mérida (from 1400 to 4000 m) are questionable. Aagard (1982) provides data on population ecology. Reproduction: One female had 2 embryos in the wet season (Aagard, 1982). Parasites: see Brennan & Reed (1974), Ferris (1921), Furman (1972a), Johnson (1972), Jones et al. (1972), Machado-Allison & Barrera (1972), Tipton & Machado-Allison (1972).

Material examined

VENEZUELA: **Mérida,** Las Vegas del Chama, 1400 m [?] *(274)* (BMNH 99.12.1.1 - holotype of *venustus*); Monte Culata, 4000 m [?] *(278)* (BMNH 99.12.1.2); Mérida *(275)* (BMNH 99.12.1.3, 10.12.3.2); Montes del Valle, 2000 m [?] *(276)* (FMNH 18188, USNM 137507); Río Mucujón, 9000-10000 ft *(276)* (FMNH 21825); Montes de Lurdes, 1630 m [?] *(279)* (USNM 123330); Cafetos de Milla, 1600 m [?] *(276)* (USNM 168228); near Tabay, 2250-3160 m *(279)* (USNM 387908, ~09, ~11, ~50); **Trujillo,** Hacienda Misisi, 2210 m *(284)* (USNM 374528 to ~30, ~33 to ~37, ~39, ~41). Total: 23.

Rhipidomys fulviventer elatturus Osgood

Etymology: Greek ελαττων *elattun* smaller, shorter, ουρα *oura* tail.

Synonyms

Rhipidomys fulviventer, sensu Osgood, 1912: 51 (not Thomas, 1896)

Rhipidomys fulviventer elatturus Osgood, 1914a: 140. Type locality "Paramo de Tama, head of Tachira River, Venezuela. Alt. 7,000 ft." (Same specimens as those mentioned by Osgood, 1912.)

Rhipidomys latimanus elatturus: Cabrera, 1961: 419 (name combination)

Rhipidomys venustus, sensu Furman, 1972a: 43 (part; not Thomas, 1900)

Holotype: FMNH 18691, adult male, skin and skull; collected at Páramo de Tamá, head of Táchira River, Táchira State, Venezuela, on 3 March 1911, by W. H. Osgood and S. G. Jewett.

Description

Small-bodied form from the Colombia-Venezuela border region. Dorsal pelage particularly long and soft; length (guard/body hairs) 14/9 to 15/11 mm. Skull with very rounded, "hourglass-shaped" interorbital region with scarcely noticeable supraorbital

ridges. Slender rostrum; nasals very long, often extending beyond plane of lacrimals. Widely bowed zygomatic arches. More rounded braincase than larger subspecies. Mesopterygoid fossa narrow and parallel-sided; small sphenopalatine fissures usually present. Parapterygoid fossae sometimes fenestrated.

Distribution

The Páramo de Tamá on the Colombia-Venezuela border and adjacent parts of the Eastern Cordillera in Colombia. How far its range extends to the north and south and whether or not it intergrades with *R. f. fulviventer* is unknown (Fig. 7.1).

Ecological notes

Habitat: Lower montane very humid forest (Holdridge classification for cloud forest, Handley, 1976). Reproduction: Two females had 2 embryos and one had 3 in March (USNM). Parasites: see Brennan & Reed (1974), Furman (1972a), Jones et al. (1972), Tipton & Machado Allison (1972).

Material examined

COLOMBIA: Santander, Cachiri *(127)* (CM 3192). **VENEZUELA: Táchira**, Páramo de Tamá, 7000 ft *(270)* (FMNH 18562, 18691 - holotype of *elatturus*); Buena Vista, c. 2400 m *(270)* (USNM 456339 to ~43, ~46 to ~48, ~50, ~51, ~53 to ~55, ~57, ~58, ~60). **Total: 19.**

Rhipidomys fulviventer fulviventer Thomas

Synonyms

Rhipidomys fulviventer Thomas, 1896b: 304. Type locality "Agua Dulce, W. Cundinamarca, Colombia"

[Rhipidomys] fulviventris Tate, 1939: 195 (incorrect subsequent spelling)

Rhipidomys fulviventer fulviventer: Gyldenstolpe, 1932: 48 (first use as subspecies name)

Rhipidomys latimanus microtis, *sensu* Cabrera, 1961: 419 (part, not *Rhipidomys microtis* Thomas, 1896)

Rhipidomys latimanus, *sensu* Corbet & Hill, 1980: 145 (part, not *Hesperomys latimanus* Tomes, 1860)

Holotype: BMNH 96.11.1.3, adult female, skin and skull; collected at "Agua Dulce, W. Cundinamarca, Colombia", on 19 September 1895, by G. D. Child.

Description

Medium-sized specimens from the Bogotá region. Dorsal colour not so bright chestnut brown as in *R. f. venustus* and often tinged with olive; flanks a little paler than dorsum. Ventral pelage usually with orange suffusion throughout. Skull with slight supraorbital ridges, so that narrowest point of interorbit lies slightly forward of centre. Parapterygoid fossae often fenestrated. Small sphenopalatine fissures often present.

Distribution

Known from the Colombian department of Cundinamarca and the Distrito Especial of Bogotá, at elevations between 1800 and 3100 m. The extent of its range to the north and south is unknown (Fig. 7.1).

Ecological notes

Montenegro-Díaz et al. (1991) report habitat as relatively undisturbed cloud forest and forest-páramo ecotone; home range 0.2 ha in forest 25 m in height. Reproduction: two females had 2 embryos; gestation of roughly one month; reproductive activity was fairly constant throughout study period from February to August. Diet: content of 5 stomachs was 68% fruit and seeds, 26% leaves and other plant matter, and 6% insects.

Material examined

COLOMBIA: Cundinamarca, Agua Dulce *(135)* (BMNH 96.11.1.3 - holotype of *fulviventer*); Fanabistá *(not located)* (BMNH 99.10.3.9); La Aguadita, 1800 m *(134)* (BMNH 15.1.3.3); Guasca, R. Balcones, 2720 m *(130)* (FMNH 71730 to ~35, ~47); Soacha, Finca El Soche, 2630 m *(133)* (KU 124031); **Distrito Especial**, San Francisco, 2700-3000 m *(138)* (FMNH 71487, ~88, 71720 to ~22); San Cristóbal, 2800-3000 m *(138)* (FMNH 71723 to ~29). **Total: 23.**

Rhipidomys fulviventer ssp. 2

Synonyms: None

Description

Single large specimen, larger than *R. f. fulviventer*, its nearest neighbour geographically. Ventral pelage with cream hair tips over dark grey bases, with slight orange suffusion in pectoral region; length (guard/body hairs) 10/7 mm. Tail much longer than head-and-body. Interorbital region rounded, "hourglass-shaped". Mesopterygoid fossa expanded at anterior end, without sphenopalatine fissures. Parapterygoid fossae

fenestrated.

Distribution

Serranía de la Macarena, an isolated tableland just east of the Eastern Cordillera in the Colombian department of Meta (Fig. 7.1).

Material examined

COLOMBIA: Meta, La Macarena, 1140 m *(141)* (AMNH 142140). Total: 1.

Rhipidomys fulviventer ssp. 3

Synonyms: None

Description

Medium- to large-bodied specimens from southern Huila. Dorsal colour reddish brown, but not so bright as *R. f. venustus*, sometimes slightly olive brown, as in *R. f. fulviventer*; length (guard/body hairs) 13/10 mm. Ventral pelage has slight orange suffusion over dark grey bases; length (guard/body hairs) 9/7 mm. Tail much longer than head-and-body. Parapterygoid fossae fenestrated. Upper molars with high labial cingular styles.

Distribution

Known from elevations between 1600 and 2350 m in the mountains at the head of the Magdalena valley, department of Huila, Colombia, including parts of the Central and Eastern Cordilleras. May extend farther north, particularly along the Central Cordillera (Fig. 7.1).

Material examined

COLOMBIA: Huila, Acevedo, San Adolfo, R. Aguas Claras, 1600 m *(145)* (FMNH 71712); San Agustín, San Antonio, Río Ovejeras, 2250-2350 m *(148)* (FMNH 71713 to ~19, ~37); Belén, 7000 ft *(144)* (USNM 294984). Total: 10.

Rhipidomys fulviventer similis J. A. Allen

Etymology: Latin *similis* similar [to *Thomasomys popayanus*, in external appearance].

Synonyms

Rhipidomys similis J. A. Allen, 1912: 79. Type locality "Cocal, Cauca, Colombia.

Altitude, 6000 feet."

Rhipidomys latimanus similis: Cabrera, 1961: 419 (part; name combination)

Rhipidomys latimanus, *sensu* Alberico, 1983: 65 (part; not *Hesperomys latimanus* Tomes, 1860)

Holotype: AMNH 32458, adult male, skin and skull; collected at Cocal (a hamlet on the western slope of the Western Cordillera), Cauca, Colombia, on 17 June 1911, by Leo E. Miller.

Description

The largest of the subspecies of *R. fulviventer* in skull dimensions and tail length. Ventral pelage with cream or more usually pale orange hair tips over long, dark grey bases; length (guard/body hairs) 9/7 mm. Tail much longer than head-and-body. Skull with slight supraorbital ridges. Mesopterygoid fossa expanded at anterior end; sphenopalatine vacuities small to medium. Parapterygoid fossae fenestrated.

Distribution

At high elevations on both versants of the Western Cordillera of Colombia in the departments of Cauca and Valle, and possibly farther north and south (Fig. 7.1).

Material examined

COLOMBIA: **Cauca**, Cocal, 4000-6000 ft *(153)* (AMNH 32458 - holotype of *similis*, 32459, ~61, ~62, 32541, ~42); Cerro Munchique (E side), 2400 m *(152)* (AMNH 181475). Total: 7.

Rhipidomys wetzeli Gardner

Etymology: Named in honour of U.S. mammalogist Ralph M. Wetzel.

Synonyms

Rhipidomys caucensis, *sensu* Furman, 1972a: 27 (not J. A. Allen, 1913)

Rhipidomys fulviventer, *sensu* Handley, 1976: 50 (part; not Thomas, 1896; specimens from Km 125 and Cerro Duida)

Rhipidomys wetzeli: Gardner, 1988: 744 (*nomen nudum*)

Rhipidomys wetzeli Gardner, 1989: 417. Type locality "Camp VII (00°50'40"N, 65°58'10"W), 1800 m, Cerro de la Neblina, Territorio Federal Amazonas, Venezuela"

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Holotype: USNM 560697, adult female, skin and skull; collected at locality mentioned above on 2 December 1984 by Alfred L. Gardner.

Revised diagnosis

Very small specimens of *Rhipidomys* with bright orange dorsal pelage, ventral pelage with cream or pale orange hair tips over dark grey bases, dark ears, and long tail ending in a well-developed pencil of hairs; skull with very slight supraorbital ridges, globose braincase, primitive carotid circulation pattern (large stapedial foramen, groove along inner surface of squamosal and alisphenoid, leading to sphenofrontal foramen), bifurcated tip of paraoccipital process; very short molar row (crown length ≤ 4 mm).

Description

Very small specimens, especially those from Bolívar. Dorsal colour bright orange agouti, especially Bolívar specimens; length (guard/body hairs) 9/7 to 12/9 mm. Ventral pelage with cream or pale orange hair tips over dark grey bases; length (guard/body hairs) 8/6 mm. Tail medium to dark brown, almost bare on proximal half, then hairs lengthening towards tip; pencil typically 20 mm, mid-brown to orangey brown. Hind foot short and narrow; dark patch pronounced over distal metatarsals, sometimes extending proximally, but poorly delineated; long toes. Ears darker than dorsal pelage. Skull with rounded interorbit, only very slight supraorbital ridges; Bolívar specimens have a shorter interorbital waist than others. Braincase broad, rounded. Lateral process of parietal very narrow posteriorly (Bolívar) or more rectangular (Neblina, Duida). One pair of large palatal foramina in centre of palate, and occasionally another smaller pair behind. Derived carotid circulation pattern (i.e., large stapedial foramen in bulla, internal groove across squamosal and alisphenoid, opening at sphenofrontal foramen). In contrast to *R. fulviventer*, the sphenofrontal foramen in *R. wetzeli* is often situated at the triple junction of alisphenoid, orbitosphenoid and frontal bones. Accessory sphenofrontal foramen absent. Parapterygoid fossae fenestrated or thinly ossified. Sphenopalatine fissures usually present, larger and sometimes subdivided in specimens from Bolívar and Cerro Duida. Paraoccipital processes bifurcated at tip. Very small molars, with posterior half of M3 greatly reduced; small protostyle on M1-2; anteromedian flexus in M1 weak; anteromedian flexid in m1 absent.

Comparisons

R. wetzeli differs from all other *Rhipidomys* species except *R. caucensis* in its smaller size and smaller molars. It is distinguished from *R. fulviventer* by its single pair of palatal foramina (but also found in *R. fulviventer tenuicauda*), bifurcated paraoccipital

processes and lack of anteromedian flexid; it usually (but not always) has shorter and brighter dorsal pelage, shorter hairs on the proximal half of the tail, darker ears, shorter nasals, more fully ossified area of the alisphenoid anterior to the alisphenoid strut (see Gardner, 1989: 418), and a sphenofrontal foramen involving the frontal bone. It can be distinguished from *R. caucensis* by its primitive carotid circulation pattern, brighter dorsal colour, and usually longer tail.

Distribution

At middle to high elevations in the Guiana Highlands; currently known only from Venezuela, in eastern Bolívar state and central and southern Amazonas territory (Fig. 7.1).

Ecological notes

Habitat information is given by Handley (1976, under the name *"R. fulviventer"*). Reproduction: Holotype lactating when collected in December; uterus had 2 embryo scars (Gardner, 1989). Parasites: see Furman (1972a), Johnson (1972).

Material examined

VENEZUELA: Bolívar, Churi-tepui, Camp 5, 4900 ft *(326)* (AMNH 176327); Km 125, 85 km SSE of El Dorado, 1032 m *(315)* (USNM 387916, ~18, ~20 to ~22, ~25, ~26); T. F. Amazonas, Cerro Duida, Cabecera del Caño Culebra, 1400 m *(337)* (USNM 406111); Cerro Neblina, Camp II, 2200 m *(346)* (USNM 560658); Cerro Neblina, Camp VII, 1800 m *(346)* (USNM 560697 - holotype of *wetzeli*, 560826 to ~33). Total: 19.

Rhipidomys caucensis J. A. Allen

Etymology: From Cauca, the Colombian department whence the holotype originated.

Synonyms

Rhipidomys caucensis J. A. Allen, 1913: 601. Type locality "[Cerro] Munchique (altitude 8225 feet), Western Andes, Cauca, Colombia"

Rhipidomys latimanus similis, *sensu* Cabrera, 1961: 419 (part; not *Rhipidomys similis* J. A. Allen, 1912)

Rhipidomys fulviventer, *sensu* Musser & Williams, 1985: 4 (part; not Thomas, 1896)

Holotype: AMNH 32466, adult female, skin and skull; collected at Cerro Munchique,

Western Andes, Cauca, Colombia" on 24 May 1911 by Leo E. Miller (type description gives altitude of 8225 feet, specimen label has "8325 ft").

Diagnosis

Very small *Rhipidomys* specimens with bright orange-brown dorsal pelage, ventral pelage with cream or pale orange hair tips over dark grey bases, dark ears and dark tail; skull with very slight supraorbital ridges, globose braincase, derived carotid circulation (very small stapedial foramen, no groove on inner surface of squamosal and alisphenoid, sphenofrontal foramen absent); mandible with pronounced incisor root capsule; molars with strong oblique paralophules paralleling mesoloph.

Description

Very small species, similar in size and appearance to *R. wetzeli*. Dorsal colour medium orange-brown, slightly olivaceous, bright but usually rather duller than *R. wetzeli*; flanks a little paler. Ventral pelage with white or pale orange hair tips over long, dark grey bases. Pelage length (guard/body hairs): dorsal 12-14/9-11 mm, ventral 10-12/ 6-8 mm. Tail longer than head-and-body (but usually shorter than in *R. wetzeli*), medium to dark brown with paler hairs, hairs lengthening over distal 25% of shaft, moderate pencil (10-15 mm). Hind feet short and narrow; patch dark, poorly defined, but contrasting strongly with pale digits; ankles barely furred. Ears very dark.

Skull with rounded, "hourglass-shaped" interorbit with only very slight supraorbital ridges. Nasals sometimes long, extending beyond plane of lacrimals, but generally shorter, not tapering strongly rearwards. Braincase globose. Lateral process of parietal roughly triangular. 2-4 pairs of palatal foramina, the largest situated in the maxillary. Parapterygoid fossae not fenestrated but ossified with thin layer of bone. Mandible with incisive root capsule forming prominent knob bordering sigmoid notch; very short angular process. Posterior half of third upper molar greatly reduced; oblique paralophules highly developed in M1-2, paralleling mesolophs; hypoflexid in third lower molar merges with entofossetid.

Distribution

Known from middle to high elevations in the Western Cordillera (departments of Cauca, Valle and Antioquia) and at the junction of the Central and Eastern Cordilleras (department of Huila), Colombia (Fig. 7.2).

Material examined

COLOMBIA: **Antioquia**, Páramo Frontino, 3300-3500 m *(166)* (FMNH 71738, ~39); Urrao, Santa Bárbara, 2800-3100 m *(167)* (FMNH 71740 to ~42); **Cauca**, Cocal,
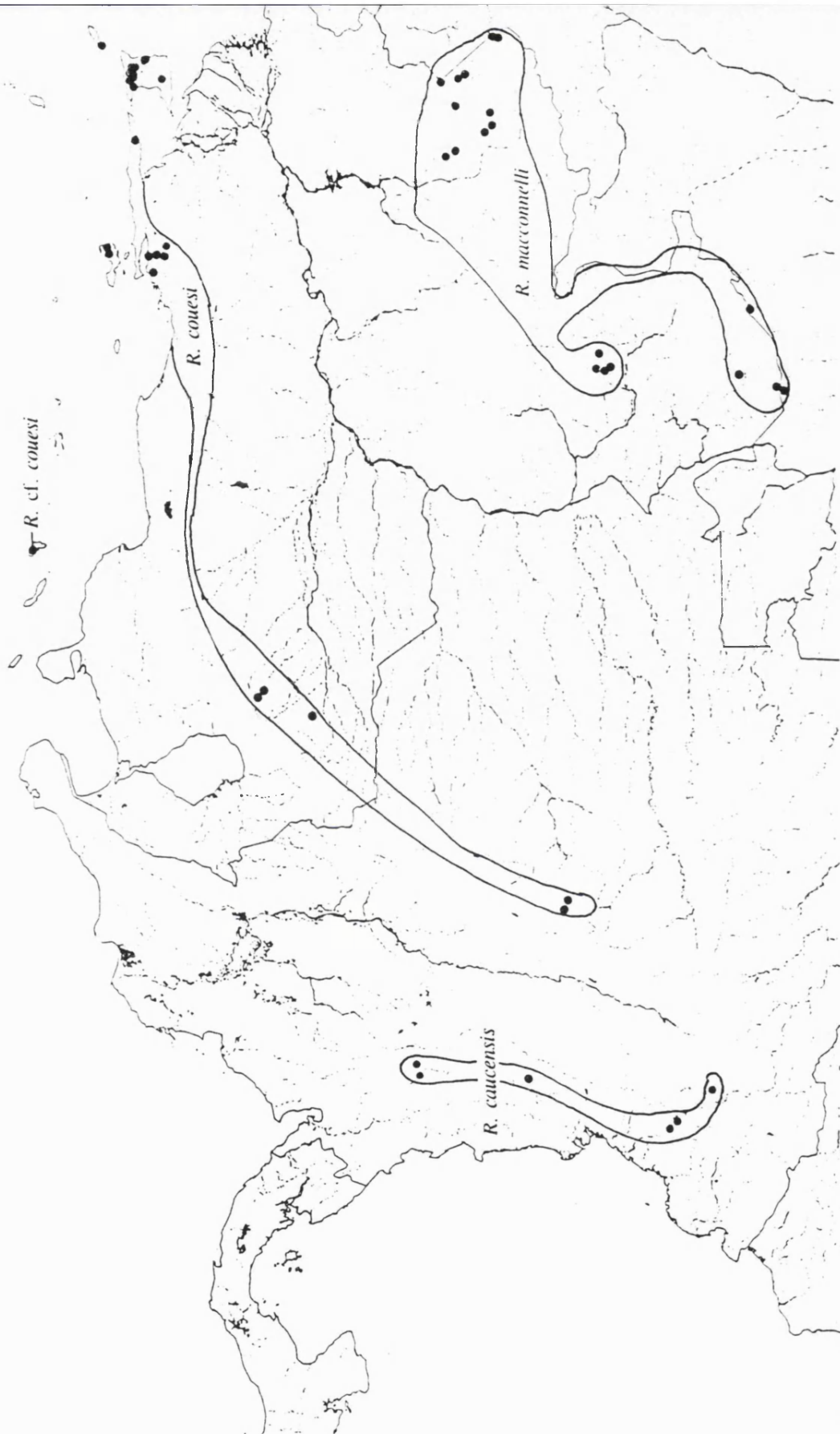
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Fig. 7.2 - Distribution of *Rhipidomys caucensis*, *R. macconnelli* and *R. couesi*.

6000 ft *(153)* (AMNH 32569, 32572); Munchique, 8325 ft *(152)* (AMNH 32466 - holotype of *caucensis*); **Huila**, San Agustín, San Antonio and Río Ovejeras, 2200-2350 m *(148)* (FMNH 71736, ~44 to ~46). **Total:** 12.

Rhipidomys ochrogaster J. A. Allen

Etymology: Greek ὠχρος *ōchros*, pale, yellow; γαστήρ *gastēr* stomach.

Synonyms

Rhipidomys ochrogaster J. A. Allen, 1901: 43. Type locality "Inca Mines, Peru (alt. 6000 feet)"

Rhipidomys leucodactylus leucodactylus, *sensu* Cabrera, 1961: 421 (part; not *Hesperomys (Rhipidomys) leucodactylus* Tschudi, 1845)

Holotype: AMNH 16481, adult female, skin and skull; collected at "Inca Mines" (= Santo Domingo), Inambari River, Región José Carlos Mariátegui (Departamento de Puno), Peru, on 14 September 1900, by H. H. Keays.

Diagnosis

Large *Rhipidomys* specimens with bright, orange-brown agouti dorsal pelage, strong orange wash to ventral pelage; tail dark, considerably longer than head and body, with long pencil; hind foot with broad, dark, indistinctly outlined patch extending onto digits. Skull moderately large, with rather slender, pointed rostrum, broad interorbit and broad, rounded braincase; supraorbital ledges well developed, divergent; parietal ridges weak; primitive carotid circulation pattern (large stapedial foramen, groove on inner surface of squamosal and alisphenoid, leading to sphenofrontal foramen).

Description

One of the larger species of *Rhipidomys* and the largest of the *R. fulviventer* group. Dorsal colour bright orange-brown, well flecked with dark guard hairs; pelage moderately soft and sleek. Ventral colour distinctly orange, due to fulvous hair tips; hair bases pale to medium-grey, making up 35-40% of hair length, less than in other species in this group; grey bases longer and darker on pectoral spot, and absent on throat and inner side of forelimbs. Pelage length (guard/body hairs): dorsal 13/10 mm, ventral 12/9 mm. Tail long and dark, with long, thick pencil. Hind foot broad, with large, ill-defined dark patch leaving only distal parts of digits golden. Ears medium to small, dark.

Skull moderately large (greatest length 37.5 mm in the two undamaged specimens) with rather slender, pointed rostrum and long nasals that taper in posterior half to a point. Interorbit broad with narrowest point central, waisted in appearance; supraorbital ledges well developed and slightly raised, diverging strongly around braincase. Braincase short, rounded and broad across the occipital; parietal ridges not pronounced, and rounded rather than inflected at anterior corner of lateral process of parietal. Incisive foramina long, penetrating between procingula of first molars. 2-3 pairs palatal foramina; medial process on rear margin of palate very slight or absent. Mesopterygoid fossa broad; sphenopalatine vacuities small or absent; parapterygoid fossae fully ossified or with only tiny gap between palatine and alisphenoid. Carotid circulation pattern primitive (i.e., large stapedial foramen in bulla, internal groove across squamosal and alisphenoid, leading to sphenofrontal foramen on alisphenoid-orbitosphenoid suture). Mandible: incisor root capsule not very prominent, forming shelf. Upper molars with well developed paralophule/mesostyle forming ridge linking paracone and mesocone.

Comparisons

Larger in external, cranial and dental dimensions than other members of the R. fulviventer group, but maintaining the basic traits of the group: intensely pigmented dorsal pelage, grey-based ventral fur, dark extremities, long tail pencil, skull with waisted interorbit, broad and rounded braincase and primitive carotid circulation pattern. These characters serve to distinguish R. ochrogaster from large members of the R. leucodactylus group that inhabit the same general area.

Distribution

Only 4 specimens known, from the vicinity of the type locality on the upper Inambari river in southeastern Peru (Fig. 7.4). The area is described by the collector of the holotype, H. H. Keays, as follows: "The country is very broken, with deep narrow cañons, and is covered with a dense undergrowth of shrubs and vines, with here or there a palmetto or a cedar rising above the surrounding vegetation" (quoted by Allen, 1900: 219).

Material examined

PERU: José Carlos Mariátegui (Puno), Inca Mines, 4000 and 6000 ft (254) (AMNH 16481 - holotype of ochrogaster, 16482); Santo Domingo, Carabaya Andes, 5500 ft (254) (BMNH 2.7.27.2, ~3). Total: 4.

Section B.

Rhipidomys macconnelli De Winton

Etymology: Named in honour of the British naturalist Frederick Vavasour McConnell, who collected the type specimen on his second expedition to Mt Roraima in 1898.

Synonyms

Rhipidomys Macconnelli De Winton, 1900: 52. Type locality "summit of Roraima, Demerara"

[Rhipidomys] maccomelli: Trouessart, 1905: 409 (incorrect subsequent spelling)

[Thomasomys] macconnelli: Thomas, 1917: 196 (name combination)

Thomasomys macconnelli macconnelli: Tate, 1939: 194 (as subspecies)

Thomasomys macconnelli subnubis Tate, 1939: 195. Holotype AMNH 131154; type locality "South slope Mt. Auyan-tepui, 3500 feet", Bolívar, Venezuela

Rhipidomys macconelli: Hershkovitz, 1959: 9 (incorrect subsequent spelling)

Holotype: BMNH 99.3.6.1, sub-adult male, in spirit with skull removed and cleaned, collected at "summit of [Mount] Roraima, Demerara" (now Guyana) in 1898 by F. V. McConnell and J. J. Quelch. Gyldenstolpe (1932) adds the altitude of 8700 ft.

Revised diagnosis

Pelage long, soft; dorsal colour dark chocolate brown, ventral dark slate overlaid with cream or pale brown; tail much longer than head-and-body, paler on ventral surface, almost bare over much of length but with pronounced terminal pencil; hind foot not short and broad as in most *Rhipidomys* but with longer, narrow metatarsals; heels bare. Skull with distinct, slightly concave supraorbital ridges; lateral process of parietal triangular and not contacting occipital, or sub-rectangular. Carotid circulation pattern derived (small stapedial foramen, no groove on inner surface of squamosal and alisphenoid, spheno-frontal foramen absent). Gall bladder absent, as in other *Rhipidomys* species.

Description

In many external characters *R. macconnelli* resembles certain *Thomasomys* species, while cranially it is closer to other *Rhipidomys*. Dorsal pelage is thick, long, soft and sleek; length (guard/body hairs) 14/12 mm; colour dark chocolate brown thickly lined with black guard hairs; bases of body hairs very dark slate, almost black, and long (80% of hair length); subterminal band orange. Flanks somewhat paler, with fewer or less conspicuous guard hairs. Ventral hairs also with long, dark slate bases, even on throat,

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under chin and on upper lip patch; hair tips white, cream or pale brown, but too short to obscure dark bases completely. Ears dark brown, matching dorsal pelage. Vibrissae shorter than in most *Rhipidomys* yet still extend beyond ear pinnae when appressed to head. Tail considerably longer than head-and-body, rather thin, bicolour - dark dorsally and pale yellowish ventrally from base almost to tip; scales conspicuous, because hairs very short over most of shaft although forming distinct pencil (5 mm to 20 mm) at tip. Hind foot less specialized for climbing, being longer (relative to head-and-body length) than in other *Rhipidomys* species on account of longer metatarsals; plantar pads smaller and separate, with gap between thenar and hypothenar; heels and ankles bare, body fur ending several millimetres above them (also on forelimbs); foot patch poorly defined, mid-brown, covering most of dorsal surface of foot; digits similar in proportions to those of other *Rhipidomys*, but digit V with claw not quite reaching base of claw of digit IV and claws less tightly curved; abundant vibrissae covering claws.

Skull: nasals narrow at anterior end; rostrum long and slender relative to broad, rounded braincase. Dorsal zygomatic root rather more slender and projecting less transversely than in many *Rhipidomys*, giving a more "streamlined" appearance. Interorbital region short, broad and rounded in dorsal view, often broadening below level of supraorbital ridges; ridges usually slightly concave rather than straight, diverging strongly rearwards. Parietal ridges often not coincidental with parietal-squamosal sutures in region anterior to lateral process of parietal, the ridges running slightly lateral to the sutures. Lateral process of parietal occasionally rectangular, but often triangular and barely or not reaching occipital. Occipital region broad. Breadth of interparietal varies: sometimes narrower than parietal ridges, sometimes nearly contacts squamosal. Palate with posterior medial peak or spine usually present; one main pair palatal foramina in middle of palate, sometimes with one or more smaller ones. Mesopterygoid fossa broadened anteriorly; sphenopalatine fissures small or absent. Parapterygoid fossae often with small medial unossified fenestration. Carotid circulation pattern derived, i.e., small stapedial foramen, no groove on inner surface of squamosal and alisphenoid, spheno-frontal foramen absent. Bulla often has small flap of ectotympanic extending dorsally over petrosal in region of stapedial foramen.

Molars broad for the genus; anteromedian flexus usually patent in M1, but anteromedian flexid often not apparent on anterior face of m1; in m1 procingulid, enamel lophids from conulids join anterior murid directly without linking to form additional transverse lophid.

Variation and comparisons

Dorsal colour varies slightly among individuals from the same locality, but overall the Cerro Duida population may be a little redder than the others, while specimens from Cerro Neblina have a tinge of olive. Variation is also associated with altitude, specimens from the tepui summits being on average richer and darker in colour than those from lower elevations. The subspecies *subnubis* was based upon a paler individual from the lower slopes of Auyán-tepui, but the differences are too inconsistent to warrant such taxonomic recognition. There is little unambiguous evidence for consistent morphometric differences correlated with altitude. Juveniles are darker and greyer than adults, but their coats are not noticeably woollier.

Rhipidomys macconnelli resembles species of *Thomasomys* externally in the long, dark bases to its fur, both dorsally and ventrally, in its bicolour tail, longer foot and less recurved claws, but differs in its tail pencil, dark foot patch and rather less bushy ungual tufts. Cranially, its supraorbital ridges are more pronounced than in *Thomasomys* species of similar size and its squamosal architecture is closer to that of other *Rhipidomys*, but the lateral process of the parietal is more like that of some *Thomasomys*. In its lack of a gall bladder it resembles other *Rhipidomys* species and differs from all other thomasomyines examined (Voss, 1991). In short, *R. macconnelli* is retained here within *Rhipidomys* as a possible basal offshoot of the genus, pending a thorough evaluation of the taxa currently included in *Thomasomys*.

Distribution

The slopes and summits of the Guiana Highland table mountains (*tepuyes*) in Venezuela and adjacent areas of Brazil and Guyana, at altitudes mostly above 1000 m (Fig. 7.2).

Ecological notes

Inhabits very humid cloud forest and dwarfed vegetation on tepuyes. Terrestrial-scansorial in habits, making runways under rocks and trees. Other habitat data in Handley (1976), Guerrero et al. (1989), Ojasti et al. (1992). Parasites: see Brennan & Goff (1977), Brennan & Reed (1974), Furman (1972a, 1972b), Johnson (1972), Jones et al. (1972), Machado-Allison & Barrera (1972), Saunders (1975), Tipton & Machado-Allison (1972). Museum specimens show a great ectoparasite load of lice nits and carpet-beetle egg cases. Teeth, even relatively unworn ones, soon acquire thick coating of tartar, more so than in most other *Rhipidomys* species.

Material examined

BRAZIL: Amazonas, Serra da Neblina *(28)* (USNM 531280). GUYANA: Cuyuni-Mazaruni, Mt Roraima, summit *(320)* (BMNH 99.3.6.1 - holotype of *macconnelli*). VENEZUELA: Amazonas, Cerro Duida *(336-338)* [includes: Caño Culebra, 50 km NNW of Esmeralda, 750 m (USNM 406070, ~72, ~75, ~76), Cabecera del Caño Culebra, 40 km NNW of Esmeralda, 1400 m, 1480 m (USNM 406078 to ~81, ~83, ~84, ~87, ~88, ~90, ~93 to ~97), Agüita, 3250 ft (AMNH 77161), Chorrera de Vegas, 4700 ft (AMNH 77071 to ~074, ~156 to ~158, ~160), Cumbre #2, Cabeceras del Valle, 5000 ft (AMNH 77044 to ~058, ~092 to ~097, ~099, ~100, ~103 to ~111, ~113 to ~119), Cumbre #13, Desfiladero, 6200 ft (AMNH 77059, ~060, ~064 to ~070, ~120, ~139 to ~141, ~143 to ~148, ~153), Cumbre #15, Loma #15, 6600 ft (AMNH 77061 to ~063, ~121, ~122, ~124, ~125, ~134, ~135), Summit, Central Camp, 4800 ft (AMNH 77076 to ~081, ~188, ~190 to ~214, ~658 to ~660), Summit, High Point Camp, Peak #7, 6800-6900 ft (AMNH 77216, ~217, ~220, ~223, ~224), Summit, Provisional Camp, 5500 ft (AMNH 77075, ~162 to ~187, ~189), Summit, Savanna Hills, 4400 ft (AMNH 77227 to ~248, ~298), Summit, Valley between Peaks 7 and 16, 6500 ft (AMNH 77225, ~226), Top of Peak #7, 7100 ft (AMNH 77082 to ~084, ~215, ~218, ~219, ~221, ~222)]; Cerro Neblina *(346)* [includes Camp II, 2200 m (USNM 560834, ~835), Camp VII, 1800 m (USNM 560836 to ~852), Camp XI (USNM 560853 to ~855)]; Bolívar, Acopán-tepui, 5000 ft *(327)* (AMNH 176308 to ~310); Arabopó ("Arabupu") 4200 ft *(321)* (AMNH 75709, ~710); Auyán-tepui *(331)* [includes Danto, 1800 m (AMNH 130949), 1100 m (AMNH 130923, ~924, 131013, ~115, ~154 - holotype of *subnubis*), Plateau, 1850 m (AMNH 130989 to 131012, 131147), Plateau, 2200 m (AMNH 130488, ~490 to ~500, ~988)]; Chimatá-tepui, camp 3, 3900 ft *(328)* (FMNH 74267, ~268); Churi-tepui *(326)* [includes 3400-3600 ft (AMNH 176306, ~311 to ~315), Camp 2, 3460 ft (AMNH 176320, ~333), Camp 4, 4370 ft (AMNH 176321), Camp 5, 4900 ft (AMNH 176322)]; Km 125 (and Km 121), 85 km SSE El Dorado, 1032 m *(315)* (USNM 387919, ~929, ~931, ~934 to ~937, ~939, ~941, ~943 to ~945, ~947, ~949, 405996, 406068, ~107); 120 km S El Dorado, 1150 m *(317)* (CM 78765, ~766); 126 km SE Río Cuyuni *(317)* (MVZ 160085, ~086); Ptari-tepui, 3800 ft *(316)* (AMNH 176300, ~301, ~303, ~304); Cerro Roraima *(320)* [includes Rondon Camp, 6800 ft (AMNH 75607 to ~624, ~626 to ~632, 75828, ~845, FMNH 53983), Summit, 8600-8650 ft (AMNH 75587, ~589 to ~606, ~840, FMNH 53982)]. Total: 356.

