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## Philippine Rodents: Chromosomal Characteristics and Their Significance for Phylogenetic Inference Among 13 Species (Rodentia: Muridae: Murinae)

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### ABSTRACT

Karyotypes are reported for 13 murines belonging to the endemic Philippine genera *Apomys*, *Archboldomys*, *Batomys*, *Bullimus*, *Chrotomys*, *Phloeomys*, and *Rhynchomys*, and the widespread genus *Rattus*. The karyotype of *Phloeomys cumingi* (2N = 44, FN = 66) differs from that of *P. pallidus* (2N = 40, FN = 60), and both are chromosomally distinct from other taxa examined. Two species of *Batomys* (2N = 52), *Chrotomys gonzalesi* (2N = 44), *Rhynchomys isarogensis* (2N = 44), and *Apomys musculus* (2N = 42) have FN = 52–53 and a predominance of telocentric chromosomes. Two other species of *Apomys* have diploid numbers of 30 and 44, and fundamental num-

bers of 50 and 88, respectively, indicating substantial chromosomal variability within that genus. *Archboldomys* (2N = 26, FN = 43) has an aberrant sex chromosome system and a karyotype that is substantially different from other taxa studied. The karyotype of *Bullimus bagobus* (2N = 42, FN = ca. 58) is numerically similar to that of the native *Rattus everetti* and the two non-native species of *Rattus*, *R. tanezumi* and *R. exulans*. Chromosomal data corroborate some phylogenetic relationships inferred from morphology, and support the hypothesis that the Philippine murid fauna is composed of separate clades representing independent ancestral invasions of the archipelago.

### INTRODUCTION

The Philippine Islands support a remarkably diverse murine rodent fauna, including at least 46 indigenous species representing 22 genera (Heaney, 1986; Heaney et al., 1987;

Heaney and Rickart, 1990; Musser and Heaney, 1992). This assemblage is also predominantly endemic: 43 species (93%) are restricted to the archipelago, and 36 species

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(78%) belong to 16 endemic genera. The high degree of endemism suggests a pattern of very few colonizations, followed by repeated speciation within the archipelago (Heaney and Rickart, 1990). Our ability to discern more detailed biogeographic patterns among Philippine murids is hampered by incomplete understanding of their phylogenetic relationships. These can be clarified only through acquisition of additional specimens, precise diagnosis of taxa, and analyses of multiple data sets.

In a survey of morphological characteristics, Musser and Heaney (1992) provided a series of alternative hypotheses of possible phylogenetic relationships among murids native to the Philippines (exclusive of the Palawan faunal region). They recognized three major divisions: (I) "OLD ENDEMICS" (species of *Phloeomys*, *Crateromys*, *Batomys*, *Carpomys*, *Apomys*, *Crunomys*, *Archboldomys*, *Chrotomys*, *Celaenomys*, and *Rhynchomys*), (II) the distinctive monotypic genus *Anonymomys*, and (III) "NEW ENDEMICS" (species of *Tryphomys*, *Abditomys*, *Bullimus*, *Tarsomys*, *Limnomys*, and indigenous species of *Rattus*). The genera in Division I, each characterized by a combination of primitive murine traits and uniquely derived specializations, comprise six distinctive clusters with uncertain phylogenetic relationships; the affinities of *Anonymomys* appear to be with members of the Sundaic fauna; and each genus in Division III is diagnosed by autapomorphic features and a suite of synapomorphies shared with *Rattus*, but otherwise phylogenetic relationships within the division are unclear (Musser and Heaney, 1992).

In addition to the indigenous fauna, there is a separate group of murines that includes several species of *Rattus* (*tanezumi mindanensis*, *rattus argentiventer*, *nitidus*, *norvegicus*, and *exulans*) as well as one species of *Mus* (*musculus castaneus*) with wide distributions outside the Philippines (Musser and Newcomb, 1983). These species have been introduced, most likely through human activity (Musser, 1977).

Against this framework of groupings derived from morphology, we present standard karyotypes for 13 species of Philippine murines belonging to 8 genera. Chromosomal

data for the endemic *Batomys*, *Apomys*, *Chrotomys*, *Rhynchomys*, *Archboldomys*, and *Bullimus* are reported for the first time. Data also are reported for endemic species of *Phloeomys* and *Rattus*, and for two non-native species of *Rattus*. We discuss the significance of these chromosomal traits for phylogenetic inference within the context of the alternative hypotheses of relationships outlined by Musser and Heaney (1992).

#### MATERIALS AND METHODS

Animals were collected from wild populations and killed with sodium pentobarbital (Nembutal) or chloroform within 24 hours of capture. Bone marrow preparations were obtained following the methods of Patton (1967) with the exception that 0.4 percent potassium chloride was used for the hypotonic treatment. Cells were processed and fixed in the field, and standard karyotypes prepared in the laboratory from stored cell suspensions following methods of Rickart et al. (1989).

Four terms are used to describe the shape of chromosomes based on the position of the centromere: **metacentric** (biarmed chromosomes with arms of nearly equal length); **submetacentric** (biarmed chromosomes with a short arm at least one third the length of the other); **subtelocentric** (biarmed chromosomes with a short arm less than one third the length of the other); **telocentric** (chromosomes with a very minute second arm or no discernable second arm). Determinations of diploid number were based on counts from a minimum of 10 cells per individual. Fundamental numbers (FN) refer to the total number of major chromosome arms (excluding very minute arms). Specimens examined were prepared as skeletons, skins with partial skeletons, or preserved in fluid and are deposited in the National Museum of Natural History, Washington, D.C. (USNM), and the Philippine National Museum, Manila (PNM).

The species we sampled are in the subfamily Murinae of the family Muridae, as outlined by Carleton and Musser (1984) and Musser and Carleton (1993), and the scientific names we use are those employed by Musser and Carleton (1993) and Musser and

Heaney (1992). Identifications of the species of *Apomys* from the central Philippines differ from those presented in Musser's (1982a) review of the genus, and are based on examination of recently acquired specimens. Specimens from Leyte and Biliran are identified as *Apomys littoralis*, whereas those from Negros probably represent an undescribed species (Heaney et al., 1989; Musser and Heaney, 1992).

#### SPECIMENS EXAMINED

*Phloeomys cumingi* (Waterhouse, 1839): Catanduanes Island, Catanduanes Province, vicinity of Barrio Summit, 250 m (13°47'N, 124°19'E), one male, four females (USNM 573154, 573330, and 573332; PNM specimens (EAR field numbers 1662 and 1663); Luzon Island, Camarines Sur Province, Mount Isarog, 4 km N, 16 km E Naga, 400 m (13°40'N, 123°19'E), one female (USNM 573509).

*Batomys granti* Thomas, 1895: Luzon Island, Camarines Sur Province, Mount Isarog, 4 km N, 22 km E Naga, 1550–1750 m (13°40'N, 123°22'E), two males, two females (USNM 458914, 458944, 458946, and 458949).

*Batomys salomonseni* (Sanborn, 1953): Leyte Island, Leyte Province, Mount Pangasugan, 10.5 km N, 4 km E Baybay, 700–1000 m (10°47'N, 124°50'E), three males, three females (USNM 458783, 458784, 459515, 459872, 459873, and 459886).

*Apomys littoralis* (Sanborn, 1952): Biliran Island, Leyte Province, 5 km N, 10 km E Naval, 850 m (11°36'N, 124°29'E), one male (USNM 459842); Leyte Island, Leyte Province, Mount Pangasugan, 10.5 km N, 4 km E Baybay, 700–1000 m (10°47'N, 124°50'E), one male, three females (USNM 458762, 458764, 459853, and 459861).

*Apomys musculus* Miller, 1911: Luzon Island, Camarines Sur Province, Mount Isarog, 4.5 km N, 20.5 km E Naga, 1125–1350 m (13°40'N, 123°21'E), two males, two females (USNM 458926, 458928, 458937, and 458938).

*Apomys* sp.: Negros Island, Negros Oriental Province, Mount Guinsayawan, 3 km N, 17 km W Dumaguete City, 1470 m

(09°22'N, 123°09'E), two males, one female (USNM 458751, 458753, and 458754).

*Archboldomys luzonensis* Musser, 1982: Luzon Island, Camarines Sur Province, Mount Isarog, 4 km N, 21.5 km E Naga, 1350–1750 m (13°40'N, 123°22'E), three males, one female (USNM 573505, 573835, 573837, and 573840).

*Chrotomys gonzalesi* Rickart and Heaney, 1991: Luzon Island, Camarines Sur Province, Mount Isarog, 4 km N, 21.5 km E Naga, 1350–1750 m (13°40'N, 123°22'E), two females (USNM 458955 and 458956).

*Rhynchomys isarogensis* Musser and Freeman, 1981: Luzon Island, Camarines Sur Province, Mount Isarog, 4 km N, 21.5 km E Naga, 1350–1750 m (13°40'N, 123°22'E), three males, one female (USNM 573575, 573901, 573905, and 573910).

*Bullimus bagobus* Mearns, 1905: Leyte Island, Leyte Province, Mount Pangasugan, 10.5 km N, 4 km E Baybay, 900 m (10°47'N, 124°50'E), one male (USNM 458789).

*Rattus everetti* (Gunther, 1879): Biliran Island, Leyte Province, 5 km N, 10 km E Naval, 850 m (11°36'N, 124°29'E), two males (USNM 458800 and 459901); Catanduanes Island, Catanduanes Province, 8.5 km W Gigmoto, 250 m (13°47'N, 124°19'E), two males (USNM 573173 and 573343); Leyte Island, Leyte Province, Mount Pangasugan, 10.5 km N, 4 km E Baybay, 700–1000 m (10°47'N, 124°50'E), four males, one female (USNM 458816, 458817, and 458820–458822); Luzon Island, Camarines Sur Province, Mount Isarog, 5 km N, 20 km E Naga, 900 m (13°40'N, 123°21'E), two males (USNM 573856 and 573857).

*Rattus exulans* (Peale, 1848): Negros Island, Negros Oriental Province, Silliman Farm, Dumaguete, 5 m (09°18'N, 123°18'E), one female (USNM 459930); Mount Guinsayawan, 3 km N, 17 km W Dumaguete City, 1470 m (09°22'N, 123°09'E), four males, three females (USNM 458835, 458837, 458840, 458841, 459931, 459932, and 459936).

*Rattus tanezumi mindanensis* (Mearns, 1905): Biliran Island, Leyte Province, 5 km N, 10 km E Naval, 850 m (11°36'N, 124°29'E), one male (USNM 459963); Negros Island, Negros Oriental Province, Mount Guinsayawan, 3 km N, 17 km W Dumaguete

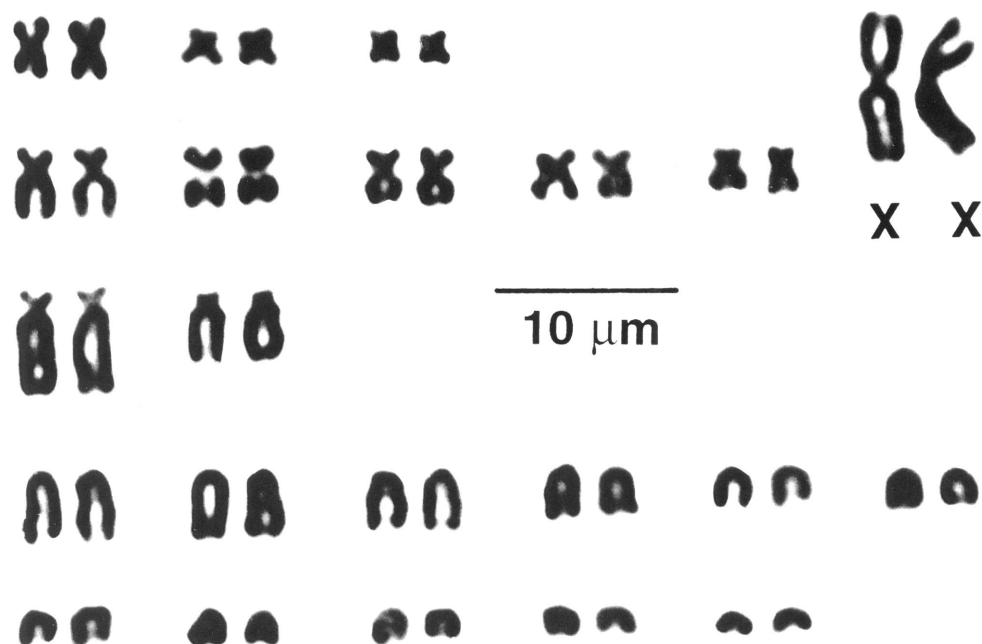


Fig. 1. Karyotype of a *Phloeomys cumingi* female (EAR 1662) from Catanduanes Island:  $2N = 44$ ,  $FN = 66$ .

City, 1470 m (09°22'N, 123°09'E), one male (USNM 459975).

#### ACKNOWLEDGMENTS

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#### CHROMOSOMAL CHARACTERISTICS

*Phloeomys cumingi* ( $2N = 44$ ,  $FN = 66$ ; fig. 1): The autosomal complement consists of one pair of medium-size and two pairs of small metacentric chromosomes, five pairs

of small to medium-size submetacentric chromosomes, one large and one medium-size pair of subtelocentric chromosomes, and 11 pairs of small to large telocentric chromosomes. The presumed X chromosome is submetacentric and the largest element in the karyotype, and the submetacentric Y chromosome is slightly smaller.

*Batomys granti* ( $2N = 52$ ,  $FN = 52$ ; fig. 2A): The karyotype consists of a graded series of 26 pairs of small to large telocentric chromosomes. The sex chromosomes cannot be differentiated from the autosomal complement, but we know that both X and Y elements are telocentric since we sampled both sexes.

*Batomys salomonseni* ( $2N = 52$ ,  $FN = 52$ ; fig. 2B): The standard karyotype is indistinguishable from that of *B. granti*.

*Apomys littoralis* ( $2N = 44$ ,  $FN = 88$ ; fig. 3A): The karyotype consists of one pair of medium-size metacentric chromosomes, two pairs of small metacentric chromosomes, one pair of large submetacentric chromosomes, and 18 pairs of small to large subtelocentric chromosomes. The sex chromosomes cannot be distinguished from the autosomal complement, but we presume the X and Y ele-

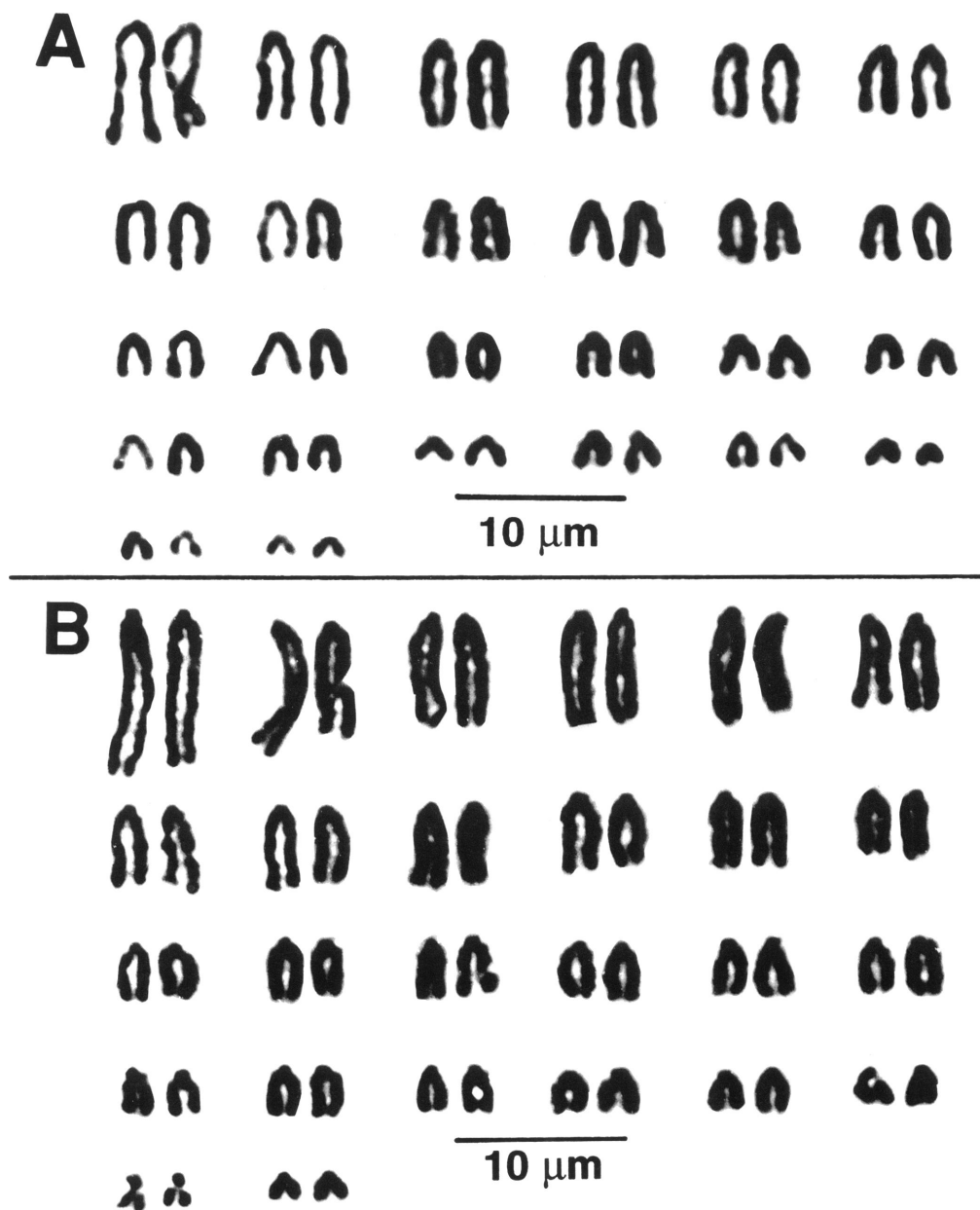


Fig. 2. Karyotypes of *Batomys*. A, *B. granti* female (USNM 458944) from Mount Isarog:  $2N = 52$ ,  $FN = 52$ . B, *B. salomonseni* male (USNM 458783) from Leyte Island:  $2N = 52$ ,  $FN = 52$ . All autosomes are telocentric, as are the X and Y chromosomes, which we cannot distinguish from the others.

ments to be subtelocentric since both sexes were studied.

*Apomys musculus* ( $2N = 42$ ,  $FN = 52$ ; fig. 3B): The complement contains one pair of medium-size metacentric chromosomes, two pairs of small metacentric chromosomes, one

pair of large submetacentric chromosomes, one pair of large subtelocentrics, and 16 pairs of small to large telocentric elements. The sex chromosomes cannot be differentiated from the autosomes, but presumably both X and Y chromosomes are telocentric.

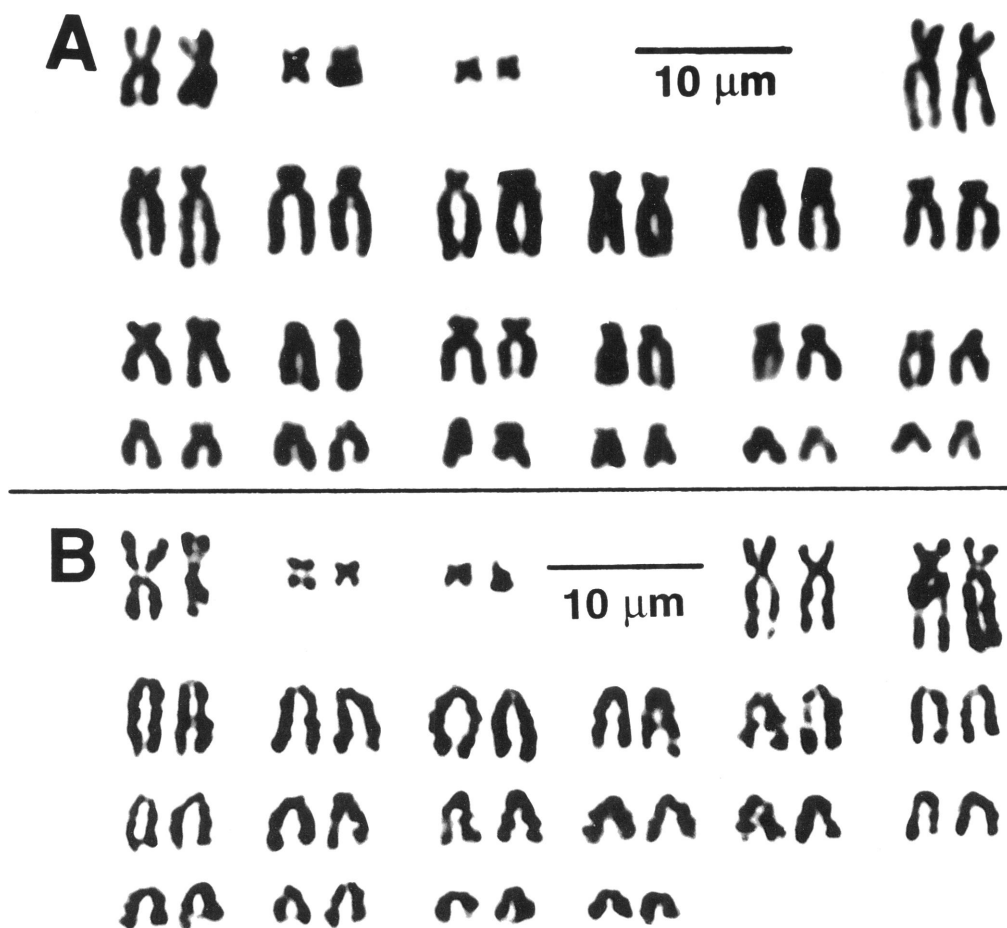


Fig. 3. Karyotypes of *Apomys*. A, *A. littoralis* male (USNM 458762) from Leyte Island:  $2N = 44$ ,  $FN = 88$ . B, *A. musculus* male (USNM 458937) from Mount Isarog:  $2N = 42$ ,  $FN = 52$ . We cannot distinguish sex chromosomes from the autosomes.

*Apomys* sp. ( $2N = 30$ ,  $FN = 50$ ; fig. 4): This sample of *Apomys* from Negros Island has an autosomal complement consisting of six pairs of medium to large-size metacentric chromosomes, three pairs of submetacentrics, and five pairs of small chromosomes that appear to be telocentric, but may include one or more biarmed pairs. The presumed X chromosome is medium-size and subtelocentric, and the Y chromosome is medium-size and submetacentric.

*Archboldomys luzonensis* ( $2N = 26$ ,  $FN = 43$ ; fig. 5A, B): The karyotype consists of five pairs of small to large metacentric chromosomes, three pairs of large to medium-size submetacentric chromosomes, four pairs of telocentric chromosomes, and an asymmet-

rical pair unique to each sex. The latter apparently constitutes an aberrant  $XX^+Y$  sex chromosome system (which will be discussed by Rickart in a future report). A large submetacentric chromosome is present in both sexes, and is the largest element in the karyotype. This large element is paired with a medium-size telocentric chromosome in karyotypes of three males, but it is paired with a much larger telocentric chromosome in the single female karyotype we examined. The female was phenotypically normal, and pregnant when captured.

*Chrotomys gonzalesi* ( $2N = 44$ ,  $FN = 52$ ; fig. 6A): The autosomal complement consists of two pairs of small metacentric chromosomes, one pair of large submetacentric chro-

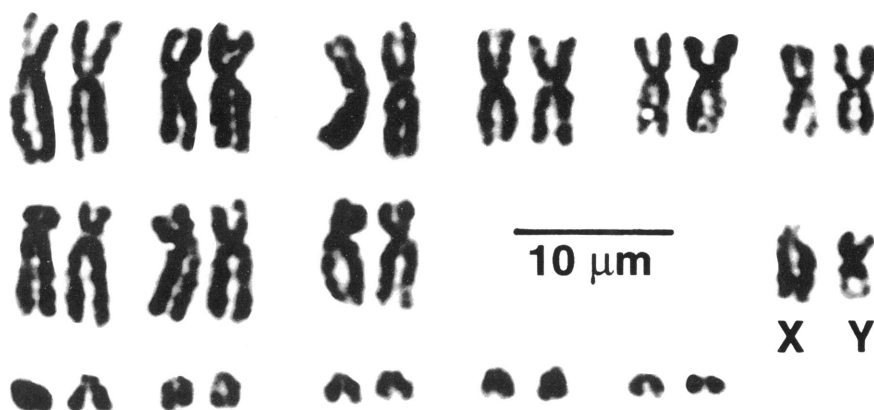


Fig. 4. Karyotype of *Apomys* sp. male (USNM 458751) from Negros Island:  $2N = 30$ ,  $FN = 50$ . The presumed X chromosome is a subtelocentric, the Y a submetacentric. Contrast this karyotype with those of *A. littoralis* and *A. musculus* in figure 3.

mosomes, one pair of large subtelocentric chromosomes, and 18 pairs of small to large telocentric elements. The X chromosomes cannot be distinguished from the autosomal complement. Because only females were examined, the Y chromosome is unknown.