Section C. The *Rhipidomys leucodactylus* group

Large-bodied species (in geographical order from north to south):

Rhipidomys couesi (J. A. Allen & Chapman)

Tree rat, tree cocoa rat, long-tailed cacao rat

Etymology: Named after Dr Elliott Coues (1842-1899), American naturalist and historian (name pronounced like the English word "cows", *fide* Cutright & Brodhead, 1981).

Synonyms

Tylomys couesi J. A. Allen & Chapman, 1893: 211. Type locality "Princestown [i.e., Prince's Town], Trinidad", further restricted to "a point twelve miles north of the southern coast and seven miles southeast of Princestown" (*ibid.*, p. 203)

Rhipidomys couesi: J. A. Allen & Chapman, 1897: 18 (new name combination)

Rhipidomys couesii: Rendall, 1897: 343 (incorrect subsequent spelling)

Rhipidomys venezuelae cumananus Thomas, 1900b: 271. Type locality Ipure, Sucre state, Venezuela, altitude 700 m

Rhipidomys sclateri couesi: Cabrera, 1961: 424 (name combination)

R[hipidomys]. sclateri cousei: Furman & Tipton, 1961: 192 (incorrect subsequent spelling)

Rhipidomys leucodactylus, *sensu* Eshelman & Morgan, 1985: 140 (subfossil material from SW Tobago; not *Hesperomys (Rhipidomys) leucodactylus* Tschudi)

Holotype: AMNH 5956 (skin)/4685 (skull), adult male, skin and skull; collected at "Princestown, Trinidad" on 6 April 1893, by Frank M. Chapman.

Revised diagnosis

Large to very large specimens of *Rhipidomys*; dorsal colour yellowish to reddish brown agouti, conspicuously flecked with dark brown/black guard hairs; ventral pelage white or creamy yellow, sometimes with pale to medium grey hair bases that are rarely noticeable; pelage moderately coarse and short; tail shaft well haired distally with medium-length pencil; hind foot broad with dark patch distinctly or indistinctly outlined extending to bases of digits II to IV. Skull large, robust, rather narrow for the genus, with flattened profile such that the interparietal lies nearly horizontal, especially in older

specimens; supraorbital ridges well developed, usually straight and weakly divergent rearwards; braincase narrow, not inflated, with squamosals oriented dorso-laterally rather than laterally; auditory bullae small; carotid circulation derived (stapedial foramen small, no internal squamosal-alisphenoid groove, no sphenofrontal foramen). Maxillary molar row approximately 5.8-6.1 mm in length (Trinidad) or rather less (mainland).

Description

Large to very large individuals, adult head-and-body length typically 150-210 mm, with tail length 100-120% HB; mainland specimens may not reach the very large sizes found in Trinidad. Adult dorsal pelage yellowish brown agouti, sometimes more reddish, well flecked with dark brown or black guard hairs; flanks a little paler, with a moderately sharp transition line to ventral colour. Ventral hairs white or creamy yellow from tip to base or with the basal 20-40% of each hair pale to dark grey, rarely apparent; grey bases usually more intense on pectoral spot, and usually absent on throat and inner surface of forelimbs. Pelage texture medium to coarse, not spinous, often rather woolly on ventral surface; pelage rather short for the size of animal - dorsal guard hairs 9-15 mm in length, body hairs 6-11 mm, ventrally much shorter (especially in lactating females): guard hairs 6-9 mm, body hairs 4-6 mm. Juvenile pelage is greyish brown and rather woolly.

Hind foot length 29-32 mm (with claw), broader than average for the genus. Dark dorsal foot patch distinctly or indistinctly outlined, usually expanding distally to reach the bases (or first phalanges) of digits II to IV; sides of foot and remainder of toes golden. Claws approximately 2 mm in length (rather longer than in most other *Rhipidomys* species), covered with claw-length tufts of pale vibrissae. Tail with rather large, dark to mid-brown scales and dark to mid-brown or reddish brown hairs; tail not bicoloured; hairs short on proximal half of shaft, lengthening towards tip, where they form a moderate pencil not exceeding 20 mm in specimens examined, although Montserin (1937) claims 2½ inches (64 mm). The same author also affirms that females have five pairs of teats, "three of which are located in the groin and two on the chest"; the skins examined, however, show only the three pairs (inguinal, abdominal and post-axial) characteristic of *Rhipidomys*. Ears medium-sized to large for the genus.

Skull large, especially in Trinidad specimens (where adult ONL usually exceeds 40 mm), slightly smaller elsewhere; generally robust, rather narrow, angular with flattened profile, especially in older individuals. Rostrum broad, heavy and rather long; nasals expanded anteriorly, parallel-sided in posterior half. Interorbit narrow, usually with pronounced, straight supraorbital ridges that diverge weakly towards the braincase

(divergence is greater in smaller specimens). Braincase narrow, not inflated, and flattened in larger individuals, with interparietal almost horizontal; parietal ridges are positioned more dorsally on braincase, so that squamosals are oriented dorsolaterally rather than laterally. Lateral process of parietal roughly rectangular. Palate with 3-4 pairs palatal foramina, and slight medial process on rear edge. Mesopterygoid fossa average to broad; sphenopalatine fissures absent or present as short, narrow slits. Auditory bullae small. Carotid circulation derived, with small stapedial foramen, no translucent groove running along internal surface of squamosal and alisphenoid, and no sphenofrontal foramen in the orbit.

Molars large (MRC mostly 5.8-6.1 mm in Trinidad, mostly 5.6-5.8 mm elsewhere). Anteromedian flexus on M1 usually deep, sometimes weaker; anteromedian style often present; oblique paralophules present on M3, often on M2 and sometimes on M1, and oblique metalophules often on M2; M3 protoflexus usually absent. Anteromedian flexid on m1 weak or strong; ectolophids usually present but weak.

Variation and comparisons

The southernmost population of *R. couesi*, from the vicinity of Villavicencio, Colombia, has a rather more slender, less angular skull than is typical in Trinidad, whereas skulls of specimens from Sucre, Venezuela, tend to be intermediate. *R. couesi* differs from *R. leucodactylus* particularly in the smaller size of its hind foot and molar row; in addition, its rather narrower skull helps to distinguish it from the more southerly populations of *R. leucodactylus*, which are closer to *R. couesi* in other dimensions. Venezuelan *R. couesi* are often similar to *R. modicus* in overall and skull size and MRC, but have a relatively narrower interorbit and broader rostrum than the latter species, as well as a hairier tail. Their broader hind feet help distinguish smaller individuals of *R. couesi* from larger specimens of *R. latimanus venezuelae* (see below), a species found on the northern slopes of the Venezuelan coastal range and Mérida Andes.

Distribution

The species is known from the island of Trinidad, the coastal lowlands of the Venezuelan state of Sucre up to approximately 1000 m altitude, Margarita island (Nueva Esparta state), the lower, southeastern-facing slopes of the Mérida Andes in Barinas state, and the foothills of the Eastern Cordillera near Villavicencio, Meta, Colombia (Fig. 7.2). By extrapolation it can be expected to occur throughout the narrow belt of lowland moist forest that borders the *llanos* along the foothills of the Venezuelan coastal range, Mérida Andes and Eastern Cordillera from Sucre in northeastern Venezuela to Meta in Colombia.

From this point southwards, where the Amazon-Orinoco forests reach the Andes, this species is replaced by the larger *R. leucodactylus*.

Ecological notes

The monograph by Montserin (1937) includes valuable data on the reproduction, life history, nesting habits and diet of *R. couesi* in Trinidad, as well as its status as a pest of cacao and the control measures taken against it. The species was found to be relatively common in plantations but difficult to trap. Trap-shyness may mean that abundance estimates based on trapping success are inadequate. Other reports (Urich, 1911; Everard and Tikasingh, 1973) suggest it is a common arboreal species in Trinidad plantations and forests. In Sucre, Nueva Esparta and Barinas states, Venezuela, *R. couesi* was taken mainly in evergreen forest or plantations and in one case inside a house (Handley, 1976; Ochoa et al., 1988). Parasites (Venezuela): see Brennan & Reed (1974), Furman (1972a), Furman & Tipton (1961), Johnson (1972), Saunders (1975).

Material examined

COLOMBIA, Cundinamarca, Ceja Alta *(not located)* (BMNH 99.10.3.7); Susumuco *(137)* (AMNH 61561, BMNH 20.12.23.8); Meta, Villavicencio *(139)* (AMNH 75239). TRINIDAD AND TOBAGO, Trinidad (USNM 256788); Caura *(261)* (AMNH 7318/5926, 7319/5927, 7320/5928, 7321/5929, 7530; BMNH 99.9.4.1); Cocal, Manzanilla Highway, 40½ mile post, 42¼ mile post, 44¾ mile post *(267)* (AMNH 188496 to ~498); Cumaca *(264)* (AMNH 169692, 169694, 169734, 169761, 212140, 212141, 212319, 235071 to ~073); Kurukai (= Curucaye, *260)* (BMNH 97.6.7.3, 97.6.7.4); Marpa (= Marper) Estate *(266)* (BMNH 33.12.4.3); Mount Aripo *(263)* (BMNH 52.242); Princestown (= Prince's Town, *268)* (AMNH 5956/4685 - holotype of *couesi*). VENEZUELA, Barinas, Altamira *(282)* (USNM 442302); Nueva Esparta, Isla Margarita, El Cafetal *(301)* (LSUMZ 1810); Isla Margarita, Cerro Matasiete *(302)* (USNM 406100); Sucre, Ensenada Cauranta, 7 km N & 5 km E Guiria *(303)* (USNM 409936); HQ Guaracayal, 24 km E Cumaná *(304)* (USNM 406098); Ipure, 2250 ft *(305)* (BMNH 0.5.1.10 - holotype of *cumananus*); Latal, 3100 ft *(307)* (AMNH 69903, 69906); Mirasol, c. 15 km S Cumanacoa, 3200 ft *(309)* (CM 6348); San Rafael, near Cumanacoa, 2950 ft *(306)* (CM 6344, 6345); Quebrada Seca (= Villarroel, *306)* (BMNH 0.5.1.9). Total: 40.

Synonym

Thomasomys spec.: Hooijer, 1959: 18 (fossilized teeth and skull fragments from Quaternary deposits near Fontein, Bonaire, Nederlandse Antillen [Dutch West Indies], collected by Dr P. Wagenaar Hummelinck in 1937).

Notes

The material described and illustrated by Hooijer (1959: 18-20 and plate III, figs. 8-10) resembles *R. couesi* more closely than it does *Delomys dorsalis*, the species with which Hooijer compared it (regarded as a species of *Thomasomys* at that time), in that the labial and lingual flexi do not interpenetrate as they do in the latter species but rather terminate close to the midline of the tooth. The fossil material differs from *R. couesi* (and from *D. dorsalis*), however, in the fact that the second and third lower molars are reported as having three roots (two anterior and one posterior), whereas in all *Rhipidomys* specimens examined there are only two, although the broad anterior root sometimes shows incipient signs of subdivision. In the first upper molar of the fossil material the anterolingual conule is slightly larger than the anterolabial (in *R. couesi* the opposite is usually true), and in the first lower molar the entoflexid makes a more distinct notch in the outer enamel of the tooth than it does in *R. couesi*. No other thomasomyine or oryzomyine species was found to resemble the illustrated fossil material more closely than *R. couesi*, but in view of the differences enumerated above it would be unwise to assert that the fossils are conspecific with this taxon, although they certainly seem to be closely related.

Rhipidomys leucodactylus (Tschudi)

Rata de las chirimoyas.

Type species of the genus.

Etymology: Greek λευκός, *leukos*, white; δακτυλός *daktulos*, toe, referring to the conspicuously pale toes that contrast with the dark upper surface of the foot in this and many other species of *Rhipidomys*.

Synonyms

H[esperomys (Rhipidomys)]. leucodactylus Tschudi, 1845: 183. Type locality "im Oststriche", i.e., the eastern region of Peru visited by Tschudi, herein restricted to the Montaña de Vitoc area, in the former department of Junín, now Región Andrés Avelino Cáceres, Peru (see taxonomic notes below)

Nyctomys leucodactylus: Fitzinger, 1867: 89 (name combination).

[Hesperomys (Rhipidomys)] anguya, sensu Trouessart, 1881 (part, not *Mus anguya* Brandt, 1835)

Hesperomys (Rhipidomys) sclateri Thomas 1887: 152 and plate XIX. Holotype BMNH 87.1.28.8. Type locality "Maccasseema" [= Makasima, on Pomeroon River], Guyana

Rhipidomys Goodfellowi Thomas, 1900b: 270. Holotype BMNH 0.6.3.7. Type locality "upper Rio Napo, at mouth of Rio Coca", Napo, Ecuador

Rhipidomys bovallii Thomas, 1911: 114. Holotype BMNH 7.6.10.3. Type locality "Potaro Highlands, towards Mt Roraima, British Guiana. Alt. 2000'"

Rhipidomys lucullus Thomas, 1911: 115. Holotype BMNH 94.10.1.11. Type locality "Garita del Sol, valley of Vitoc, Upper Peréné, Central Peru. Alt. 5700'"

Rhipidomys equatoris Thomas, 1915: 312. Holotype BMNH 15.1.1.39. Type locality "San Domingo [= Santo Domingo de los Colorados], W. Ecuador (79°6'W., 0°13'S.). Alt. 1600'"

Rhipidomys rex Thomas, 1927: 600. Holotype BMNH 27.11.1.125. Type locality "Chinchavita, 3000'", Huánuco, Peru

Rhipidomys leucodactylus equatoris: Cabrera, 1961: 421 (name combination)

Rhipidomys leucodactylus goodfellowi: Cabrera, 1961: 421 (name combination)

Rhipidomys leucodactylus leucodactylus: Cabrera, 1961: 421 (part, excluding *Rhipidomys ochrogaster*, as subspecies)

Rhipidomys couesi, sensu Handley, 1976: 50 (part; specimen from Cerro Duida; not *Tylomys couesi* J. A. Allen & Chapman)

R[hipidomys]. leucodactylus aratayae Guillotin & Petter, 1985: 541. Holotype in MNHN. Type locality "saut Pararé, sur la rivière Arataye (4°3'N, 52°40'W)", French Guiana

Rhipidomys sp. 2: Woodman et al., 1991: 5 (specimens from Cuzco Amazónico, Peru)

Rhipidomys sp.: Woodman et al., 1995: 6 (specimens from Cuzco Amazónico, Peru)

Holotype: MHNN (771), adult, sex unknown, skin and skull. No locality data associated with specimen.

Taxonomic notes

As explained in the taxonomic notes for the genus, Tschudi's name *leucodactylus*, like *Rhipidomys*, becomes available from its use on page 183 of the *Untersuchungen über die Fauna peruana (Therologie)*, published in the fourth instalment of the work in 1845. Where it appears on page 16 of this work (published in 1844) and on p. 252 of the "Mammalium conspectus" (Tschudi, 1843) it is a *nomen nudum*. In his description of the material, Tschudi (1845: 183-4) mentions only that he found this species "im Oststriche", i.e., the region east of the Andean Cordillera in central Peru, where it was associated with crop fields (his first specimen was shot while gnawing a pineapple) and human habitations. He also states that Prof. Poeppig reported it from Tocache on the Huallaga river. Cabrera's (1961: 421) restriction of the type locality "on the basis of Tschudi's text" to the upper Huallaga is thus evidently based on a misinterpretation: Tschudi's own specimens came from the region he himself visited and not from the Huallaga, which lies much farther north. Tschudi (1846, 1847) describes his excursion from Lima over the Cordillera to the Montaña de Vitoc, the area between the rivers Anamayo and Tulumayo in the former department of Junín. There he saw many plantations, especially of pineapples. Although he does not specifically mention *Rhipidomys* in this context, this is the only area east of the Andes that he describes from first-hand experience. Given also the close similarity between the holotype of *leucodactylus* and other specimens collected later in the same area, it is justifiable to restrict the type locality of this taxon to the Montaña de Vitoc and to reject Cabrera's (1961) mistaken suggestion.

Wagner (1845: 147) also described a specimen of *Rhipidomys* under the name *Hesperomys leucodactylus*, but one belonging to a different species from Tschudi's material. I attribute Wagner's type specimen to *R. mastacalis* (Lund, 1840) (q.v.), which is thus a senior subjective synonym of *leucodactylus* Wagner. I have been unable to resolve the question of which *leucodactylus* - Tschudi's or Wagner's - was published first in 1845: no month of publication appears in either work, and no clues have been found in the accession records of several libraries consulted. In the absence of any clear priority, and in accordance with the Principle of the First Reviser (Code, 1985: Article 24), I consider that relative precedence should be given to *leucodactylus* Tschudi. This step best serves stability by retaining the name for the taxon with which it has always been associated; in contrast, to my knowledge Wagner's name has been cited only three times

this century (Tate, 1932: 5; Moojen, 1952: 75; and Vieira, 1955: 419); of these, only Tate associated the name with *Rhipidomys*. Furthermore, it avoids the inconvenience of having to provide a replacement name for the type species of the genus. Thus *leucodactylus* Wagner should be rejected as a junior homonym.[1]

Revised diagnosis

Large to very large *Rhipidomys* specimens; dorsal pelage yellowish to reddish brown agouti, rather coarse but not spinous, and sleek or rather woolly in texture; ventral pelage white or yellowish, with grey hair bases that may be apparent, often with orange suffusion on upper thorax; hind foot large, broad, with broad, dark patch covering most of foot and extending onto digits; tail long, abundantly furred distally, with long pencil. (In more southerly populations grey bases to ventral hairs sometimes absent, hind foot patch less extensive, and tail with moderate rather than long pencil.) Skull large, robust and broad, with flattish profile in larger specimens; supraorbital ridges well developed, usually weakly divergent; braincase broad; squamosal oriented dorsolaterally, especially in larger specimens; carotid circulation pattern derived (stapedial foramen small, no internal squamosal-alisphenoid groove, no sphenofrontal foramen). Maxillary molar row usually greater than 6.0 mm in length.

Description

Large to very large individuals (the largest *Rhipidomys* specimens examined belong to this species), with adult head-and-body length often exceeding 180 mm, and tail length 95-130% of HB or more; males often rather larger than females. Dorsal pelage mid-brown agouti, varying in tone from greyish to yellowish to reddish, with conspicuous dark guard hairs; flanks a little paler. Ventral pelage white, cream or yellowish, the hair bases (approximately 40% of hair length) very pale to medium grey, often apparent when fur slightly ruffled; grey bases often (but not always) absent on throat and inner surface of forelimbs; orange suffusion to pectoral area, especially on midline, common in lowland specimens and found occasionally in others. Distinctness of lateral dividing line depends on ventral colour: it is more distinct when ventral fur is white, less when it is yellowish or suffused with orange. Pelage texture rather coarse but not spinous; sometimes sleek (particularly in lowland specimens) but often a little woolly, especially ventrally but also dorsally to a certain extent; length moderate - dorsal guard hairs 12-16 mm, body fur

[1] These nomenclatural acts are unavailable until published in an available work, and should not be cited from this thesis.

10-12 mm, ventral 8-11 mm and 5-7 mm - varying somewhat with altitude. Juvenile pelage dull grey-brown dorsally, greyish-white ventrally, woolly.

Hind foot large and very broad, length 32-38 mm (including claw) in adults. Dark patch covering most of dorsal surface of foot and extending onto first or even second phalanges of digits II to V, sometimes also digit I; sides of foot and tips of toes silvery or golden. Claws moderately large for genus (roughly 2 mm in length), covered by pale claw-length vibrissae. Tail reddish to very dark brown, not bicoloured; shaft well clothed in hair, tipped with long, bushy pencil usually over 15 mm in length, sometimes reaching 40 mm. Ears moderately large. The rehydrated soft palate of one specimen (MPEG 2508, Amapá, Brazil) showed seven palatal ridges.

Skull large and robust, adult ONL usually greater than 40 mm; relatively broad. Rostrum deep and broad; nasals usually expanded at anterior end and parallel-sided in posterior half. Zygomatic notch small; anterior edge of zygomatic plate sometimes leaning a little rearwards. Supraorbital ridges well developed, sometimes converging anteriorly on top of interorbital region, so that narrowest part of interorbital constriction is formed by orbital wall ventrolateral to the ridges, and providing almost an hourglass shape to the region; other specimens have narrowest point of constriction well forwards on the ridges themselves. Braincase moderately broad and slightly inflated, although profile can be flattish in larger specimens, with interparietal almost horizontal and occiput vertical; parietal ridges are positioned more dorsally on braincase, so that squamosals are oriented dorsolaterally rather than laterally. Lateral process of parietal roughly rectangular. Palate with 3-5 pairs palatal foramina; medial process on rear edge usually present. Mesopterygoid fossa broad, especially anteriorly; sphenopalatine fissures absent or present as short, narrow slits. Region anterior to alisphenoid strut well ossified. Auditory bullae small. Carotid circulation derived, with small stapedial foramen, no translucent groove running along internal surface of squamosal and alisphenoid, and no sphenofrontal foramen in the orbit.

Molars large to very large (MRC mostly 6.0-7.0 mm). Anteromedian flexus on M1 usually deep; anteromedian style often present; oblique paralophules present on M3, often on M2 and sometimes on M1, and oblique metalophules often on M2; oblique lophule sometimes also associated with anterolabial conule of M1. Anteromedian flexid on m1 usually pronounced.

Variation and comparisons

Considerable geographic variation is present in this species. Karyotypic or

molecular data may in the future demonstrate that it is composite, but on the basis of currently available material it cannot be split unquestionably into separate taxa even at the subspecies level. The most divergent populations occur in the Peruvian region of Inka (i.e., the former departments of Cuzco and Madre de Dios) and the Ucayali valley, where pelage is often shorter without grey bases to ventral hairs, tails are less hairy with shorter pencils, and hind feet have a narrower dark patch; skulls are generally rather smaller, with less pronounced supraorbital ridges, narrower mesopterygoid fossa and smaller molars.

Adult specimens that are smaller than normal occur sporadically within the range of *R. leucodactylus* but can be attributed to this species on account of other characteristics, particularly a very hairy tail, large hind feet and/or long molar row. They include the three individuals from Los Pozos on the dry southern coastal plain of Ecuador, the holotypes of *goodfellowi* and *sclateri* (a subadult), a specimen from Machu Picchu, southeastern Peru, and an individual from Cerro Galeras in eastern Ecuador. All but the last of these specimens are females, a fact consistent with the sexual dimorphism in size that is more apparent in the larger species of *Rhipidomys*. Although small in head-and-body length, the Cerro Galeras male (a skin with no associated skull) has large feet but is also notable for its much smaller ears than normal for the species; more material from this area is needed to assess the significance of these anomalies.

The specimen from Cerro Neblina, Venezuela, has melanistic pelage, which may be associated with the high humidity of the locality (A. L. Gardner, personal communication). The specimen from Cerro Duida, Venezuela, attributed by Handley (1976) to *R. couesi* is a juvenile and has not yet developed the adult characters that might determine its identification; its colour is compatible with the young of either species and its molar row length (6.0 mm) lies in the area of overlap between them. Since no other *R. couesi* have been found south or east of the *llanos*, I prefer the more parsimonious interpretation of this individual as belonging to *R. leucodactylus*.

Specimens of *R. leucodactylus* are found in Colombia as far north as the Serranía de la Macarena. They contrast clearly with *R. couesi* from the vicinity of Villavicencio, just north of Macarena, (which are rather smaller and slenderer than those from Trinidad) in their larger overall size, broader hind foot, more abundantly haired tail, longer and broader skull, more pronounced supraorbital ridges and larger molars. To the northeast, Guyanan specimens of *R. leucodactylus* (i.e., the holotypes of *sclateri* and *bovallii*) differ from Trinidadian *R. couesi* particularly in their larger hind feet, darker coloration, longer

tail pencils and larger molars. Comparisons of *R. leucodactylus* with its neighbours to the south and southeast will be dealt with under the relevant species.

Distribution

Rhipidomys leucodactylus is found in the rainforests of the Guianas and Amazonia, within a perimeter drawn from Amapá in the east to northern Guyana in the north, around the eastern, southern and western flanks of the Guiana Highlands towards the Serranía de la Macarena and the Andean foothills of southern Colombia, south through Ecuador to southeastern Peru and northern Bolivia as far as the Cochabamba *yungas* (tropical valleys), and northeastwards through Rondônia towards the Tapajós and lower Amazon; in addition it occurs in the submontane valleys of eastern Peru, and through the Huancabamba depression to the western Andean slopes and valleys of NW Peru and Ecuador. It may prove to occur also in the Chocó region of western Colombia, and possibly the forested Maracaibo lowlands of Venezuela (Fig. 7.3).

Ecological notes

The six specimens from San Jerónimo, southern Loreto, Peru, were captured in houses or thatched roofs. Specimens from Chinchavito and Chihuangala, Peru, were captured on rafters in houses. Terborgh et al. (1984) and Woodman et al. (1995) provide ecological information on this species at Cocha Cashu and Cuzco Amazónico, Peru. Handley (1976) and Ochoa et al. (1988) described habitats in southern Venezuela. Females may become pregnant while still lactating: one individual (USNM 559408, Pakitza, Río Manu, Peru), captured when nursing a litter of three young in a desk drawer, was pregnant with four 20 mm embryos at the same time. *R. leucodactylus* has long been known to damage crops: the holotype was captured while gnawing fruit in a pineapple field (Tschudi, 1845); it is listed as a pest by Aguilar et al. (1977). Parasites (Venezuela): see Johnson (1972), Saunders (1975).

Material examined

BOLIVIA: **Cochabamba**, Yungas de Cochabamba, 1000 m *(10)* (BMNH 34.9.2.172). BRAZIL: **Amazonas**, Altamira, right bank Rio Juruá *(27)* [(MVZ) JLP15923]; Condor, left bank Rio Juruá *(25)* [(MVZ) JLP15683, ~704, ~724]; Rio Juruá, near Eirunepé *(26)* (MZUSP 895); Penedo, right bank Rio Juruá *(24)* [(MVZ) JLP15426]; **Amapá**, Mazagão, Boa Fortuna, upper Igarapé Rio Branco *(34)* (MPEG 2508); **Pará**, Amorim, Rio Tapajós *(38)* (AMNH 95508); Posto Monte Dourado, 105 km S + 170 km W Macapá *(35)* (USNM 399451); **Rondônia**, Usina Hidrelétrica de Samuel, Rio Jamari *(22)* (UFPB 1259). COLOMBIA: **Caquetá**, Florencia, 1000 ft *(143)* (AMNH
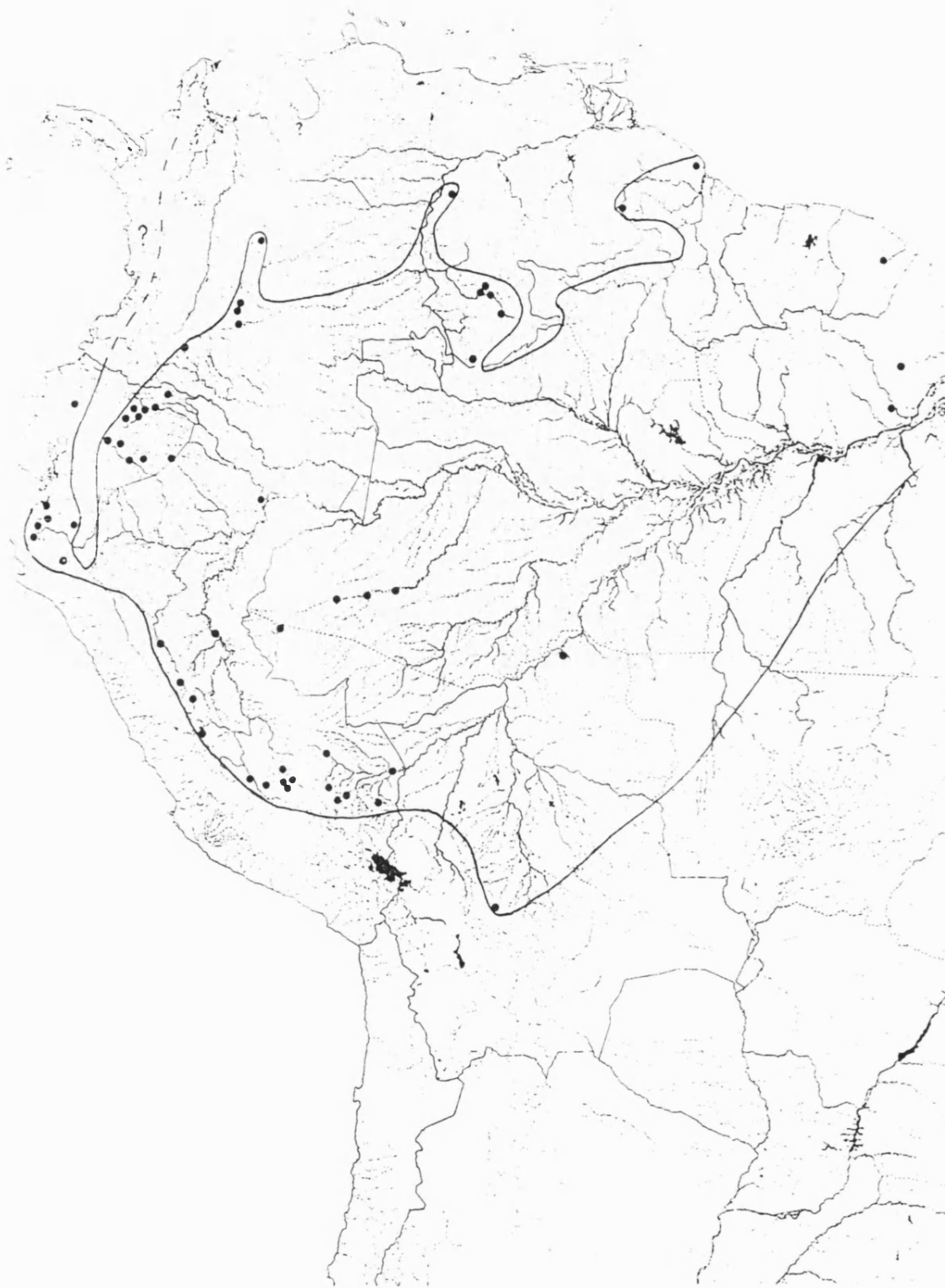
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Fig. 7.3 - Distribution of *Rhipidomys leucodactylus*.

33744); **Meta**, Serranía La Macarena, 1140 m *(141)* (AMNH 142141). **ECUADOR: El Oro**, Los Pozos *(195)* (AMNH 67507 to ~09); **Loja**, Alamor, Florida *(196)* (AMNH 213199, USNM 461648); Malacatos, 1600 m *(197)* (FMNH 53394, ~96 to ~99); **Napo**, mouth of Río Coca *(179)* (BMNH 0.6.3.7 - holotype of *goodfellowi*); Laguna Cuyabeno ("Laguna Grande" *177)* (FMNH 125049); Cerro Galera *(184)* (BMNH 54.495); Cerro Guataracu *(183)* (USNM 267499, 267502); Limoncocha *(178)* (USNM 528359, ~398); San José de Payamino *(180)* (MVZ 170910 to ~15); San José Nuevo (includes San José, San José abajo, *(181)* (AMNH 68189, 68191, FMNH 31083, MCZ 52617); Río Suno abajo *(182)* (AMNH 68190); **Pastaza**, Canelos *(188)* (AMNH 67510, 67681); Río Copataza, 650 m, 750 m *(191)* (FMNH 53400, ~01, 54274, ~75); Mera *(187)* (USNM 548392); Montalvo, Río Bobonaza *(190)* (FMNH 41477, -78, MCZ 38682); Río Pindo Yacu *(189)* (FMNH 43211); **Pichincha**, Santo Domingo *(175)* (BMNH 15.1.1.39 - holotype of *equatoris*, 15.1.1.40). **GUYANA: Cuyuni-Mazaruni**, Potaro Highlands, Venamo River, 2000 ft *(200)* (BMNH 7.6.10.3 - holotype of *bovallii*); **Pomeroon-Supenaam**, Makasima ("Maccasseema"), Pomeroon River *(198)* (BMNH 87.1.28.8 - holotype of *sclateri*). **PERU**: Central Peru *(not located)* (BMNH 85.4.1.2); **Andrés Avelino Cáceres (Huánuco)**, Chihuangala, 4000 ft *(232)* (BMNH 27.11.1.126 to ~129); Río Chinchao, Hacienda Buena Vista, 3500 ft *(232)* (FMNH 24805 to ~16, ~18 to ~23, ~25 to ~31, MCZ 26945, MNRJ 11662); Chinchavito, 3000 ft *(231)* (BMNH 27.11.1.125 - holotype of *rex*); **(Junín)**, Amable María, 2000 ft *(236)* (BMNH 85.4.1.3); La Garita del Sol *(237)* (BMNH 94.10.1.11 - holotype of *lucullus*); Montaña de Vitoc *(237)* (MHNN 771 - holotype of *leucodactylus*); Utcuyacu *(237)* (AMNH 63858); **(Pasco)**, Pozuzo, 2400 ft *(233)* (FMNH 24832 to ~34); **Grau (Piura)**, Canchaque, 1230 m *(224)* (FMNH 81290 to ~93); Cerro Cortezo, Las Trancas *(222)* (USNM 304560); Lancones, Cerro La Mesa, Sitio Añalquis *(223)* (USNM 282285, ~86, ~96); **Inka (Cuzco)**, Hac. Amaibamba, Río Santa María, 5250 ft *(243)* (MCZ 39687); Cosñipata ("Cosnipata", *245)* (BMNH 13.2.3.13); Machu Picchu, San Miguel Bridge, 6000 ft *(244)* (USNM 194493); Marcapata (includes Hacienda Cadena, Camante, 1000 m, 2000 m, *246-247)* (BMNH 3.2.9.6, ~7, FMNH 66413 to ~15, 68635, ~47, ~49 to ~54, 78697, ~98); Mercedes, below Quillabamba *(239)* (MCZ 39688 to ~91); Ocobamba *(240)* (BMNH 98.11.6.19, ~20, 99.10.5.5, USNM 86919); Quincemil *(248)* (FMNH 75229); San Fernando, Río San Miguel, 4500 ft *(242)* (BMNH 22.1.1.69, FMNH 43394, USNM 194495 to ~99); Santa Ana, 3000 ft *(241)* (USNM 194501); **(Madre de Dios)**, Reserva

Cuzco Amazónico (includes Albergue 252) (KU 144051 to ~57, MUSM CP42(F), CP64(F), CP73(F), RAC359(F), MVZ 168938, 168959); Pakitza (250) (USNM 559405 to ~408); Puerto Maldonado, 4.5 km W, (251) (USNM 390138, ~39); José Carlos Mariátegui (Puno), La Pampa, 2500 ft (253) (MCZ 39498); Loreto, mouth Río Curaray (219) (AMNH 71906, ~07); mouth of Río Mazán (220) (BMNH 32.8.4.33b); Lago Miraño, Río Napo (not located) (BMNH 32.8.4.31, 32.8.4.32); San Jerónimo, W bank Río Ucayali, 1000 ft (221) (BMNH 28.5.2.180 to ~185); Los Libertadores-Wari (Ayacucho), Huanhuachayo, 1580 m (238) (AMNH 241643). VENEZUELA: T. F. Amazonas, Acanaña (339) (USNM 406104); Cerro Duida, Cabecera del Caño Culebra, 1400 m (337) (USNM 495592); Boca Mavaca, 138 m (342) (USNM 374543, 406101, ~102); Cerro Neblina, Camp VII, 1800 m (346) (USNM 560825); Tamatama, 135 m (340) (USNM 409937). Total: 173.