*Rhynchomys isarogensis* ( $2N = 44$ ,  $FN = 52/53$ ; fig. 6B): The autosomal complement contains two pairs of small metacentric chromosomes, one pair of large submetacentric chromosomes, one pair of large subtelocentric chromosomes, and 17 pairs of small to large telocentric elements. The presumed X chromosome is telocentric and cannot be distinguished from the other large telocentric autosomes. The Y chromosome is distinctive, about the same size as the X chromosome, and submetacentric. X and Y chromosomes of approximately the same size (isomorphic) is an unusual configuration for mammals. In its evolutionary history, most of the Y chromosome is deleted because its only functional genes are those determining sex (J. L. Patton, in litt.).

*Bullimus bagobus* ( $2N = 42$ ,  $FN = 58$ ; fig. 7A): The karyotype consists of seven pairs of small metacentric chromosomes, one pair of large subtelocentric chromosomes, and 13 pairs of small to large telocentric elements. The sex chromosomes cannot be distinguished from the autosomal complement, but presumably are included within the telocentric series (based on the general similarity to karyotypes of *Rattus*, fig. 7B; table 2).

*Rattus everetti* ( $2N = 42$ ,  $FN = 64$ ; fig. 7B): The autosomal complement consists of seven pairs of small metacentric chromosomes, four pairs of small to large subtelocentric chromosomes, and nine pairs of small to large telocentric chromosomes. The presumed X chromosome is telocentric, as is the Y.

*Rattus exulans* ( $2N = 42$ ,  $FN = 60$ ; not figured): Specimens from Negros Island yielded standard karyotypes that were indistinguishable from those documented for other populations of this species (table 2). The autosomal complement consists of seven pairs of small metacentric chromosomes, one pair of large and one pair of small subtelocentric chromosomes, and 11 pairs of small to large telocentric chromosomes. Both the presumed X and the Y chromosomes are telocentric.

*Rattus tanezumi mindanensis* ( $2N = 42$ ,  $FN = 60$ ; not figured): Karyotypes of individuals from Biliran and Negros islands are closely similar to those documented for specimens from Luzon and elsewhere in Asia (table 2). The standard karyotype also resembles that of *Rattus exulans* (table 2).

#### SIGNIFICANCE OF CHROMOSOMAL DATA

In their recent review of morphological and distributional characteristics of Philippine murines, Musser and Heaney (1992) provided alternative hypotheses of phylogenetic relationships among what appear to be mono-

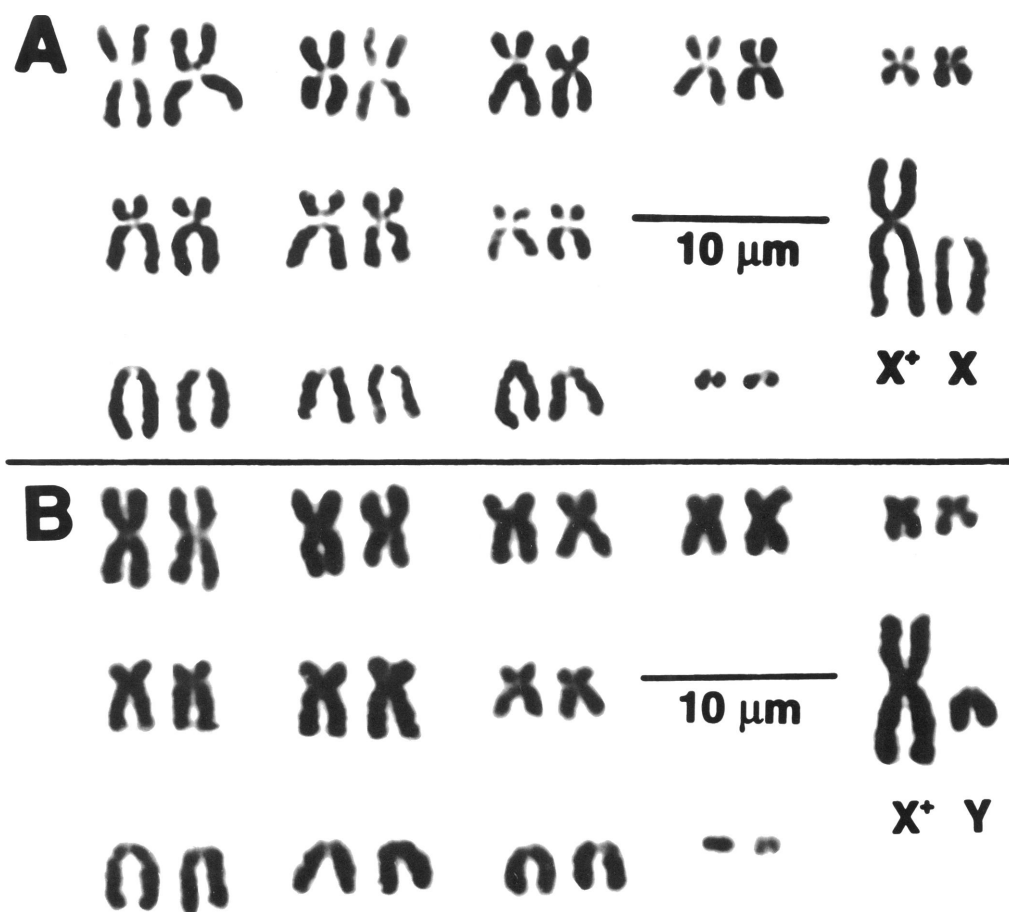


Fig. 5. Karyotypes of a female (A, USNM 573840) and male (B, USNM 573835) *Archboldomys luzonensis* from Mount Isarog:  $2N = 26$ ,  $FN = 43$ . The sex chromosomes are dimorphic in both sexes.

phyletic clusters of species and genera. They recognized three major divisions containing generic groups as follows:

#### DIVISION I (OLD ENDEMICIS)

- Phloeomys* Group
- Crateromys* Group (*Crateromys*, *Batomys*, and *Carpomys*)
- Apomys* Group
- Crunomys* Group (*Crunomys* and *Archboldomys*)
- Chrotomys* Group (*Chrotomys* and *Celaenomys*)
- Rhynchomys* Group

#### DIVISION II (*Anonymomys*)

- Anonymomys*

#### DIVISION III (NEW ENDEMICIS)

- Tryphomys* and *Abditomys*
- Bullimus*
- Tarsomys*
- Limnomys*
- Rattus*

It is in the context of this review that we discuss three levels of significance of the chromosomal data presented in the previous section: first, as another character set useful for diagnosing the species of Philippine murines and distinguishing among them; second, as additional information about phylogenetic relationships among the Philippine endemics and use in testing the phylogenetic alternatives suggested by Musser and Heaney (1992);



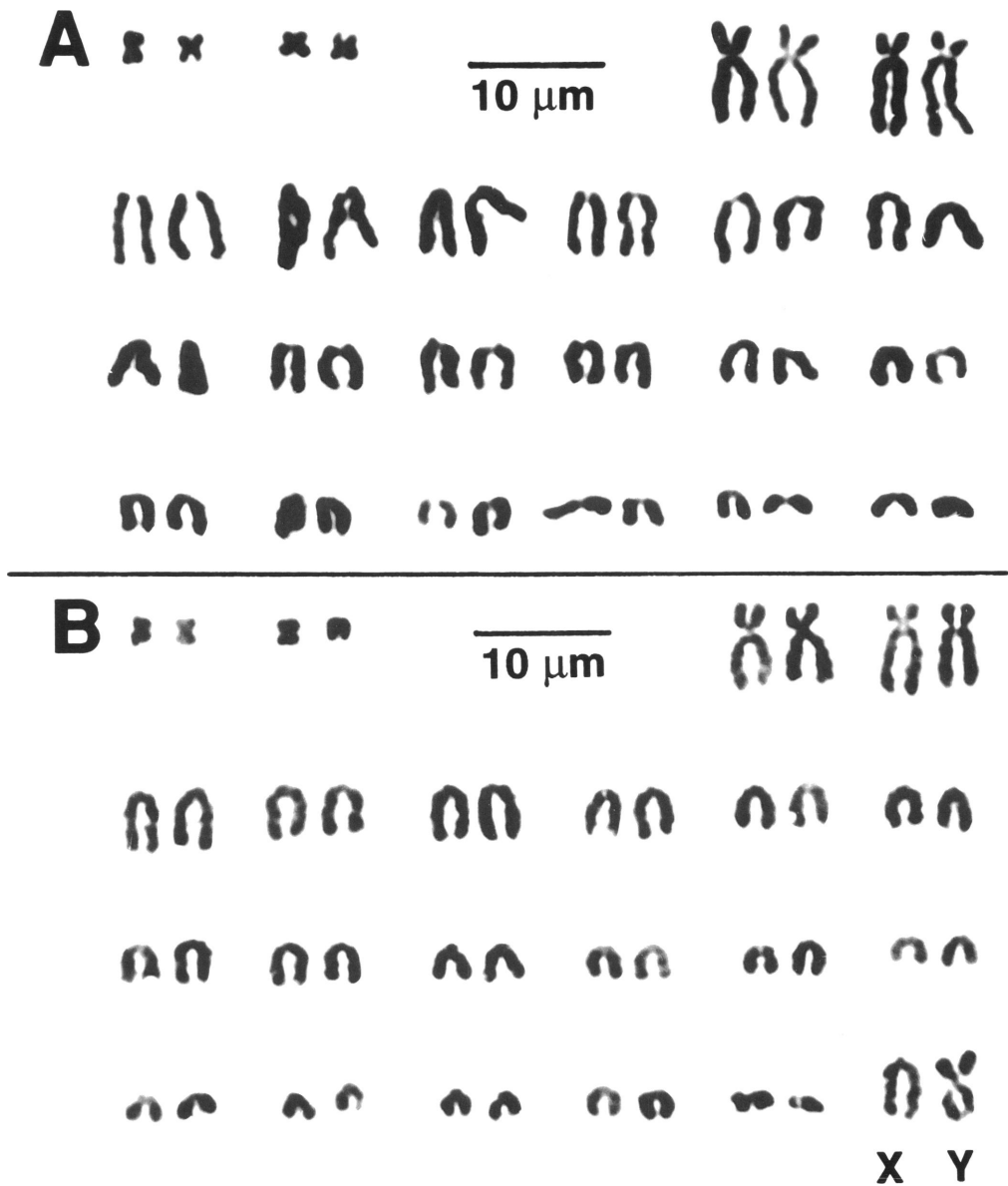


Fig. 6. Karyotypes of shrew rats from Mount Isarog. A, *Chrotomys gonzalesi* female (USNM 458956): 2N = 44; FN = 52. B, *Rhynchomys isarogensis* male (USNM 573575): 2N = 44, FN = 53. Each species has two pairs of small metacentrics, one pair of large submetacentrics, and one pair of large subtelocentrics.

and third, as a clue to estimating phylogenetic alliances between the Philippine murines and those native to other regions in the Indo-Australian region. To help us evaluate the significance of the Philippine data we have extracted karyotypic information (2N, FN, the number of metacentric, submetacentric,

subtelocentric, and telocentric autosomes, and morphology of the sex chromosomes) from the literature and our own unpublished results and summarized them in tables 1 and 2 and figure 8. By plotting diploid number against fundamental number of Indo-Australian murines, we wanted to determine if the