Rhipidomys modicus Thomas

Etymology: Latin *modicus*, moderate, medium

Synonyms

Hesperomys (Rhipidomys) leucodactylus, *sensu* Thomas, 1882: 100 (part, not Tschudi, 1845; specimen from Huambo).

Hesperomys latimanus, *sensu* Thomas, 1884 (part, not Tomes, 1860; same specimen as above).

Rhipidomys modicus Thomas, 1926: 161. Type locality "Puca Tambo, 5100'", San Martín, Peru.

Rhipidomys lucullus, *sensu* Thomas, 1927: 601 (part, not Thomas, 1911; specimen from Chinchavito).

Rhipidomys leucodactylus modicus: Cabrera, 1961: 422 (name combination).

Holotype: BMNH 25.6.3.69, adult female, skin and skull; collected at "Puca Tambo, 5100 [feet]", San Martín, Peru, "about 50 miles east of Chachapoyas" (Thomas, 1926: 157), on 3 January 1926 by R. W. Hendee.

Revised diagnosis

Medium to large *Rhipidomys* specimens; dorsal pelage mid to dark yellowish to

reddish brown agouti, well streaked with dark guard hairs, rather coarse and short; ventral pelage with white tips, grey bases present or absent, orange pectoral spot sometimes present; hind foot moderately large, broad, with dark patch usually broad, sometimes extending onto digits; tail long, shaft lightly haired, pencil rarely exceeding 15 mm; ears rather small. Skull moderate in size and robustness; rostrum short and tapering, nasals with gradually tapering sides; zygomatic plate not broad; supraorbital ridges squared rather than raised, diverging strongly; interorbit broad, with narrowest point forward; braincase oval, moderately broad, not greatly flattened, although interparietal oriented more dorsally than posteriorly; carotid circulation derived (stapedial foramen small, no internal squamosal-alisphenoid groove, no sphenofrontal foramen). Maxillary molar row less than 6.0 mm in length.

Description

Moderate to large individuals: adult head-and-body length 130-165 mm, tail length up to 135% head-and-body length. Dorsal colour medium to dark yellowish to reddish brown agouti, often a little redder on the rump, well flecked with dark brown/black guard hairs. Ventral hairs with white tips over grey bases that vary in length (from absent to 50% of hair length) and intensity (from pale to dark); orange pectoral spot sometimes present. Pelage usually rather coarse (but not spinous) and short, sometimes a little woolly; dorsal guard hairs 9-12 mm, body hairs 6-9 mm; ventral guard hairs 6-10 mm, body hair 3-7 mm. Hind foot 28-30 mm (including approx. 1.5 mm claw), broad, with broad dark patch covering most of upper surface of foot and extending onto digits (rather narrower and not covering toes in some more northerly specimens); sides of foot and remainder of digits pale or silvery; claw vibrissae generally not extending beyond claw tips. Tail medium to dark brown, shaft hairs short except near tip; pencil mostly 5-10 mm, rarely longer than 15 mm. Ears rather small.

Skull moderate in size and robustness, broader and heavier in old specimens, a little more slender in some others. Rostrum short and rather pointed; nasals have sides that taper gradually instead of narrowing abruptly in the anterior half and then continuing roughly parallel in the posterior part. Zygomatic notch small; zygomatic plate not broad. Interorbital region broad, with narrowest point forward of centre; supraorbital ledges not raised but squared instead, straight or slightly concave, diverging strongly towards the parietals. Braincase oval, moderately broad and not greatly flattened. Parietal ridges usually positioned well to the sides of the braincase (rather than more dorsally). Interparietal oriented more dorsally than posteriorly, but not forming sharp angle with

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occipital. Lateral process of parietal rectangular, sometimes narrowing posteriorly. Palate with incisive foramina not greatly expanded; 2-3 pairs palatal foramina; rear edge of bony palate slightly peaked. Mesopterygoid fossa usually penetrating between hypocones of third upper molars, moderately broad; sphenopalatine fissures absent or present as tiny slits beside basisphenoid/presphenoid. Parapterygoid fossae well ossified. Bullae small. Carotid circulatory pattern derived, i.e., stapedial foramen small, no internal groove across squamosal and alisphenoid, no sphenofrontal foramen. Upper molar row shorter than 6.0 mm (mean 5.5 mm, range 5.0-5.8, sd = 0.22; n = 11). Anteromedian flexus moderate in M1, anteromedian flexid weak to moderate in m1; oblique paralophules usually present in M2, sometimes also in other teeth.

Variation and comparisons

Adult *R. modicus* are similar in size to juvenile *R. leucodactylus* but substantially smaller than adults of the latter species in external dimensions, skull length and toothrow length; in addition, the rostrum tends to be relatively shorter and more pointed and the supraorbital ledges are less pronounced. Although similar in size to Bolivian material, *R. modicus* has a broader interorbit than *R. austrinus*, and usually a more robust skull than specimens from Chijchipani, although a specimen of *R. modicus* from near La Peca in northern Peru is rather more delicate than the remainder of the sample examined. The presence of grey bases to the ventral fur varies even within localities: one specimen from Chanchamayo has fur with grey bases (50% of hair length) all over the ventral surface; in another, such grey bases are distributed only along the sides of the belly, and in a third the hairs are white to the base throughout.

Distribution

Known from eastern Andean valleys in northern and central Peru, at elevations between 700 and 1800 m. Collecting localities for *R. modicus* in central Peru are identical with or close to localities where specimens of *R. leucodactylus* have been taken (Fig. 7.4).

Ecological notes

The holotype was "trapped in brush near stream" and the specimen from Chinchavito was trapped in an abandoned shed (specimen labels).

Material examined

PERU: **Andrés Avelino Cáceres (Huánuco)**, Chinchavito, 3000 ft *(231)* (BMNH 27.11.1.130); **(Junín)**, Chanchamayo, 1000 m, 1100 m, 1200 m *(235)* (BMNH 7.6.15.13; FMNH 65757, 65758; MHNG 755/52, USNM 172957); Río Saco Alto, 13
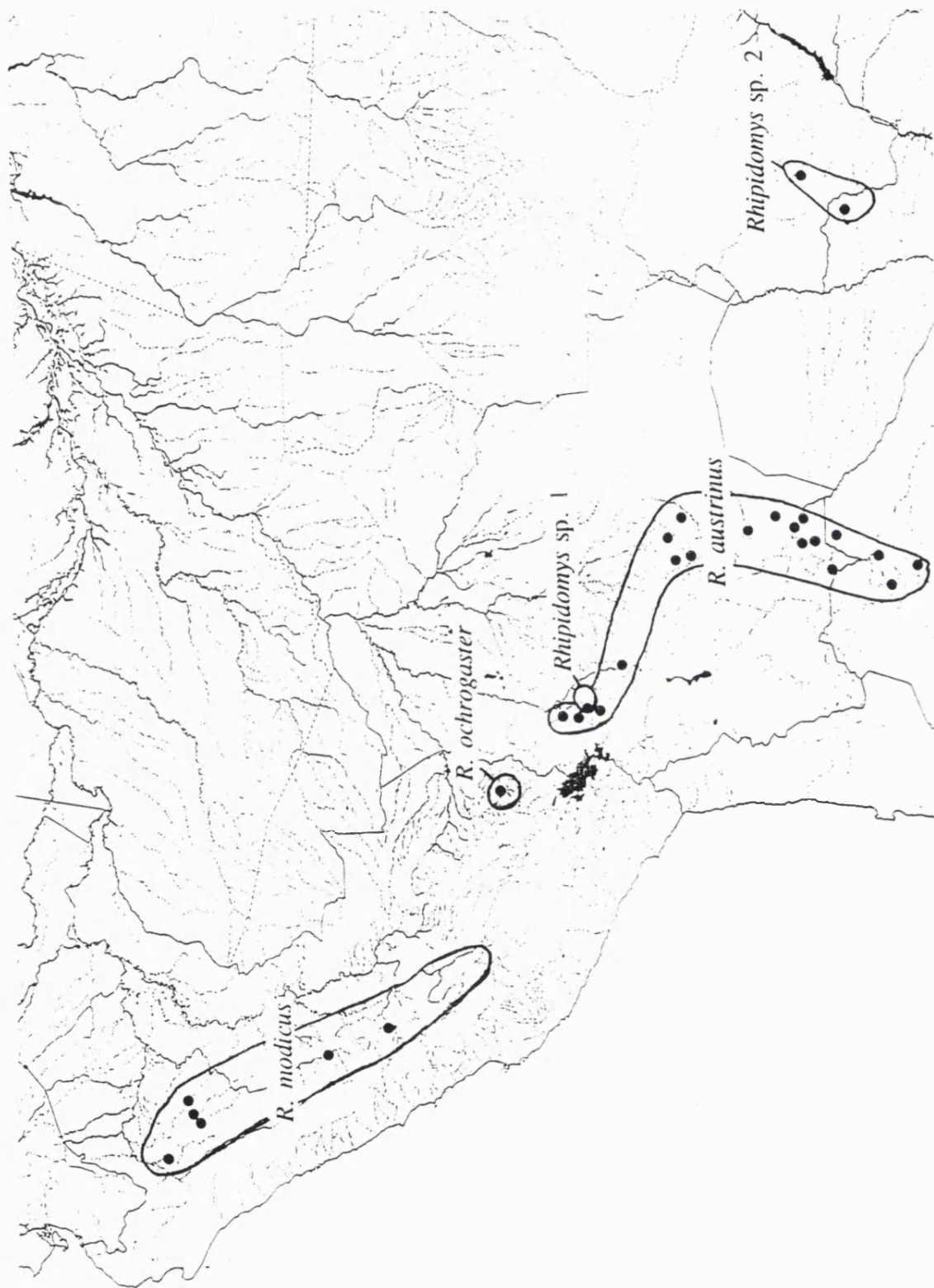
Fig. 7.4 - Distribution of *Rhipidomys ochrogaster, R. modicus, R.* sp. 1, *R. austrinus* and *R.* sp. 2.

miles N of La Merced, 2376 ft *(234)* (AMNH 231197); **Nor Oriental del Marañón (Amazonas)**, Huambo, 3700 ft *(227)* (BMNH 81.9.7.21); La Peca Nueva, 12 km E, 5775 ft *(226)* (LSUMZ 21873); **San Martín (San Martín)**, Moyobamba *(229)* (FMNH 19363, 19364); Puca Tambo, 5100 ft *(228)* (BMNH 26.5.3.69 - holotype of *modicus*). Total: 12.

Rhipidomys sp. 1

Synonym

Rhipidomys couesi, *sensu* Voss, 1991: 34 [not *R. couesi* (J. A. Allen & Chapman)].

Diagnosis

Moderate to large *Rhipidomys* specimens. Dorsal pelage reddish-orange brown agouti, finely streaked by dark guard hairs, fine and soft; ventral hairs with pale cream tips over dark grey bases, occasionally white to roots, slightly woolly; hind foot moderate in size with distinct dark patch to bases digits II-IV; tail moderately long, sparsely haired, medium pencil. Skull moderate size, not very robust; short, tapering rostrum; interorbit not very broad, with heavy supraorbital ledges converging far forward, concave; braincase long, rather inflated; carotid circulatory pattern derived.

Description

Specimens examined with adult head-and-body length up to 170 mm and tail length 105-115% HB. Dorsal pelage relatively bright reddish-orange brown, slightly flecked by dark brown/black guard hairs; texture fine and soft. Ventral pelage creamy-white with mid to dark grey bases (40% of hair length, occasionally absent); throat hair white to base; texture sometimes rather woolly. Pelage rather short (guard hairs/body fur): dorsal 10 mm/7 mm; ventral 7 mm/5 mm. Abnormal moult pattern observed: head, rump and forelimbs moulted first into adult pelage, leaving a saddle of juvenile pelage on the back and on the hind limbs (specimen AMNH 262992). Hind foot moderate in size (27-29 mm, including approx. 1.5 mm claw); distinctly outlined dark patch to base digits II-IV; sides of foot and digits white or yellow; long claw vibrissae. Tail rather longer than head-and-body; shaft sparsely haired, pencil up to approx. 12 mm. Ears rather small and dark.

Skull moderate in size, not very robust. Rostrum short, broad at base and tapering

to tip. Interorbit moderate in breadth, with heavy supraorbital ledges (i.e., expanded laterally rather than dorsally) converging in a concave curve to a point far forward in the interorbital region, very different from the more hourglass-shaped interorbit of *R. austrinus* from western Bolivia. Braincase long, broad, rather inflated. Lateral process of parietal a shallow rectangle. Incisive foramina usually long, broad and pear-shaped; palate with 2-4 pairs palatal foramina (plus a pair of venous foramina adjacent to the mesopterygoid fossa); medial process on rear edge of palate absent to moderate. Mesopterygoid fossa parallel-sided or slightly expanded anteriorly; sphenopalatine fissures absent or narrow slits. Carotid circulatory pattern derived, i.e., stapedial foramen small, no internal groove across squamosal and alisphenoid, no sphenofrontal foramen.

Upper molar row of sample examined in range 5.6-6.25 mm (mean = 5.94 mm, s.d. = 0.18, n = 14). Molars mostly large, with complex occlusal surface. Anteromedian flexus of M1 usually well defined; anteromedian style usually absent. Oblique anterolabial lophule (M1), oblique paralophules (M1-3) and oblique metalophule (M2) usually present. Anteromedian flexid on m1 distinct; ectolophids sometimes present; oblique metalophulids occasionally present (m2-3). In some specimens cingular elements are reduced in upper molars, so that labial flexi are not blocked at the edge of the tooth and lingual styles are absent.

Comparisons

Externally this species resembles the following one (*R. austrinus*), but it differs (especially from the nearby population of *R. austrinus*) in the shape of the skull, particularly as regards the heavy supraorbital ledges and inflated braincase. It can be distinguished from *R. modicus* by the same features plus its narrower interorbit and rather less robust skull and the reduced lingual cingulum of the upper molars. The same combination of characters and its overall size will distinguish it from *R. leucodactylus*.

Distribution

Known only from a single locality at 850 m elevation at Chijchipani, Departamento La Paz, Bolivia; this is situated near Coroico, about 60 km NE of the city of La Paz (Fig. 7.4).

Material examined

BOLIVIA: La Paz, Chijchipani, 850 m *(7)* (AMNH 262290, ~991, ~992, 263134 to ~137, ~142, ~143, ~145, ~155 to ~163). Total: 19.

Rhipidomys austrinus Thomas

Etymology: Latin *austrinus*, from the south

Synonyms

Rhipidomys austrinus Thomas, 1921: 183. Type locality "Sierra de Santa Barbara, S.E. Jujuy [...] Sunchal, 1200 m", Argentina.

Rhipidomys collinus Thomas, 1925: 578. Holotype BMNH 25.2.1.39. Type locality "Sierra Santa Rosa, 1000 m", near Itaú, Tarija, Bolivia.

Rhipidomys leucodactylus austrinus: Cabrera, 1961: 420 (name combination).

Rhipidomys leucodactylus collinus: Cabrera, 1961: 421 (name combination).

Rhipidomys leucodactylus, sensu Cendrero, 1972: 1032 (part, not *R. leucodactylus* Tschudi)

R[hipidomys]. couesi, sensu Emmons & Feer, 1990: 184 [part, not *R. couesi* (J. A. Allen & Chapman)].

Holotype: BMNH 21.1.1.17, young adult male, skin and skull; collected at "Sierra de Santa Barbara, S.E. Jujuy [...] Sunchal, 1200 m", Argentina, on 6 June 1920, by E. Budin.

Revised diagnosis

Moderate to large *Rhipidomys* specimens; dorsal pelage greyish brown to bright orange brown agouti, soft and dense, sharp lateral transition line; ventral pelage with creamy white tips and medium to dark grey bases, soft; hind foot medium to large, broad, with distinctly outlined dark patch extending to base of digits II to V (less distinct and more extensive in northwestern population); tail long, medium to dark brown, shaft with short hairs and short to medium pencil; ears large and oval. Skull moderate in size and robustness; rostrum short and deep, not tapering greatly; nasals narrowing sharply behind tips, then tapering gently; interorbit narrow, either hourglass-shaped with squared edges or waisted anteriorly with slightly raised supraorbital ridges; braincase rather flattened or very slightly inflated; bullae prominent; carotid circulation derived. Molars moderate to large.

Description

Specimens examined with adult head-and-body length up to 170 mm and tail length 110-135% HB. Dorsal pelage varying from greyish brown agouti to bright orange brown agouti, darker in Pitiguaya population; dark brown/black guard hairs tend to be more conspicuous in larger, older specimens, less obvious in others. Sharp lateral

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transition to ventral colour: overall creamy grey impression given by creamy white hair tips over mid to dark grey bases (50% of hair length, more in Pitiguaya specimens); throat usually white to base of hairs, sometimes with some grey bases; orange pectoral spot not observed. Pelage texture soft, dense, sleek and long, especially in southern populations; length (guard hairs/body fur): dorsal 14-19 mm/9-14 mm, ventral 7-12 mm/ 5-9 mm. Hind foot moderate to large (28-33 mm, including 1.5 mm claw), broad, with distinctly outlined dark patch extending to base of digits II to V, rarely onto phalanges (except in Pitiguaya specimens, in which the outline of the patch is also indistinct), with sides of foot and remainder of digits pale or golden; claw vibrissae long and abundant. Tail long, mid to dark brown; small scales (up to 20 per 10 mm length, mid-shaft); shaft with short hairs; pencil short to medium length, up to 10 mm. Ears large and oval, especially in southern populations.

Skull moderate in size and robustness. Rostrum short and deep, tapering relatively little. Nasals broad at tip, narrowing sharply, then tapering gently in posterior half. Zygomatic notch usually small, but often absent in Pitiguaya specimens in which the anterior edge of the zygomatic plate drops straight down from the dorsal root. Interorbital region narrow either with squared edges, in which case the outline is usually rather hourglass-shaped, especially in Pitiguaya specimens, or with slightly raised supraorbital ridges converging to an anterior waist. Braincase not especially broad or inflated, often rather flattened. Lateral process of parietal rectangular, often narrowing posteriorly. Incisive foramina relatively long and elliptical or pear-shaped; palate with 3-4 pairs palatal foramina, plus a pair of venous foramina beside the mesopterygoid fossa; moderate to large medial process on rear edge. Mesopterygoid fossa parallel-sided or slightly broadened anteriorly; sphenopalatine fissures absent, slit-like or occasionally a little broader and extending half the length of the basisphenoid. Auditory bullae prominent, slightly inflated. Carotid circulatory pattern derived, i.e., stapedial foramen small, no internal groove across squamosal and alisphenoid, no sphenofrontal foramen.

Upper molar row mostly 5.5 to 6.1 mm (observed range 5.3-6.3 mm, mean = 5.81, s.d. = 0.24, n = 23). Anteromedian flexus well defined; anteromedian style usually absent (usually present in Pitiguaya specimens). Oblique anterolabial lophule (M1) present or absent; oblique paralophule (M1-3) and oblique metalophule (M2) absent or slight (more common in Pitiguaya material); labial cingular ridge sometimes does not link styles to adjacent cusps. Anteromedian flexid moderate; ectolophids absent; no oblique metalophulids. In Pitiguaya specimens, the protoflexid and hypoflexid expand medially,

pinching the medial side of the protoconid and hypoconid. In more southerly specimens the occlusal enamel pattern is generally simple, not convoluted, whereas it is rather more complex in the Pitiguaya population.

Comparisons

Rhipidomys austrinus can be distinguished from the Chijchipani species by the shape of its interorbit and braincase; from *R. modicus* by its less robust skull, narrower interorbit, less pointed rostrum and more inflated bullae; and from the larger species farther north by these characters and its size.

Distribution

This species occurs in the eastern Andean foothills and valleys and adjacent forested plains at altitudes from 360 m to at least 1750 m, from southern Jujuy, Argentina, northwards to Santa Cruz de la Sierra, Bolivia; to the west in La Paz department it has been found in the same valley systems as the preceding species (*Rhipidomys* sp. 1), but at higher altitudes (1500-1770 m) (Fig. 7.4).

Ecological notes

The collecting locality at Villa Montes (8 km S, 10 km E), Departamento Tarija, Bolivia, 467 m, was described on the specimen label as "E. bank Río Pilcomayo. Habitat: dense forest 15 m height, dense understory of 6 m shrubs, 86% ground cover of forbs, grasses and bromeliads." The two specimens from Jujuy, Argentina, were collected in nut trees ("nogales"), and the two from the Chimasi Yungas, La Paz, Bolivia, were found "in [a] corn sack". Ojeda & Mares (1989) provide some general habitat information for NW Argentina.

Material examined

ARGENTINA: Jujuy, Sierra Santa Bárbara, Sunchal, 1200 m, 1600 m *(4)* (BMNH 21.1.1.17 - holotype of *austrinus*, 21.1.1.18). BOLIVIA: (CM 5050, 5051); Chuquisaca, Porvenir, 675 m *(16)* (AMNH 262259); La Paz, Chimasi Yungas, 1500 m *(5)* (BMNH 1.6.7.33, 1.6.7.34); Pitiguaya, 5600-5800 ft (including La Florida, Río Unduavi, 1700 m - *8)* (AMNH 72631 to 72635, 72718; UMMZ 156295); Santa Cruz, Río Ariruma, 7 km SE Ariruma, 1750 m *(12)* (AMNH 264199); Camiri, 1000 m *(15)* (AMNH 271599 to ~601; USNM 545228); Estancia Cuevas, 1 km NE *(11)* (AMNH 264198; MNLP NK22803); Florida, near Floripondio *(not located)* (FMNH 72881 to ~83); Ingenio Mora, 7 km E, 3 km N, 490-580 m *(14)* (AMNH 247782); Molina [?], Tabacal, 1610 m *(not located)* (USNM 270913); Tarija, Cuyambuyo, 4 km N, 980 m *(21)* (UMMZ 155864, ~865); Itaú valley, foot of Sierra Santa Rosa, 1000 m *(20)*

(BMNH 25.2.1.39 - holotype of *collinus*); Tapecua, 1500 m *(19)* (AMNH 264200; MNLP NK23393); Taringuiti, 360 m *(18)* (UMMZ 155866); Villa Montes, 8 km S, 10 km E, 467 m *(17)* (AMNH 246827). **Total:** 33.

Rhipidomys sp. 2

Synonyms: None

Diagnosis

Moderate to large *Rhipidomys* specimens. Dorsal pelage dull, medium-brown agouti well streaked with dark brown guard hairs; ventral hairs creamy with grey bases; pelage short, rather woolly; hind foot large and broad with well-defined, narrow dark patch; tail moderately long, well haired with medium length pencil. Skull moderate in size; rostrum short and broad; interorbit narrow, edges beaded, diverging little from the middle of the region; braincase moderately broad, slightly flattened especially in older specimens; bullae small; carotid circulatory pattern derived. Upper molar row moderate in length, less than 6.0 mm.

Description

Moderate to large individuals, with observed adult head-and-body length up to 175 mm and tail length 110-120% of HB. Dorsal pelage dull, medium-brown agouti, not bright orange, well streaked with dark brown guard hairs; short and not particularly soft in texture. Ventral hairs probably with creamy tips (all specimens are rather dirty and discoloured) over medium to dark grey bases (40-50% of hair length), sometimes paler, white to base on throat; pectoral spot with darker grey bases; texture woolly and dense (possibly an artifact of preservation). Some specimens have an orange ventral tinge, which may or may not be an artifact. Pelage length (guard hairs/body fur): dorsal 12 mm/8 mm, ventral 7-10 mm/5-7 mm. Hind foot moderately large (30-33 mm, including approx. 1.5 mm claw), broad; dark patch well-defined and narrow, extending to base of digit III, occasionally also to the adjacent digits; sides of foot and digits golden or creamy. Tail medium or reddish brown, moderately well haired, with pencil up to 20 mm in length, usually less. Ears large and medium brown.

Skull moderate in size and robustness. Rostrum short and broad, not tapering greatly; zygomatic notch barely visible from above. Interorbit rather narrow, with beaded

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edges (not pronounced ridges) that are usually straight and diverge little from the centre of the region. Braincase moderately broad, not inflated, slightly flattened in older specimens; parietal ridges weak and irregular in outline anterior to lateral process of parietal. Interparietal broad. Incisive foramina usually long, broad and pear-shaped; palate with 3-4 pairs palatal foramina plus one pair venous foramina adjacent to the mesopterygoid fossa; medial process on rear edge absent to moderate. Mesopterygoid fossa parallel-sided or slightly broadened anteriorly; sphenopalatine fissures usually absent, rarely narrow slits; foramen ovale small. Auditory bullae small, not inflated, with short, wide bony tubes.

Observed range of upper molar row 5.35 to 5.85 mm (mean = 5.62, s.d. = 0.13, n = 27). Molars generally regular and rounded in outline, with thick enamel. Anteromedian flexus in M1 well defined; anteromedian style usually absent. Oblique anterolabial lophule usually absent; oblique paralophule always present in M3 (except in Paraguay specimen), usually also in M1-2; oblique metalophule absent or slight in M2. Labial and lingual cingulum present. In m1, anteromedian flexid absent or weakly defined and soon obliterated by wear; oblique metalophulids absent in m1-3; ectostylids often large, but ectolophids weak. Upper labial flexi and lower lingual flexids very narrow.

Comparisons

This species is similar to *R. austrinus* in external and skull size, but has duller, shorter and harsher pelage, a narrower foot patch, and often a rather hairier tail; the skull has a relatively broader braincase, palatal bridge and mesopterygoid fossa, and smaller bullae. In comparison with *R. macrurus* of central Brazil, specimens from Maracaju are similar in dorsal pelage colour and texture but have considerably larger and broader hind feet, more conspicuous grey bases to the ventral pelage, and a much hairier tail with a longer pencil; they are larger in head-and-body, skull and molar row lengths, although the very largest *R. macrurus* may be similar in size to the smallest adults from Maracaju.

Distribution

Known from the vicinity of Maracaju, Mato Grosso do Sul, Brazil and from the Parque Nacional del Cerro Corá, Amambay, Paraguay, some 150 km to the SW of Maracaju (Fig. 7.4). The range of the species presumably includes the forested parts of the hill country of the Serra de Maracaju and the Sierra de Amambay along the Brazil-Paraguay border. It is separated by the Chaco of Paraguay from the range of *Rhipidomys austrinus* in southern Bolivia and northwestern Argentina.

Material examined

BRAZIL: **Mato Grosso do Sul, Maracaju,** 500 m *(117)* (AMNH 134513, ~514, ~516, ~519 to ~522, ~824, ~826, ~828, ~836, ~842 to ~844, ~846 to ~848, ~850, ~853, ~855, ~863, ~865, ~898; MNRJ 4296, 4297, 4442, 30018, 30024). **PARAGUAY: Amambay,** Parque Nacional Cerro Corá *(218)* (USNM 554544). **Total: 29.**

Medium and small-bodied species (in approximate geographical order clockwise from Ecuador):

Rhipidomys latimanus (Tomes)

Etymology: Latin *latus* broad, *manus* hand

Synonyms: See under subspecies.

Revised diagnosis

Medium-sized *Rhipidomys* specimens with reddish, orange or yellowish brown dorsal pelage, intensely pigmented or not and with or without evident agouti effect; ventral pelage creamy white, with or without inconspicuous grey bases to hairs; hind foot moderately large and robust with rather narrow dark patch rarely extending onto digits; tail with short to medium-length pencil of hairs. Skull moderately rounded in younger specimens, becoming more flattened in older ones; supraorbital ledges or ridges pronounced; parapterygoid fossae not fenestrated; bullae small; carotid circulatory pattern derived (stapedial foramen small, no internal squamosal-alisphenoid groove, no sphenofrontal foramen); incisor root capsule on mandible not forming prominent knob.

Distribution

Andean slopes and valleys from extreme northern Peru, through Ecuador and Colombia to the Sierra Nevada de Santa Marta in the north of that country, in Venezuela from the Mérida Andes through the hills and coastal plains of Lara and Falcón to the northern Coastal Range at least as far east as the Federal District, and in the Darién mountains of eastern Panama, at elevations between sea level and 2000 m, locally higher (Fig. 7.5).

Although the differences between the samples from Ecuador and Mérida appear

sufficient for them to deserve the status of separate species, the occurrence of forms that intergrade to a greater or lesser extent in various parts of Colombia, particularly in the north of the country, suggests that the whole assemblage should be treated as a single species. Three major variants are here regarded as subspecies, as described below.

Subspecies:

Rhipidomys latimanus latimanus (Tomes)

Synonyms

H[esperomys]. latimanus Tomes, 1860: 213. Type locality probably Pallatanga, Chimborazo province, Ecuador.

[Hesperomys (] Myoxomys [)] latimanus: Tomes, 1861: 284 (name combination).

Hesperomys (Rhipidomys) leucodactylus, sensu Thomas, 1882: 106 (part; not of Tschudi)

Rhipidomys microtis Thomas, 1896b: 304. Holotype BMNH 96.11.1.2; type locality "Saliña del Vatan [possibly near Quebrada Batán], Western Cundinamarca, Colombia".

Rhipidomys pictor Thomas, 1904b: 193. Holotype BMNH 1.1.6.4; type locality "Rio Verde, [Pichincha province,] N.W. Ecuador. Alt. 1000 m."

Rhipidomys mollissimus J. A. Allen, 1912: 78. Holotype AMNH 32243; type locality "Mira Flores [= Miraflores] (alt. 6200 ft.), west slope of Central Andes, near Palmira, Cauca [now Valle], Colombia."

Rhipidomys cocalensis J. A. Allen, 1912: 79. Holotype AMNH 32376; type locality "Cocal, Cauca, Colombia, Altitude, 4000 feet."

Rhipidomys quindianus J. A. Allen, 1913: 600. Holotype AMNH 32970; type locality "El Roble (altitude 7200 feet), Central Andes [Quindío department], Colombia."

Rhipidomys scandens Goldman, 1913: 8. Holotype USNM 178987; type locality "near head of Rio Limon (altitude 5,000 feet), Mount Pirri [= Cerro Pirre], Eastern Panama".

[Rhipidomys] similis, sensu Tate, 1939: 195 (part; not of J. A. Allen. Tate believed *quindianus* to be the young of *R. similis.*)

Rhipidomys latimanus latimanus: Cabrera, 1961: 419 (as subspecies).

Rhipidomys latimanus similis: Cabrera, 1961: 419 (part; not *R. similis* J. A. Allen. Attribution of *cocalensis.*)

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Rhipidomys latimanus microtis: Cabrera, 1961: 419 (as subspecies).

Rhipidomys latimanus mollissimus: Cabrera, 1961: 419 (as subspecies).

Rhipidomys latimanus pictor: Cabrera, 1961: 419 (as subspecies).

R[hipidomys]. scadens: Cuervo-Díaz et al., 1986: 498 (incorrect subsequent spelling).

Rhipidomys venustus, *sensu* Lawrence, 1993: 102 (part; not of Thomas. Attribution of
   quindianus.)

Holotype: BMNH 7.1.1.95, adult male, skin and skull; "believed to have been collected at Pallatanga, on the western slopes of the Cordillera [in Chimborazo province, Ecuador, by L. Fraser in 1859]; but the exact locality is not certain, from the specimens having been unfortunately mixed together" (Tomes, 1860: 211).

Diagnosis

Dorsal pelage intensely pigmented orange-brown agouti, rarely duller, finely flecked with dark brown or black guard hairs; ears small; tail, ears and feet moderately dark; tail pencil medium length. Skull with moderate to slender braincase, not excessively flattened; interorbit moderately broad with supraorbital ledges converging strongly to the front of the region.

Description

Medium-sized specimens, adult head-and-body length usually 120-140 mm (old adults sometimes considerably larger); tail 120-150% of HB. Dorsal pelage rather dark orange-brown agouti, saturate, finely flecked with dark brown/black guard hairs; flanks rather paler; texture moderately soft, not normally woolly. Ventral colour creamy white; hairs white to base, sometimes with inconspicuous pale grey bases (rarely dark), especially at sides of belly and on pectoral spot, not on throat. Pelage length (guard hairs/ body fur) dorsal: 11-12/9-10; ventral 6-9/4-6. Hind foot usually 26-28 mm (including approx. 1.5 mm claw), thinly haired; foot patch dark, narrow over metatarsals and broadening distally at the bases of toes III-V, distinctly or indistinctly outlined; claw vibrissae usually long and abundant. Tail medium to dark brown, short hair on shaft, distally a little longer; pencil ranging from 3 to 20 mm, usually c. 10 mm. Ears small to medium in size, rather dark.

Skull moderate in size, rather slender, with slender rostrum. Supraorbital ledges well developed, sometimes slightly raised into ridges, straight (rarely curved) and converging to a point well forward; interorbit not broad. Braincase oval, not angular and not greatly flattened except in old specimens; interparietal at a large angle to the horizontal; lateral process of parietal approximately rectangular. Palate with 3-4 pairs

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palatal foramina; medial spine on rear edge present or absent. Parapterygoid fossae well ossified, broad and flat, not greatly recessed. Sphenopalatine fissures either absent or present as narrow slits beside presphenoid. Auditory bullae small. Mandible not very robust; incisor root capsule not prominent but usually forming shelf-like projection.

Upper molar row length mostly 4.7-5.3 mm. M1 anteromedian flexus weak to moderate; anteromedian style sometimes present; oblique paralophules usually present, especially in M2-3; protoflexus often absent in M3. Anteromedian flexid in m1 often weak, soon obliterated by wear, or not apparent (the two conulids fused together); oblique metalophulids (around base of metaconids) common in m3. Lower m2-3 sometimes with three roots.

Variation and comparisons

Specimens from SW Colombia (Nariño, Cauca - flanks of Western Cordillera) are usually a little paler than Ecuadorean specimens; the holotype of *mollissimus*, from the eastern side of the Cauca valley a little farther north at Miraflores (Valle - Central Cordillera), is a duller, darker greyish brown, but agrees in other respects with the typical form; specimens from Antioquia at the northern end of the Western and Central Cordilleras are more intensely red-brown, and those from eastern Panama ("scandens") are bright orange-brown with little dark flecking, particularly on the sides of the body. In Cundinamarca (western slopes of Eastern Cordillera) specimens are similar to the Ecuadorean population but with more conspicuous flecking, especially in older adults. The hind foot is rather larger and fleshier in the Panama population, and sometimes also in Cundinamarca, Cauca and Antioquia, with relatively shorter and broader digits; in Panama especially the foot patch is broader (to bases of toes II-V). The ear is smaller in Cundinamarca and *mollissimus* than in other populations, and a little larger in Ecuador. Skulls may be slightly broader and flatter in Colombia than in Ecuador, and more likely to have a medial process on the rear edge of the palate. The three specimens from Perico, northern Peru, are very bright dorsally with long guard hairs, and pure creamy white ventrally; their hind feet are broad with stout digits and a very narrow patch; their skulls are broader and more robust than other members of this subspecies, except perhaps those from Panama.