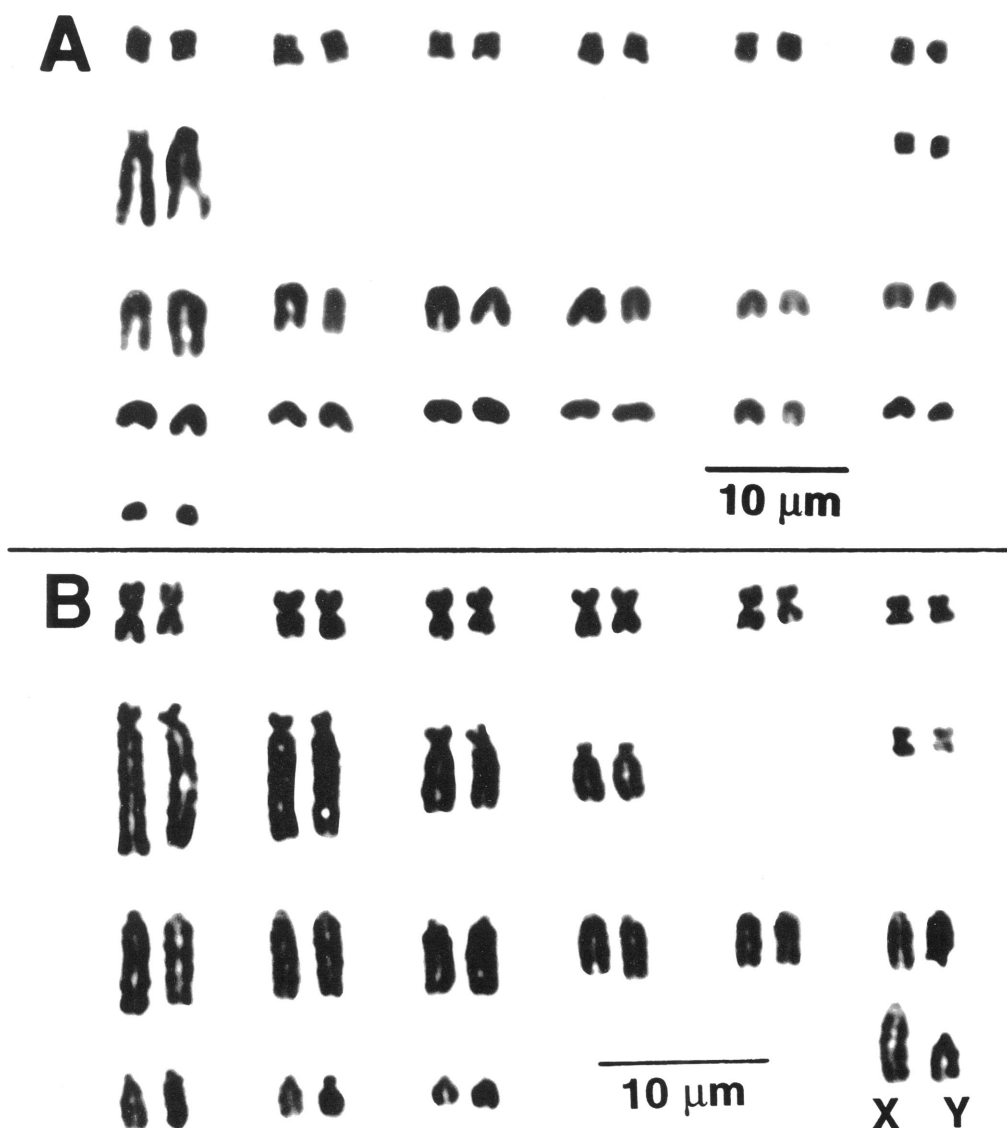


Fig. 7. Karyotypes of New Endemics. A, *Bullimus bagobus* female (USNM 458789) from Leyte Island:  $2N = 42$ ,  $FN = 58$ . B, *Rattus everetti* male (USNM 573343) from Catanduanes Island:  $2N = 42$ ,  $FN = 64$ .

Philippine species showed dispersion, cohesion, or trends compared with samples from outside the Philippine Archipelago, aspects which are brought out in the discussion that follows.

Our discussion is bounded by a cautionary reminder and two assumptions. We remind readers that our knowledge of the chromosomal features of Philippine endemics comes from standard karyotypes, preparations that

yield only gross chromosomal morphology, diploid and fundamental numbers. We assume that chromosomal complements that are similar, either primitive or derived patterns, share homologous units. We also accept for now the assertion of Viegas-Pequignot et al. (1983, 1985) that a high diploid number combined with a moderately low fundamental number defining a karyotype consisting of either all telocentric pairs, or

predominantly telocentric pairs with one or two pairs of small metacentric autosomes, and biarmed sex elements is primitive for murines. This assumption is a hypothesis, one we recognize to be based on the principle of commonality, which may or may not correspond to the real primitive condition (Qumsiyeh and Baker, 1988). However, the hypothesis can be tested by the methodology of outgroup analyses if G-band sequences become available for Philippine murines.

Among the murines Viegas-Pequignot et al. (1983) studied, chromosomes of the African *Malacomys longipes* are closest to the presumed ancestral complement. The karyotype of that species consists of a diploid number of 48, a fundamental number of 52, and an autosomal complement of all telocentric pairs except for one pair of small metacentric chromosomes. We consider examples of derived karyotypes to be those of the Sulawesi *Echiothrix* or those from several species of Sundaic *Maxomys*—all have many biarmed elements and high fundamental numbers (table 1; fig. 8).

#### DIVISION I (OLD ENDEMICS)

##### PHLOEOMYS Group

The slender-tailed cloud rats, genus *Phloeomys*, are endemic to the Luzon faunal region. There are two named species: *Phloeomys cumingi* from southern Luzon, Marinduque, and Catanduanes, and *P. pallidus* from central and northern Luzon (Thomas, 1898; Heaney et al., 1987, 1991). Schauenberg (1978) recognized only *P. cumingi*, and suggested that the name *pallidus* represented a seasonal or individual color variant. The karyotype reported here for specimens of *P. cumingi* from southern Luzon and Catanduanes ( $2N = 44$ ,  $FN = 66$ ; fig. 1) is substantially different from that documented by Jotterand-Bellomo and Schauenberg (1988) for specimens originating in Aurora Province, east-central Luzon ( $2N = 40$ ,  $FN = 60$ ). Although those authors used the name *Phloeomys cumingi* in their report, Aurora Province is within the presumed range of *P. pallidus* (Heaney et al., 1991). Furthermore, the published photographs of specimens from this region (Schauenberg, 1978; Jotterand-Bellomo and Schauenberg, 1988) clearly de-

pict individuals with the extensive pale dorsal markings characteristic of *P. pallidus*, rather than the uniformly dark brown pelage of *P. cumingi* (Heaney et al., 1991).

Karyotypes from the two species of *Phloeomys* differ by at least two Robertsonian translocations and three non-Robertsonian events. Differences of this magnitude are strong evidence that *cumingi* and *pallidus* represent separate species. This chromosomal evidence is a significant addition to the suite of traits defining each kind of *Phloeomys* and our knowledge of the diversity within this genus.

The distinctive characteristics associated with *Phloeomys* have prompted some researchers to isolate it either in its own subfamily (the Phloeomyinae) of Muridae or separate family (see the discussion in Musser and Heaney, 1992: 59). The unique morphological specializations of *Phloeomys* led Musser and Heaney (1992) to view it as a separate group, only distantly related to the other Old Endemic Philippine genera. However, they did identify a few derived traits that potentially linked *Phloeomys* with the *Crateromys* Group (which includes *Batomys*).

If the chromosomal complements of the species of *Batomys* ( $2N = 52$ ,  $FN = 52$ ; fig. 2A, B) are representative of the *Crateromys* Group, they appear to argue against a close association with the species of *Phloeomys*, at least with species of *Batomys*, which differ strikingly in chromosome number, size, and shape. Accepted by themselves, the chromosomal traits of *Phloeomys* would appear to falsify the alternative hypothesis suggested by Musser and Heaney (1992: 82) that "*Phloeomys* and members of the group are more closely related to each other than to any other Philippine endemic or to any other genus from the Indo-Australian region." However, as we previously cautioned, the karyotypes we examined provided only gross morphology of chromosomes—banding and other staining techniques might change the interpretation.

The derived chromosomal complement, as well as most morphological traits examined (Musser and Heaney, 1992), simply underscore the uniqueness of *Phloeomys*. As a single character set, karyological results are consistent with the hypothesis formulated by Musser and Heaney (1992: 81) that "*Phleo-*

TABLE 1  
Summary of Karyotypic Data from Samples of Old Endemics from the  
Indo-Australian Region

Species	Autosomes					Sex		FN	References
	2N	M	SM	ST	T	X	Y		
<i>Pseudomys</i>									
<i>praeconis</i>									
Australia	48	2	0	0	21	T	T	52	Baverstock et al., 1977a
<i>fumeus</i>									
Australia	48	2	0	0	21	ST	ST	54	Baverstock et al., 1977a
<i>nanus</i>									
Australia	48	2	0	0	21	M	M	54	Baverstock et al., 1977a
<i>alboconereus</i>									
W Australia, mainland	48	2	0	0	21	T	ST	53	Baverstock et al., 1977a
S Australia	48	2	0	0	21	ST	ST	54	Baverstock et al., 1977a
W Australia, Bernier Is	48	2	0	0	21	M	ST	54	Baverstock et al., 1977a
<i>hermannsburgensis</i> <sup>a</sup>									
Australia	48	2	0	0	21	SM	ST	54	Baverstock et al., 1977a
<i>desertor</i> <sup>b</sup>									
Australia	48	2	0	0	21	SM	?	54	Baverstock et al., 1977a
<i>higginsii</i>									
Australia	48	2	0	1	20	T	T	54	Baverstock et al., 1977a
Tasmania	48	2	0	0	21	T	T	52	Dartnall, 1970
<i>occidentalis</i>									
Australia	48	2	0	1	20	T	T	54	Baverstock et al., 1977a
<i>delicatus</i>									
Australia, N Territory	48	2	0	1	20	SM	SM	56	Baverstock et al., 1977a
Australia, Queensland	48	2	0	2	19	SM	M	58	Baverstock et al., 1977a
<i>novaehollandiae</i>									
Australia	48	2	0	1	20	SM	T	55	Baverstock et al., 1977a
<i>australis</i> <sup>c</sup>									
Australia	48	2	0	2	19	T	T	56	Baverstock et al., 1977a
<i>gracilicaudatus</i>									
Australia	48	2	0	3	18	M	SM	60	Baverstock et al., 1977a
<i>shortridgei</i>									
Australia	48	2	0	0	21	ST	ST	54	Baverstock et al., 1977a
<i>fuscus</i>									
Tasmania	48	2	0	3	18	T	T	56	Baverstock et al., 1977a
Australia, NSW	48	2	0	3	18	SM	M	60	Baverstock et al., 1977a
<i>Leggadina</i>									
<i>forresti</i> <sup>d</sup>									
Australia	48	2	0	0	21	T	T	52	Baverstock et al., 1977a
<i>lakedownensis</i>									
Australia	48	1	0	0	22	T	T	50	Baverstock et al., 1977a
<i>Mesembriomys</i>									
<i>gouldii</i>									
Australia, N Territory	48	2	0	0	21	T	T	52	Baverstock et al., 1977a
Australia, Queensland	47	2	0	0	21	T	O	52-♀ 51-♂	Baverstock et al., 1977a

TABLE 1—(Continued)

Species	Autosomes					Sex		FN	References
	2N	M	SM	ST	T	X	Y		
<i>Conilurus</i>									
<i>penicillatus</i>									
Australia	48	2	0	0	21	T	T	54	Baverstock et al., 1977a
<i>Leporillus</i>									
<i>conditor</i>									
Australia	48	2	0	2	20	?	?	56	Baverstock et al., 1977a
<i>Notomys</i>									
<i>fuscus</i> <sup>e</sup>									
Australia	48	1	0	0	22	ST	ST	52	Baverstock et al., 1977c
<i>alexis</i>									
Australia	48	2	0	0	21	SM	ST	54	Baverstock et al., 1977c
<i>mitchelli</i>									
Australia	48	2	0	3	18	ST	ST	60	Baverstock et al., 1977a
<i>cervinus</i> <sup>f</sup>									
Australia	48	3	0	12	8	M	ST	80	Baverstock et al., 1977c
<i>Zyzomys</i>									
<i>woodwardi</i>									
Australia	44	0	1	1	19	T	T	48	Baverstock et al., 1977a
<i>argurus</i>									
Australia	44	0	1	1	19	T	T	48	Baverstock et al., 1977a
<i>Melomys</i>									
<i>burtoni</i> <sup>g</sup>									
Australia	48	2	0	0	21	T	T	52	Baverstock et al., 1977a
<i>cervinipes</i> <sup>h</sup>									
Australia	48	2	0	1	20	T	T	54	Baverstock et al., 1977a; Martin, 1969
<i>Uromys</i>									
<i>caudimaculatus</i> <sup>i</sup>									
Australia, Cape York	46	0	0	3	19	T	T	52	Baverstock et al., 1976b, 1977a
Australia, Atherton	46	2	0	1	19	T	T	52	Baverstock et al., 1976b, 1977a
Papua New Guinea	48	2	0	2	19	T	T	56	Donnellan, 1989
<i>neobritannicus</i>									
New Britain	32	11	1	1	2	T	T	58	Donnellan, 1989
<i>hadrourus</i> <sup>j</sup>									
Australia	48	2	0	2	20	?	?	56	Baverstock et al., 1977a
<i>Hydromys</i>									
<i>chrysogaster</i>									
Australia	48	2	0	0	21	T	T	52	Baverstock et al., 1977a; Martin, 1969
Tasmania	48	2	0	0	21	T	T	52	Dartnall, 1970
<i>Xeromys</i>									
<i>myoides</i>									
Australia	48	2	0	0	21	T	T	52	Baverstock et al., 1977a

TABLE 1—(Continued)

Species	2N	Autosomes				Sex		FN	References
		M	SM	ST	T	X	Y		
<i>Crossomys</i>									
<i>moncktoni</i>									
Papua New Guinea	48	2	0	4	17	T	T	60	Donnellan, 1989
<i>Leptomys</i>									
<i>elegans</i>									
Papua New Guinea	48	2	0	1	20	T	T	54	Donnellan, 1989
<i>Parahydromys</i>									
<i>asper</i>									
Papua New Guinea	48	2	0	0	21	T	T	52	Donnellan, 1989
<i>Mallomys</i>									
<i>rothschildi</i>									
Papua New Guinea	48	2	0	0	21	T	T	52	Donnellan, 1989
<i>Anisomys</i>									
<i>imitator</i>									
Papua New Guinea	46	2	1	0	19	T	T	52	Donnellan, 1989
<i>Lorentzimys</i>									
<i>nouhuysi</i>									
Papua New Guinea	46	2	1	0	19	T	T	52	Donnellan, 1989
<i>Pogonomys</i>									
<i>loriae</i>									
Papua New Guinea	46	2	1	0	19	T	T	52	Donnellan, 1989; Dennis and Menzies, 1979
<i>macrourus</i>									
Papua New Guinea	46	2	1	0	19	T	T	52	Donnellan, 1989
<i>sylvestris</i>									
Papua New Guinea	46	2	1	0	19	T	T	52	Dennis and Menzies, 1979
<i>Chiruromys</i>									
<i>forbesi</i>									
Papua New Guinea	44	0	2	0	19	T	T	48	Dennis and Menzies, 1979
<i>vates</i>									
Papua New Guinea	44	0	2	0	20	?	?	48	Dennis and Menzies, 1978
<i>Phloeomys</i>									
<i>pallidus</i> <sup>k</sup>									
Phil., EC Luzon	40	4	5	0	10	SM	SM	60	Jotterand-Bellomo and Schauenberg, 1988
<i>cumingi</i>									
Phil., S. Luzon	44	3	5	2	11	SM	SM	66	Present report
<i>Batomys</i>									
<i>granti</i>									
Phil., S Luzon	52	0	0	0	25	T	T	52	Present report
<i>salomonseni</i>									
Phil., Leyte	52	0	0	0	25	T	T	52	Present report
<i>Apomys</i>									
<i>littoralis</i>									
Phil., Leyte	44	3	1	17	0	ST	ST	88	Present report

TABLE 1—(Continued)

Species	Autosomes					Sex		FN	References
	2N	M	SM	ST	T	X	Y		
<i>musculus</i> Phil., S Luzon	42	3	1	1	15	T	T	52	Present report
sp. Phil., Negros	30	6	3	0	5	ST	SM	50	Present report
<i>Archboldomys</i> <i>luzonensis</i> <sup>1</sup> Phil., S Luzon	26	5	3	0	4	SM	T	43	Present report
<i>Chrotomys</i> <i>gonzalesi</i> Phil., S Luzon	44	2	1	1	17	?	?	52	Present report
<i>Rhynchomys</i> <i>isarogensis</i> Phil., S Luzon	44	2	1	1	17	T	SM	52-♀ 53-♂	Present report
<i>Margaretamys</i> <i>beccarii</i> Sulawesi	42	2	0	0	18	T	T	46	Musser, 1981
<i>elegans</i> Sulawesi	42	0	7	0	13	T	T	52	Musser, ms.
<i>Echiothrix</i> <i>luecura</i> Sulawesi	40	3	14	0	2	SM	T	75-♂ 76-♀	Musser, 1990
<i>Haeromys</i> <i>minahassae</i> Sulawesi	48	2	0	0	21	SM	SM	54	Musser, 1990
<i>Maxomys</i> <i>hellwaldii</i> Sulawesi	34	4	7	2	3	ST	T	61-♂ 62-♀	Musser, ms
<i>musschenbroekii</i> Sulawesi	36	6	5	0	6	ST	T	59-♂ 60-♀	Musser, ms
<i>bartelsii</i> Java	48	8	0	3	12	T	T	70	Van Peenen et al., 1974; Duncan et al., 1974
<i>inas</i> Malay Peninsula	42	10	10	0	0	M	T	83-♂ 84-♀	Yong, 1969a
<i>rajah</i> Malay Peninsula	36	6	3	0	8	M	ST	56	Yong, 1969a
<i>whiteheadi</i> Malay Peninsula	36	8	1	8	0	M	T	71-♂ 72-♀	Yong, 1969a
<i>moi</i> Vietnam	52	4	2	4	14	SM	SM	74	Duncan and Van Peenen, 1971

TABLE 1—(Continued)

Species	2N	Autosomes				Sex		FN	References
		M	SM	ST	T	X	Y		
<i>surifer</i>									
Vietnam	52	4	2	0	19	M	?	66	Duncan and Van Peenen, 1971
Vietnam	52	4	2	0	19	M	M	66	Cao and Tran, 1984
Thailand	52	4	1	1	19	M	ST	66	Markvong et al., 1973
Malay Peninsula	52	4	2	0	19	M	ST	66	Yong, 1969a
<i>Niviventer</i>									
<i>fulvescens</i>									
Vietnam, Con Sol Isl	46	3	0	1	18	T	T	54	Duncan et al., 1970
Vietnam	46	3	0	4	15	T	T	60	Cao and Tran, 1984
Thailand	46	3	0	4	15	T	T	60	Yosida, 1973
Thailand	46	3	0	1	18	T	T	54	Markvong et al., 1973; Tsuchiya et al., 1979
Malay Peninsula	46	3	0	1	18	T	T	54	Yong, 1969a
Java	46	3	0	4	15	T	T	60	Duncan et al., 1974
Hong Kong	46	3	0	4	15	ST	T	61	Yong, 1969b
								62	
<i>langbianis</i>									
Vietnam	46	3	0	1	18	T	T	54	Cao and Tran, 1984
<i>cremoriventer</i>									
Malay Peninsula	46	3	0	1	18	T	T	54	Yong, 1969a
Java	46	3	0	4	15	T	T	60	Duncan et al., 1974
<i>confucianus</i>									
N Thailand	46	3	3	1	15	T	T	60	Markvong et al., 1973
<i>rapit</i>									
Malay Peninsula	46	3	0	4	15	T	T	60	Yong, 1969a
<i>lepturus</i>									
Java	46	3	0	0	19	T	T	52	Duncan et al., 1974
<i>hinpoon</i>									
Thailand	46	3	0	1	18	T	T	54	Marshall, 1977
<i>Lenothrix</i>									
<i>canus</i>									
Malay Peninsula	46	3	0	5	14	SM	T	63-♂ 64-♀	Yong, 1969a; Yosida, 1973
<i>Pithecheir</i>									
<i>parvus</i>									
Malay Peninsula	50	3	1	3	16	M	ST	64	Yong et al., 1982
<i>Hapalomys</i>									
<i>longicaudatus</i>									
Malay Peninsula	50	0	0	1	23	M	ST	54	Yong et al., 1982
<i>Chiropodomys</i>									
<i>gliroides</i>									
Thailand	42	0	0	0	21	?	?	42	Marshall, 1977; Tsuchiya et al., 1979
Malay Peninsula	42	1	1	0	18	M	SM	48	Yong, 1973
<i>Vandeleuria</i>									
<i>oleracea</i>									
N Thailand	26	2	5	0	5	T	ST	40-♀ 41-♂	Gropp et al., 1972



TABLE 1—(Continued)

Species	2N	Autosomes				Sex		FN	References
		M	SM	ST	T	X	Y		
NE Thailand	28	1	5	0	7	T	ST	40-♀ 41-♂	Winking et al., 1979
E Thailand	28	1	5	0	7	T	SM	40-♀ 41-♂	Winking et al., 1979
N India	28	1	5	0	7	T	T	40	Sharma and Raman, 1972
S India	28	1	5	0	7	T	T	40	Satya Prakash and Aswathanarayana, 1973, 1976
<i>Mus</i>									
<i>platythrix</i> <sup>m</sup>									
S India	26	0	0	0	12	T	T	26	Yosida, 1979; Kumari et al., 1984
<i>shortridgei</i>									
Thailand	46	1	0	0	21	T	T	48	Markvong et al., 1973
<i>pahari</i>									
Thailand	48	0	0	0	23	T	T	48	Markvong et al., 1973
<i>caroli</i>									
Thailand	40	0	0	0	19	T	T	40	Markvong et al., 1973
Japan, Ryukyu Isls	40	0	0	0	19	T	T	40	Tsuchiya, 1981
<i>cervicolor</i>									
Thailand	40	0	0	0	19	T	T	40	Markvong et al., 1973
<i>cookii</i>									
Thailand	40	0	0	0	19	T	T	40	Markvong et al., 1973
<i>fulvidiventris</i>									
Sri Lanka	40	0	0	0	19	T	T	40	Markvong et al., 1975
<i>booduga</i>									
Peninsular India	40	0	0	0	19	T	T	40	Matthey and Petter, 1968; Sen and Sharma, 1983
<i>terricolor</i> <sup>n</sup>									
N Peninsular India	40	0	0	19	0	SM	T	79	Markvong et al., 1975; Sen and Sharma, 1983
S Peninsular India	40	0	3	0	16	SM	T	47-♂ 48-♀	Matthey and Petter, 1968; Manjunatha and Aswathanarayana, 1979; Sen and Sharma, 1983
<i>musculus (castaneus)</i>									
Thailand	40	0	0	0	19	T	T	40	Markvong et al., 1973
<i>Bandicota</i>									
<i>savilei</i>									
Thailand	44	8	0	0	13	T	T	60	Markvong et al., 1973
Thailand	44	8	2	3	8	T	?	70-♀	Tsuchiya et al., 1979
<i>indica</i>									
Thailand	46	9	1	2	10	ST	T	71-♂ 72-♀	Markvong et al., 1973
Thailand	44	11	1	2	7	T	?	72-♀	Tsuchiya et al., 1979
<i>bengalensis</i> <sup>o</sup>									
India	42	6	0	2	12	T	T	58	Sharma and Raman, 1973

TABLE 1—(Continued)

Species	2N	Autosomes				Sex		FN	References	
		M	SM	ST	T	X	Y			
<i>Millardia</i>										
<i>meltada</i>										
Peninsular India	50	1	0	2	21	M	T	57-♂ 58-♀	Raman and Sharma, 1977; Yosida, 1978	
<i>gleadowi</i>										
NW India	40	1	0	2	16	M	T	47-♂ 48-♀	Raman and Sharma, 1977	
<i>Cremnomys</i>										
<i>blanfordi</i>										
Peninsular India	36	0	0	0	17	T	ST	36-♀ 37-♂	Rao and Lakhotia, 1972; Sharma and Gadi, 1977	
<i>cutchicus</i>										
Peninsular India	36	0	0	0	17	T	T	36	Sharma and Gadi, 1977; Raman and Sharma, 1977	
<i>Golunda</i>										
<i>elliotti</i>										
Peninsular India	54	1	0	0	25	SM	T	57-♂ 58-♀	Krishna and Aswathanarayana, 1979	
<i>Tokudaia</i>										
<i>osimensis</i>										
Japan, Amamioshima Is	25	4	3	4	1	SM	O	48	Tsuchiya et al., 1989	
<i>muenninki</i>										
Japan, Okinawa Is	44	1	3	0	17	SM	SM	52	Tsuchiya et al., 1989	
sp.										
Japan, Tokunoshima Is	45	1	3	6	12	T	T	54	Tsuchiya et al., 1989	

<sup>a</sup> Autosomal pair 9 is heteromorphic in some specimens (Baverstock et al., 1977a).

<sup>b</sup> Only a female was karyotyped.

<sup>c</sup> Autosomal pair 2 is polymorphic for a subtelocentric/telocentric combination (Baverstock et al., 1977a).