Compared with *Rhipidomys latimanus venezuelae* (see below), *R. l. latimanus* is darker and more intensely pigmented, with more frequently dark-based ventral pelage; its fur is a little shorter and slightly less soft because of the abundance of stiffer guard hairs; the hind foot is a little more slender, especially in Ecuadorean specimens, with relatively

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longer digits; it is also darker, as is the tail; the ear is smaller and usually darker. The skull, particularly the rostrum, is more slender with more prominent supraorbital ledges and a rather more rounded braincase than *R. l. venezuelae* specimens of equivalent age. The procingulid of the first lower molar is less frequently cleft into two separate conulids. With regard to *R. modicus*, *R. l. latimanus* is rather smaller overall with a more brightly pigmented skin, smaller skull and molars, and narrower interorbit.

Distribution

From Perico in the Chinchipe valley of northern Peru, close to the border with Ecuador, possibly linking northwards along the eastern Andean slopes with the population in the upper Napo valley (700-1100 m); on the western flanks and valleys of the Ecuadorean Andes from about 2° S northwards to Nariño in Colombia (700-1700 m); also in the Colonche range of western Ecuador (about 450 m); in Colombia, on both sides of the upper and middle Cauca valley (Cauca, Valle, Antioquia departments - 700-2000 m), spilling over in places to the opposite slopes of the Western and Central Cordilleras (2200 m at El Roble) and extending to the eastern side of the Magdalena valley in Cundinamarca and Boyacá (1000-1300 m); a population in the mountains of eastern Panama (1250-1550 m), close to the Colombian border, is similar enough not to warrant separate subspecific status (Fig. 7.5).

Ecological notes

Parasites: see Durette-Desset (1971), Johnson (1972), Quentin (1970).

Material examined

COLOMBIA: **Antioquia**, Río Negrito, 15 km E Sonsón, 1850 m *(164)* (FMNH 70256); San Jerónimo, 720-850 m *(165)* (FMNH 70233, ~35 ~37, ~41 to ~45, ~47, ~49); Valdivia, 900-1500 m *(168)* (FMNH 70250 to ~55, ~57 to ~59, ~61); **Boyacá**, Muzo, 1300 m *(128)* (AMNH 72051, BMNH 20.12.23.9 to ~11, FMNH 71711); **Cauca**, Charguayaco, 1900-2000 m *(154)* (AMNH 181448, ~52); Cocal, 4000 ft *(153)* (AMNH 32376 - holotype of *cocalensis*); Cerro Munchique, 1500 m *(152)* (FMNH 88542); Río Munchique, 1200 m *(153)* (FMNH 90357, ~58); Sabanetas, 1900-2000 m *(151)* (AMNH 181447, ~50, ~53, ~54, FMNH 89269, ~70, ~72); Uribe, 1900 m *(150)* (MNHN 1981-586); **Cundinamarca**, west (BMNH 99.10.3.8); Paime, 1038 m *(132)* (AMNH 74126); Quebrada Batán ("Salina del Vatan") *(131)* (BMNH 96.11.1.2 - holotype of *microtis*); **Nariño**, San Pablo, 1500 m *(149)* (BMNH 99.9.3.1, ~.4); **Quindío**, El Roble, 7200 ft *(163)* (AMNH 32970 - holotype of *quindianus*, 32974); **Valle**, near Cali *(157)* (MNHN 1983-472); Miraflores, 6200 ft *(161)* (AMNH 32243 - holotype of *mollissimus*);
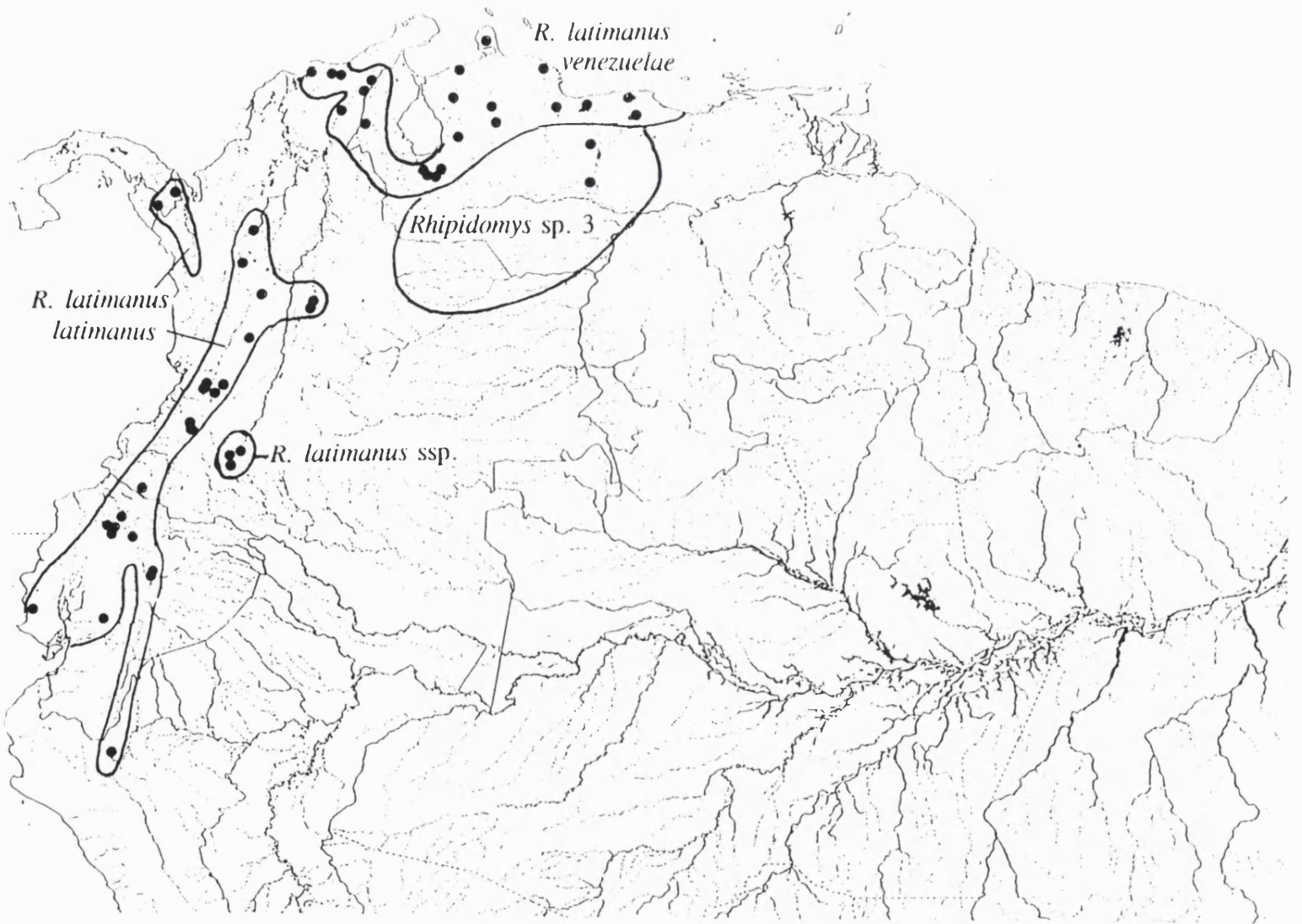
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Fig. 7.5 - Distribution of *Rhipidomys latimanus* and R. sp. 3.

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Peñas Blancas, Río Pichindé, c. 1800 m *(156)* (USNM 507263, ~64). ECUADOR: Bolívar, Ríos Chimbo and Coco (confluence of), 2400 ft *(193)* (AMNH 62123); Chimborazo, Pallatanga, 4950 ft *(192)* (BMNH 7.1.1.95 - holotype of *latimanus*); Guayas, Cerro Manglar Alto, 1500 ft *(194)* (AMNH 66618); Imbabura, Hacienda Chinipamba, near Peñaherrera, 1500 m *(169)* (UMMZ 77244 to ~47); Napo, near Archidona, 3500 ft *(185)* (BMNH 34.9.10.112); near Río Napo, 2400 ft *(186)* (BMNH 34.9.10.113); Pichincha, Gualea, 2900-5000 ft *(172)* (AMNH 46742 to ~44, BMNH 15.7.12.27, ~28, 34.9.10.111); Mindo, 4213-5500 ft *(174)* (AMNH 46661, 46736 to ~38, ~40, ~41, BMNH 13.10.2.35, ~36, 13.10.24.54 to ~56, 34.9.10.110); Mojanda, S. side, 8000 ft *(176)* (AMNH 47005, 47021); Nanegal, 4000 ft *(172)* (AMNH 46760, BMNH 98.5.1.2); Pachijal, 3000 ft *(174)* (AMNH 46662, ~69, 46735); Pacto, 5500 ft *(171)* (AMNH 46651, 46775); Río Blanco, below Mindo, 4000 ft *(173)* (AMNH 46739); Río Verde, 3200 ft *(170)* (BMNH 1.1.6.4 - holotype of *pictor*). PANAMA: Darién, Cerro Malí, 4700-4800 ft *(215)* (USNM 338265, 339060); Cerro Pirre ("Mount Pirri"), 5100 ft *(217)* (USNM 178987 - holotype of *scandens*); Cerro Tacarcuna, 4100 ft *(216)* (USNM 338264). PERU: Nor Oriental del Marañón (Cajamarca), Perico *(225)* (MCZ 17042, ~43, ~46). Total: 96.

Rhipidomys latimanus ssp.

Synonyms: None.

Diagnosis

Dorsal pelage reddish brown agouti with olive tinge, conspicuously flecked with dark brown or black guard hairs; ventral pelage always with grey bases to hairs and creamy or pale orange tips. Skull with broad braincase and narrow interorbital region; bullae moderate in size.

Description

This subspecies differs from the nominotypical subspecies in pelage colour and skull proportions, as indicated above. In the slight olive tinge to its dorsal coloration; noticeably grey-based ventral pelage sometimes with an orange wash; long, narrow nasals; narrow interorbit with less pronounced supraorbital ridges; broad, rounded braincase; and larger bullae than other *R. latimanus*, this form resembles *Rhipidomys fulviventer*, a

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species found at higher altitudes in the same area. It differs from the latter species, however, in the texture and length of its pelage, its narrow, well-defined foot patch, its short tail pencil, its dark but not extremely dark ears, the lack of fenestration in the parapterygoid fossae, the poorly developed mandibular incisor root capsule, and of course its derived carotid circulatory pattern. These characters justify its inclusion in *R. latimanus*, but it is distinct enough to warrant subspecies status. The specimens known from Pitalito are rather smaller than those from San Adolfo.

Distribution

At the head of the Magdalena valley, Huila department, Colombia, at 1350-1400 m altitude (Fig. 7.5). Whether its range connects down the semi-arid valley with that of the Cundinamarca population of *R. l. latimanus* (a distance of nearly 500 km) deserves investigation. At higher altitudes (1600 m and above) it is replaced by *R. fulviventer* and *R. caucensis*.

Material examined

COLOMBIA: **Huila**, Pitalito, *(147)* (FMNH 71709, ~10); San Adolfo, 1400 m (includes Río Aguas Claras, 1400 m - *145)* (FMNH 71703 to ~08, 71743). **Total:** 9.

Rhipidomys latimanus venezuelae Thomas

Synonyms

Rhipidomys venezuelæ Thomas, 1896b: 303. Type locality "Merida, Venezuela, alt. 1630 metres."

R[hipidomys]. v[enezuelae]. typicus Thomas, 1900b: 271 (referring to material from the type locality in comparison with *Rhipidomys venezuelae cumananus*).

Rhipidomys venezuelae venezuelae: Gyldenstolpe, 1932: 46 (as subspecies).

[Rhipidomys] venezuelanus: Tate, 1939: 195 (incorrect subsequent spelling).

Rhipidomys mastacalis venezuelae: Cabrera, 1961: 423 (name combination).

R[hipidomys]. mastacalis, sensu Corbet & Hill, 1980: 145 (part; not *Mus mastacalis* Lund).

Holotype: BMNH 96.11.1.1, adult male, skin and skull; collected at "Merida, Venezuela, alt. 1630 metres" on 5 March 1896 by Salomón Briceño Gabaldón.

Revised diagnosis

Rhipidomys latimanus specimens with reddish to yellowish brown dorsal pelage with little to moderate agouti effect; hind foot of medium breadth with relatively short digits, foot pale brown with faint, darker patch on metatarsals; tail pale to medium brown with short to moderate pencil; ears large, pale. Skull elongated, becoming angular and flattened in older specimens; supraorbital ridges not highly divergent; frontals long; bullae moderate in size.

Description

Medium-sized rats (adult head-and-body length usually 130-150 mm, tail length usually 110-135% HB); older individuals occasionally much larger. Dorsal pelage varying from fairly rich reddish-brown (sometimes more intensely orange brown) in specimens from more mesic areas to a duller, sandier colour in those from drier parts; in the former the sparse guard hairs are often brown rather than black and contrast poorly with the body hairs so that little agouti effect is apparent, whereas the latter are more conspicuously flecked with dark guard hairs. Sides of head and body generally paler. Ventral pelage white or cream-coloured to base of hairs or sometimes with pale grey bases, especially at the sides of the belly; some specimens have a small pectoral patch with grey bases and occasionally orange tips. One very melanistic specimen has been examined (MHNG 802/67) that has long, dark grey hair bases throughout but agrees in all other respects with the surrounding Mérida population. Pelage relatively soft and fine; length (guard hairs/body fur): dorsal 10-13/8-10 mm; ventral 6-9/4-7 mm. Hind foot length usually 27-29 mm in males, sometimes a little less in females; foot moderately broad with proportionally rather short and thick digits; foot usually pale brown with faint, indistinctly outlined, mid-brown patch which varies from very narrow to moderately broad; claw vibrissae long. Tail usually pale to medium brown, sometimes darker; shaft with short hairs, lengthening only close to tip; pencil short (usually ≤ 6 mm, rarely longer). Ears large relative to body size, pale to medium brown.

Skull elongated, becoming flattened and angular with age. Rostrum broad, not tapering greatly in adults; posterior part of nasals roughly parallel-sided. Frontals and therefore interorbital region long; supraorbital ridges well developed in older specimens, but not usually greatly divergent and not always straight: sides of interorbital region may be rounded. Braincase not inflated, interparietal facing more dorsally than posteriorly; lateral process of parietal rectangular; squamosal root of zygomatic arch positioned low on side of braincase and often prolonged posteriorly in a slight ridge running along the

dorsal edge of the subsquamosal fenestra. Incisive foramina large, compatible with broad rostrum; 3-4 pairs palatal foramina, the largest usually the rearmost; medial process usually present on rear edge of palate; soft palate with two complete ridges (and possibly a third) anterior to the molars and six partial ridges between the molars. Mesopterygoid fossa expanded anteriorly; sphenopalatine fissures either absent or small slits; parapterygoid fossae not fenestrated and often recessed, trough-like. Auditory bullae moderate in size.

Anteromedian flexus and flexid usually pronounced, sometimes weak. Oblique paralophules often present in upper molars. M3 not excessively reduced in length. Lower molars with oblique metalophulid occasionally well developed, curving round the labioposterior base of the metaconid; m3 mesolophid often very short.

Variation and comparisons

Dorsal colour varies with habitat: sandier-coloured specimens come from seasonally dry areas, particularly the Caribbean coastal plain in Falcón (e.g., at Capatárida), the Tocuyo basin in Lara, Venezuela, and the César valley, Colombia; those from the cordilleras and more mesic enclaves on the coastal plain are usually more saturate red or orange brown. Lowland specimens also have shorter pelage. Ventral colour varies little; grey hair bases found principally in specimens from higher altitudes (> 2000 m) in Mérida and from the Serranía de Perijá, where the hind foot and tail may also be darker. Specimens from drier areas have rather darker ears that contrast with their paler fur more than occurs in specimens that have more intensely pigmented pelage. Skulls from Perijá are smoother and less angular, with supraorbital ledges rather than raised ridges; the mesopterygoid fossa is also narrow and not expanded. The single skull from the César valley is smaller, more slender and more rounded than most others attributed to the subspecies.

Comparisons with *R. l. latimanus* were given under that subspecies. Relative to *R. couesi* specimens of similar age-class from NE Venezuela, *R. l. venezuelae* is smaller, with softer, more streaked dorsal pelage, a less hairy tail and a narrower hind foot.

Distribution

Northern Colombia, northwestern and northern Venezuela, at low to lower-middle altitudes in the Sierra Nevada de Santa Marta, Serranía de Perijá, Mérida Andes (notably the Chama valley), and Cordillera de la Costa (as far east as Miranda and Guárico states), as well as the lowlands of the César valley and the hills and plains of Lara and Falcón (Fig. 7.5).

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Ecological notes

O'Connell (1989) discussed the population dynamics of *Rhipidomys venezuelae* (reported as *"R. mastacalis"*) in premontane rain forest in Guatopo National Park, on the southern slopes of the Venezuelan coastal range. Habitat data of SVP specimens may be found in Handley (1976). Parasites: see Brennan & Reed (1974), Ferris (1921), Furman (1972a), Hopkins (1949), Johnson (1972), Jones et al. (1972), Machado-Allison & Barrera (1972), Saunders (1975), Tipton & Machado-Allison (1972).

Material examined

COLOMBIA: **César,** El Orinoco, Río César *(126)* (USNM 280447); **La Guajira,** La Concepción, 3000 ft *(121)* (MCZ Bangs Coll. 8360, 8361); Pueblo Viejo (= El Pueblito), 2000 ft *(122)* (AMNH 38948, ~49; BMNH 9.4.15.1; MCZ Bangs Coll. 8110, 8111; USNM 85544); San Francisco *(122)* (AMNH 38947); Monte Elías, Sierra Negra, 5000 ft *(123)* (USNM 270392); Las Marimondas (= Marimonda), [20 km S. of] Fonseca *(124)* (USNM 280441 to ~446); Sierra Negra, [E. of] Villanueva *(125)* (USNM 280307 to ~329, ~435 to 440); **Magdalena,** Hacienda Cincinnati *(119)* (AMNH 32667); Palomino *(120)* (AMNH 38950, 51); Santa Marta *(not plotted)* (BMNH 0.5.6.10). VENEZUELA: no locality (FMNH 7048; USNM 115317); **Aragua,** Estación Biológica Rancho Grande, 1050 m *(294)* (USNM 517589 to ~591); Campamento Rafael Rangel, 800-1200 m *(not located)* (USNM 314182, 317728); **Carabobo,** Hacienda El California, 4 km NNW of Montalbán, 1000 m *(293)* (USNM 442303); **Distrito Federal,** Los Venados, 1470, 1500 m *(295)* (USNM 371247, ~250); **Falcón,** Capatárida, 40 m *(289)* (USNM 442296); La Pastora, 14 km ENE Mirimire, 190 m *(292)* (USNM 442137); Cerro Santa Ana, Península de Paranaguá, 560-595 m *(291)* (USNM 456363, ~365, ~366, ~368, ~370 to ~372, ~562); Hacienda Socopito, Río Socopo, 80 km NW of Carora, 470 m *(288)* (USNM 442275); Cerro Socopo, 84 km NW of Carora, 1260 m *(287)* (USNM 442133); **Lara:** Caserío Boro, 13 km W of El Tocuyo, 900 m *(285)* (USNM 456374); Río Tocuyo, 500 m *(286)* (AMNH 130987, 131027 to ~084); **Mérida,** Río Albarregas *(275)* (BMNH 99.12.1.7); La Azulita *(271)* (FMNH 21828); Río Chama (includes Cafetos de Chama, 1600 m, 1630 m; Montaña de Chama, 2020 m - *274)* (AMNH 21316, ~20, 24344, ~51; BMNH 99.12.1.5, ~.9; MHNG 802/65, ~/67; USNM 123325); Montañas de Hechisera (= Echicera), 2000 m *(277)* (USNM 172973); Mérida (includes Mérida, 1630 m, 2500 m; Cafetos de Mérida, 1600 m, 1630 m; Montes de Mérida, 1630 m; Montes del Arenal, 1630 m - *275)* (AMNH 24345 to ~48, ~50 ~52;

BMNH 96.11.1.1 - holotype of *venezuelae*, 99.12.1.4, -.6, -.8, 3.1.5.1, 5.2.5.13, 8.4.24.4; MHNG 728/08, 802/60 to -/62, -/66; MZUSP 2007; USNM 123324, -28, -34, -36); Río Milla, 1700 m (includes Cafetos de Milla, 1600 m, 1630 m; Montes de Milla, 1600 m - *276)* (AMNH 21318, 24342, -43, 33159; BMNH 99.12.1.10; FMNH 18887; MHNG 802/59, -/63, -/64; USNM 172956); Montes de la otra banda *(not located)* (USNM 123335); Hacienda Santa Catalina, Río Chama 4500 ft *(273)* (FMNH 21826); Montañas de la Sierra, 2500 m *(279)* (FMNH 29443; UMMZ 57089); Cañada La Sucia, near Jají, *(272)* (FMNH 21827); Montes del Vallecito, 2000 m *(276)* (AMNH 33161); **Trujillo,** Isnotu, 930 m *(283)* (USNM 371251); **Zulia,** Misión Tukuko, 200-400 m *(269)* (USNM 448629, -30). **Total:** 188.

Rhipidomys sp. 3

Synonyms

Rhipidomys ?venezuelae, sensu Poulton, 1982: 79 (specimens from Aguaro-Guariquito
National Park, Guárico, Venezuela; not *R. venezuelae* Thomas).

Rhipidomys sp.: Eisenberg et al., 1979: 192; O'Connell, 1982: 176; 1989: 537; August,
1984: 77 (specimens from Fundo Pecuario Masaguaral, Guárico, Venezuela).

Description

In view of the fact that only one skin and one immature skull referrable to this form have been examined, the following description is necessarily cursory and provisional. Skin: size rather smaller than *Rhipidomys latimanus venezuelae* (no collector's measurements available); possibly not fully adult. Dorsal colour rather pale greyish brown with a pinkish tinge; ventral fur white to base; length (guard hairs/body fur) dorsal 11/8, ventral 6/4; texture rather coarse. Tail pale coloured; shaft with moderate length hairs, lengthening distally; pencil 8 mm. Hind foot (length 26.5 c.u., measured dry) pale with faint but sharply delineated patch occupying half the width of the metatarsals. Ear relatively large. Skull young (DAC 1), and therefore not representative of adult size or shape; nasals relatively long; braincase rounded; lateral process of parietal large, deep and rectangular; incisive foramina broad; palate short, with 5 pairs palatal foramina (including pair beside anterior end of mesopterygoid fossa); parapterygoid fossae not fenestrated; sphenopalatal fissures large for the genus, extending along 1/3 of the

length of the basisphenoid and part of the presphenoid; carotid circulatory pattern derived. Molars: crown length of upper molar row 5.1 mm; M1 with anteromedian flexus shallow, no anteromedian style; lingual styles weak in M1-3; M3 much reduced in posterior part (behind hypoflexus); lower m1 with distinct anteromedian flexid, transverse lophid in procingulid; m3 mesolophid almost completely foreshortened.

Distribution

The llanos of Venezuela, where it is found in *bajío* habitat - a mosaic of moderately flooded savanna with low-stature forest (O'Connell, 1989) (Fig. 7.5).

Ecological notes

The population dynamics of this taxon at Masaguaral is compared with that of *R. l. venezuelae* in northern Guárico by O'Connell (1989). Two specimens were captured at Aguaro-Guariquito National Park, one (an adult male) in the branches of a low tree, the other (adult female) in thick, dense grass in dry open parkland (Poulton, 1982).

Material examined

VENEZUELA: Guárico, Fundo Pecuario Masaguaral, 55 km S of Calabozo *(300)* [USNM 521019 (skull), 521020 (skin)]. **Total:** 1 (?)

Rhipidomys nitela Thomas

Etymology: Latin *nitela*, variant of *nitedula*, dormouse

Synonyms

Rhipidomys nitela Thomas, 1901: 148. Type locality: see below, under "Holotype".

Rhipidomys venezuelæ fervidus Thomas, 1904a: 34. Type locality: La Unión, lower Caura valley, Bolívar, Venezuela.

Rhipidomys venezuelæ yuruanus J. A. Allen, 1913: 601. Holotype: AMNH 30735; type locality: Río Yuruán, Bolívar, Venezuela.

Rhipidomys milleri J. A. Allen, 1913: 602. Holotype: AMNH 36332; type locality: "Minehaha Creek (altitude 500 feet), Lower Essequibo River, British Guiana".

R[hipidomys]. v[enezuelae]. nitela: J. A. Allen, 1913: 602 (name combination).

Rhipidomys venezuelae milleri: Gyldenstolpe, 1932: 47 (name combination).

Rhipidomys mastacalis nitela: Cabrera, 1961: 423 (name combination).

Rhipidomys mastacalis fervidus: Cabrera, 1961: 423 (name combination).

Rhipidomys nitela tobagi Goodwin, 1961: 16. Holotype: AMNH 184555; type locality:

  Little Tobago island, Trinidad and Tobago.

R[hipidomys]. n[itela]. milleri: Goodwin, 1961: 16 (name combination).

Rhipidomys mastacalis, sensu Handley, 1976: 50 (specimens from Venezuela; not *Mus*

  mastacalis Lund).

Rhipidomys masticalis: Gardner, 1989: 412 (incorrect subsequent spelling for *mastacalis*,

  sensu Handley; not *Mus mastacalis* Lund).

Rhipidomys mastacalis cearanus, sensu Patterson, 1992: 26 (specimens from Rio Tapajós,

  Brazil; not *Rhipidomys cearanus* Thomas).

Holotype: BMNH 1.6.4.81, adult male, skin and skull; collected on 12 October 1900
by J. J. Quelch, at "Kwaimattat, Kanuku Mts." This is the locality given in the published
report (Thomas, 1901: 149) and recorded in the museum's accession register for the
whole type series; the labels attached to all the skins, however, are marked "Quatata [or
"Quatatat"], Kanuku Mts., B. Guiana, 240'." Kwaimattat and Quatatat, now spelt
Kwaimatta and Kwatata, are localities in Guyana some 25 km apart in the savannas north
of the Kanuku Mountains.

Revised diagnosis

  Small to medium-sized *Rhipidomys* specimens; dorsal pelage short, dull grey-
brown to richer reddish or orange brown; ventral pelage short, creamy white to roots or
with inconspicuous pale grey hair bases; hind foot short and slender with small plantar
pads, dark patch distinctly outlined or not; tail moderately long to long with short to
medium-length pencil. Skull small; rostrum short, blunt, rarely pointed; interorbit with
squared or ledged edges, sometimes raised; braincase oval, not inflated, flattened in older
individuals; bullae small; carotid circulation pattern derived (stapedial foramen small, no
internal squamosal-alisphenoid groove, no sphenofrontal foramen); molar row short, not
exceeding 5 mm.

Description

  Small to medium-sized mice (adult head-and-body length mostly 110-140 mm)
with moderately long to long tails (mostly 110-140% of HB length). Dorsal pelage
varying from dull greyish brown agouti to reddish or orange brown with little dark
flecking; often slightly redder on the rump than on the shoulders; pale patch behind the
ear in some specimens. Ventral colour creamy white to roots or with inconspicuous pale
(occasionally darker) grey bases to the hairs, especially at the sides of the belly and on
pectoral spot but sometimes throughout; lateral dividing line sharp when hair bases are

white, blurred when they are grey. Texture fine and soft, usually short (especially ventrally): length (guard hairs/body fur), dorsal 8-11/6-8 mm, ventral 5-6/3-4 mm. Hind foot short (24-27 mm, c.u.) and relatively slender for the genus; plantar pads small and often rather separate; dark patch varying in darkness and distinctness, only rarely extending onto first phalanx of digits; digits and sides of foot white to mid-brown; claws small with moderately abundant vibrissae. Tail slender, pale to dark brown; hairs short along shaft except near tip; pencil short to moderate, 5-15 mm. Ears pale to dark, moderately large.

Skull varying from small and delicate to medium-sized and rather more robust. Rostrum short, usually rather broad, occasionally narrower and more pointed; nasals usually shorter than premaxillaries, parallel-sided in posterior half. Interorbit broad; edges squared or ledged, sometimes raised as slight ridges, straight or slightly curved; narrowest point usually well forward in the region, sometimes further back (as in the holotype). Braincase oval in dorsal view, elongated in some specimens; not inflated, but rounded in younger specimens and becoming flatter with age; lateral process of parietal rectangular. Incisive foramina usually narrow and almost elliptical in shape; number of pairs of palatal foramina variable; palatal bridge usually with well defined posterior medial process. Mesopterygoid fossa usually narrow, sometimes broadened at anterior end; sphenopalatine fissures absent or small slits, rarely more open; parapterygoid fossae sometimes not fully ossified, leaving medial fenestration. Bullae not extremely small. Mandible with small, shelf-like incisor root capsule.

Molars small (observed extremes of upper molar row 3.8 to 5.0 mm), usually with relatively low cusps. Posterior part of M3 usually greatly reduced. Complexity of occlusal enamel pattern highly variable, some having smooth outlines, others highly convoluted. Anteromedian flexus in M1 usually well defined, occasionally with anteromedian style; oblique paralophules present or absent in M1-3; anteromedian flexid in m1 usually weak or absent; transverse lophid in m1 procingulid occasionally absent; m3 mesolophid usually greatly foreshortened.

Variation and comparisons

A large range of variation is included within the bounds of Rhipidomys nitela, but character states are not distributed in a manner amenable to division at subspecies level (see chapter 6). Only the salient features of the main samples are described here. The type series from the Kanuku Mountains, Guyana, is greyish brown, average in size, with a rather short braincase and average molars. The sample from the savannas of Suriname is

similar but a little smaller with more slender skulls; the Sipaliwini specimen has a particularly long tail. The "milleri" series from the lower Potaro region of Guyana is average in external proportions but very small in skulls and teeth; pelage rather darker than the Kanuku series (but the skins are a little greasy); skull broad, sometimes flattened, with blunt rostrum, weak supraorbital ridges. Specimens from the highlands of Bolívar state, Venezuela, and from Limão in the southern foothills (Roraima state, Brazil) are rather more brightly coloured than the Kanuku series and often have pale grey bases to their ventral fur (darker in the Arabopó specimen), but in size and skull characters are similar. The holotype of *R. fervidus* from the lower Caura valley is an intense reddish brown in dorsal colour, although not as bright as *R. latimanus*, for example, and white ventrally; it is also larger both externally and in skull size; the skull is rather elongated, with strong supraorbital ridges and a broad braincase; its molars have complex enamel patterns. The "yuruanus" sample (from the Río Yuruán in the Cuyuní basin north of the highlands in eastern Bolívar) is very similar to this specimen in most respects. Specimens from the lower Rio Tapajós (Pará state, Brazil) are also large and brightly pigmented, but have a narrower braincase and palate and broader interorbit than "yuruanus". The specimen from Little Tobago is similar in size and colour to the Kanuku series but has a slender, pointed rostrum and a more domed braincase; it also has relatively large sphenopalatine vacuities. The specimen from Bonda is similar to the last in size and in its pointed rostrum, but its skull is more elongated with a flatter braincase.

Rhipidomys nitela is easily distinguished from *R. macconnelli*, with which it is sympatric in the upper parts of its range in the Guiana Highlands, by its paler dorsal colour, whiter underparts, shorter pelage, shorter and relatively broader hind foot, not bicoloured tail (although it may be a little paler proximally on the ventral surface), more elongated and less inflated skull with shorter rostrum, and smaller molars. In comparison with *R. wetzeli*, which is sympatric with *R. macconnelli* in some areas and thus may be with *R. nitela*, the latter species is larger, has duller, shorter pelage, and a larger and more robust skull, with a longer tooth row and a derived carotid circulatory pattern. *R. nitela* is distinguished from *R. latimanus* by a combination of its small size, short feet, smaller molars and bullae, short and broad rostrum, and broader interorbit, as well as its often duller coloration. In comparison with *R. emiliae* its molar row length is similar but it is smaller overall and has more slender feet with shorter digits.

Distribution

The Guiana Highlands and adjacent forested lowlands from central Venezuela to
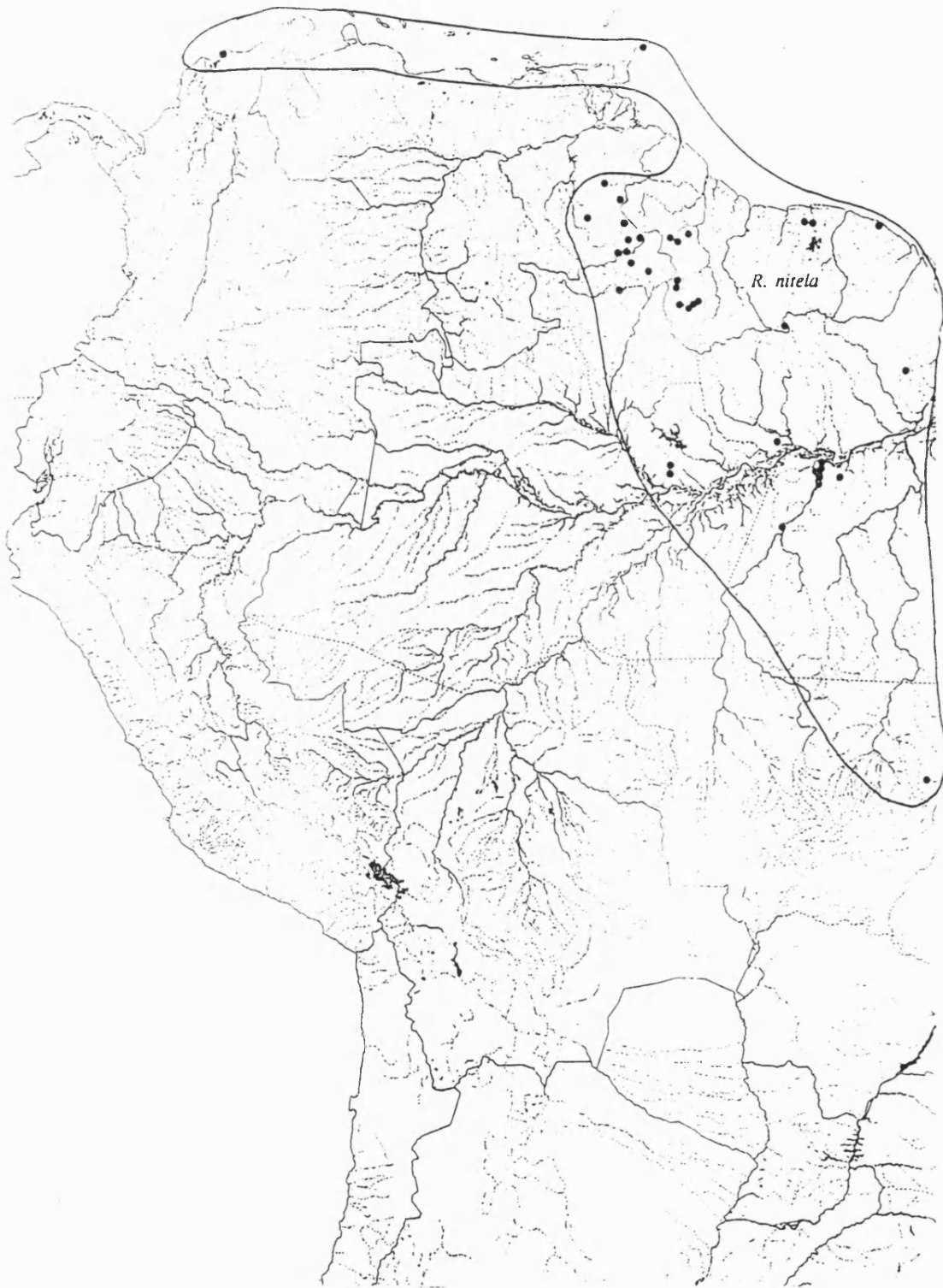
235

Fig. 7.6 - Distribution of *Rhipidomys nitela*.