<sup>d</sup> Autosomal pair 1 is heteromorphic in some specimens (Baverstock et al., 1976a).

<sup>e</sup> Baverstock et al. (1977c) have described the striking polymorphisms in certain autosomal pairs and the sex chromosomes.

<sup>f</sup> Baverstock et al. (1977c) have noted the variation in size and centromere position seen in the sex chromosomes.

<sup>g</sup> Reported under *M. littoralis* (Baverstock et al., 1977a).

<sup>h</sup> In addition to the standard 48 chromosomes there are supernumerary elements bringing the diploid number to 60 (Baverstock et al., 1977a).

<sup>i</sup> Baverstock et al. (1976b) amplified the chromosomal differences between northern and southern Australian populations of *U. caudimaculatus*.

<sup>j</sup> The karyotype, discussed under *M. sp.* by Baverstock et al. (1977a), was taken from a specimen that was later designated as a paratype of the new species *M. hadrourus* (Winter, 1984), which was recently transferred to *Uromys* (Musser and Carleton, 1993).

<sup>k</sup> Karyotype was originally reported under *P. cumingi* (see discussion in text of present report).

<sup>l</sup> Unique pattern of the sex chromosomes is discussed in text.

<sup>m</sup> Kumari et al. (1984) recorded a male with a diploid number of 24.

<sup>n</sup> Karyotypic data are reported under *M. dunni*; *terrlicolor* is an older name (Musser and Carleton, 1993). A range from 47 to 52 has been recorded for the fundamental number because one autosomal pair may consist of telocentrics (Manjunatha and Aswathanarayana, 1979), biarmed chromosomes, or be heteromorphic (Matthey and Petter, 1968; Sen and Sharma, 1983).

<sup>o</sup> In some samples either the X or Y chromosomes are biarmed, reflecting variation in constitutive heterochromatin and affecting magnitude of the fundamental number (Sharma and Raman, 1973).

*mys* is unique and phylogenetically distant not only from any other Philippine murine, but also from genera in any other regional fauna" and falsify the alternative hypothesis that *Phloeomys* "has a closer phylogenetic alliance with genera native to island groups and continents outside of the Philippines." If high number of telocentric chromosomes and low number of biarmed components is more primitive than a complement characterized by mostly biarmed elements (see Viegas-Pequignot et al., 1983, 1985), the karyotypes of *Phloeomys* are far more derived than those characterizing many Old Endemics native to Australia, New Guinea, Sulawesi, and Indochina (table 1). Based on the relationship between diploid and fundamental numbers, the species of *Phloeomys* actually cluster with those of *Rattus* and related genera of New Endemics (fig. 8); this superficial similarity clashes with results from morphology, but is based only on gross chromosomal structure and is probably convergent.

#### CRATEROMYS Group

Species of *Crateromys*, *Carpomys*, and *Batomys* constitute this cluster, but chromosomal data are available only for two of the four known species of *Batomys*, all of which occur in the Luzon and Mindanao faunal regions (Heaney et al., 1987; Musser and Heaney, 1992). The species *salomonseni* was originally described in the monotypic genus *Mindanaomys* (Sanborn, 1953), now viewed as a synonym of *Batomys* (Misonne, 1969; Musser, 1981). The karyotype of *B. salomonseni* consists of 52 telocentric chromosomes and is indistinguishable from that of *B. granti* (fig. 2A, B), offering no evidence to support the recognition of *Mindanaomys*, and demonstrating that standard karyotypes are not useful in distinguishing between these two species.

Among the Philippine murines sampled, karyotypes from the species of *Batomys* most closely resemble those of *Chrotomys* and *Rhynchomys* ( $2N = 44$ ,  $FN = 52-53$ ; fig. 6A, B; table 1), and *Apomys musculus* ( $2N = 42$ ,  $FN = 52$ ; fig. 3B). Apparently, *Batomys* differs from *Chrotomys* and *Rhynchomys* by four Robertsonian translocations and the nature of the Y chromosome, and from *Apomys*

*musculus* by five Robertsonian translocations. However, the similarity between the chromosomal complements of the two species of *Batomys* and those of the other taxa noted above primarily reflects the high numbers of telocentric chromosomes possessed by the two groups, which are presumably primitive features.

The significance of the chromosomal traits of *Batomys* is likewise ambiguous in exposing possible phylogenetic alliances between that genus and those in faunas occurring outside the Philippine Archipelago. The species of *Batomys*, along with *Golunda ellioti* from peninsular India and two species of *Maxomys* from the Indo-Sundaic region, exhibit the highest diploid numbers (52 and 54) among Indo-Australian murines, but nothing else about the chromosomal complements of these species suggests significant phylogenetic links between them (table 1; fig. 8). Except for a pair of small metacentric autosomes and a biarmed X chromosome, the complement of *Golunda* consists of telocentric elements. In karyotypic traits, *Batomys* is more similar to *Golunda* than to any native Philippine genus, but again the similarity likely reflects the retention of primitive features. Although the species of *Maxomys* and *Batomys* share the same diploid number, the *Maxomys* karyotypes are characterized by many biarmed elements and no close relationship is indicated in this group.

A primitive chromosomal complement (as illustrated by conventional preparations) excludes *Batomys* from the New Endemic cluster with their more derived karyotypes. Beyond this observation the karyotypes are uninformative in assessing phylogenetic relationships.

#### APOMYS Group

With eight recognized species, *Apomys* is the largest endemic genus of Philippine murines (Musser 1982a; Heaney et al., 1987). Data presented here demonstrate that the radiation of this group has involved considerable chromosomal evolution. The three species examined differ both in diploid and fundamental numbers, indicating major Robertsonian and non-Robertsonian rearrangements. The karyotypes of *Apomys lit-*

*toralis* ( $2N = 44$ ,  $FN = 88$ ; fig. 3A) and *A. musculus* ( $2N = 42$ ,  $FN = 52$ ; fig. 3B) are separated by one Robertsonian translocation and a series of 18 non-Robertsonian events (possibly the addition of heterochromatic short arms in *A. littoralis*). The species of *Apomys* from Negros Island ( $2N = 30$ ,  $FN = 50$ ; fig. 4) differs from *A. musculus* by at least six Robertsonian translocations and the different nature of the sex chromosomes (biarmed). The impressive chromosomal contrasts seen among these three species is strikingly discordant with the close morphological similarities they share (Musser, 1982a). Their shared morphological features define a tight monophyletic cluster; their distinctive chromosomal traits indicate substantial genetic differences.

*Apomys* was poorly defined when proposed by Mearns (1905), and was subsequently included within *Rattus* by some authors (Ellerman, 1947–48; Sanborn, 1952; Ellerman and Morrison-Scott, 1966). Musser (1982a) was the first to provide a detailed description of the genus and to define those morphological characters that distinguish it from *Rattus*. Species of *Apomys* share certain derived dental features with those of *Melomys* from the New Guinea and Australian region (Musser, 1982a) and some species of *Niviventer* from the Indo-Malayan area (Musser and Heaney, 1992). Based entirely on occlusal molar patterns, some authors have suggested a close phylogenetic relationship between *Apomys* and *Melomys* (Ellerman, 1941; Johnson, 1962; Misonne, 1969), but Musser and Heaney (1992: 84) suspected the similar cusp topography to have evolved independently because “derived cranial and external traits of most species of *Melomys* or *Niviventer* are not shared with *Apomys* . . . , and the apomorphic characters of *Apomys* are not shared with either *Melomys* or *Niviventer*.”

Chromosomal data are informative at certain levels about relationships among these groups. Karyotypes from the three species of *Apomys* (figs. 3 and 4) show clear differences from those of Indo-Australian species of *Rattus* in diploid and fundamental numbers and chromosome shape and size categories (fig. 7B; Baverstock et al., 1977b; tables 1 and 2; fig. 8) and are consistent with the hypothesis that *Apomys* is not a component of the New Endemic cluster.

The species of *Apomys* from Negros and *A. littoralis* are isolated among Indo-Australian murines by their chromosomal traits. The Negros animal has a relatively common fundamental number (50), but its diploid number of 30 is one of the lowest recorded for Indo-Australian species (table 1; fig. 8). The combination of  $2N = 44$  and  $FN = 88$  (the highest fundamental number recorded for Indo-Australian murines) excludes *A. littoralis* from any other murine group for which chromosomal data are available (table 1; fig. 8). However, if most of the biarmed autosomes seen in *A. littoralis* are the result of the addition of heterochromatic short arms, then the basic chromosomal complement is closely similar to that characterizing *A. musculus*. One of Musser and Heaney's (1992: 85) alternative hypotheses about the relationships of *Apomys*, that “species of *Apomys* are allied to groups native to other archipelagos and island continents and not to the Philippines,” is not supported by chromosomal data from samples of *A. littoralis* and the Negros species.

The karyotype of *Apomys musculus* does resemble those from some species of *Melomys* and from other endemic Australian genera (as well as *Niviventer*) in number of chromosome arms ( $FN$  is within the range 48–60; table 2; fig. 8), the predominance of telocentric chromosomes, and the presence of two pairs of small metacentric chromosomes (Baverstock et al., 1977a; table 1). Whether or not these similarities reflect close phylogenetic alliance or reveal only the sharing of retained primitive features is unknown; we suspect the latter.

Among all murines for which we summarized chromosomal data, and particularly among the Philippine murines sampled, *Apomys musculus* ( $2N = 42$ ,  $FN = 52$ ; fig. 3B) is most similar to species of *Chrotomys* ( $2N = 44$ ,  $FN = 52$ ; fig. 6A) and *Rhynchomys* ( $2N = 44$ ,  $FN = 52/53$ ; fig. 6B), apparently differing by a single Robertsonian translocation in the autosomes (because sex chromosomes could not be distinguished from the autosomal complement in *A. musculus* and *Chrotomys*, we are ignorant about possible differences in these elements). Otherwise, all three share two pairs of small metacentric chromosomes, one pair of large submetacentric chromosomes, and one pair of large subtelo-

centric chromosomes in a large field of telocentric autosomes. This shared and probably derived chromosomal pattern of biarmed elements of *Apomys musculus* and two species of shrew rats adds credibility to one of the alternative hypotheses formulated by Musser and Heaney (1992: 84) on the basis of a very few shared derived morphological traits: "Species of *Apomys* are more closely related to shrew rats than to members of the *Phloeomys* or *Crateromys* groups in Division I."

#### CRUNOMYS Group

Of the two genera included in this group of small-bodied shrew rats, *Crunomys* and *Archboldomys* (Musser and Heaney, 1992), only the latter is documented by chromosomal characteristics. *Archboldomys*, containing the sole species *A. luzonensis*, was described by Musser (1982b) on the basis of a single specimen from Mount Isarog, southeastern Luzon.

Musser and Heaney (1992: 89) proposed several alternative phylogenetic hypotheses regarding relationships among the Philippine shrew rats. One postulated close phylogenetic affinity with *Chrotomys* and *Rhynchomys*, an alliance weakly supported by some morphological features. Another proposed that each group of shrew rats was more closely related to genera native to regions outside of the Philippine Archipelago than they were to each other. And a third described the premise that if the *Chrotomys* and *Rhynchomys* groups formed a monophyletic cluster, the *Crunomys* Group may be a sister taxon to that assemblage.

The karyotype of *Archboldomys* (fig. 5), represented only by conventional preparations, differs markedly from those of other sampled species in the number, shape, and size categories of chromosomes. The low diploid number, high number of biarmed chromosomes relative to number of telocentric elements, and the peculiar pattern of the sex chromosomes define a highly derived karyotype compared to those characteristic of species of *Batomys*, *Chrotomys*, *Rhynchomys*, and *Apomys musculus*, and provide no clues as to the phylogenetic relationships of *Archboldomys* among Philippine murines. Whether or not this distinctive karyotype is

unique to the *Crunomys* Group as a whole can only be determined by wider sampling. The unique karyotype of *Archboldomys* and the occurrence of *Crunomys* outside the Philippines on Sulawesi (*Crunomys celebensis*) suggests that it may constitute a clade that is not phylogenetically close to the large-bodied Philippine shrew rats *Chrotomys* and *Rhynchomys* (the first alternative hypothesis referred to above) or to any other group of native Philippine murines (Musser, 1982b; Musser and Heaney, 1992).

Possible relationships between *Archboldomys* and Indo-Australian murines occurring outside the Philippines is equally enigmatic based on chromosomal information. The same low diploid number of 26 has been recorded only for populations of a *Mus* and *Vandeleuria*, and only *Tokudaia osimensis* from the Ryukyu Islands has a lower number (table 1; fig. 8). Nothing else in the karyotypes of these species, or in their derived morphological traits, indicates a close phylogenetic relationship with *Archboldomys*.

#### CHROTOMYS Group and RHYNCHOMYS Group

The large-bodied Philippine shrew rats, *Rhynchomys* and *Chrotomys*, have distinctive cranial, limb, and pelage morphologies that reflect, respectively, semisaltatorial and semifossorial activity and differing adaptations toward vermivory (Musser and Freeman, 1981; Musser et al., 1982; Rickart and Heaney, 1991; Rickart et al., 1991). These specializations are so distinct that Thomas (1898) placed *Rhynchomys* (together with *Echiothrix* of Sulawesi) in the Rhynchomyinae, and associated *Chrotomys* (as well as *Celaenomys*) with the Hydromyinae of New Guinea and Australia. The separation of *Rhynchomys* and *Chrotomys* has been retained by some subsequent authors (Ellerman, 1941; Simpson, 1945; Misonne, 1969). However, among the alternative hypotheses about shrew rat relationships that were postulated by Musser and Heaney (1992: 89) was one noting that as "distinctive as members of the *Chrotomys* and *Rhynchomys* groups are in their morphology, certain derived traits suggest that they form a monophyletic assemblage that excludes all other described Indo-Australian murines." Musser and Heaney also



questioned any close association of the shrew rats with genera occurring outside the Philippines.

Standard karyotypes of *Chrotomys* and *Rhynchomys* ( $2N = 44$ ,  $FN = 52$ ,  $53/54$ ; fig. 6A, B) are similar and may be identical (the nature of the *Chrotomys* Y chromosome is not known). Most of the karyotype of each contains telocentric chromosomes (17 pairs), but both share the biarmed complement, presumably derived, of two pairs of small metacentric autosomes, one pair of large submetacentric chromosomes, and one pair of large subtelocentric elements. This chromosomal evidence provides strong support for the close association of *Chrotomys* and *Rhynchomys*, possibly as sister taxa, as postulated in one of the alternative hypotheses listed by Musser and Heaney (1992).

Chromosomal evidence does not support any close phylogenetic alliance between the Philippine large-bodied shrew rats and those murines native to regions outside the archipelago, especially those on Sulawesi and in the New Guinea–Australian region. Substantial differences between chromosomal complements of Philippine *Rhynchomys* and Sulawesi *Echiothrix* ( $2N = 40$ ,  $FN = 75$ ; table 1; fig. 8; also compare fig. 6 with fig. 10 in Musser, 1990: 15) support the view that the morphological resemblance of these genera is convergent (see the discussion in Musser and Heaney, 1992: 89).

Karyotypes of the species of *Chrotomys* and *Rhynchomys* do resemble those of many Australian and some New Guinean genera of Old Endemics, particularly *Hydromys*, *Xeromys*, and *Parahydromys*; these three “hydromyines” are thought by some to be related

to *Chrotomys* and *Rhynchomys* (Misonne, 1969, for example). All share a fundamental number of 52, a predominance of telocentric chromosomes, and two pairs of small metacentric chromosomes (Baverstock et al., 1977a; Donnellan, 1989; table 1; fig. 8). This karyotype is so prevalent among Australian murines that Baverstock et al. (1977a: 115) argued “that the common and widespread occurrence of such a distinctive karyotype in the same zoogeographic region (Australasia) emphasizes homology” and close phylogenetic relationship among the taxa sampled, although they also admitted that the shared characteristics could “be due to karyotypic convergence.” Because most of the similarity is based on the large number of telocentric chromosomes, presumably a primitive conformation, convergence would reflect the independent reacquisition of those primitive features.

A similar karyotype (with either one or two small metacentrics in an all-telocentric field) is found in species of *Haeromys* ( $2N = 48$ ,  $FN = 54$ ) and *Margaretamys* ( $2N = 42$ ,  $FN = 46$ ), and *Golunda* ( $2N = 54$ ,  $FN = 58$ ) from peninsular India (table 1; fig. 8). Even the African *Malacomys longipes* is characterized by a comparable karyotype ( $2N = 48$ ,  $FN = 52$ , one pair of small metacentric and 22 pairs of telocentric chromosomes), one that has been defined as primitive for murine rodents (Viegas-Pequignot et al., 1983, 1985). The chromosomal complements of these species are more similar to those of the Australian and New Guinea Old Endemics than are karyotypes of either *Chrotomys* or *Rhynchomys*. In fact, the karyotype of *Haeromys* is identical to that of several Australian Old

Fig. 8. The relationship between diploid and fundamental numbers among Indo-Australian murines. Compiled from data listed in tables 1 and 2. Hollow symbols indicate samples with the same combination of  $2N$  and  $FN$  but from different geographic regions. Abbreviations A, *Anisomys*; Apl, *Apomys littoralis*; Apm, *Apomys musculus*; Aps, *Apomys* sp.; Arc, *Archboldomys*; B, *Bandicota*; Bag, *Batomys granti*; Bas, *Batomys salomonseni*; Be, *Berylmys*; Bu, *Bunomys*; Bul, *Bullimus*; C, *Conilurus*; Ch, *Chiruromys*; Chr, *Chrotomys*; Cm, *Cremnomys*; Cp, *Chiropodomys*; Cr, *Crossomys*; D, *Diplothrix*; E, *Echiothrix*; G, *Golunda*; H, *Hydromys*; Ha, *Haeromys*; Hp, *Hapalomys*; L, *Leggadina*; Ld, *Leopoldamys*; Le, *Leporillus*; Lo, *Lorentzimys*; Lp, *Leptomys*; Lt, *Lenothrix*; M, *Mesembriomys*; Ma, *Mallomys*; Me, *Melomys*; Mi, *Millardia*; Mg, *Margaretamys*; Mu, *Mus*; Mx, *Maxomys*; N, *Notomys*; Nv, *Niviventer*; P, *Pseudomys*; Pa, *Parahydromys*; Phc, *Phloeomys cumingi*; Php, *Phloeomys pallidus*; Pi, *Pithecheir*; Po, *Pogonomys*; Pu, *Paruromys*; R, *Rattus*; Re, *Rattus everetti*; Rhy, *Rhynchomys*; S, *Sundamys*; T, *Tokudaia*; Ta, *Taeromys*; U, *Uromys*; V, *Vandeleuria*; X, *Xeromys*; Z, *Zyzomys*.

TABLE 2

Summary of Karyotypic Data for Selected Samples from Species of *Rattus*, *Rattus*-like Groups from the Malayan-Australia Region, and the New Endemics *Sundamys*, *Leopoldamys*, and *Berylmys* from Indo-Malaya, *Bullimus* from Philippines, *Bunomys*, *Taeromys*, and *Paruromys* from Sulawesi, and *Diplothrix* from Japan<sup>a</sup>

Species	2N	Autosomes				Sex		FN	References
		M	SM	ST	T	X	Y		
<i>Rattus</i>									
<i>norvegicus</i> <sup>b</sup>									
Thailand	42	7	0	4	9	T	T	64	Markvong et al., 1973
Vietnam	42	7	0	3	10	T	T	62	Duncan and Van Peenen, 1971
Vietnam	42	7	0	4	9	T	T	64	Cao and Tran, 1984
Malay Peninsula	42	7	0	4	9	T	T	64	Yong, 1969a
Calcutta	42	7	0	3	10	T	T	62	Gadi and Sharma, 1983
SE Asia, Oceania	42	7	0	3	10	T	T	62	Yosida, 1973
Sakhalin, Kamchatka	42	7	0	3	10	T	T	62	Bekasova and Mezhova, 1983
Armianskaya	42	7	0	4	9	T	T	64	Kral, 1971
Ussurijsk	42	7	0	4	9	T	T	64	Kral, 1971
<i>nitidus</i>									
Kathmandu	42	8	0	2	10	T	T	62	Gadi and Sharma, 1983
Vietnam	42	7	0	3	10	T	T	62	Duncan and Van Peenen, 1971
Vietnam	42	7	0	1	12	T	T	58	Cao and Tran, 1984
Thailand	42	8	0	2	10	T	T	62	Markvong et al., 1973
<i>turkestanicus</i>									
Tadzhikskaya	42	7	0	6	7	ST	T	69-♂ 70-♀	Kral, 1971; Bekasova and Mezhova, 1983
Afghanistan	42	7	0	7	6	ST	T	71-♂ 72-♀	Niethammer and Martens, 1975
Nepal	42	7	0	4	9	ST	T	65-♂ 66-♀	Niethammer and Martens, 1975
N India	42	7	0	4	9	T	T	64	Gadi and Sharma, 1983
N India	42	7	0	2	11	ST	T	61-♂ 62-♀	Caldarini et al., 1989
<i>losea</i>									
Thailand	42	7	0	2	11	T	T	60	Markvong et al., 1973; Tsuchiya et al., 1979
Vietnam	42	7	0	3	10	T	T	62	Duncan and Van Peenen, 1971
<i>argentiventer</i>									
Thailand	42	7	0	2	11	T	T	60	Markvong et al., 1973
Vietnam	42	7	0	3	10	T	T	62	Duncan and Van Peenen, 1971
Java	42	7	0	2	11	T	T	60	Yosida et al., 1971
Malay Peninsula	42	7	0	2	11	ST	T	61-♂ 62-♀	Yong, 1969a
<i>tanezumi</i> <sup>c</sup>									
Thailand	42	7	0	2	11	T	T	60	Markvong et al., 1973
Vietnam, mainland	42	7	0	2	11	T	T	60	Duncan and Van Peenen, 1971
Vietnam, mainland	42	7	0	1	12	T	T	58	Cao and Tran, 1984
Vietnam, Con Son Is	42	7	0	2	11	T	T	60	Duncan et al., 1970
Malay Peninsula	42	7	0	2	11	T	T	60	Yong, 1969a; Yosida et al., 1971
India	42	7	0	3	10	T	T	62	Raman and Sharma, 1977; Gadi and Sharma, 1983
N India	42	7	0	2	11	T	T	60	Caldarini et al., 1989
SW India	42	7	0	1	12	T	T	58	Lakhotia et al., 1973
Hong Kong	42	7	0	0	13	T	T	56	Yosida et al., 1971; Yosida, 1980



TABLE 2—(Continued)

Species	Autosomes					Sex		FN	References
	2N	M	SM	ST	T	X	Y		
Taiwan	42	7	0	3	10	T	T	62	Yosida et al., 1971
Japan	42	7	0	0	13	T	T	56	Yosida et al., 1971; Yosida, 1980
<b>Philippines</b>	<b>42</b>	<b>7</b>	<b>0</b>	<b>3</b>	<b>10</b>	<b>T</b>	<b>T</b>	<b>62</b>	Yosida et al., 1971
<b>Philippines</b>	<b>42</b>	<b>7</b>	<b>0</b>	<b>2</b>	<b>11</b>	<b>T</b>	<b>T</b>	<b>60</b>	Present report
<i>rattus rattus</i> <sup>d</sup>									
Russia	38	9	0	2	7	T	T	60	Bekasova and Mezkhova, 1983
Sakhalin	38	9	0	2	7	T	T	60	Bekasova and Mezkhova, 1983
Galapagos Is	38	9	0	2	7	T	T	60	Patton and Myers, 1974
Australia	38	9	0	2	7	T	T	60	Yosida et al., 1971; Yosida, 1980
New Zealand	38	9	0	2	7	T	T	60	Yosida et al., 1971; Yosida, 1980
Papua New Guinea	38	9	0	2	7	T	T	60	Yosida et al., 1971; Yosida, 1980
U.S., California	38	9	0	2	7	T	T	60	Yosida et al., 1974
India <sup>e</sup>	38	9	0	3	6	T	T	62	Raman and Sharma, 1977; Gadi and Sharma, 1983
Sri Lanka	40	8	0	2	9	T	T	60	Yosida et al., 1972; Yosida, 1980
<i>tiomanicus</i>									
Malay Peninsula	42	7	0	4	9	T	T	64	Yong, 1969a
Pulau Tioman	42	7	0	4	9	T	T	64	Yong et al., 1972
Pulau Perhentian									
Besar	42	7	0	5	8	T	T	62	Yong et al., 1972
Pulau Tengool	42	7	0	5	8	T	T	62	Yong et al., 1972
<i>exulans</i>									
Malay Peninsula	42	7	0	2	11	T	T	60	Yong, 1969a
Thailand	42	7	0	2	11	T	T	60	Markvong et al., 1973; Tsuchiya et al., 1979
Vietnam	42	7	0	2	11	T	T	60	Duncan and Van Peenen, 1971
SE Asia, Oceania	42	7	0	2	11	T	T	60	Yosida, 1973
Papua New Guinea	42	7	0	2	11	T	T	60	Dennis and Menzies, 1978
<b>Philippines</b>	<b>42</b>	<b>7</b>	<b>0</b>	<b>2</b>	<b>11</b>	<b>T</b>	<b>T</b>	<b>60</b>	Present report
<i>hoffmanni</i>									
Sulawesi	42	7	0	2	11	ST	T	61-♂ 62-♀	Musser and Holden, 1991
<i>everetti</i>									
<b>Philippines</b>	<b>42</b>	<b>7</b>	<b>0</b>	<b>7</b>	<b>6</b>	<b>T</b>	<b>T</b>	<b>70</b>	Tabuena, 1977
<b>Philippines</b>	<b>42</b>	<b>7</b>	<b>0</b>	<b>4</b>	<b>9</b>	<b>T</b>	<b>T</b>	<b>64</b>	Present report
<i>sikkimensis</i> <sup>f</sup>									
Thailand	42	8	0	6	6	T	T	70	Markvong et al., 1973
Hong Kong	42	8	0	6	6	T	T	70	Yong, 1969b; Yosida et al., 1971
<i>remotus</i>									
Thailand, Samui Is	42	7	0	4	9♂	T	T	64	Markvong et al., 1973
"Rattus"—Sulawesi									
<i>xanthurus</i>									
Sulawesi	42	7	0	1	12	ST	T	59-♂ 60-♀	Musser and Holden, ms
"Rattus"—Sunda Shelf									
<i>annandalei</i> <sup>h</sup>									
Malay Peninsula	42	6	0	3	11	T	T	60	Yong, 1969a
Malay Peninsula	42	7	0	1	12	T	T	58	Yosida, 1973