Amapá, and the northern, eastern and southeastern Amazon basin from the Rio Negro to the lower Tapajós and Xingu and the Serra do Roncador in northeastern Mato Grosso. Isolated specimens have been collected at Bonda on the northern coast of Colombia and Little Tobago island, Trinidad and Tobago, suggesting that this taxon may also occur all along the Caribbean coast of South America (Fig. 7.6).

Ecological notes

According to specimen labels and published reports, *R. nitela* is often found in buildings (e.g., J. A. Allen, 1911; Husson, 1978). Handley (1976, listed as "*R. mastacalis*") gives habitat data in Venezuela. The vegetation at San Ignacio de Yuruaní, Bolívar, Venezuela, where several specimens were collected, is described in detail by Voss (1991). Data on *R. nitela* near Manaus is given by Malcolm (1988). Parasites: see Brennan & Yunker (1969), Furman & Tipton (1961).

Material examined

BRAZIL: **Amapá,** mouth of Rio Branco, Rio Maracá *(34)* (MNRJ 20649); **Amazonas,** Fazenda Esteio, 80 km NNE of Manaus *(30)* (USNM 555635); Manaus-Itacoatiara road, km 50 (includes Manaus - *29)* (MNRJ 19614 to ~16, MPEG 7209); **Mato Grosso,** Serra do Roncador, 264 km N of Xavantina *(115)* (BMNH 81.378, ~379); **Pará,** Aramanaí, Rio Tapajós *(39)* (AMNH 94810 to ~13); Aveiro, E bank Rio Tapajós *(43)* (NHR 371, 385.5, 7479); Boim, Rio Tapajós *(40)* (MCZ 30844); Curuá-Una, 44 km S and 40 km E of Santarém *(37)* (MPEG 9087); Cachoeira Espelho, 52 km SSW Altamira, E bank Rio Xingu *(45)* (MZUSP 21316); Marai [= Igarapé Marói], E bank Rio Tapajós *(41)* (NHR 7393, 7403); Oriximiná, Porto Trombetas, Rio Saracazinho km 43 *(36)* (MPEG 10113); Tauari, E bank Rio Tapajós *(42)* (MCZ 30837, ~38, ~43); **Roraima,** Fazenda Deus-me-ajude *(31)* (MZUSP 27517, ~18); Limão, Rio Cotinga *(32)* (AMNH 75405 to ~10, 75519, 75832, ~47). COLOMBIA: **Magdalena,** Bonda *(118)* (MHNG 1706.75). GUYANA: **Cuyuni-Mazaruni,** Kalacoon (= Kalakun) *(199)* (AMNH 207387); **Potaro-Siparuni,** Anandabaru *(201)* (AMNH 75829); Karisparu, 2000 ft *(202)* (BMNH 69.395); Minnehaha Creek, 500 ft *(203)* (AMNH 36330, ~31, ~32 - holotype of *milleri,* ~33 to ~38); **Upper Takutu-Upper Essequibo,** Kwatata, 240 ft *(204)* (BMNH 1.6.4.81 - holotype of *nitela,* ~82 to ~86). SURINAME: **Nickerie,** Sipaliwini savanna, near Sipaliwini airstrip *(257)* (RMNH 22360); **Para,** Zanderij airport *(256)* (RMNH 22354 to ~56); **Saramacca,** Matta, 15 km W of Zanderij airport *(255)* (RMNH 21971 to ~74, 22353). TRINIDAD AND TOBAGO: **Tobago,** Little Tobago

island *(258)* (AMNH 184555 - holotype of *tobagi*, 184556). **VENEZUELA: Amazonas,** Cerro Duida, Caño Culebra, 750 m *(336)* (USNM 406109, ~110); **Bolívar,** Arabupu [= Arabopó], 4200 ft *(321)* (AMNH 75637); Auyán-tepui, 1100 m *(330)* (AMNH 131112, ~113, ~165); El Dorado, 145 km S, 1380 m *(319)* (CM 78767); El Manaco, 59 km SE of El Dorado, 150 m *(314)* (USNM 387914, ~15, 406069); La Colonia, 53 km NE of Icabarú, 915 m *(324)* (USNM 442285); La Unión *(332)* (BMNH 4.5.7.34 - holotype of *fervidus*, ~35); La Vuelta *(333)* (BMNH 4.5.7.36); Maurá, 45 km NE of Icabarú, 800 m (includes Santa Lucia de Surukún, 851 m, Vetania, 800 m - *325)* (USNM 442277 to ~283, ~286 to ~288, ~291, ~293); San Ignacio de Yuruaní (includes 12 km SW, 850 m, 5.2 km NE - *322)* (AMNH 257273 to ~75; MHNLS 8067, 8072, 8074, 8093; USNM 448612 to ~28); Santa Elena, 940 m *(323)* (AMNH 135457); Uruyén, Camarata valley *(329)* (AMNH 135456); Río Yuruán *(313)* (AMNH 30725, ~27 to ~35 - holotype of *yuruanus*, ~36, ~37). **Total: 128.**

Rhipidomys emiliae (J. A. Allen)

Etymology: Named in honour of the naturalist Dr Emilie Snethlage, director of the Museu Goeldi in Belém, who collected the holotype and donated it to the American Museum of Natural History.

Synonyms

Œcomys emiliæ J. A. Allen, 1916: 525. Type locality: Rio Moju, Pará, Brazil.

Oryzomys [(Oecomys)] emiliae: Ellerman, 1941: 358 (name combination).

Rhipidomys emiliae: Goodwin, 1953: 306 (name combination).

Rhipidomys mastacalis cearanus, sensu Cabrera, 1961: 422 (part; not *Rhipidomys cearanus* Thomas).

Rhipidomys mastacalis ssp. Pine et al., 1972: 468 (specimens from Serra do Roncador, Mato Grosso, Brazil).

Rhipidomys mastacalis, sensu Pine, 1973: 54 (specimens from Belém region, Brazil; not *Mus mastacalis* Lund)

Holotype: AMNH 37495, subadult male, skin only; collected at "Rio Mojú, Pará, Brazil" on 28 February 1914, by E. Snethlage (specimen ex Museu Goeldi, Belém).

Revised diagnosis

Medium-sized *Rhipidomys* specimens with dull greyish-brown to brighter orange-brown agouti dorsal pelage and cream or white ventral pelage; hind foot broad with long toes; tail with moderate pencil. Skull

with moderate supraorbital ridges diverging from a point well forward, resulting in broad interorbit; braincase narrow, becoming angular in older specimens, and moderately flattened; palatal bridge in adults longer than molar row; molars and bullae small; carotid circulatory pattern derived (stapedial foramen small, no internal squamosal-alisphenoid groove, no sphenofrontal foramen).

Description

Medium-sized mice, adult head-and-body length generally 120-150 mm, with moderately long tails. Dorsal colour varies from dull, dark, greyish-brown to brighter reddish or orange-brown agouti, with noticeable dark flecking due to abundant dark guard hairs. Ventral fur pure white or cream to base of hairs, some specimens having pale grey hair bases at sides of belly, occasionally more extensively; pectoral spot with grey hair bases present in some. Pelage length (guard hairs/body fur): dorsal 10-11/7-8 mm; ventral 5-6/3-4 mm. Hind foot moderate in size (25-28 mm), broad, with relatively long toes; dark patch narrow to broad, usually ill-defined, leaving sides of foot and toes pale. Tail mid- to dark brown, moderately well haired, with medium-length pencil (10-15 mm). Ears large, brown and bare; occasionally there is a pale patch of fur behind the ear. Vibrissae long.

Skull medium in size. Rostrum not especially short, but sometimes strongly curved down rather than straight in profile; when the rostrum is curved, the zygomatic notch cannot be seen from above. Supraorbital ridges squared or slightly raised, usually straight, diverging from a point well forward in the region; interorbit broad. Braincase rather narrow, with straight parietal ridges; occiput narrow and angular especially in older specimens; top of braincase often flattened, but interparietal usually directed postero-dorsally rather than dorsally; lateral process of parietal rectangular. Palatal bridge relatively long, compared with the short molar row; mesopterygoid fossa usually narrow, sometimes broader anteriorly; sphenopalatine vacuities absent or very small; bullae small.

Molar row short, not exceeding 5 mm; third upper molar reduced in posterior half. Anteromedian flexus and flexid distinct; anteromedian style often present in M1; oblique paralophules usually present in M1-3.

Variation and comparisons

The co-occurrence of certain character states in some specimens and not others raises the possibility that *Rhipidomys emiliae* as defined here may contain two different forms. Those specimens with a highly recurved rostrum tend to have squared rather than raised supraorbital edges, darker pelage and longer hind feet; craniodental measurements are apparently not different. Because some of the individuals involved may have been reared in captivity, and because other specimens appear to be intermediate in some or all of these characters, the two varieties have not been formally separated here.

Rhipidomys emiliae is distinguished from *R. nitela* by its larger head-and-body length, tail length and skull size, although there is some overlap with older specimens in the Tapajós sample of *nitela*. Were it not for the fact that the two taxa sympatric at the Serra do Roncador appear to belong to *R. nitela* and *R. emiliae*, there would be little reason to separate these forms at species level. *R. emiliae* can be distinguished from its neighbour to the east, *R. macrurus*, by its longer rostrum and palatal bridge, broader interorbit, and smaller molars and bullae.

Distribution

The eastern fringe of the Amazonian rainforest, from the region of Belém eastwards into Maranhão and southwards to the Serra do Roncador in Mato Grosso, between the headwaters of the Rio Xingu and the Araguaia valley (Fig. 7.7).

Ecological notes

Snethlage noted on the label of the holotype that the rat was often found in houses and plantations. Pine (1973) considered the species somewhat uncommon at Utinga, Belém. At the Serra do Roncador, one specimen was caught in a house, two in gallery forest and one at the cerrado-dry forest ecotone. For details of the study area at Roncador, see Fry (1970).

Material examined

BRAZIL: **Maranhão**, Alto da Alegria, [c. 40 km SW of] Turiaçu *(51)* (BMNH 25.5.21.8; MNRJ 2153, 2154); **Mato Grosso**, Serra do Roncador, 264 km N of Xavantina *(115)* (BMNH 81.374 to ~377); **Pará**, Belém (includes Bosque Municipal, Bussuquiara, Utinga - *48)* (MNRJ 24195; MPEG 484, 12633, ~34, 15258, ~59; USNM 394679, ~81, ~83, ~84, ~85, 461410, 545997, ~98); Capim [= São Domingos do Capim], Estrada BR14, km 87 *(49)* (MZUSP 10397, ~98); Rio Moju *(47)* (AMNH 37495 - holotype of *emiliae*); Serra dos Carajás, área N1, Casa de Pedra *(46)* (MPEG 12132). **Total: 25.**

Rhipidomys macrurus (Gervais)

Etymology: Greek μακρός makros, long, ουρα oura, tail

Synonyms

Mus (Hesperomys) macrurus Gervais, 1855: 111. Type locality: Crixás ("Trixas"), Goiás, Brazil.

Hesperomys macrourus: Gervais, 1855: 112 (incorrect original spelling).

[Hesperomys (Rhipidomys)] macrurus: Trouessart, 1881: 136 (name combination).

Rh[ipidomys]. macrurus: Thomas, 1896b: 303 (name combination).

Rhipidomys cearanus Thomas, 1910: 501. Type locality: "S[ão]. Paulo, on the top of the Serra [da Ibiapaba], at about 900 metres", Ceará, Brazil.

Rhipidomys venezuelae cearanus: Gyldenstolpe, 1932: 47 (name combination).

Rhipidomys mastacalis cearanus: Cabrera, 1961: 422 (name combination).

Rhipidomys mastacalis macrurus: Cabrera, 1961: 423 (name combination).

Rhipidomys mastacalis, sensu Hooper & Musser, 1964: 6 (specimen from "Goyaz"; not Mus mastacalis Lund).

Rhipidomys paricola, sensu Carvalho, 1983: 83 (part; not R. paricola Thomas, an Oecomys)

Rhipidomys masticalis: Goff et al., 1983: 183 (incorrect subsequent spelling of mastacalis; specimen from Parque Nacional Serra da Canastra, Minas Gerais, Brazil; not Mus mastacalis Lund)

Holotype: In the MNHN collections. Collected at "Trixas" [= Crixás], Goiás, Brazil, in May 1844 by Castelnau and Deville.

Revised diagnosis

Medium-sized Rhipidomys specimens with dull, reddish-grey-brown dorsal pelage and white underparts; tail slightly to much longer than head-and-body length, with short to moderate pencil; hind foot short to moderate. Skull with short rostrum and small zygomatic notch; supraorbital edges squared or slightly ridged, curved rather than straight, giving rounded appearance to interorbit; braincase broad, rounded; bullae moderately large; carotid circulatory pattern derived. Karyotype with $2n = 44$ chromosomes, low fundamental number (48, 49 and 51 found).

Description

A medium-sized species, adult head-and-body length mostly 125-145 mm; tail

moderate to rather long: usually 100%-120% of HB in the south, up to 140% in the north. Dorsal colour basically dull, reddish-grey brown, a little brighter on the head and rump and paler on the flanks; guard hairs dark reddish brown, abundant but not very conspicuous. Ventral fur white or pale cream to base of hairs, or with unapparent pale grey bases (not on throat); small pectoral spot sometimes present with grey bases and orange tips to hairs. Pelage length (guard hairs/body fur): dorsal 11-15/7-10 mm, ventral 7-9/4-6 mm; texture medium fine. Hind foot short to moderate in length, typically 24-26 mm c.u. in the south, 26-28 mm c.u. in the east and north, relatively broad and robust; dark foot patch distinctly outlined or not, fairly narrow to broad, occasionally extending onto digits; sides of foot and digits golden; claw vibrissae long and abundant. Tail medium to dark reddish brown, distal half well haired, pencil short to moderate (up to 15 mm, approx.). Ears large, medium brown.

Skull with short, blunt rostrum and short, narrow nasals broadening at the anterior tip. Zygomatic notch very small in dorsal view; zygomatic plate rather broad. Interorbit usually with biconcave outline due to curved supraorbital edges, which are squared or slightly ridged. Braincase broad and rounded, becoming angular only in the largest specimens; occiput broad. Incisive foramina roughly pear-shaped, broader in posterior half; occasionally more regularly elliptical. Palatal bridge and mesopterygoid fossa short and broad, less so in the east; medial process on posterior margin of bridge usually present; sphenopalatine fissures absent or occasionally very small. Bullae moderately large. Carotid circulation derived (small stapedial foramen, no translucent internal groove across squamosal and alisphenoid, no sphenofrontal foramen).

Upper molar row approximately 5.1 mm (mostly 4.8 to 5.4 mm); M3 often not greatly reduced in posterior half. Anteromedian flexus often weakly developed; oblique paralophules often in M3, less frequent in M2; hypoflexus in M2 sometimes cuts deeply into mure, becoming almost confluent with mesoflexus. Anteromedian flexid weak or absent; m3 mesolophid distinct or foreshortened.

Karyotype: two specimens from Brasília had $2n = 44$, FN = 48 and 49, the second with a heterozygous pericentric inversion in pair 10 (details in Svartman & Almeida, 1993); a specimen from Mocambinho in the São Francisco valley, northern Minas Gerais, had $2n = 44$, FN = 51 (Leila Pessoa, personal communication).

Phallic morphology was described and illustrated by Hooper & Musser (1964).

Variation

Specimens from Ceará tend to be slightly darker and those from the Brasília area

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greyer, and some may be a little brighter orange. The hind foot and tail are shorter in the samples from Anápolis and Brasília and somewhat longer elsewhere. The skull has a relatively longer rostrum in the Ceará sample, and a longer, narrower palate and mesopterygoid fossa in specimens from the São Francisco valley. The latter also have rather larger molars (mean = 5.24, s.d. 0.18, n = 18 for São Francisco valley specimens; compared with mean = 5.05, s.d. = 0.17, n = 102 for a combined sample from Goiás, the Federal District and Ceará).

Distribution

This species has been found in gallery forests in the cerrado domain of Goiás and central Mato Grosso, in the adjoining semi-deciduous woods of the São Francisco basin, and in the mesic forest of the Serra da Ibiapaba in western Ceará. It may be expected to occur (or to have occurred in the past) in the chain of forests that stretch through Piauí and eastern Maranhão, linking the Serra da Ibiapaba with the other areas. The exact boundaries of its range are unknown but probably coincide with the limits of the cerrado in the west, southwest and south, where it contacts the Amazonian forest, the Pantanal and the Atlantic forests, respectively; eastwards it is probably restricted to more mesic areas within the dry forests bordering the caatinga (Fig. 7.7).

Ecological notes

For an analysis of habitat and reproductive data for *R. macrurus* in Ceará, see Cerqueira et al. (1989); for parasites, see Fonseca (1959). During a 7-month study near Brasília, only 3 individuals were captured a total of 7 times in 12 170 trap nights (Nitikman & Mares, 1987). Mares et al. (1989) summarizes ecological data on specimens collected in that area (see also references therein); Gettinger (1992a, 1992b) reports on parasites from there. Dietz (1983) gives brief notes on the natural history of *R. macrurus* (as "*R. mastacalis*") in the Serra da Canastra National Park, Minas Gerais; parasites from there are described by Whitaker & Dietz (1987).

Material examined

BRAZIL: **Bahia,** (BMNH 49.12.8.4); Barreiras *(64)* (MNRJ 4168, 4174); Bom Jesus da Lapa *(65)* (MNRJ 4142); São Marcelo, Rio Preto *(63)* (FMNH 21162); **Ceará,** Guaraciaba do Norte (includes: Sítio Areias; Sítio Cacimba do Meio; Sítio Convento; Sítio Flores; Sítio Flores do Meio; Sítio Mandu; Sítio Mazagão; Sítio Quati; Sítio Riacho Fundo; Sítio Rua Nova; Sítio São Tomé - *54)* (MNRJ 12531, ~533, ~564, ~587, 17307 to ~311, ~313 to ~318, ~424, ~427, ~429, ~432, ~433 ~435, ~437, ~438); Ibiapina, Sítio Pejuaba *(52)* (MNRJ 17401); São Benedito (includes: Sítio Abrigo; Sítio Alto; Sítio
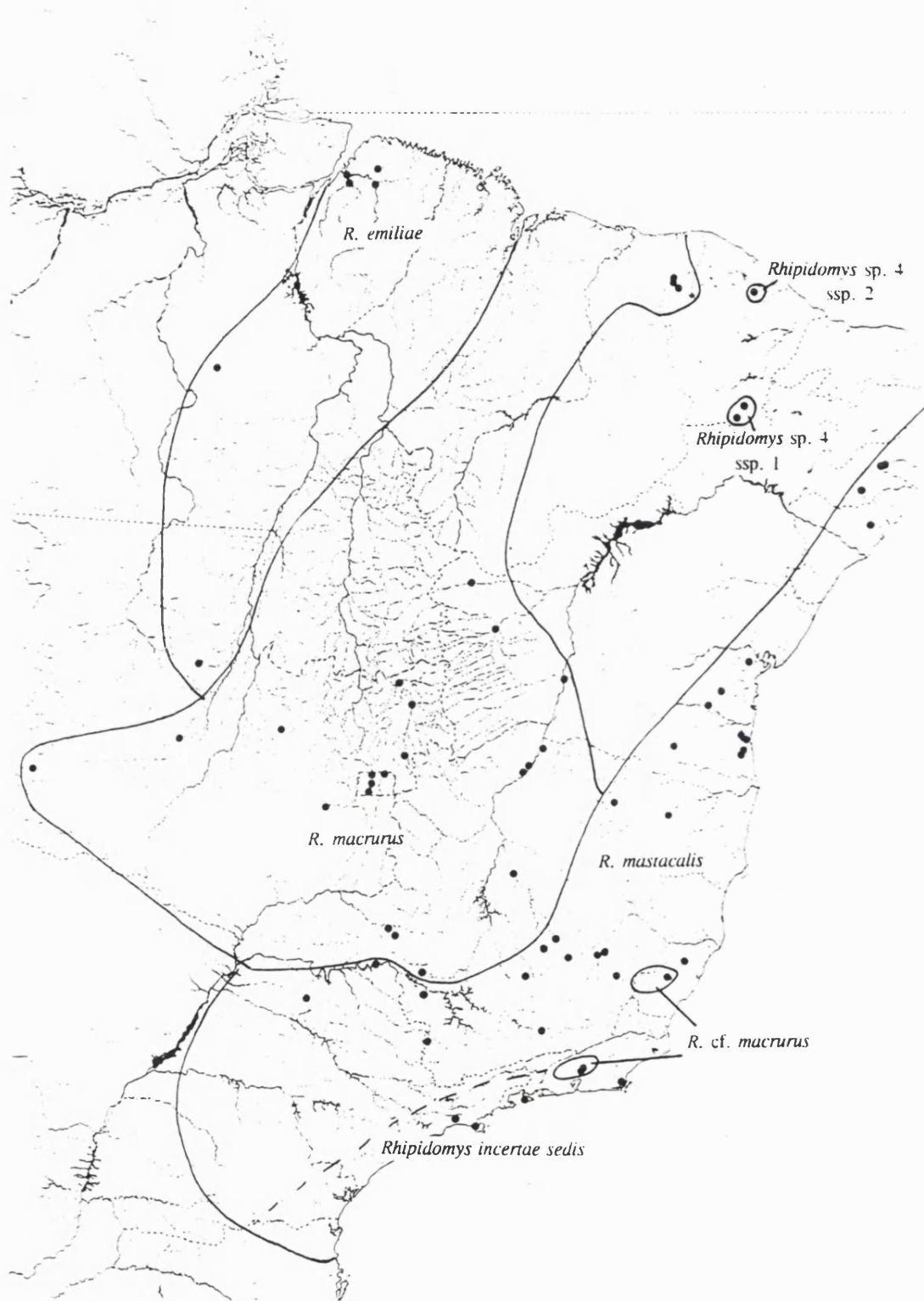
Fig. 7.7 - Distribution of *Rhipidomys emiliae*, *R. macrurus*, *R.* sp. 4 and *R. mastacalis*.

Bananeira do Bandeira; Sítio Barra; Sítio Barroquinha; Sítio Boa Vista do Epaminondas; Sítio Bom Jardim; Sítio Buenos Aires; Sítio Cabeceiras; Sítio Cantinho; Sítio Cigarro; Sítio Cinta da Soledade; Sítio Cinta de São José; Sítio Guaribas do Amaral; Sítio Juçara; Sítio Lagoa da Tereza; Sítio Macapá; Sítio Mundo Novo; Sítio Pimenteira; Sítio Piraguara; Sítio Potós; Sítio Queimados dos Martins; Sítio São Francisco dos Lopes; Sítio São José da Boa Vista; Sítio Santa Luzia; Sítio São José; Sítio Tamandaré - 53) (MNRJ 12364, ~377, ~389, ~390, ~392, ~394, ~395, ~397 to ~400, ~497, ~498, ~502, ~523 to ~530, ~532, ~534 to ~541, ~543 to ~546, ~548 to ~559, ~561 to ~563, ~565 to ~580, ~586, ~588 to ~600, 17355, ~386 to ~399, ~402 to ~413, ~415, ~416, ~425, ~426, ~430, ~434, ~436, ~439); São Paulo, Serra de Ibiapaba (53) (BMNH 11.4.25.7 - holotype of *R. cearanus*); **Distrito Federal**, Brasília (including Jardim Zoológico - 106) (MNRJ 21373 to 21403, 21971 to ~73); Fazenda Água Limpa, 20 km S of Brasília (105) (OMNH 17447 to ~52, 19086); Parque Nacional de Brasília (includes Granja do Ipê, Ribeirão Bananal - 107) (FMNH 128325; MNRJ 24790); Reserva do IBGE, 25 km S of Brasília, c. 1000 m (105) (MNRJ 25926; OMNH 17453 to ~58); **Goiás**, Anápolis, 1000 m (112) (AMNH 134502 to ~504, ~523, ~524, ~669, ~762, ~888, 202653 to ~656; MNRJ 3361, 3366, 3367, 4066, 4305, 4317, 4323, 4333, 4335, 4350, 30016, 30017); Formosa, Rio Canabrava (111) (MNRJ 22848); Nova Roma, Cana Brava (110) (MCZ 33991, ~92, 34037, ~38, ~45, ~48, ~58, ~59, ~60; MZUSP 3991, ~93, ~94, 4005, ~06, ~08, ~10, ~15, ~30); **Mato Grosso**, Chapada dos Guimarães, Casa de Pedra (116) (MNRJ 24914); Xavantina, Rio das Mortes (114) (MNRJ 30023); **Minas Gerais**, Barro Alto, Rio São Francisco (102) (MCZ 33989, ~990, ~993, 34039, ~040, ~042, ~043; MZUSP 3979, 3982, 3992, 3996, 4004, 4011, 4014, 4021, 4028); Lassance, Fazenda São Francisco (99) (UFMG Faz. S. Francisco.37); Manga, Mocambinho (104) (MNRJ 28874); Pedrinópolis, Mata dos Adolfos (86) (UFMG Nova Ponte.05); Perdizes, Mata de galeria João Alonso (87) (UFMG Nova Ponte.46); Riacho da Cruz, Rio São Francisco (103) (MCZ 34041); São Roque de Minas, (includes Fazenda dos Quartéis, Casca d'Anta - 88) (IBAMA/MG 107, 140); Parque Nacional Serra da Canastra (includes: 19-25 km W of São Roque de Minas, Fazenda Barreiro, Fazenda das Pedras, Retiro Maria do Carmo, Zezim Cândido - 88) (MSUMZ 29269 to ~74, 29601 to ~05); **Locality unknown** (UFPB 945). **Total: 273.**

Rhipidomys cf. *macrurus*

Specimens from the mountain ranges in the Atlantic forest of SE Brazil that have karyotypes with low fundamental number (FN = 49 or 50) are known from Monte Verde (Serra do Caparaó, Espírito Santo), Garrafão (Serra dos Órgãos, Rio de Janeiro) and Casa Grande (Serra do Mar, São Paulo). They may be expected to occur also in the higher parts of the Serra da Mantiqueira (on the borders of Minas Gerais, Rio de Janeiro and São Paulo) and Serra de Paranapiacaba (southern São Paulo and Paraná), and even as far south as Santa Catarina and northern Rio Grande do Sul. In view of the possible disjunction between the range of *R. macrurus* as described above and these mountains, there is doubt as to whether these specimens might not belong to a separate taxon.

Specimen examined

BRAZIL: **Espírito Santo,** Hotel Fazenda Monte Verde, 24 km SE of Venda Nova *(77)* (UFPB 345). **Total:** 1.

Rhipidomys incertae sedis

Allocation of non-karyotyped specimens from coastal São Paulo, Rio de Janeiro and extreme southern Minas Gerais to either the last or the next species is uncertain. The specimens listed below have therefore been left *incertae sedis*.

Ecological notes

Life history notes on the sample from Teresópolis and general ecological information on the habitat there are given by Davis (1945, 1947). Guitton et al. (1986) investigated parasites on specimens from Ilha Grande.

Material examined

BRAZIL: **Minas Gerais,** Lima Duarte, Parque Estadual Ibitipoca *(91)* (UFMG Ibitipoca.09); **Rio de Janeiro,** Ilha Grande, Praia Vermelha *(81)* (MNRJ 24365, 24389); Teresópolis, Fazenda Carlos Guinle [= Faz. Comari] *(79)* (FMNH 53877; MNRJ 2357, 2359, 7044 to 7053, 11652 to ~654); **São Paulo,** Boracéia, 800 m *(83)* (MZUSP 10816; USNM 460531, ~532); Casa Grande *(83)* (MZUSP 11445; USNM 543005); São Sebastião *(82)* (MZUSP 880). **Total:** 25.

Etymology: Presumably from the Greek μυσταξ, μυστακος *mustax, mustakos*, moustache.

Synonyms

[Mus] mastacalis: Lund, 1839: 233 (nomen nudum).

Mus mastacalis Lund, 1840a: 24. Type locality: Lagoa Santa, Minas Gerais, Brazil.

Mus mustacalis: Lund, 1840b: 7 (incorrect subsequent spelling).

Mus mystacalis: Wagner, 1843: 750 (incorrect subsequent spelling).

Mus maculipes Pictet & Pictet, 1844: 67. Type locality: Bahia, Brazil.

Hesperomys leucodactylus Wagner, 1845: 147 (not of Tschudi). Type locality: "Rio Parana", i.e. Porto do Rio Paraná (today Igarapava), São Paulo, Brazil.

Hesperomys [(Calomys)] Anguya, sensu Burmeister, 1854: 168 (part; not *Mus anguya* Azara; includes *H. leucodactylus* Wagner).

Mus masculipes: Burmeister, 1854: 185 (incorrect subsequent spelling)

H[esperomys (Calomys)]. mystacalis: Burmeister, 1855: 7 (name combination; part).

H[esperomys (Calomys)]. maculipes: Burmeister, 1855: 8 (name combination).

H[esperomys (Holochilus)]. physodes, sensu Giebel, 1859: 542 footnote (part; not *Mus physodes* Olfers; includes "*Mus mystacalis* Lund").

H[esperomys (Calomys)]. expulsus, sensu Giebel, 1859: 546 footnote (part; includes "Pictets *M. masculipes*"; not *Mus expulsus* Lund).

[Hesperomys (Rhipidomys)] mastacalis: Trouessart, 1881: 136 (name combination).

Rhipidomys mastacalis: Winge, 1888: 54 (first use of current name combination).

[Oryzomys] musculipes: Trouessart, 1899: 528 (name combination and incorrect subsequent spelling of *maculipes*).

[Œcomys] maculipes: Tate, 1932: 21 (name combination).

Rhipidomys maculipes: Laemmert et al., 1946: 38 (name combination).

Rhipidomys mastacalis mastacalis: Cabrera, 1961: 423 (as subspecies).

R[hipidomys]. mastacalis cearanus, sensu Tipton & Machado-Allison, 1972: 35 (specimen from Pernambuco; not *R. cearanus* Thomas).

Rhipidomys masatacalis: Voss & Myers, 1991: 428 (incorrect subsequent spelling).

R[hipidomys]. cereanus: Zanchin et al., 1992a: 121, fig. 1 (incorrect subsequent spelling).

Holotype: UZM 291 (skin), L.16 (skull and part skeleton); collected at Lagoa Santa, Minas Gerais, Brazil, in or before 1839 by Peter Wilhelm Lund.

Revised diagnosis

Medium-sized *Rhipidomys* specimens with grey-brown to more intense red-brown dorsal pelage and cream or white underparts; hind foot broad, moderate in length; tail moderate to long with short to medium-length pencil. Skull: rostrum moderate in length, not especially broad; supraorbital ridges straight, diverging from front of interorbital region; braincase not greatly inflated or rounded; incisive foramina narrow; palatal bridge long and narrow; carotid circulation derived. Karyotype: $2n = 44$, FN $= 74$.

Description

The specimen from Fazenda União, eastern Rio de Janeiro state, is illustrated in Figure 1.1. Mice of moderate size, adult head-and-body length usually 125-145 mm; tail 120%-140% of HB, occasionally longer. Dorsal pelage varies from greyish-brown to bright red-brown (especially at some more coastal localities); some specimens are a duller, richer chocolate brown; agouti effect varies from barely noticeable in the redder forms to more conspicuous in the greyer and browner. Ventral pelage cream or white to roots or with inconspicuous pale grey bases, especially at sides of belly. Pelage length (guard hairs/body fur): dorsal 9-13/6-9 mm, ventral 7-9/4-6 mm; texture moderately fine. Hind foot broad, medium length (mostly 26-29 mm c.u.); medium to dark brown patch, often broad and ill-defined, not normally extending onto toes; sides of foot and toes pale. Tail light to dark brown; hairs short proximally, longer on distal half, with short to moderate pencil. Ears medium to large, usually mid-brown.

Rostrum short to moderate in length, relatively slender; nasals tend to taper regularly from anterior to posterior end. Supraorbital edges squared or more often slightly raised, usually nearly straight rather than curved, and diverging from front of interorbital region; interorbit usually broad. Braincase not especially broad or rounded, often a little flattened especially in older specimens; lateral process of parietal rectangular. Incisive foramina narrow and elliptical or slightly broader in posterior half; palatal bridge relatively narrow, often longer than molar row; medial process on rear edge usually present; mesopterygoid fossa moderate in width; sphenopalatine vacuities absent or small slits. Bullae small in specimens from coastal regions, larger in those from drier areas inland. Carotid circulation derived (small stapedial foramen, no translucent internal groove across squamosal and alisphenoid, no sphenofrontal foramen).

Molars moderate in size, mean approximately 5.0 mm. Hypocone of M3 often

greatly reduced. Anteromedian flexus moderate to weak; anteromedian flexid present or absent; oblique paralophules often present M1-3; oblique metalophules sometimes present, especially on M2-3.

The karyotypes of specimens from Lagoa Santa (Minas Gerais), Unacau (S Bahia) and Serra dos Cavalos (Pernambuco) are described by Zanchin et al. (1992a).

Variation and comparisons

Specimens from Pernambuco are usually deep, intense red-brown compared with those from farther south, while the São Felipe sample from near Salvador is brighter orange-brown. Near Ilhéus and Jequié specimens may be browner or redder; the individual from Santa Teresa, Espírito Santo, is very red. Specimens from Minas Gerais, especially the three presumed to be from the Rio Jequitinhonha, are greyer and more evidently agouti. These three also have rather longer hind feet (29-30 mm) and a more "streamlined" skull, with slightly more evident zygomatic notches and large bullae. Large bullae are also found in specimens from Vitória da Conquista, in dry forest bordering the caatinga.

Rhipidomys mastacalis is similar in most external characters to *R. macrurus*; the differences between them are no greater than the geographical variations that exist within each species. Cranially, too, there is convergence, and although the "standard" form of each is distinctive, individual specimens may be difficult to allocate with certainty. *R. mastacalis* typically has a narrower skull with a less inflated braincase and straighter supraorbital ridges; the palatal bridge is narrower and longer, and the bullae are smaller. Intermediate forms do exist, however. Were it not for the karyological distinction, the two taxa might well be thought to be conspecific.

Distribution

In the Atlantic forest domain of eastern Brazil, down the coast from Pernambuco (possibly from Rio Grande do Norte), through Alagoas and eastern Bahia to the coastal plain and foothills of Espírito Santo and Rio de Janeiro, and inland through eastern and southern Minas Gerais to the interior of São Paulo Fig. 7.7). In view of the extent of deforestation in this region, particularly along the coastal plain, this species' habitat may already have disappeared over much of its original range.

Ecological notes

About 59% of the *R. mastacalis* collected by SEPSFA around Ilhéus were taken in young forest, 21% in old forest and 9% in swamp forest; *Rhipidomys* proved to be less important as a host for the yellow fever virus than most rodents (Laemmert et al., 1946).

The species was considered rare in the Parque Florestal Estadual do Rio Doce, although two individuals were caught in a house (Fonseca & Kierulff, 1988; Stallings, 1988). *Rhipidomys* is implicated in damage to cacao at Uruçuca, Bahia, by Cruz (1983). Fonseca (1959) reports on parasites from Caruaru.

Material examined

BRAZIL: **Alagoas,** Anádia, Sítio Vale Verde *(62)* (MNRJ 17450); **Bahia,** (MHNG 275.38 - holotype of *maculipes*); Almada (near Ilhéus), Río do Braço *(72)* (MNRJ 9127, 9131, 9132, 9336, 9431, 9436, 9448, 9453, 9473, 9606, 9707); Buerarema (near Ilhéus), Ribeirão da Fortuna *(74)* (MNRJ 9411, 11651); Ilhéus *(73)* ((KU 39320; MNRJ 10682, ~684, ~721, ~786, ~787, ~858, ~862, ~952, 11214, ~548); Jequié, Fazenda Baixa Bonita *(68)* (MNRJ 17300 to ~306, ~312); São Felipe *(66)* (MNRJ 22274 to ~79); Três Braços, Fazenda Nova Esperança *(67)* (USNM 545062); Fazenda Unacau, 8 km SE of São José *(75)* (UFPB 425, 426); Uruçuca, Estação Central de Experimentação de Cacau *(71)* (MNRJ 30022); Urucutuca, Aritaguá, Ilhéus *(73)* (MNRJ 9021, 9128, 9129, 9280, 9383, 9459, 9506, 9657, 9670, 9685, 9686, 30019, ~20); Vitória da Conquista (includes Sítio Cachoeiro dos Porcos, Sítio Caititu de Graciano - *70)* (MNRJ 17375 to ~377, ~447); **Espírito Santo,** Santa Teresa, Floresta da Capela São Braz *(76)* (MNRJ 5393); **Minas Gerais,** Engenho Velho, Highway BR 262, km 53 *(92)* (UFMG 604); Lagoa Santa *(97)* (BMNH 88.1.28.1; MNRJ 30033); Parque Florestal Estadual do Rio Doce, Hotel *(94)* (UFMG Rio Doce.25P); Passos *(89)* (MNRJ 30014) Rio Jequitinhonha (uncertain locality - *100)* (UFMG Jequi.91, ~98, ~100); Rio Manso *(96)* (UFMG Rio Manso.04, ~.s/n); Salinas *(101)* (MNRJ 30015, ~21); Santa Bárbara, Reserva Peti *(95)* (UFMG CEMIG.7, ~.70, ~.140, ~.141); Serra do Cipó, 1400 m *(98)* (MNRJ 4212); **Pernambuco,** Caruaru (includes Sítio Brejo do Buraco, Fazenda Caruaru, Sítio Quandus, Fazenda Santa Maria, Sítio Serra dos Cavalos - *59-60)* (MNRJ 12361 to ~363, ~365, ~366, ~368 to ~375, ~378, ~380 to ~384, ~386, ~388, ~391, ~393, ~503, ~506 to ~522, 17346, ~352, ~354, ~357 to ~360, ~362 to ~369, ~381, ~448); Garanhuns, Sítio Cavaquinho *(61)* (MNRJ 12500); Serra dos Cavalos, 13 km ESE of São Caitano *(58)* (UFPB 946, 947); **São Paulo,** São José do Rio Preto *(84)* (USNM 460533). **Total:** 141.

Synonyms: See under subspecies.

Diagnosis

Moderately large *Rhipidomys* specimens with yellowish to reddish-grey-brown agouti dorsal pelage and cream underparts; tail long with medium-length pencil; hind foot large, broad, with short toes; ears large; vibrissae very long and thick. Skull large and robust, with well-developed supraorbital ridges and broad occiput; palate short; bullae and molars relatively large. Carotid circulatory pattern derived.

Distribution

Known from mesic forests isolated within the semi-arid caatinga of northeastern Brazil.

2 subspecies:

Rhipidomys sp. 4 ssp. 1

Rato palmeira

Synonyms

Rhipidomys cearanus, *sensu* Moojen, 1943: 10 (not *Rhipidomys cearanus* Thomas).

Holochilus sciureus, *sensu* Freitas, 1957: 131 (part; not *Holochilus sciureus* Thomas).

Rhipidomys mastacalis, *sensu* Mares et al., 1981: 84 (part; not *Mus mastacalis* Lund).

Diagnosis

As for the species. Dorsal pelage yellowish-grey-brown with conspicuous agouti effect; ventral pelage rather woolly in texture. Skull with very short, broad palatal bridge and broad mesopterygoid fossa.

Description

Moderate to large-bodied rats, adult head-and-body length mostly 130-160 mm, the largest in the sample being 190 mm; tail 110%-130% of HB. Dorsal pelage yellowish-grey-brown, sometimes greyer, sometimes redder, but always with conspicuous speckling from dark guard hairs and hair tips. Ventral pelage white or pale cream, sometimes with pale grey bases on abdomen. Tail light to rather dark, moderately haired, with medium-length pencil. Hind foot large and broad, 27-30 mm c.u.; toes short; dark patch often poorly defined. Ears large. Mystacial vibrissae very long and thick.

Skull large and robust. Rostrum moderately long; nasals narrow; zygomatic plate broad. Supraorbital ridges well developed, straight, diverging from front of interorbital

region. Braincase large, rather angular, with broad occiput; lateral process of parietal rectangular; hamular process of squamosal long and almost horizontal. Incisive foramina roughly elliptical, penetrating between anterior roots of first molars. Palatal bridge broad, shorter than molar row; 3 pairs palatal foramina. Mesopterygoid fossa broad; bullae rather inflated. Carotid circulation derived (small stapedial foramen, no translucent internal groove across squamosal and alisphenoid, no sphenofrontal foramen).

Upper incisors robust, more opisthodont than in most *Rhipidomys*. Molars rather large (MRC: mean = 5.18, s.d. = 0.13, n = 23). Anteromedian flexus and flexid well defined; oblique paralophules present M1-3; M3 not greatly reduced.

Comparisons

External characters serve to distinguish these rats from the nearest *Rhipidomys* to the east and west, *R. mastacalis* and *R. macrurus* respectively. Body size is larger for equivalently aged specimens, the hind foot is longer and broader, and the vibrissae are longer and thicker. Dorsal colour is greyer, and the ventral pelage tends to be a little woolly rather than sleek. The skulls are somewhat similar to old *R. macrurus*, although the rostrum is often relatively longer.

Distribution

Known only from the vicinity of Crato, in the isolated mesic enclave of the Cariri, southern Ceará state, NE Brazil (Fig. 7.7).

Ecological notes

Specimen labels indicate that the rats were taken in fields, trees and palms.

Material examined

BRAZIL: Ceará, Crato (includes Sítio Arisco, Sítio Baixa do Maracujá, Sítio Belo Horizonte, Sítio Caiana, Sítio Grangeiro, Sítio Passagem 1ª, Sítio Passagem 2ª, Sítio Recreio 1º - *56-57)* (KU 27308; MNRJ 1530, 10170, 17298, ~299, ~347 to ~349, ~351, ~353, ~378 to ~380, ~417 to ~423, 30012, ~013; USNM 304587, ~588). Total: 24.

Rhipidomys sp. 4 ssp. 2

Synonyms

Rhipidomys cearanus, sensu Freitas, 1957: 131 (part; not *Rhipidomys cearanus* Thomas).

Diagnosis

As for the species. Dorsal pelage reddish brown, conspicuously agouti. Skull with

moderately long rostrum, short but not broad palatal bridge, and broad braincase.

Description

Moderate sized rats, adult head-and-body length mostly 130-150 mm; tail 120%-140% of HB. Dorsal pelage rather redder-brown than the previous subspecies, with evident agouti effect. Ventral pelage white or pale cream, sometimes with pale grey bases on abdomen. Tail light to rather dark, moderately haired, with medium-length pencil. Hind foot large and broad, 28-30 mm c.u.; toes short; dark patch often poorly defined. Ears large.

Skull large and robust. Rostrum relatively longer than in the previous form; zygomatic plate broad. Supraorbital ridges well developed, straight, diverging from front of interorbital region. Braincase large, rather angular, with broad occiput. Palatal bridge shorter than molar row but less broad than in Crato specimens. Mesopterygoid fossa also narrower. Bullae rather inflated. Carotid circulation derived (small stapedial foramen, no translucent internal groove across squamosal and alisphenoid, no sphenofrontal foramen).

Molars rather large (MRC: mean = 5.45, s.d. = 0.12, n = 15). Anteromedian flexus and flexid well defined; oblique paralophules present M1-3; M3 not greatly reduced; M2 hypoflexus often penetrating into mure, becoming almost continuous with mesoflexus.

Distribution

Known only from the vicinity of Pacoti, in the isolated mesic enclave of the Serra de Baturité, northern Ceará state, NE Brazil (Fig. 7.7).

Ecological notes

Specimen labels indicate that 12 specimens were taken in canefields, two in coffee plantations, two in second-growth forest and one in a quarry. One female had four embryos. For ecological and biogeographical notes on Baturité, see Gomes (1978) and Nascimento & Lima-Verde (1989).

Material examined

BRAZIL: Ceará, Pacoti (includes Sítio Cebola, Sítio Ladeira, Sítio Ouro, Sítio Pirajá, Sítio Santa Rosa - 55) (MNRJ 17373, ~428, ~431, ~440 to ~446, 30005 to ~011). Total: 17.

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CHAPTER 8 - CONCLUSIONS

Rhipidomys is a highly plesiomorphic genus within the Sigmodontinae, sharing few derived character states with other taxa. In its convergent supraorbital ridges and absence of a gall bladder it bears some resemblance to the Oryzomyini, but it lacks the diagnostic characters used by Voss & Carleton (1993) to define that tribe. It also possesses few apomorphies that unquestionably delimit it from other plesiomorphic genera, particularly *Thomasomys*. The main characters distinguishing *Rhipidomys* from *Thomasomys* - pelage colour, tail colour, tail pencil, foot patch, shape of interorbit, development of parietal ridges, lateral process of parietal, squamosal conformation - have to be taken in combination, because for each one individually there may be exceptions among the species of one or both genera.

A definitive diagnosis of *Rhipidomys* has been constrained by the heterogeneous nature of *Thomasomys*. I have not attempted to formally challenge the unity of *Thomasomys* because to do so would have entailed broadening this revision far beyond its intended scope. Nevertheless, it is badly in need of revision and should probably be split into a number of independent parts, some of which are likely to prove more closely related to *Rhipidomys* than to their current congeners. It is hoped that this examination of *Rhipidomys* will provide a basis for such comparisons. Once relations among the taxa currently included in *Thomasomys* have been clarified, the arrangement of *Rhipidomys* proposed in this study will then need to be reassessed in the light of the new understanding. It may be found that *Rhipidomys* becomes more readily diagnosable if taxa are added from a dismembered *Thomasomys*, or it may be appropriate to combine *R. macconnelli* and/or the *R. fulviventer* group with parts of that genus, or even to grant them separate generic status.

Within *Rhipidomys* there is a lack of discrete morphological characters that might distinguish clearly among the included species. The carotid circulation pattern appears to be the most consistent of those that do exist, but it is not entirely congruent with the distribution of other character states, as shown by my inclusion of *R. caucensis* (with derived circulation) in the otherwise primitive-circulation *R. fulviventer* group. Most other characters (e.g. interorbital shape, ventral coloration) have states that are not clearly delimited and intermediate forms can and do exist, even within the same sample. Hence the reliance placed on morphometric methods to help reveal "natural" groupings among specimens and samples.

The results of analyses of measurement error (%ME) and ontogenetic and sexual variation allowed the most variable measurements to be dropped from subsequent analyses, but it was notable that several of the measurements that proved most taxonomically useful (especially PB1, MFB and BW) had relatively large %ME. Such small structures are not easy to measure precisely, but evidently the greatest care should be taken to reduce investigator error, given the importance of these dimensions in discriminating between taxa. Care is also required when skulls are being cleaned to avoid damage to the delicate structures of the basicranium. It is unfortunate that so much of the older type material, which may be irreplaceable now because of habitat destruction, lacks precisely these diagnostic structures.

It is hoped that the expanding investigation of alternative character sets, such as karyotypes, allozymes and DNA sequences, will provide new information of taxonomic value. Indeed, karyological data will be essential in distinguishing "sibling" species such as those present in southeastern Brazil, and are likely to prove important in elucidating the taxonomic boundaries of R. nitela, which seems to vary in diploid number. Very few populations have so far been surveyed, and most of these have been represented by only one or two individuals. It is possible that other specimens have been karyotyped but have not been reported. In the case of a wide-ranging genus like Rhipidomys, it is especially important for such findings to be published so that researchers working with material from other parts of the continent may make comparisons. Although it is becoming increasingly common for newly collected material to be karyotyped and tissue samples preserved, such practices should ideally be regarded as standard procedure, as normal as the preservation of skin and skull.

The opposing tendencies of taxonomists to "split" species into smaller units and to "lump" them into more embracing ones usually occur in alternating phases; "splitting" is a response to the perception of hitherto unrecognized variation, often as a result of the availability of new kinds of data, whereas "lumping" occurs as an attempt to put some order into an otherwise confusing array of nominal taxa. The current trend in Neotropical muroid systematics seems to be towards recognizing and defining an increasing number of local forms, with the result that few species are now considered to have continent-wide distributions (even if formal revisions have not yet been conducted). In this study, both processes have played their part. New species have been recognized in the Venezuelan llanos, the southern Andes and Brazil, and it is shown that the blanket use of the name R. mastacalis for non-Andean forms is not appropriate. In contrast, the relations among

the large-bodied forms in Peru are confusing, and for want of clear distinctions most of them have been subsumed in the single species *R. leucodactylus*; similar considerations apply to *R. latimanus* and *R. nitela*. These are evidently taxa that require further investigation. The final total of 18 species recognized (28 species and subspecies) is thus intermediate between the 42 nominal taxa already described and the 7 to 14 species accepted in recent compilations (Corbet & Hill, 1986; Musser & Carleton, 1993). The species and subspecies to which nominal taxa have been allocated are listed in Appendix II.

Biogeographical hypotheses have been brought to bear in SE Brazil, where morphological evidence alone is insufficient to identify unknown-karyotype specimens with one or other of the karyomorphs present in the region. The hypothesis of a northerly, low altitude, coastal/interior form with high fundamental number (*R. mastacalis*) and a southerly, higher altitude, montane form with low FN (*R.* cf. *macrurus*) requires testing through the accumulation of more karyological data, which may then be used to identify distinguishing characters in external and cranial morphology. Altitude also seems to separate other pairs of *Rhipidomys* species: *R. fulviventer* and *R. latimanus* in Colombia and Venezuela, and *R. austrinus* and *R.* sp. 1 in NW Bolivia. The latter case seems to parallel the pattern of distribution in SE Brazil, and it would be interesting to see whether there is also a karyological difference between the species involved there. Another environmental boundary which may separate species is that between forest and cerrado. Again, the hypothesis requires extensive testing, particularly in areas where drier forests and cerrado meet. Since *Rhipidomys* is restricted to the more mesic conditions of gallery forest in the latter domain, a comparative ecological study is needed of gallery habitat and semi-deciduous forest; precise habitat notes should always be provided with voucher specimens. A similar situation exists in Venezuela, where the llanos and the submontane forests of the northern coast range appear to be inhabited by different species. Aridity is another factor influencing the distribution of *Rhipidomys*: without suitable habitat connecting mesic enclaves in the caatinga of NE Brazil, the local populations at Crato and Pacoti have become (or remained) sufficiently distinct to be regarded as a separate species.

Almost every species of *Rhipidomys* presents major gaps in its known distribution which should be investigated, and only a selection of cases deserving attention can be mentioned. In the case of *R. fulviventer*, collecting is needed particularly in the Eastern Cordillera of Colombia both north and south of Cundinamarca, and in the mountain knot

where the Central and Western Cordilleras meet in Nariño, to establish whether there is any contact between the subspecies recognized. With the rapid clearance of Andean forests, once continuous populations are likely to become increasingly fragmented. Montenegro-Díaz et al. (1991) report that the species is apparently sensitive to habitat disturbance, so it may already have disappeared from some areas. Surveys should therefore investigate its current status. At lower altitudes, too, little is known of species ranges. The whole extent of the eastern foothills of the Andes from NE Venezuela to N Argentina is probably occupied by large-bodied *Rhipidomys* species, but major stretches have not been sampled. In particular, the relationship of the populations from Meta in Colombia and Barinas and Sucre in Venezuela, all allocated here to *R. couesi*, needs to be clarified through collections made in intermediate areas, and points of possible contact or intergradation between *R. leucodactylus, R.* sp. 1 and *R. austrinus* in Bolivia should be sampled. Throughout the Amazon basin the forest canopy may well harbour at least one large and one small species of *Rhipidomys*; the few specimens known from the region have been allocated to *R. leucodactylus* and *R. nitela*, but future karyological and molecular work on new samples from a wider area may indicate that a reassessment of their relationships is called for.

The unexpected occurrence of *Rhipidomys nitela* in northern Colombia and its almost accidental discovery in Little Tobago and French Guiana suggest that this species may be more widely distributed than previously imagined, and that small mammal faunas are not being adequately sampled by the collecting techniques currently used. *Rhipidomys* probably occurs at low densities in most areas, and depending on the type of forest may be more arboreal in some places than in others. Population density will be seriously underestimated if traps are set only on the ground, so canopy trapping is essential, but even that may not produce many specimens. Some species may also be restricted to relatively undisturbed forest, as at Teresópolis in SE Brazil (Davis, 1947) and as mentioned above in Cundinamarca (Montenegro-Díaz et al, 1991). Given the rate of forest clearance throughout South America and not just in the Amazon basin, ecologically viable populations may no longer exist in many areas. The species of *Rhipidomys* should be added to the list of those considered in the assessment of areas for conservation.

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APPENDIX I - Specimens used in preparatory studies

A. Measurement Error

Set 1, "Brasília":

Specimens from the collections of the Museu Nacional, Rio de Janeiro: 21373, 21374, 21375, 21377, 21378, 21379, 21381, 21382, 21386, 21387, 21388, 21389, 21390, 21392, 21393, 21394, 21395, 21396, 21399, 21400, 21401, 21402, 21971, 21972, 24790; all collected in Brasília.

Set 2, *Rhipidomys "couesi"*

Specimens from the collections of the Natural History Museum, London:

Trinidad: 97.6.7.3, 97.6.7.4, 99.9.4.1; Guyana: 87.1.28.8; Venezuela (Sucre): 0.5.1.9, 0.5.1.10; Ecuador (Napo): 0.6.3.7; Peru (Loreto): 28.5.2.180, 28.2.5.182, 28.2.5.184; (Cuzco): 98.11.6.19, 98.11.6.20, 99.10.5.5, 3.2.9.6, 13.2.3.13, 22.1.1.69; Bolivia (La Paz):1.6.7.33.

Specimens from the collections of the American Museum of Natural History:

Peru (Junín): 231197; Bolivia (La Paz): 72632.

B. Ontogenetic variation and sexual dimorphism

Rhipidomys macconnelli

Specimens from the collections of the American Museum of Natural History, collected by the Tyler-Duida Expedition at Cerro Duida, Venezuela:

DAC 1, females 77060, 77070, 77105, 77109, 77113, 77120, 77135, 77144, 77191, 77214, 77223, 77230;

males 77048, 77059, 77061, 77064, 77100, 77146, 77169, 77182, 77204, 77236;

DAC 2, females 77044, 77047, 77077, 77106, 77110, 77114, 77179, 77183, 77211, 77226, 77234, 77241, 77244;

males 77050, 77076, 77082, 77148, 77195, 77206, 77217, 77218, 77221, 77237, 77242;

DAC 3, females 77045, 77046, 77049, 77053, 77072, 77073, 77078, 77080, 77081, 77115, 77116, 77118, 77139, 77143, 77157, 77163, 77173, 77174, 77175, 77178, 77207;

males 77051, 77062, 77069, 77071, 77092, 77093, 77093, 77099, 77103, 77107, 77117, 77140, 77162, 77170, 77171, 77185, 77194, 77198, 77210, 77229, 77232, 77233, 77245, 77298.

Rhipidomys "cearanus"

Specimens from the collections of the Museu Nacional, Rio de Janeiro, collected by the Serviço Nacional da Peste in the vicinity of São Benedito, Ceará, Brazil:

DAC 0, females 12600, 17309, 17391, 17392, 17397, 17405;

males 12541, 12544, 12558, 12594, 12597, 12599, 17386, 17387, 17390, 17398;

DAC 1, females 12536, 12566, 17308, 17317, 17394, 17409, 17429, 17435;

males 12525, 12543, 12549, 12555, 12589, 17307, 17308, 17311, 17404, 17406;

DAC 2, females 12397, 12548, 17313, 17315, 17403, 17425, 17432;

males 12538, 12570, 12576, 12577, 17402, 17437;

DAC 3, females 12400, 12497, 12527, 12529, 12530, 12531, 12540, 12557, 12572, 12573, 12575, 12579, 12590, 12591, 12598, 17310, 17316, 17406, 17408, 17411, 17424, 17433;

males 12394, 12534, 12550, 12567, 12568, 17410;

DAC 4, females 12528, 12535, 12537, 12539, 12552, 12563, 12569, 17415;

males 12526, 12556, 12565, 12571, 17407, 17434.

APPENDIX II - Allocation of nominal taxa within *Rhipidomys*

Original name	Allocation in this revision
Rhipidomys leucodactylus aratayae Guillotin & Petter, 1985	*Rhipidomys leucodactylus*
Rhipidomys austrinus Thomas, 1921	*Rhipidomys austrinus*
Rhipidomys bovallii Thomas, 1911	*Rhipidomys leucodactylus*
Rhipidomys caucensis J. A. Allen, 1913	*Rhipidomys caucensis*
Rhipidomys cearanus Thomas, 1910	*Rhipidomys macrurus*
Rhipidomys cocalensis J. A. Allen, 1912	*Rhipidomys latimanus latimanus*
Rhipidomys collinus Thomas, 1925	*Rhipidomys austrinus*
Tylomys couesi J. A. Allen, 1893	*Rhipidomys couesi*
Rhipidomys venezuelae cumananus Thomas, 1900	*Rhipidomys couesi*
Rhipidomys fulviventer elatturus Osgood, 1914	*Rhipidomys fulviventer elatturus*
Oecomys emiliae J. A. Allen, 1916	*Rhipidomys emiliae*
Rhipidomys equatoris Thomas, 1915	*Rhipidomys leucodactylus*
Rhipidomys venezuelae fervidus Thomas, 1904	*Rhipidomys nitela*
Rhipidomys fulviventer Thomas, 1896	*Rhipidomys fulviventer fulviventer*
Rhipidomys goodfellowi Thomas, 1900	*Rhipidomys leucodactylus*
Rhipidomys latimanus Tomes, 1860	*Rhipidomys latimanus latimanus*
Hesperomys (Rhipidomys) leucodactylus Tschudi, 1845	*Rhipidomys leucodactylus*
Hesperomys leucodactylus Wagner, 1845 (junior homonym of the above)	*Rhipidomys mastacalis*
Rhipidomys lucullus Thomas, 1911	*Rhipidomys leucodactylus*
Rhipidomys macconnelli De Winton, 1900	*Rhipidomys macconnelli*
Mus macrurus Gervais, 1855	*Rhipidomys macrurus*
Mus maculipes Pictet & Pictet, 1844	*Rhipidomys mastacalis*
Mus mastacalis Lund, 1840	*Rhipidomys mastacalis*
Rhipidomys microtis Thomas, 1896	*Rhipidomys latimanus latimanus*
Rhipidomys milleri J. A. Allen, 1913	*Rhipidomys nitela*
Rhipidomys modicus Thomas, 1926	*Rhipidomys modicus*
Rhipidomys mollissimus J. A. Allen, 1912	*Rhipidomys latimanus latimanus*

Rhipidomys *nitela* Thomas, 1901	*Rhipidomys nitela*
Rhipidomys *ochrogaster* J. A. Allen, 1901	*Rhipidomys ochrogaster*
Rhipidomys *pictor* Thomas, 1904	*Rhipidomys latimanus latimanus*
Rhipidomys *quindianus* J. A. Allen, 1913	*Rhipidomys latimanus latimanus*
Rhipidomys *rex* Thomas, 1927	*Rhipidomys leucodactylus*
Rhipidomys *scandens* Goldman, 1913	*Rhipidomys latimanus latimanus*
Hesperomys *(Rhipidomys) sclateri* Thomas, 1887	*Rhipidomys leucodactylus*
Rhipidomys *similis* J. A. Allen, 1912	*Rhipidomys fulviventer similis*
Thomasomys macconnelli *subnubis* Tate, 1939	*Rhipidomys macconnelli*
Oryzomys *tenuicauda* J. A. Allen, 1899	*Rhipidomys fulviventer*
	tenuicauda
Rhipidomys nitela *tobagi* Goodwin, 1961	*Rhipidomys nitela*
Rhipidomys *venezuelae* Thomas, 1896	*Rhipidomys latimanus venezuelae*
Rhipidomys *venustus* Thomas, 1900	*Rhipidomys fulviventer venustus*
Rhipidomys *wetzeli* Gardner, 1989	*Rhipidomys wetzeli*
Rhipidomys venezuelae *yuruanus* J. A. Allen, 1913	*Rhipidomys nitela*

APPENDIX III - Gazetteer and maps of *Rhipidomys* collecting localities.

Entries in the gazetteer are arranged first by country (in alphabetical order) and then by major administrative divisions thereof. Each entry consists of:

1.   Locality number, as marked on the maps and noted under "Material examined"; as far as practicable, within each country numbering starts in the north and/or west and proceeds roughly clockwise;

2.   Specific locality; spellings follow the most recent authority, usually the gazetteers of the United States Board on Geographic Names, but modified especially in the case of Brasil to obey current orthographic rules; names as given on specimen labels or in the literature, where significantly different from the currently accepted form, are quoted in parentheses; common nouns as parts of place names (e.g., Fazenda, Río - see list below) are given in the language of the country concerned; other modifiers (e.g., mouth of, 3 km by road NE of) are generally given in English;

3.   Altitude in metres (an original height in feet follows in parentheses); altitudes in square brackets [ ] are derived from maps or other sources and not from specimen labels, field notes or published accounts;

4.   Geographical coordinates; the source of these is indicated in notes at the end of the gazetteer unless it is the same as the source of the locality reference itself;

5.   Source of the locality reference (in parentheses): information attached to specimens examined is represented by the collection acronym (see Materials and Methods); where no specimen from the locality was examined for this study, references to literature or correspondence ("*in litt.*") are given (in such cases specimen identifications are provisional and based upon written descriptions, photographs and/or known ranges).

       To avoid repetition, taxa present at each locality are indicated at the most inclusive geographical level possible.

Portuguese (P), Spanish (S) and French (F) words used in the gazetteer: *Boca* (P,S) mouth; *Cabecera* (S) headwaters; *Cachoeira* (P) waterfall, rapids; *Cafetos* (S) coffee plantation; *Campamento* (S) camp; *Caño* (S) stream, gully; *Caserío* (S) hamlet, settlement; *Cerro* (S) mountain; *Chorrera* (S) waterfall; *Cordillera* (S) mountain range; *Cumbre* (S) peak, summit; *Desfiladero* (S) narrow pass; *Ensenada* (S) bay; *Estação* (P), *Estación* (S) station; *Estancia* (S) farm, ranch; *Estrada* (P) road, highway; *Fazenda* (P), *Finca* (S) farm, ranch; *Floresta* (P) forest; *Hacienda* (S) ranch; *Igarapé* (P) creek; *Ilha* (P), *Isla* (S) island; *Lago* (P,S) lake; *Laguna* (S) lagoon, lake; *Mata* (P) forest; *Montaña*

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(S) mountain, wilderness; *Monte* (S) Mount, woods, wilderness; *Oeste* (P,S) west; *Páramo* (S) Paramo (high altitude moorland); *Parque Florestal Estadual* (P) State Forest Park; *Parque Nacional* (P,S) National Park; *Pico* (S) Peak; *Porto* (P) port; *Posto* (P) trading/administrative post; *Quebrada* (S) stream, gully; *Reserva* (P,S) reserve; *Reserva Biológica* (P,S) Biological Reserve; *Ribeirão* (P) river, stream; *Rio* (P), *Río* (S), *Rivière* (F) river; *Salina* (S) salt pan; *Saut* (F) falls; *Serra* (P), *Serranía, Sierra* (S) mountain range; *Sitio* (S) farm; *Sítio* (P) farm, locality; *Talud* (S) slope; *Usina hidrelétrica* (P) hydroelectric power station; *Valle* (S) valley; *Vega* (S) (water)meadow; *Vía* (S) road, highway.

ARGENTINA

Salta - *R. austrinus*

1 Aguaray, 22°16'S 63°44'W² (Ojeda & Mares, 1989)

2 Río Santa María, 23°17'S 64°14'W² (Ojeda & Mares, 1989)

Jujuy - *R. austrinus*

3 Cerro Calilegua, 1700 m, 23°35'S 64°54'W² (Olrog, 1979)

4 El Sunchal, Sierra Santa Bárbara, 1200 m (type locality of *Rhipidomys austrinus* Thomas), 1600 m, 24°16'S 64°27'W² (BMNH)

BOLIVIA

La Paz

5 Chimasi Yungas, 1500 m, c. 15°30'S 67°53'W² (BMNH) *R. austrinus*

6 Zongo, 30 km N by road, 15°53'S 67°52'W (S. Anderson, *in litt.*) *R. austrinus?*

7 Chijchipani, 850 m, 16°08'S 67°44'W¹ (AMNH, MNLP, MSB) *Rhipidomys* sp. 1

8 Pitiguaya, 1710 m (5600 ft), 1770 m (5800 ft), (also includes La Florida, Río Unduavi, 1700 m) 16°21'S 67°47'W⁶ (AMNH, UMMZ) *R. austrinus*

Cochabamba

9 El Choro, [2500 m], 16°56'S 66°42'W² (S. Anderson, *in litt.*; species unknown)

10 Yungas, 1000 m, possibly c. 17°10'S 65°50'W⁷ (BMNH) *R. leucodactylus*

Santa Cruz - *R. austrinus*

11 Estancia Cuevas, 1 km NE, Highway km 101 from Santa Cruz, 1300 m, 18°11'S 63°44'W¹ (AMNH, MNLP)

12 Río Ariruma, 7 km by road SE of Ariruma, 1750 m, 18°20'S 64°13'W¹ (AMNH)

13   La Hoyada, 30 km S of Valle Grande, 18°45'S 64°06'W (S. Anderson, *in litt.*)

14   Ingenio Mora, 7 km E, 3 km N, 490-580 m, 18°28'S 63°12'W[2] (AMNH)

15   Camiri, 1000 m, 20°05'S 63°34'W[7] (USNM)

      Florida, nr. Floripondio, not located (FMNH)

Chuquisaca - *R. austrinus*

16   Porvenir, 675 m, 20°45'S 63°13'W[1] (AMNH, MSB)

Tarija - *R. austrinus*

17   Villa Montes, 8 km S and 10 km E, 467 m, 21°15'S 63°30'W[2] (AMNH)

18   Taringuiti, c. 35 km by road SE of Villa Montes, 360 m, 21°28'S 63°17'W[1] (UMMZ)

19   Tapecua, 1500 m, 21°26'S 63°55'W[1] (AMNH, MNLP)

20   Valle del Itaú, foot of Sierra Santa Rosa, 1000 m (type locality of *Rhipidomys collinus* Thomas), 21°44'S 63°52'W[7] (BMNH)

21   Cuyambuyo, 4 km N by road, Fábrica de papel, Río Sidras, 980 m, 22°13'S 64°36'W[7] (UMMZ)

Not located

      Molina [or Molino?], Tabacal, 1610 m (USNM) *R. austrinus*

BRASIL

Rondônia

22   Usina Hidrelétrica de Samuel, Rio Jamari, 08°45'S 63°28'W[3] (UFPB) *R. leucodactylus*

Acre

23   Rio Juruá, above Cruzeiro do Sul, c. 07°38'S 72°36'W[2] (Cruzeiro do Sul), (J.L. Patton, *in litt.*) *R. leucodactylus*

Amazonas

24   Penedo, right bank Rio Juruá, 06°50'S 70°45'W[1] (MVZ) *R. leucodactylus*

25   Condor, left bank Rio Juruá, 06°45'S 70°51'W[1] (MVZ) *R. leucodactylus*

26   Rio Juruá [nr. Eirunepé], c. 06°40'S 69°52'W[2] (MZUSP) *R. leucodactylus*

27   Altamira, right bank Rio Juruá, 06°35'S 68°54'W[1] (MVZ) *R. leucodactylus*

28   Serra da Neblina, 00°45'N 66°01'W[8] (USNM) *R. macconnelli*; see also Venezuela, T. F. Amazonas, Cerro Neblina (localities 345-6)

29   Manaus, Estrada Manaus-Itacoatiara, km 50, c. 02°40'S 59°55'W[4] (MNRJ, MPEG) *R. nitela*

30   Fazenda Esteio, 80 km NNE of Manaus, (and INPA forest reserves, Malcolm, 1988) 02°25'S 59°50'W[1] (USNM) *R. nitela*

Roraima - *R. nitela*

31   Fazenda Deus-me-ajude, 04°16'N 61°02'W[1] (MZUSP)

32   Limão, Rio Cotinga, 03°56'N 60°30'W[2] (AMNH)

33   Ilha de Maracá, 03°22'N 61°26'W (Barnett & Cunha, 1994)

      Monte Roraima: see under Venezuela, Estado Bolívar, Cerro Roraima (locality 320)

Amapá

34   Boa Fortuna, upper Igarapé Rio Branco, 00°33'N 52°12'W[3] (MNRJ, MPEG) *R. leucodactylus*

34   Mouth of Rio Branco, Rio Maracá, 00°32'N 52°12'W[2] (MNRJ) *R. nitela*

Pará

35   Posto Monte Dourado, 105 km S and 170 km W of Macapá, W of Rio Jari, c. 00°50'S 52°33'W[9] (USNM) *R. leucodactylus*

36   Oriximiná, Porto Trombetas, Rio Saracazinho km 43, 01°42'S 56°23'W[4] (MPEG) *R. nitela*

37   Curuá-Una, 44 km S and 40 km E of Santarém, 02°50'S 54°22'W[1] (MPEG) *R. nitela*

38   Igarapé Amorim ("Amorim"), Rio Tapajós, 02°26'S 55°00'W[10] (AMNH) *R. leucodactylus*

39   Aramanaí ("Aramanaý"), Rio Tapajós, 02°45'S 54°59'W[10] (AMNH) *R. nitela*

40   Boim, W bank Rio Tapajós, 02°49'S 55°10'W[2] (MCZ) *R. nitela*

41   Igarapé Marói ("Marai"), E bank Rio Tapajós, 02°51'S 55°03'W[3] (NHR) *R. nitela*

42   Tauari ("Tauary"), E bank Rio Tapajós, 03°05'S 55°06'W[10] (MCZ) *R. nitela*

43   Aveiro ("Aveiros"), E bank Rio Tapajós, 03°15'S 55°10'W[2] (NHR) *R. nitela*
      Rio Tapajós, not plotted (NHR) *R. nitela*

44   Parque Nacional da Amazônia, c. 04°30'S 56°15'W[9] (George et al., 1988) *R. nitela*

45   Cachoeira Espelho, 52 km SSW Altamira, E bank Rio Xingu, 03°39'S 52°22'W[1] (MZUSP) *R. nitela*

46   Serra dos Carajás, área N1, Casa de Pedra, c. 06°00'S 51°30'W[3] (MPEG) *R. emiliae*

47   Rio Moju (type locality of *Oecomys emiliae* J.A. Allen), c.01°40'S 48°25'W[2]

(AMNH) *R. emiliae*

48 Belém (also includes: Bosque Municipal; Utinga; Bussuquiara), 01°27'S 48°29'W² (MNRJ, MPEG, USNM) *R. emiliae*

49 São Domingos do Capim ("Capim"), Estrada BR14 km 87, 01°41'S 47°47'W¹¹ (MZUSP) *R. emiliae*

50 Estrada Belém-Brasília [highway], km 94, c. 01°19'S 47°42'W⁴ (Carvalho & Toccheton, 1969) *R. emiliae*

Maranhão - *R. emiliae*

51 Alto da Alegria, [c. 40 km SW of] Turiaçu ("Tury-assu", "Jury-assu"), 01°41'S 45°21'W² (Turiaçu), (BMNH, MNRJ)

Ceará

52 Ibiapina, Sítio Pejuaba, c. 03°55'S 40°54'W² (MNRJ) *R. macrurus*

53 São Benedito (includes: Sítio Abrigo; Sítio Alto; Sítio Bananeira do Bandeira; Sítio Barra; Sítio Barroquinha; Sítio Boa Vista do Epaminondas; Sítio Bom Jardim; Sítio Buenos Aires; Sítio Cabeceiras; Sítio Cantinho; Sítio Cigarro; Sítio Cinta da Soledade; Sítio Cinta de São José; Sítio Guaribas do Amaral; Sítio Juçara; Sítio Lagoa da Tereza; Sítio Macapá; Sítio Mundo Novo; Sítio Pimenteira; Sítio Piraguara; Sítio Potós; Sítio Queimados dos Martins; Sítio São Francisco dos Lopes; Sítio São José da Boa Vista; Sítio Santa Luzia; Sítio São José; Sítio Tamandaré), c. 04°03'S 40°53'W² (MNRJ) *R. macrurus*

53 São Paulo, Serra de Ibiapaba, [c. 1000 m] (type locality of *Rhipidomys cearanus* Thomas), c. 04°03'S 40°53'W² (São Benedito), (BMNH) *R. macrurus*

54 Guaraciaba do Norte (includes: Sítio Areias; Sítio Cacimba do Meio; Sítio Convento; Sítio Flores; Sítio Flores do Meio; Sítio Mandu; Sítio Mazagão; Sítio Quati; Sítio Riacho Fundo; Sítio Rua Nova; Sítio São Tomé), c. 04°10'S 40°46'W² (MNRJ) *R. macrurus*

55 Pacoti (includes: Sítio Cebola; Sítio Ladeira; Sítio Ouro; Sítio Pirajá; Sítio Santa Rosa), c. 04°13'S 38°56'W² (MNRJ) *Rhipidomys* sp. 4 ssp. 2

56 Crato (also includes: Sítio Arisco; Sítio Baixa do Maracujá; Sítio Belo Horizonte; Sítio Caiana; Sítio Passagem 1ª; Sítio Passagem 2ª; Sítio Recreio 1º), c. 07°14'S 39°23'W² (MNRJ, USNM) *Rhipidomys* sp. 4 ssp.1

57 Crato, Sítio Grangeiro, 06°53'S 39°12'W² (KU, USNM) *Rhipidomys* sp. 4 ssp. 1

Pernambuco - *R. mastacalis*

58 Serra dos Cavalos, 13 km ESE of São Caitano, c. 08°21'S 36°06'W² (São

Caitano), (UFPB)

59 Caruaru, Fazenda Caruaru, [850 m], 08°22'S 36°01'W[5] (MNRJ)

59 Caruaru, Sítio Serra dos Cavalos, [750 m], 08°21'S 36°02'W[5] (MNRJ)

59 Caruaru, Fazenda Santa Maria, [850 m], 08°23'S 36°02'W[5] (MNRJ)

60 Caruaru (includes: Sítio Brejo do Buraco; Sítio Quandus) c. 08°17'S 35°58'W[2] (MNRJ, MNHN)

61 Garanhuns, Sítio Cavaquinho, c. 08°54'S 36°29'W[2] (MNRJ)

Alagoas - *R. mastacalis*

62 Anádia, Sítio Vale Verde, 09°42'S 36°18'W[2] (MNRJ)

Bahia

Bahia [state of] (type locality of *Mus maculipes* Pictet & Pictet), not plotted (MHNG) *R. mastacalis*

63 São Marcelo, Rio Preto, 11°02'S 45°32'W[2] (FMNH) *R. macrurus*

64 Barreiras, [c. 500 m], 12°08'S 45°00'W[2] (MNRJ) *R. macrurus*

65 Bom Jesus da Lapa, [447 m], 13°15'S 43°25'W[2] (MNRJ) *R. macrurus*

66 São Felipe, 12°51'S 39°06'W[2] (MNRJ) *R. mastacalis*

67 Três Braços, 37 km N and 34 km E of Jequié, Fazenda Nova Esperança, 13°32'S 39°45'W[1] (USNM) *R. mastacalis*

68 Jequié, Fazenda Baixa Bonita, [c. 200 m], 13°51'S 40°05'W[2] (MNRJ) *R. mastacalis*

69 Vitória da Conquista, Sítio Batalha, 14°48'S 40°54'W[2] (MNRJ) *R. mastacalis*

70 Vitória da Conquista (includes: Sítio Cachoeira dos Porcos; Sítio Caititu de Graciano), c. 14°51'S 40°51'W[2] (MNRJ) *R. mastacalis*

71 Uruçuca, Estação Central de Experimentação de Cacau, 14°35'S 39°16'W[4] (MNRJ) *R. mastacalis*

72 Almada, Rio do Braço, 14°40'S 39°15'W[4] (MNRJ) *R. mastacalis*

73 Urucutuca, Aritaguá, Ilhéus, 14°40'S 39°07'W[4] (MNRJ, FMNH) *R. mastacalis*

74 Ribeirão da Fortuna, Buerarema, 14°58'S 39°14'W[4] (MNRJ) *R. mastacalis*

75 Fazenda Unacau, 8 km SE of São José, c. 15°06'S 39°16'W[4] (UFPB) *R. mastacalis*

Espírito Santo

76 Santa Teresa, [659 m], Floresta da Capela São Braz, 19°55'S 40°36'W[2] (MNRJ) *R. mastacalis*

77 Hotel Fazenda Monte Verde, 24 km SE Venda Nova, c.20°19'S 40°59'W[4] (Venda

Nova), (UFPB) *R.* cf. *macrurus*

Rio de Janeiro

78   Fazenda União, Casimiro de Abreu, 20 m, 22°45'S 42°02'W[12] (L. Geise, *in litt.*) *R. mastacalis*

79   Teresópolis ("Therezopolis"), Fazenda [Carlos] Guinle [= Fazenda Comari], 22°27'S 42°57'W[4] (MNRJ, FMNH) *Rhipidomys inc. sedis*

80   Garrafão, Serra dos Órgãos, Magé, 300 m, 22°29'S 43°00'W[4] (L. Geise, *in litt.*) *R.* cf. *macrurus*

81   Praia Vermelha, Ilha Grande, 23°09'S 44°21'W[12] (MNRJ) *Rhipidomys inc. sedis*

São Paulo

82   São Sebastião, 23°48'S 45°25'W[2] (MZUSP) *Rhipidomys inc. sedis*

83   Biritiba Mirim, Casa Grande, 23°38'S 45°54'W[11] (MZUSP, USNM) *Rhipidomys inc. sedis, R.* cf. *macrurus*

83   Boracéia, 800 m, 23°39'S 45°54'W[3] (MZUSP, USNM) *Rhipidomys inc. sedis*

84   São José do Rio Preto, 20°48'S 49°23'W[2] (USNM) *R. mastacalis*

85   Porto do Rio Paraná [= Igarapava] (type locality of *Hesperomys leucodactylus* Wagner), 19°59'S 47°46'W[3] (NMW) *R. mastacalis*

Minas Gerais

86   Pedrinópolis, Mata dos Adolfos, c. 19°13'S 47°28'W[2] (UFMG) *R. macrurus*

87   Perdizes, Mata de galeria João Alonso, c. 19°21'S 47°17'W[2] (UFMG) *R. macrurus*

88   Parque Nacional Serra da Canastra (includes: 19-25 km W of São Roque de Minas; Fazenda Barreiro, 1 km N of park; Casca d'Anta; Fazenda das Pedras; Fazenda dos Quartéis; Retiro Maria do Carmo; Zezim Cândido) c. 20°15'S 46°40'W[3] (IBAMA/MG, MSUMZ) *R. macrurus*

89   Passos, 20°43'S 46°37'W[2] (MNRJ) *R. mastacalis*

90   Poços de Caldas, 21°48'S 46°34'W[2] (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", *in litt.*) *R. mastacalis*

91   Lima Duarte, Parque Estadual Ibitipoca, c. 1100 m, c. 21°33'S 43°55'W[3] (UFMG) *Rhipidomys inc. sedis*

92   Engenho Velho, highway BR-262 km 53, c. 20°15'S 42°12'W[13] (UFMG) *R. mastacalis*

93   Parque Florestal Estadual do Rio Doce, Rio Turvo, 19°42'S 42°30'W[14] (Stallings, 1989) *R. mastacalis*

94 Parque Florestal Estadual do Rio Doce, Hotel, 19°46'S 42°37'W[14] (UFMG) *R. mastacalis*

95 Santa Bárbara, Reserva Peti, c. 19°52'S 43°20'W[3] (UFMG) *R. mastacalis*

96 Rio Manso, 20°16'S 44°19'W[2] (UFMG) *R. mastacalis*

97 Lagoa Santa, Rio das Velhas (type locality of *Mus mastacalis* Lund), 19°38'S 43°53'W[2] (BMNH, MNRJ, UZM) *R. mastacalis*

98 Serra do Cipó, 1400 m, c. 19°25'S 43°35'W[9] (MNRJ) *R. mastacalis*

99 Lassance, Fazenda São Francisco, 600 m, c. 17°54'S 44°34'W[2] (UFMG) *R. macrurus*

100 Jequitinhonha, [region of], c. 16°30'S 41°00'W[13] (UFMG) *R. mastacalis*

101 Salinas, [450 m], 16°10'S 42°17'W[2] (MNRJ) *R. mastacalis*

102 Barro Alto, Rio São Francisco, 15°28'S 44°24'W[11] (MCZ, MZUSP) *R. macrurus*

103 Riacho da Cruz, Rio São Francisco, 15°20'S 44°14'W[11] (MCZ) *R. macrurus*

104 Manga, Mocambinho, área B, 14°55'S 43°55'W[13] (MNRJ) *R. macrurus*

Distrito Federal - *R. macrurus*

105 Fazenda Água Limpa, 20 km S of Brasília, c. 1000 m, 15°58'S 47°57'W[15] (OMNH)

105 Reserva do IBGE, 25 km S of Brasília, c. 1000 m, 15°58'S 47°54'W[1] (MNRJ, OMNH)

106 Brasília, [c. 1000 m] (also includes: Fundação Zoobotânica; Jardim Zoológico), c. 15°47'S 47°55'W[2] (MNRJ, FMNH)

107 Parque Nacional de Brasília (includes Granja do Ipê, Ribeirão Bananal), 15°35'S 47°54'W[16] (MNRJ)

108 Reserva Biológica de Águas Emendadas, 15°33'S 47°35'W (Svartman & Almeida, 1993)

Goiás - *R. macrurus*

109 Mouth of Rio São Domingos, 13°36'S 46°48'W[9] (MZUSP)

110 Cana Brava, Nova Roma, 13°51'S 46°56'W[11] (MCZ, MZUSP)

111 Formosa, Rio Canabrava, [162 km N of Brasília], c. 15°05'S 47°05'W[17] (MNRJ)

112 Anápolis ("Annapolis"), 1000 m, 16°20'S 48°58'W[2] (AMNH, MNRJ)

113 Crixás ("Trixas" - type locality of *Mus (Hesperomys) macrurus* Gervais), 14°27'S 49°58'W[2] (Gervais, 1855)

Mato Grosso

114 Xavantina, Rio das Mortes, [250 m], 14°40'S 52°21'W[2] (MNRJ) *R. macrurus*

115 Serra do Roncador, 264 km N Xavantina (includes: Base Camp; Fazenda Casa), 12°54'S 51°52'W³ (BMNH) *R. emiliae, R. nitela*

116 Chapada dos Guimarães, Casa de Pedra, c. 15°26'S 55°45'W² (MNRJ) *R. macrurus*

Mato Grosso do Sul

117 Maracaju, 500 m, c. 21°38'S 55°09'W² (AMNH, MNRJ) *Rhipidomys* sp. 2

COLOMBIA

Magdalena

118 Bonda, 11°14'N 74°08'W² (MHNG) *R. nitela*

119 Cincinati ("Hacienda Cincinnati"), 1480 m, 11°06'N 74°06'W² (AMNH) *R. latimanus venezuelae*

120 Palomino, [c. 600 m], 11°02'N 73°39'W² (AMNH) *R. latimanus venezuelae*

Santa Marta [region of], 825 m (2700 ft), not plotted (BMNH) *R. latimanus venezuelae*

La Guajira - *R. latimanus venezuelae*

121 La Concepción, 915 m (3000 ft), 11°03'N 73°27'W³ (MCZ)

122 El Pueblito ("Pueblo Viejo"), [610 m (2000 ft); specimen labels of W.W. Brown, Jr. give 8000 ft, in error], 10°59'N 73°27'W³ (AMNH, BMNH, MCZ, USNM)

122 San Francisco, [c. 1000 m; specimen labels of W.W. Brown, Jr. give 6000 ft, in error], c. 10°59'N 73°27'W³ (AMNH)

123 Monte Elias, Sierra Negra, 1525 m (5000 ft), c. 10°51'N 72°43'W¹⁸ (USNM)

124 Marimonda ("Las Marimondas"), [c. 20 km S of] Fonseca, 1000 m, 10°52'N 72°43'W¹⁹ (USNM)

125 Sierra Negra, [E of] Villanueva, 1500 m, 10°37'N 72°54'W² (USNM)

César - *R. latimanus venezuelae*

126 El Orinoco, Río César, [158 m], 10°10'N 73°24'W² (USNM)

Santander

127 Cachirí, 1890 m, 07°30'N 73°01'W² (CM) *R. fulviventer elatturus*

Boyacá

128 Muzo, 1300 m, 05°32'N 74°06'W² (AMNH, BMNH, FMNH) *R. l. latimanus*

129 Páez, Vereda El Tunjo, 05°05'N 73°03'W² (ICN, *in litt.*) *R. leucodactylus?*

Cundinamarca

130 Guasca, Río Balcones, 2720 m, c. 04°50'N 73°48'W²⁰ (FMNH) *R. f. fulviventer*

131 Quebrada Batán ("Salina del Vatan", type locality of *Rhipidomys microtis* Thomas), [c. 700 m], 05°27'N 74°11'W[21] (BMNH) *R. l. latimanus*

132 Paime, 1038 m, 05°22'N 74°10'W[2] (AMNH) *R. l. latimanus*

133 Finca El Soche, 15 km W Soacha, 2630 m, 04°32'N 74°19'W[5] (KU) *R. f. fulviventer*

133 San Miguel, Soacha, [c. 2000 m], 04°28'N 74°12'W[2] (M. Alberico, *in litt.*) *R. f. fulviventer*

134 La Aguadita, 1800 m, 04°23'N 74°20'W[20] (BMNH) *R. f. fulviventer*

135 Agua Dulce (type locality of *Rhipidomys fulviventer* Thomas), 04°33'N 73°58'W[5] (BMNH) *R. f. fulviventer*

136 Reserva Biológica Carpanta, 3000-3100 m, 04°34'N 73°41'W (Montenegro-Díaz et al., 1991) *R. f. fulviventer*

137 Susumuco, [c. 1000 m], 04°12'N 73°45'W[20] (AMNH, BMNH) *R. couesi*

Ceja Alta, not located (BMNH) *R. couesi*

Fanabistá, W Cundinamarca, not located (BMNH) *R. f. fulviventer*

Distrito Especial *R. f. fulviventer*

138 Bogotá, El Delirio, 04°33'N 74°04'W[2] (M. Alberico, *in litt.*)

138 Bogotá, San Cristóbal, 2800 m, 2900 m, 3000 m, 04°34'N 74°05'W[2] (FMNH)

138 Bogotá, San Francisco, 2700 m, 2750 m, 2800 m, 3000 m, 04°35'N 74°05'W[5] (FMNH)

Meta

139 Villavicencio, [498 m], 04°09'N 73°37'W[2] (AMNH) *R. couesi*

140 Serranía de la Macarena, Campamento Guapayita, c. 03°00'N 73°45'W[3] (ICN, *in litt.*) *R. leucodactylus*

141 Serranía de la Macarena ("Mt. Macarena"), 1140 [m], c. 02°45'N 73°55'W[2] (AMNH) *R. fulviventer* ssp.2, *R. leucodactylus*

142 Serranía de la Macarena, southern end, c. 02°20'N 73°50'W[21] (ICN, *in litt.*) *R. leucodactylus?*

Caquetá

143 Florencia, 305 m (1000 ft), 01°36'N 75°36'W[2] (AMNH) *R. leucodactylus*

Huila

144 Belén, 45 km SW of La Plata, 2135 m (7000 ft), 02°15'N 76°05'W[2] (USNM) *R. fulviventer* ssp. 3

145 San Adolfo, 1400 m, (also includes Río Aguas Claras, 1400 m, 1600 m) 01°37'N 75°59'W^2 (FMNH) *R. latimanus* ssp. (at 1400 m), *R. fulviventer* ssp. 3 (at 1600 m)

146 Suaza, Vda. San Calixto, 01°59'N 75°48'W (M. Alberico, *in litt.*) *R. latimanus* ssp.

147 Pitalito, 1350 m, 01°51'N 76°02'W^2 (FMNH) *R. latimanus* ssp.

148 San Antonio (includes: Río Ovejeras, 2350 m; left bank Río Magdalena, 2250 m, 2300 m, 2350 m; right bank Río Magdalena, 2200 m), 01°57'N 76°29'W^2 (FMNH) *R. fulviventer* ssp. 3, *R. caucensis*

Nariño

149 San Pablo, 1500 m, 01°06'N 78°01'W^3 (BMNH) *R. l. latimanus*

Cauca

150 Uribe, 1900 m, 02°32'N 76°50'W^2 (MNHN) *R. l. latimanus*

151 Sabanetas, 1900 m, 2000 m, 02°32'N 76°53'W^2 (AMNH, FMNH) *R. l. latimanus*

152 Hacienda El Mirador, Cerro Munchique, 02°30'N 76°57'W (M. Alberico, *in litt.*) *R. l. latimanus*

152 Cerro Munchique, 1500 m, 2400 m (E side), 2540 m (8325 ft, type locality of *Rhipidomys caucensis* J.A. Allen), 02°32'N 76°57'W^2 (AMNH) *R. l. latimanus* (at 1500 m), *R. fulviventer similis* (at 2400 m), *R. caucensis* (at 2540 m)

153 Cocal, 1220 m (4000 ft, type locality of *Rhipidomys cocalensis* J.A. Allen), 1830 m (6000 ft, type locality of *Rhipidomys similis* J.A. Allen), 02°31'N 77°03'W^{21} (AMNH) *R. l. latimanus* (at 1220 m), *R. fulviventer similis* (at 1220 m, 1830 m), *R. caucensis* (at 1830 m)

153 Río Munchique, 1200 m, 02°36'N 77°03'W^{21} (FMNH) *R. l. latimanus*

154 Charguayaco, 2000 m, 02°40'N 76°57'W^3 (AMNH) *R. l. latimanus*

Valle

155 Estación Corea, Farallones de Cali, 2580 m, 03°22'N 76°41'W^{22} (Alberico, 1983) *R. fulviventer similis*

156 Pichindé, 1800 m (includes Finca El Cairo, Finca La Esperanza, Finca La Flora, Finca La Playa, Finca Los Cárpatos, Quebrada Honda), 03°26'N 76°37'W^2 (Alberico, 1983) *R. fulviventer similis, R. l. latimanus*

156 Peñas Blancas, Río Pichindé, c. 1800 m, 03°25'N 76°35'W^{23} (USNM) *R. l. latimanus*

156 El Saladito, 03°29'N 76°37'W[22] (M. Alberico, *in litt.*) *R. l. latimanus*

157 near Cali, c. 03°27'N 76°31'W[2] (MNHN) *R. l. latimanus*

157 El Silencio, Cali, 1500 m, c. 03°27'N 76°31'W[2] (Alberico, 1983) *R. l. latimanus*

158 Finca La Cabaña, Via Cali-Buenaventura km 27, 03°34'N 76°37'W[22] (M. Alberico, *in litt.*) *R. l. latimanus*

159 La Cumbre, Hacienda La María, 2200 m, 03°39'N 76°33'W[22] (Alberico, 1983) *R. l. latimanus*

160 Candelaria, El Carmelo, 1050 m, 03°25'N 76°21'W[22] (M. Alberico, *in litt.*) *R. l. latimanus*

161 Miraflores, 1890 m (6200 ft, type locality of *Rhipidomys mollissimus* J. A. Allen), 03°35'N 76°10'W[3] (AMNH) *R. l. latimanus*

162 El Cairo, Cerro del Inglés, 04°46'N 76°18'W[22] (M. Alberico, *in litt.*) *R. caucensis*

Quindío

163 El Roble (type locality of *Rhipidomys quindianus* J.A. Allen), 2200 m (7200 ft), 04°41'N 75°36'W[2] (AMNH) *R. l. latimanus*

Antioquia

164 Río Negrito, 15 km E of Sonsón, 1850 m, 05°42'N 75°18'W[21] (FMNH) *R. l. latimanus*

165 San Jerónimo, 35 km NW of Medellín, 720 m, 800 m, 850 m, 06°27'N 75°45'W[2] (FMNH) *R. l. latimanus*

166 Páramo Frontino, 3300 m, 3500 m, 06°28'N 76°04'W[2] (FMNH) *R. caucensis*

167 Urrao, Santa Bárbara, 2800 m, 3100 m, 06°25'N 76°15'W[3] (FMNH) *R. caucensis*

168 Valdivia (includes: 9 km S, 1400 m; 10 km S, 1500 m; La Cabaña; Quebrada Valdivia, 900 m), c. 07°11'N 75°27'W[2] (FMNH) *R. l. latimanus*

ECUADOR

Imbabura

169 Peñaherrera (includes Hacienda Chinipamba), 1500 m, c. 00°21'N 78°32'W[2] (UMMZ) *R. l. latimanus*

Pichincha

170 Río Verde, 975 m (3200 ft, type locality of *Rhipidomys pictor* Thomas), c. 00°12'N 78°52'W[3] (BMNH) *R. l. latimanus*

171 Pacto ("Pagto"), 1680 m (5500 ft), 00°09'N 78°45'W[2] (AMNH) *R. l. latimanus*

172 Gualea, 885 m (2900 ft), 1370 m (4500 ft) [also includes: below Gualea, c. 915 m (c. 3000 ft); near Gualea, 1525 m (5000 ft)], 00°07'N 78°44'W^2 (AMNH, BMNH) *R. l. latimanus*

172 Nanegal, 915 m (3000 ft), 1220 m (4000 ft), 1680 m (5500 ft), 00°07'N 78°40'W^2 (AMNH, BMNH) *R. l. latimanus*

173 Río Blanco, below Mindo, 1220 m (4000 ft), 00°00' 78°50'^{24} (AMNH) *R. l. latimanus*

174 Pachijal ("Pachejal", "Pechijal", "Pachihal"), 915 m (3000 ft), c. 00°04'S 78°48'W^{25} (AMNH) *R. l. latimanus*

174 Mindo, 1285 m (4213 ft), 1680 m (5500 ft) [also includes: below Mindo, 1220 m (4000 ft)], 00°03'S 78°46'W^{25} (AMNH, BMNH) *R. l. latimanus*

175 Santo Domingo de los Colorados ("San Domingo"), 490 m (1600 ft, type locality of *Rhipidomys equatoris* Thomas), 00°15'S 79°09'W^2 (BMNH) *R. leucodactylus*

176 Mojanda, S side, 2440 m (8000 ft), 00°02'S 78°17'W^{24} (AMNH) *R. l. latimanus*

Napo

177 Laguna Cuyabeno ("Laguna Grande"), Río Cuyabeno, 210 m, 00°00' 76°11'W^1 (FMNH) *R. leucodactylus*

178 Limoncocha, 00°24'S 76°37'W^2 (USNM) *R. leucodactylus*

179 Mouth of Río Coca, [c. 260 m] (type locality of *Rhipidomys goodfellowi* Thomas), 00°29'S 76°58'W^2 (BMNH) *R. leucodactylus*

180 San José de Payamino, 300 m, 00°30'S 77°17'W^2 (MVZ) *R. leucodactylus*

181 San José Nuevo ("San José"; "San José Abajo"), 00°26'S 77°20'W^3 (AMNH, FMNH, MCZ) *R. leucodactylus*

182 Río Suno abajo, c. 00°42'S 77°08'W^2 (AMNH) *R. leucodactylus*

183 Cerro Guataracu ("Cerro Guataraco"), c. 00°40'S 77°35'W^3 (USNM) *R. leucodactylus*

184 Cordillera de Galeras ("Cerro Galera"), 1200 m, 00°50'S 77°32'W^2 (BMNH) *R. leucodactylus*

185 near Archidona ("Archidina"), 1070 m (3500 ft), 00°55'S 77°48'W^2 (BMNH) *R. l. latimanus*

186 near Río Napo, 730 m (2400 ft), c. 01°05'S 77°55'W^{26} (BMNH) *R. l. latimanus*

Pastaza - *R. leucodactylus*

187 Mera, [1160 m], 01°28'S 78°08'W^2 (USNM)

188 Canelos, c. 550 m (c. 1800 ft), 01°35'S 77°45'W² (AMNH)

189 Río Pindo Yacu, 02°07'S 76°03'W² (FMNH)

190 Montalvo, Río Bobonaza (also includes "Río Bobonazo") 02°04'S 76°58'W² (FMNH, MCZ, UMMZ)

191 Río Copataza, 650 m, 750 m, c. 02°07'S 77°27'W² (FMNH)

Chimborazo

192 Pallatanga, 1510 m (4950 ft, probable type locality of *Hesperomys latimanus* Tomes), 01°59'S 78°57'W² (BMNH) *R. l. latimanus*

Bolívar

193 Ríos Chimbo and Coco [confluence of], 730 m (2400 ft), 02°05'S 79°00'W³ (AMNH) *R. l. latimanus*

Guayas

194 Cerro de Manglaralto ("Cerro Manglar Alto"), Camp 2, 460 m (1500 ft), 01°48'S 80°35'W²⁴ (AMNH) *R. l. latimanus*

El Oro - *R. leucodactylus*

195 Los Pozos, near Arenillas, c. 90 m (c. 300 ft), c. 03°33'S 80°04'W² (Arenillas), (AMNH)

Loja - *R. leucodactylus*

196 Alamor, Florida, 04°02'S 80°02'W² (AMNH, USNM)

197 Malacatos, 1600 m, 04°14'S 79°15'W² (FMNH)

GUYANA

Pomeroon-Supenaam - *R. leucodactylus*

198 Makasima ("Maccasseema"), Pomeroon River (type locality of *Hesperomys (Rhipidomys) sclateri* Thomas), 07°15'N 58°43'W² (BMNH)

Cuyuni-Mazaruni

199 Kalakun ("Kalacoon"), 06°24'N 58°39'W² (AMNH) *R. n. nitela*

200 Potaro Highlands, Venamo River, 610 m (2000 ft, type locality of *Rhipidomys bovallii* Thomas), c. 06°00'N 61°20'W²⁷ (BMNH) *R. leucodactylus*

Mount Roraima: see under Venezuela, Estado Bolívar, Cerro Roraima (locality 320)

Potaro-Siparuni - *R. nitela*

201 Anandabaru River ("Anundabaru"), 04°59'N 59°44'W² (AMNH)

202 Karisparu, 610 m (2000 ft), 04°52'N 59°29'W² (BMNH)

203 Minnehaha Creek ("Minehaha Creek"), 150 m (500 ft, type locality of *Rhipidomys*

milleri J.A. Allen), 05°08'N 59°07'W² (AMNH)

Upper Takutu-Upper Essequibo - *R. nitela*

204 Kwaimatta ("Kwaimattat"), Kanuku Mountains (type locality of *Rhipidomys nitela* Thomas), 03°49'N 59°20'W² (BMNH)

204 Kwatata ("Quatata", "Quatatat"), Kanuku Mountains, 75 m (240 ft), 03°38'N 59°30'W² (BMNH)

205 Nappi Creek, 40 km E of Lethem, Kanuku Mountains, c. 03°25'N 59°34'W² (ROM, *in litt.*)

206 Rewa River, c. 03°00'N 58°50'W²⁷ (ROM, *in litt.*)

207 Kwitaro River [E of Shea], c. 02°50'N 59°00'W²⁷ (ROM, *in litt.*)

208 Bono Wau, near Shea, c. 02°51'N 59°06'W² (Shea), (ROM, *in litt.*)

209 Sand Creek, 32 km ("20 miles") E of Dadanawa, c. 02°50'N 59°20'W²⁷ (ROM, *in litt.*)

210 Dadanawa, 56 km ("35 miles") WSW, c. 02°50'N 59°30'W² (Dadanawa), (ROM, *in litt.*)

211 Wariwau ("Wau Wau"), 02°43'N 59°12'W² (ROM, *in litt.*)

GUYANE FRANÇAISE

212 Rivière Arataye, Saut Pararé (type locality of *Rhipidomys leucodactylus aratayae* Guillotin & Petter), 04°03'N 52°40'W (Guillotin & Petter, 1985) *R. leucodactylus*

213 Paracou, 15 km by road SSE of Sinnamary, 05°17'N 52°55'W (R. S. Voss, pers. comm.) *R. nitela*

NEDERLANDSE ANTILLEN

Bonaire

214 near Fontein, 12°15'N 68°18'W²⁸ (Hooijer, 1959; Quaternary fossil material) *Rhipidomys* cf. *couesi*

PANAMÁ

Darién *R. l. latimanus*

215 Cerro Malí, 1435 m (4700 ft), 1465 m (4800 ft), 08°07'N 77°14'W²⁹ (USNM)

216 Cerro Tacarcuna, 1250 m (4100 ft), 08°10'N 77°18'W²⁹ (USNM)

217 Cerro Pirre ("Mt. Pirri"), near head of Río Limón, 1525 m (5000 ft, type locality

of *Rhipidomys scandens* Goldman), 07°49'N 77°43'W² (USNM)

PARAGUAY

Amambay - *Rhipidomys* sp. 2

218 Parque Nacional Cerro Corá, c. 22°40'S 55°59'W² (USNM)

PERÚ (by Region; former Departments in parentheses)

Loreto

(**Loreto**) *R. leucodactylus*

219 Mouth of Río Curaray, 02°22'S 74°05'W² (AMNH)

220 Mouth of Río Mazán ("boca Rio Masan"), 03°28'S 73°11'W² (BMNH)

221 San Jerónimo, W bank Río Ucayali, 305 m (1000 ft), 07°52'S 74°48'W² (BMNH)
     Lago Miraño, Río Napo (not located; between 00°55'S 75°15'W and 03°25'S
     72°40'W)

Grau

(**Piura**) *R. leucodactylus*

222 Cerro Cortezo, Las Trancas, 04°14'S 80°21'W² (USNM)

223 Lancones, Cerro La Mesa, Sitio Añalquis, c. 04°35'S 80°30'W² (USNM)

224 Canchaque, 1230 m, 05°24'S 79°36'W² (FMNH)

Nor Oriental del Marañón

(**Cajamarca**) *R. l. latimanus*

225 Perico, [c. 500 m], 05°15'S 78°45'W² (MCZ)

(**Amazonas**) *R. modicus*

226 La Peca Nueva ("La Peca"), 12 trail km E, 1760 m (5775 ft), 05°34'S 78°17'W³
     (LSUMZ)

227 Huambo, 1130 m (3700 ft), 06°22'S 77°28'W² (BMNH)

San Martín

(**San Martín**)

228 Pucatambo ("Puca Tambo"), 1555 m (5100 ft, type locality of *Rhipidomys modicus*
     Thomas), 06°10'S 77°16'W² (BMNH) *R. modicus*

229 Moyobamba, c. 855 m (c. 2800 ft), 06°03'S 76°58'W² (FMNH) *R. modicus*

230 Tocache Viejo, 08°12'S 76°32'W³⁰ (Tschudi, 1845) *R. leucodactylus?*

Andrés Avelino Cáceres

(**Huánuco**)

231 Chinchavito ("Chinchavita"), 915 m (3000 ft), 09°29'S 75°55'W² (BMNH) *R. leucodactylus, R. modicus*

232 Chihuangala, 1220 m (4000 ft), c. 09°31'S 75°57'W³⁰ (BMNH) *R. leucodactylus*

232 Río Chinchao, Hacienda Buena Vista, c. 1070 m (3500 ft), c. 09°31'S 75°57'W³¹ (FMNH, MCZ) *R. leucodactylus*

(Pasco)

233 Pozuzo, 730 m (2400 ft), 10°04'S 75°32'W² (FMNH) *R. leucodactylus*

(Junín)

234 Río Saco Alto, 21 km ("13 miles") N of La Merced, 725 m (2376 ft), c. 11°00'S 75°22'W⁴ (AMNH) *R. modicus*

235 Chanchamayo, 1000 m, 1100 m, 1200 m, c. 11°03'S 75°18'W³ (BMNH, FMNH, USNM) *R. modicus*

236 Amable María, 610 m (2000 ft), 11°07'S 75°19'W³ (BMNH) *R. leucodactylus*

237 Montaña de Vitoc (type locality of *Hesperomys (Rhipidomys) leucodactylus* Tschudi, as restricted herein), [c. 1000 m], c. 11°15'S 75°20'W⁴ (MHNN) *R. leucodactylus*

237 Utcuyacu, 11°17'S 75°18'W⁴ (AMNH) *R. leucodactylus*

237 La Garita del Sol, Vitoc valley, 1750 m (5740 ft, type locality of *Rhipidomys lucullus* Thomas), c. 11°17'S 75°21'W³ (BMNH) *R. leucodactylus*

Los Libertadores-Wari

(Ayacucho) *R. leucodactylus*

238 Huanhuachayo ("Huanhuanchayo"), 1580 m, 12°44'S 73°47'W²³ (AMNH)

Inka

(Cuzco) *R. leucodactylus*

239 Mercedes, below Quillabamba, 12°27'S 72°39'W² (MCZ)

240 Ocobamba, 12°48'S 72°24'W² (BMNH, USNM)

241 Santa Ana, 915 m (3000 ft), 12°52'S 72°43'W² (USNM)

242 San Fernando, Río San Miguel, 1375 m (4500 ft), 13°00'S 73°15'W² (BMNH, FMNH, USNM)

243 Hacienda Amaibamba, Río Santa María, 1600 m (5250 ft), 13°03'S 72°28'W³² (MCZ)

244 Machu Picchu, San Miguel Bridge, 1830 m (6000 ft), 13°06'S 72°38'W³ (USNM)

245 Cosñipata ("Cosnipata"), 1000 m, 13°04'S 71°11'W² (BMNH)

246 Marcapata (includes: below Marcapata, 1000 m, 2000 m; Camante, 2000 m), c.

13°30'S 70°55'W² (BMNH, FMNH)

247 Marcapata, Hacienda Cadena, 1000 m, 13°24'S 70°43'W² (FMNH)

248 Quincemil ("Quince Mil"), 680 m, 13°16'S 70°38'W² (FMNH)

(Madre de Dios) *R. leucodactylus*

249 Cocha Cashu Biological Station, c. 380 m, 11°55'S 71°18'W[33] (Terborgh et al., 1984)

250 Pakitza, 57 airline km above mouth of Río Manú, c. 350 m, 11°55'S 71°15'W[34] (USNM)

251 Puerto Maldonado, 4.5 km W, N bank Río Madre de Dios, Tambopata, 12°36'S 69°11'W² (USNM)

252 Reserva Cuzco Amazónico (formerly "Albergue"), 14 km E of Puerto Maldonado, 200 m, 12°33'S 69°03'W[35] (MVZ, KU, MUSM)

José Carlos Mariategui

(Puno)

253 La Pampa, 765 m (2500 ft), 13°39'S 69°36'W² (MCZ) *R. leucodactylus*

254 Santo Domingo [includes: Inca Mines, 1220 m, 1830 m (4000 ft, 6000 ft, type locality of *Rhipidomys ochrogaster* J.A. Allen); Carabaya Andes, 1680 m (5500 ft)], 13°51'S 69°41'W² (AMNH, BMNH) *R. ochrogaster*

SURINAME - *R. nitela*

Saramacca

255 Matta, 15 km W of Zanderij airport, 05°28'N 55°21'W² (RMNH)

Para

256 Zanderij airport (bunker nearby), c. 40 km S of Paramaribo, c. 05°26'N 55°08'W³ (RMNH)

Nickerie

257 Sipaliwini savanna, near Sipaliwini airstrip, 02°06'N 56°02'W² (RMNH)

TRINIDAD AND TOBAGO

Tobago

258 Little Tobago Island (type locality of *Rhipidomys nitela tobagi* Goodwin), 11°18'N 60°30'W² (AMNH) *R. nitela*

259 Robinson Crusoe cave, Remnant cave and Effigy cave, S of Crown Point airport, 10 m, 11°09'N 60°50'W[36] (Eshelman & Morgan, 1985; Quaternary fossil

material) *R. couesi*

Trinidad - *R. couesi*

260 Curucaye ("Kurukai"), 10°40'N 61°27'W^2 (BMNH)

261 Caura, c. 150 m (c. 500 ft), 10°43'N 61°21'W^2 (AMNH, BMNH)

262 Arima, Spring Hill Estate, 10°38'N 61°17'W^2 (Vesey-Fitzgerald, 1936)

263 Mount Aripo, 10°43'N 61°15'W^2 (BMNH)

264 Cumaca, 10°42'N 61°09'W^2 (AMNH)

265 Turure Forest, 42 km (26 miles) E of Port of Spain and 5 km (3 miles) W of Sangre Grande, 10°37'N 61°10'W^{46} (Everard & Tikasingh, 1973)

266 Marper Estate ("Marpa Estate"), 10°30'N 61°05'W^{46} (BMNH)

267 Cocal, Manzanilla Highway (40^1/$_2$, 42^1/$_4$, 44^3/$_4$ mile posts), edge of Nariva swamp, c. 10°27'N 61°02'W^{46} (AMNH)

268 Prince's Town ("Princestown"), 11 km (7 miles) SE (type locality of *Tylomys couesi* J.A. Allen), 10°13'N 61°20'W^{46} (AMNH)

VENEZUELA

Zulia - *R. latimanus venezuelae*

269 Tucuco ("Misión Tukuko"), 200-400 m, 09°50'N 72°52'W^2 (USNM)

Táchira - *R. fulviventer elatturus*

270 Buena Vista, 41 km S of San Cristóbal, near Páramo de Tamá, 2370-2422 m, 07°27'N 72°26'W^{37} (USNM)

270 Páramo de Tamá, 2135 m (7000 ft, type locality of *Rhipidomys fulviventer elatturus* Osgood), 07°25'N 72°26'W^2 (FMNH)

Mérida

271 La Azulita, 1135 m (3500 ft), 08°43'N 71°27'W^2 (FMNH) *R. latimanus venezuelae*

272 Cañada La Sucia, near Jají, c. 08°34'N 71°21'W^2 (Jaji), (FMNH) *R. latimanus venezuelae*

273 Río Chama, [at Hacienda Santa Catalina], 1375 m (4500 ft), 08°32'N 71°21'W^3 (BMNH, FMNH) *R. latimanus venezuelae*

274 Río Chama [also includes: Cafetos de Chama, 1600 m, 1630 m; Montaña de Chama, 2020 m; Las Vegas del Chama, 1400 m (type locality of *Rhipidomys venustus* Thomas)], c. 08°33'N 71°13'W^{38} (AMNH, BMNH, MHNG, USNM) *R. fulviventer venustus*, *R. latimanus venezuelae*

275 Río Albarregas, 08°35'N 71°09'W^2 (BMNH) *R. latimanus venezuelae*

275 Mérida, (type locality of *Rhipidomys venezuelae* Thomas), (also includes: Mérida, 2165 m, 2500 m, Cafetos de Mérida, Montes de Mérida, Montes del Arenal, 1600 m, 1630 m), c. 08°36'N 71°08'W² (AMNH, BMNH, MHNG, USNM) *R. fulviventer venustus*, *R. latimanus venezuelae*

275 Mérida, 3.1 km SE, 2250 m; 4.1 km SE, 2600 m, c. 08°35'N 71°07'W³⁸ (Aagaard, 1982) *R. fulviventer venustus*

276 Río Milla, 1700 m (also includes: Cafetos de Milla, 1600 m, 1630 m; Montes de Milla, 1600 m), c. 08°38'N 71°07'W³⁸ (AMNH, FMNH, MHNG, USNM) *R. fulviventer venustus*, *R. latimanus venezuelae*

276 Río Mucujún ("R. Mucujón"), slope of Páramo San Antonio, 2745-3050 m (9000-10000 ft), c. 08°38'N 71°07'W³⁸ (FMNH) *R. fulviventer venustus*

276 Montes del Vallecito, 2000 m, c.08°39'N 71°06'W³ (AMNH) *R. latimanus venezuelae*

276 Montes del Valle, 2000 m, c.08°40'N 71°06'W³ (FMNH, USNM) *R. fulviventer venustus*

277 Echicera ("Montañas de Hechisera"), 2000 m [?], c. 08°40'N 71°10'W³ (USNM) *R. latimanus venezuelae*

278 Monte Culata, 4000 m, c. 08°45'N 71°05'W³ (BMNH) *R. fulviventer venustus*

279 Tabay, 2.9 km E, 2450 m, c. 08°38'N 71°04'W³⁸ (Aagaard, 1982) *R. fulviventer venustus*

279 Tabay, 6 km ESE, Middle Refugio, 2250 m, 08°37'N 71°02'W³⁷ (USNM) *R. fulviventer venustus*

279 Tabay, 7 km SE, La Coromoto, 3130-3160 m, 08°36'N 71°01'W³⁷ (USNM) *R. fulviventer venustus*

279 La Mucuy, trail to La Coromoto, First Refugio, 2500 m, c. 08°37'N 71°02'W³⁸ (MBUCV, *in litt.*) *R. fulviventer venustus*

279 Montañas de la Sierra, 2500 m [?], c. 08°36'N 71°00'W³ (FMNH, UMMZ) *R. latimanus venezuelae*

279 Lourdes ("Montes de Lurdes"), 1630 m, c. 08°36'N 71°00'W³ (USNM) *R. fulviventer venustus*

"Montes de la otra banda", 1600 m, not located (USNM) *R. latimanus venezuelae*

Barinas - *R. couesi*

280 Reserva Forestal de Ticoporo, 250-260 m, c. 08°00'N 70°46'W (Ochoa et al.,

1988)

281 Barinitas, 3 km NW, 500 m, 08°45'N 70°25'W (Díaz de Pascual, 1984)

282 Altamira, 794 m, 08°50'N 70°30'W[37] (USNM)

Trujillo

283 Isnotú, 10 km WNW of Valera, 930 m, 09°32'N 70°40'W[37] (USNM) *R. latimanus venezuelae*

284 Hacienda Misisí, 14 km E of Trujillo, 2210 m, 09°21'N 70°18'W[37] (USNM) *R. fulviventer venustus*

Lara - *R. latimanus venezuelae*

285 Caserío Boro, 10 & 13 km NW of El Tocuyo, 537 m, 900 m, 09°53'N 69°47'W[37] (USNM)

286 Río Tocuyo, 500 m, 10°16'N 69°56'W[2] (AMNH)

Falcón - *R. latimanus venezuelae*

287 Cerro Socopo, 84 km NW of Carora, 1260 m, 10°28'N 70°48'W[37] (USNM)

288 Hacienda Socopito, Río Socopito, 80 km NW of Carora, 470 m, 10°30'N 70°44'W[37] (USNM)

289 Capatárida, 40 m, 11°10'N 70°37'W[37] (USNM)

290 Yabuquiva, 25 km SW of Pueblo Nuevo, Península de Paraguaná, 575 m, 11°49'N 70°06'W[37] (USNM)

291 Cerro Santa Ana, 15 km SSW of Pueblo Nuevo, Península de Paraguaná, 560-595 m, 11°49'N 69°58'W[37] (USNM)

292 La Pastora (near), 14 km ENE of Mirimiri, 190 m, 11°12'N 68°37'W[37] (USNM)

Carabobo - *R. latimanus venezuelae*

293 Hacienda El California, 4 km NNW of Montalbán, 1000 m, 10°15'N 68°21'W[37] (USNM)

Aragua - *R. latimanus venezuelae*

294 Estación Biológica Rancho Grande, 13 km NW of Maracay, 1050 m, 10°21'N 67°40'W[37] (USNM)

Campamento Rafael Rangel (also "Camp Rangel"), 800-1200 m, not located (USNM)

Distrito Federal

295 Los Venados, 1470 m, 1500 m, 10°32'N 66°54'W[37] (USNM) *R. latimanus venezuelae*

295 Pico Avila, 5 km NNE of Caracas, near Hotel Humboldt, 2095-2223 m (partly in

307

Estado Miranda) 10°33'N 66°52'W³⁷ (USNM) *R. fulviventer* ssp. 1

296 Los Canales de Naiguatá, Parque Nacional El Avila, 800 m, c. 10°35'N 66°45'W⁵ (MBUCV, *in litt.*) *R. latimanus venezuelae*

Miranda

297 La Carbonera, San Eusebio, 2200 m, c. 10°28'N 66°32'W² (MBUCV, *in litt.*) *R. fulviventer* ssp. 1

Guárico

298 Parque Nacional Guatopo, 40 km SSE of Caracas, 710 m, 10°03'N 66°26'W³⁹ (O'Connell, 1989) *R. latimanus venezuelae*

299 San José de Tiznados, 09°23'N 67°33'W² (MBUCV, *in litt.*) *Rhipidomys* sp. 3

300 Masaguaral, 55 km S of Calabozo, 75 m, 08°24'N 67°35'W³⁹ (USNM) *Rhipidomys* sp. 3

Nueva Esparta *R. couesi*

301 Isla Margarita, El Cafetal, 740 m, c. 11°01'N 63°55'W³ (LSUMZ)

302 Isla Margarita, Cerro Matasiete, 3 km NE of La Asunción, 410-415 m, 11°03'N 63°51'W³⁷ (USNM)

Sucre

303 Ensenada Cauranta, 7 km N and 5 km E of Guiria, 4 m, 10°38'N 62°15'W³⁷ (USNM) *R. couesi*

304 Headquarters Guaracayal, 24 km E Cumaná, 0 m, 10°27'N 63°57'W³⁷ (USNM) *R. couesi*

305 Ipure, near Cumaná, 685 m (2250 ft, type locality of *Rhipidomys venezuelae cumananus* Thomas), possibly = Los Ipures, at 10°22'N 64°10'W⁴ (BMNH) *R. couesi*

306 Villarroel ("Quebrada Seca"), near Cumaná, [c. 200 m], 10°19'N 63°57'W⁴ (BMNH) *R. couesi*

306 San Rafael, near Cumanacoa, 900 m (2950 ft), c. 10°15'N 63°55'W³ (CM) *R. couesi*

307 Carapas, Cerro Turumiquire, 1710 m (5600 ft), c. 10°12'N 63°56'W³ (AMNH) *R. fulviventer tenuicauda*

307 Latal, 945 m (3100 ft), c. 10°10'N 63°55'W⁴⁰ (AMNH) *R. fulviventer tenuicauda*, *R. couesi*

308 Los Palmales (type locality of *Oryzomys tenuicauda* J.A. Allen), c. 10°17'N

63°45'W³ (AMNH) *R. fulviventer tenuicauda*

309 Mirasol, c. 15 km S of Cumanacoa, 975 m (3200 ft), c. 10°10'N 63°50'W³⁸ (CM) *R. couesi*

310 Cerro Turumiquire, 1830 m (6000 ft), 10°07'N 63°52'W² (FMNH) *R. fulviventer tenuicauda*

Monagas *R. fulviventer tenuicauda*

311 Caripe, 360 m, 860 m, 10°10'N 63°30'W⁴ (MBUCV, *in litt.*)

311 Caripe, behind Las Delicias, 1400 m, 10°11'N 63°28'W⁴ (MBUCV, *in litt.*)

311 San Agustín, 5 km NW of Caripe, 1160-1340 m (also includes Hacienda San Fernando, 1320-1340 m), 10°12'N 63°32'W³⁷ (USNM)

312 Cerro Espejo, Caripe, 1500 m, 10°05'N 63°16'W⁴ (MBUCV, *in litt.*)

Bolívar

313 Río Yuruán (type locality of *Rhipidomys venezuelae yuruanus* J.A. Allen), c. 06°48'N 61°50'W² (AMNH) *R. nitela*

314 El Manaco, Km 74, 59 km SE of El Dorado, 150 m, 06°17'N 61°19'W³⁷ (USNM) *R. nitela*

315 Km 125 (also "Km 121"), 85 km SSE of El Dorado, 1032 m, 05°59'N 61°26'W³⁷ (USNM) *R. wetzeli, R. macconnelli*

316 Ptari-tepui, 1160 m (3800 ft), 05°46'N 61°46'W² (AMNH) *R. macconnelli*

317 120 km S of El Dorado, 1150 m, c. 05°42'N 61°23'W³⁸ (CM) *R. macconnelli*

317 126 km SE of Río Cuyuní (by road), 1400 m, c. 05°39'N 61°23'W³⁸ (MVZ) *R. macconnelli*

318 132 km SE of Río Cuyuní (by road), 1430 m, c. 05°36'N 61°20'W³⁸ (MVZ, *in litt.*) *R. macconnelli*

319 145 km S of El Dorado, 1380 m, c. 05°30'N 61°15'W³⁸ (CM) *R. nitela*

320 Cerro Roraima ("Mount Roraima"), [includes: Rondon Camp, 2075 m (6800 ft); Summit (type locality of *Rhipidomys macconnelli* De Winton); Summit, 2625 m (8600 ft), 2640 m (8650 ft)], c. 05°12'N 60°44'W² (AMNH, BMNH, FMNH) *R. macconnelli*. For convenience, all localities on Roraima have been listed under Venezuela, although parts of the mountain lie in Brasil and Guyana.

321 Arabopó ("Arabupu"), 1280 m (4200 ft), 05°06'N 60°44'W² (AMNH) *R. macconnelli, R. nitela*

322 San Ignacio de Yuruaní, (includes: 12 km SW by road, 850 m; 5.2 km NE), c.

05°02'N 61°08'W[41] (AMNH, MHNLS, USNM) *R. nitela*

323 Santa Elena de Uairén ("Sta. Elena"), 940 m, 04°37'N 61°08'W[2] (AMNH) *R. nitela*

324 La Colonia, 53 km NE of Icabarú, 915 m, 04°35'N 61°19'W[37] (USNM) *R. nitela*

325 Santa Lucia de Surukún, 45 km NE of Icabarú, 851 m, 04°33'N 61°25'W[37] (USNM) *R. nitela*

325 Maurá, 46 km NE of Icabarú, 800 m, 04°33'N 61°25'W[37] (USNM) *R. nitela*

325 Vetania, 46 km NE of Icabarú, 800 m, 04°33'N 61°25'W[37] (USNM) *R. nitela*

326 Churi-tepui [includes: lower slopes, 1035 m (3400 ft); camp 2, 1055 m (3460 ft); 1060 m (3470 ft); 1080 m (3540 ft); 1100 m (3600 ft); camp 4, 1335 m (4370 ft); camp 5, 1495 m (4900 ft)], c. 05°13'N 61°54'W[2] (AMNH) *R. wetzeli* (at camp 5), *R. macconnelli*

327 Acopán-tepui, 1525 m (5000 ft), 05°12'N 62°04'W[2] (AMNH) *R. macconnelli*

328 Chimatá-tepui ("Chimanta tepui"), camp 3, 1190 m (3900 ft), 05°18'N 62°10'W[2] (FMNH) *R. macconnelli*

329 Uruyén, Camarata Valley, 05°41'N 62°25'W[2] (AMNH) *R. nitela*

330 Auyán-tepui, southern slope, 1100 m (type locality of *Thomasomys macconnelli subnubis* Tate), c. 05°45'N 62°27'W[42] (AMNH) *R. macconnelli*, *R. nitela*

331 Auyán-tepui (includes: Danto, 1800 m; Plateau, 1850 m, 2200 m), c. 05°55'N 62°32'W[2] (AMNH) *R. macconnelli*

332 La Unión, Río Caura ("lower Orinoco"), (type locality of *Rhipidomys venezuelae fervidus* Thomas), 06°55'N 64°55'W[2] (BMNH) *R. nitela*

333 La Vuelta, Río Caura ("lower Orinoco"), c. 07°25'N 65°10'W[3] (BMNH) *R. nitela*

334 Serranía de los Pijiguaos, 300-660 m, c. 06°29'N 66°43'W (Ochoa et al., 1988) *R. leucodactylus*

Amazonas

335 Cerro Marawaca or Marahuaca (includes: campamento Sima, 1150 m; cumbre, 2550 m; talud oeste, 1250 m), 03°34'N 65°27'W[2] (Guerrero et al., 1989) *R. macconnelli*

336 Cerro Duida, Caño Culebra, 50 km NNW of Esmeralda, 750 m, 825 m, 03°37'N 65°41'W[37] (USNM) *R. macconnelli*, *R. nitela*

337 Cerro Duida, Cabecera del Caño Culebra, 40 km NNW of Esmeralda, 1400 m, 1480 m, 03°30'N 65°43'W[37] (USNM) *R. wetzeli*, *R. macconnelli*, *R.*

leucodactylus

338 Cerro Duida ("Mount Duida"), |includes: Agüita, 990 m (3250 ft); Chorrera de Vegas, 1435 m (4700 ft); Cumbre #2, Cabeceras del Valle, 1525 m (5000 ft); Cumbre #13, Desfiladero, 1890 m (6200 ft); Cumbre #15, Loma #15, 2015 m (6600 ft); Summit, Central Camp, 1465 m (4800 ft); Summit, High Point Camp, Peak #7, 2075 m (6800 ft), 2105 m (6900 ft); Summit, Provisional Camp, 1680 m (5500 ft); Summit, Savanna Hills, 1340 m (4400 ft); Summit, Valley between Peaks 7 and 16, 1985 m (6500 ft); Top of Peak #7, 2165 m (7100 ft)], c. 03°25'N 65°40'W[2] (AMNH) *R. macconnelli*

338 Cerro Duida, Cabecera del Caño Negro, 32 km NW of Esmeralda, 1400 m, 03°26'N 65°43'W[37] (USNM) *R. macconnelli*

339 Acanaña, 48 km NW of Esmeralda, Río Cunucunuma, 145 m, 03°32'N 65°48'W[37] (USNM) *R. leucodactylus*

340 Tamatama, Rio Orinoco, 135 m, 03°10'N 65°49'W[37] (USNM) *R. leucodactylus*

341 Caserío La Esmeralda, Alto Orinoco, 180 m, 03°10'N 65°33'W[2] (MBUCV, *in litt.*) *R. leucodactylus?*

342 Boca Mavaca, 84 km SSE of Esmeralda, 138 m, 02°30'N 65°13'W[37] (USNM) *R. leucodactylus*

343 Cerro de Tamacuare, 01°15'N 64°47'W (Ojasti et al., 1992) *R. macconnelli*

344 Cerro Aracamuri, Cumbre Sur, 1500 m, 01°26'N 65°47'W[43] (MBUCV, *in litt.*) *R. macconnelli*

345 Cerro Neblina, Base Camp, Río Baria, 140 m, c. 01°00'N 66°10'W[44] (MBUCV, *in litt.*) *R. leucodactylus*

346 Cerro Neblina, Camp II, c. 2.5 km NE Pico Phelps (= Neblina), 2200 m, 00°50'N 65°59'W[45] (USNM) *R. wetzeli, R. macconnelli*

346 Cerro Neblina, Camp VII, 5.1 km NE Pico Phelps (= Neblina), 1800 m, 1850 m (type locality of *Rhipidomys wetzeli* Gardner), 00°51'N 65°58'W[45] (USNM) *R. wetzeli, R. macconnelli, R. leucodactylus*

346 Cerro Neblina, Camp XI, c. 00°52'N 65°58'W[45] (USNM) *R. macconnelli*
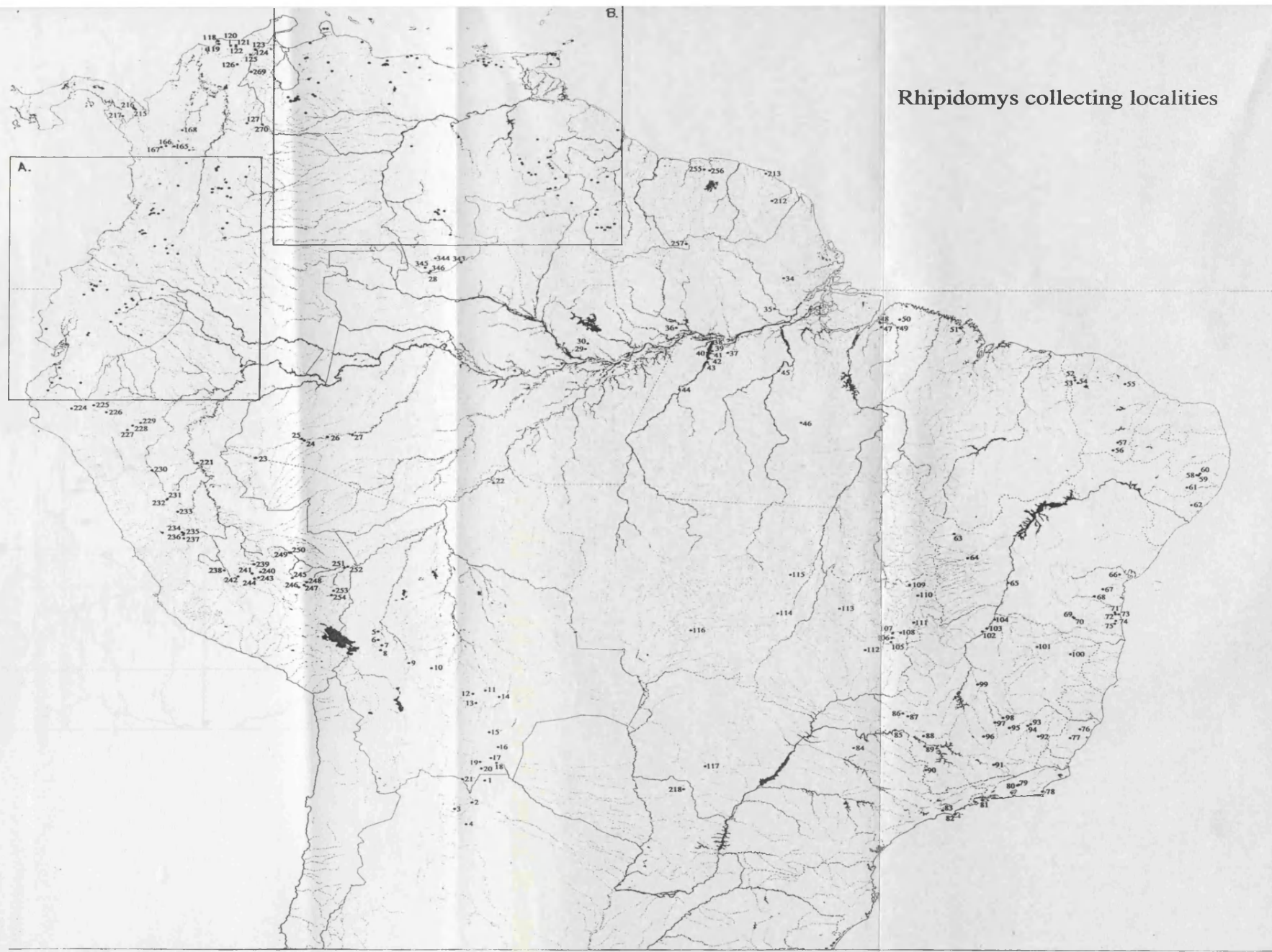
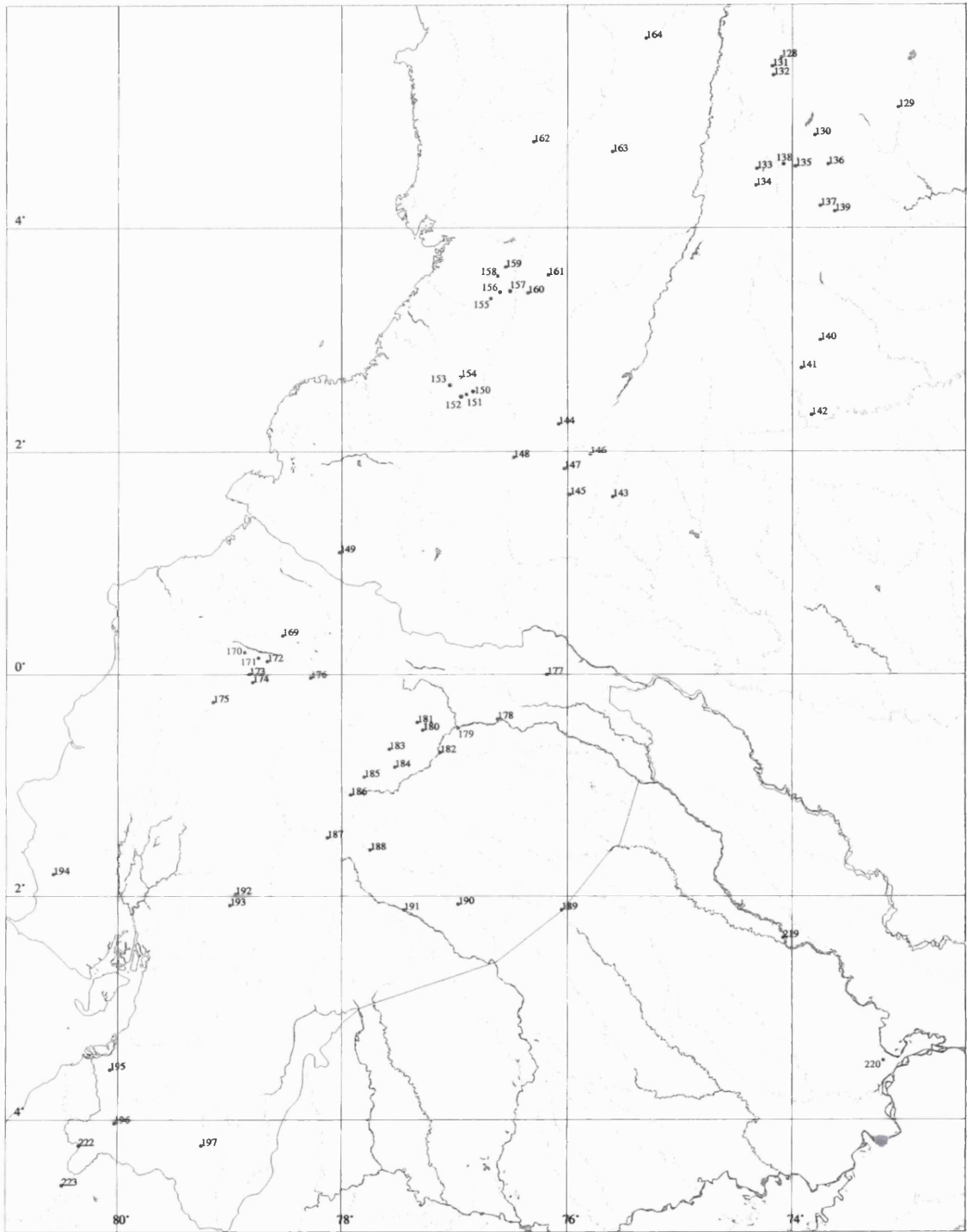### Notes - Sources of geographical coordinates

[1] Specimen label

[2] United States Board on Geographic Names (USBGN) gazetteer series (Argentina, 1968; Bolivia, 2nd ed., 1992; Brazil, 1963; British West Indies, 1955; Colombia,

1964; Ecuador, 2nd ed., 1987; Guyana, 1976; Panama, 1969; Paraguay, 1957; Peru, 1955; Surinam, 1974; Venezuela, 1961)

[3] Ornithological Gazetteer of the Neotropics series (Brazil: Paynter & Traylor, 1991; Colombia: Paynter & Traylor, 1981; Ecuador: Paynter & Traylor, 1977; Guianas: Stephens & Traylor, 1985; Peru: Stephens & Traylor, 1983; Venezuela: Paynter, 1982)

[4] Maps of the Americas series, scale 1:250 000

[5] Maps of the Americas series, scale 1:100 000

[6] Estimated from USBGN and map in G.H.H. Tate's field notes (AMNH)

[7] Mapa de la República de Bolivia, 1980, 3rd ed., scale 1:1 000 000. Instituto Geográfico Militar, La Paz.

[8] Times World Atlas

[9] International Travel Map 154 - South America North East, 1989, scale 1:4 000 000, International Travel Map Productions, Vancouver

[10] Hershkovitz, 1977

[11] P.E. Vanzolini, personal gazetteer

[12] Rio de Janeiro, Mapa Rodoviário e Político, 1986, scale 1:400 000, Geomapas, São Paulo

[13] Mapa do Brasil, 1983, Guia Quatro Rodas, suplemento, Editora Abril, Rio de Janeiro

[14] Interpolated on map in Stallings, 1989

[15] Nitikman & Mares, 1987

[16] Alho, Pereira & Paula, 1986

[17] Interpolated from data in Mello, 1977

[18] Maps of the World series, scale 1:1 000 000

[19] Hershkovitz, 1947

[20] Map of Cundinamarca, scale 1:250 000, Instituto Geográfico Agustín Codazzi, Bogotá

[21] Cartas Geográficas de los Departamentos de Colombia. Ministerio de las Relaciones Exteriores, Bogotá

[22] Mapa Vial, Valle del Cauca, scale 1:250 000. Secretaria de Obras Públicas, 1978 (Michael Alberico, *in litt.*)

[23] Gardner & Patton, 1976

[24] Mapa Geográfica, República del Ecuador, scale 1:500 000. Instituto Geográfico
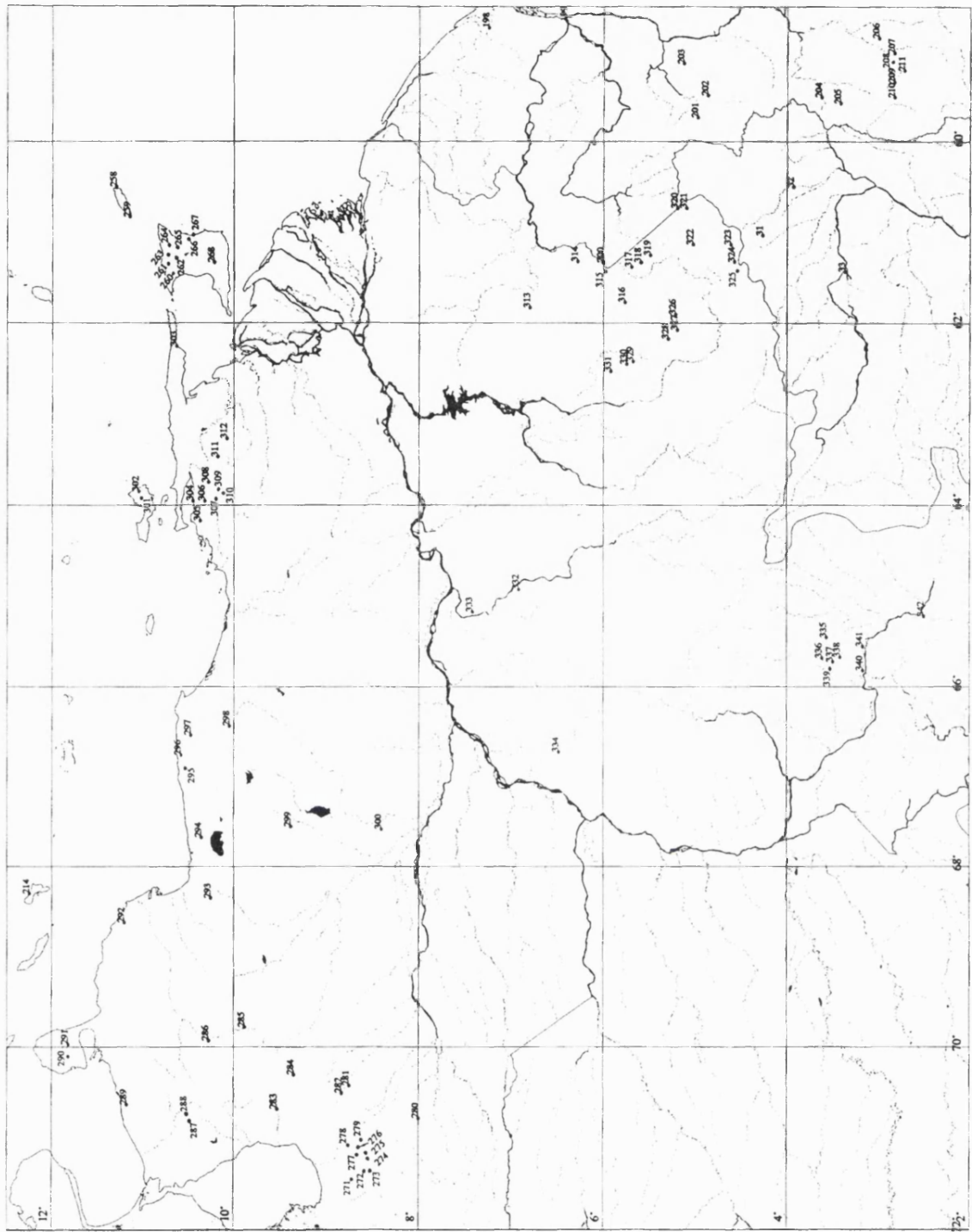
Militar, Quito, 1979

[25] Maps of Ecuador, scale 1:50 000. Instituto Geográfico Militar, Quito, Interamerican Geodetic Survey

[26] International Travel Map 153 - South America North West, 1987, scale 1:4 000 000, International Travel Map Productions, Vancouver

[27] Map of Guyana, Scale 1:1 000 000. Ministry of Agriculture, Georgetown, 1975

[28] Atlas van Tropisch Nederland, 1938 (facsimile, 1990)

[29] Fairchild & Handley, 1966

[30] República del Perú, Mapa Físico-Político, scale 1:1 000 000. Instituto Geográfico Militar del Perú, 1978

[31] Interpolated on item 30, from information in Ornithological Gazetteer of Peru (item 3)

[32] Map of Departamento de Cuzco, scale 1:747 000. Instituto Geográfico Nacional, Lima, 1986

[33] Terborgh et al., 1984

[34] Ascorra et al., 1991

[35] Woodman et al., 1991

[36] Ordnance Survey map of Tobago, scale 1:25 000

[37] Handley, 1976

[38] Atlas de Venezuela, Ministerio del Ambiente y de los Recursos Naturales Renovables, 2nd ed., 1979

[39] O'Connell, 1989

[40] Tate, 1931

[41] Voss, 1991

[42] Mapa físico y político de la República de Venezuela, scale 1:1 000 000, 1955

[43] MBUCV, *in litt.*

[44] Interpolated on item 26

[45] Gardner, 1989

[46] Map of Trinidad Showing Motor Roads and Other Means of Communication, scale 1:250 000. Lands and Surveys Department, Trinidad and Tobago, 1969

Rhipidomys collecting localities

A.

315

B.