TABLE 2—(Continued)

Species	2N	Autosomes				Sex		FN	References
		M	SM	ST	T	X	Y		
“ <i>Rattus</i> ”—New Guinea–Australia									
<i>lutreolus</i>									
Australia	42	7	0	2	11 <sup>i</sup>	T	T	60	Baverstock et al., 1977b
Tasmania	42	7	0	2	11	T	T	60	Dartnall, 1970
<i>tunneyi</i>									
Australia <sup>j</sup>	42	7	0	3	10	T	T	62	Baverstock et al., 1977b
<i>fuscipes</i>									
Australia <sup>k</sup>	38	9	0	2	7	T	T	60	Baverstock et al., 1977b
Australia	38	9	0	1	8	T	T	58	Yosida, 1973; Martin, 1969
<i>leucopus</i>									
Australia <sup>l</sup>	34	10	1	2	3	T	T	60	Baverstock et al., 1977b
Papua New Guinea	34	10	1	2	3	T	T	60	Dennis and Menzies, 1978
Papua New Guinea	34	10	1	1	4	T	T	58	Yosida, 1973
<i>sordidus</i>									
Australia	32	11	0	3	1	T	T	60	Baverstock et al., 1977b
Australia <sup>m</sup>	32	12	0	2	1	T	T	60	Yosida, 1973; Martin, 1969
<i>colletti</i>									
Australia <sup>n</sup>	42	7	0	2	11	T	T	60	Baverstock et al., 1977b
<i>villosissimus</i> <sup>o</sup>									
Australia	50	3	0	2	19	T	T	60	Baverstock et al., 1977b
<i>niobe</i>									
Papua New Guinea	32	11	1	2	1	T	T	60	Dennis and Menzies, 1978
<i>verecundus</i>									
Papua New Guinea	32	11	1	2	1	T	T	60	Dennis and Menzies, 1978
<i>steini</i> <sup>p</sup>									
Papua New Guinea	32	11	1	2	1	T	T	60	Dennis and Menzies, 1978
<i>mordax</i> <sup>p</sup>									
Papua New Guinea	32	11	1	2	1	T	T	60	Dennis and Menzies, 1978
<i>Sundamys</i>									
<i>muelleri</i> <sup>q</sup>									
Malay Peninsula	42	6	0	2	12	SM	T	59-♂ 60-♀	Yong, 1968
Malay Peninsula	42	6 <sup>q</sup>	0	3	11	SM	T	61-♂ 62-♀	Yosida, 1973
<i>Leopoldamys</i>									
<i>edwardsi</i>									
Malay Peninsula	42	3	0	4	13	T	T	56	Yong, 1968
Vietnam	42	2	0	8	10	T	T	62	Cao and Tran, 1984
<i>sabanus</i>									
Malay Peninsula	42	2	0	4	14	T	T	54	Yong, 1968; Yosida, 1973
Thailand	42	2	0	4	14	T	T	54	Markvong et al., 1973; Tsuchiya et al., 1979
Vietnam	42	2	0	4	14	T	T	54	Duncan and Van Peenen, 1971; Cao and Tran, 1984
<i>neilli</i>									
Thailand	44	2	0	2	16	T	T	50	Marshall, 1977; Tsuchiya et al., 1979

TABLE 2—(Continued)

Species	Autosomes					Sex		FN	References
	2N	M	SM	ST	T	X	Y		
<i>Berylmys</i>									
<i>bowersii</i>									
Malay Peninsula	40	7	1	5	6	T	T	66	Yong, 1968; Yosida, 1973
Thailand	40	7	1	5	6	T	T	66	Markvong et al., 1973
<i>berdmorei</i>									
Thailand	40	7	1	5	6	T	T	66	Markvong et al., 1973
Vietnam <sup>r</sup>	40	7	1	5	6	T	T	66	Duncan et al., 1970
<i>Bullimus</i>									
<i>bagobus</i>									
Philippines	42	7	0	1	12	T	T	58	Present report
<i>Bunomys</i>									
<i>chrysocomus</i>									
Sulawesi	42	7	0	1	12	T	T	58	Musser, ms; Duncan, 1976
<i>andrewsi</i>									
Sulawesi	42	7	0	1	12	T	T	58	Musser, ms
<i>penitus</i>									
Sulawesi	42	7	0	2	11	T	T	60	Musser, ms
<i>Taeromys</i>									
cf. <i>arcuatus</i>									
Sulawesi	42	6	0	2	12	SM	ST	60	Musser, ms
<i>celebensis</i>									
Sulawesi	39	4	0	1	14	T	O	49-♂	Musser, ms
	40	4	0	1	14	T	T	50-♀	Musser, ms
<i>Paruromys</i>									
<i>dominator</i>									
Sulawesi	38	0	1	4	13	T	T	48	Musser, ms
<i>Diplothrix</i>									
<i>legatus</i>									
Ryukyu Is	42	7	0	3	10	M	ST	64	Tsuchiya, 1979

<sup>a</sup> Samples are selective because we list only information obtained from specimens which we are confident were correctly identified. The notation "*Rattus*" indicates groups that are now placed in that genus but will probably be excluded as separate monophyletic clusters (see Musser and Carleton, 1993).

<sup>b</sup> Additional chromosomal polymorphisms found in samples of *R. norvegicus* caught in the wild are reported by Diaz de la Guardia et al. (1981) and Tsuchiya (1980).

<sup>c</sup> What has been called "*Asian Rattus rattus*" with  $2N = 42$  is distinct from the European or Oceanic *R. rattus* with  $2N = 38$  (Yosida et al., 1971; Yosida, 1980). Baverstock et al. (1983: 978) noted that if "the chromosomal, electrophoretic and laboratory hybridization data are considered together, it seems that the  $2n = 38$  and  $2n = 42$  forms are best considered as incipient species," and in the places where "they meet, they may introgress, become sympatric without interbreeding or one may replace the other depending upon the prevailing biological conditions." If the Asian populations are considered a separate species, they should be called *R. tanezumi* (Musser and Carleton, 1993). Some geographic samples of *R. tanezumi* have subtelocentric and telocentric polymorphisms in pairs 1, 9, and 13 (see, for example, Yosida et al., 1971; Markvong et al., 1973; Raman and Sharma, 1977; Tsuchiya et al., 1979; Yosida and Harada, 1985; reported under *R. rattus*).

<sup>d</sup> Seven pairs of the metacentric chromosomes range from medium to small; in size and gradation they are closely similar to the seven metacentric pairs in most of the other species of *Rattus*. The other two metacentric pairs are large chromosomes and represent fusion of one pair (*R. rattus* from Sri Lanka) or two pairs (*R. rattus rattus*) of telocentric chromosomes (Yosida, 1980).

<sup>e</sup> Most researchers recognize only pairs 1 and 9 as subtelocentrics in the complement of the  $2N = 38$  karyotype

Endemics, and Musser (1990) suggested that the resemblance reflected the conservation of a primitive karyotype and not close phylogenetic alliance.

In summary, the points of chromosomal resemblance between the Philippine shrew rats and species of Old Endemics from Australia and New Guinea may reflect simply the retention of a primitive karyotypic conformation. The points of dissimilarity between these two groups (pairs of large submetacentric and subtelocentric chromosomes in *Chrotomys* and *Rhynchomys*), which are derivations, unite the Philippine shrew rats and exclude them from close relationship with the New Guinea–Australian fauna. There is no compelling evidence from karyotypes that *Chrotomys* and *Rhynchomys* are closely related to the “hydromyines,” a hypothesis supported by morphological characters (Musser and Heaney, 1992) as well as spermatozoal traits for *Chrotomys* (Breed and Musser, 1991).

### DIVISION III (NEW ENDEMICIS)

Of the six genera placed in this assemblage by Musser and Heaney (1992), chromosomal characteristics are known for only *Bullimus* and *Rattus*.

*Bullimus* is another genus that was incompletely defined when described by Mearns (1905), and as with *Apomys*, it was subsequently placed within *Rattus* by some authors (Thomas, 1907; Ellerman, 1941; Missonne, 1969). Musser and Heaney (1992) provided an emended diagnosis of *Bullimus* with a list of characters that define it as a distinct group. Nevertheless, they placed it within their Division III along with *Rattus* and other New Endemics sharing a similar morphological grade. The karyotype of *Bullimus bagobus* (2N = 42, FN = 58; fig. 7A) clearly places it close to species of *Rattus* (fig. 7B), as well as the Sulawesi *Bunomys* (table 2; fig. 8), but provides no additional resolution.

TABLE 2—(Continued)

←  
(Yosida, 1980, for example), but Indian investigators also include pair 13 as subtelocentric rather than telocentric (Raman and Sharma, 1977; Gadi and Sharma, 1983).

<sup>f</sup> Karyotypes of this species have been reported under the name *Rattus sladeni*. However, the karyotype of “*Rattus sladeni*” reported by Duncan and Van Peenen (1971: 337) and based on USNM 357664 from Vietnam is an example of *R. tanezumi molliculus*.

<sup>g</sup> Markvong et al. (1973) noted that pair 11 is heteromorphic.

<sup>h</sup> We do not know if the differences in autosomal elements reflect population variation or different interpretations of photographic prints.

<sup>i</sup> Pair 5 is heteromorphic in some individuals (Baverstock et al., 1977b).

<sup>j</sup> Baverstock et al. (1977b) also recorded variation in the diploid numbers in some samples (41 or 43 instead of 42).

<sup>k</sup> Some specimens of *R. fuscipes assimilis* were found to have 39 chromosomes instead of 38 (Baverstock et al., 1977b).

<sup>l</sup> The karyotype is slightly different in *R. leucopus cooktownensis* (Baverstock et al., 1977b).

<sup>m</sup> Recorded by Yosida (1973) under *R. conatus*. Dennis and Menzies (1978) discussed samples of the *sordidus* group from New Guinea.

<sup>n</sup> Five pairs of metacentrics consist of large chromosomes formed by fusions of telocentrics and are not homologous to the metacentric pairs found in most other species of *Rattus*, and most of the telocentric pairs have resulted from fission of small metacentrics, as Baverstock et al. (1977b) have clearly shown in their illustrations of karyotypes.

<sup>o</sup> The low number of metacentric pairs and high number of telocentric pairs reflect fission of metacentric pairs 14–19 and fusion of telocentric pairs 2 and 3, and 8 and 9 (Baverstock et al., 1977b).

<sup>p</sup> Dennis and Menzies (1978) discussed karyotypes of samples from lowlands and highlands which they identified as *R. ruber*; the lowland sample is actually *R. mordax* and the highland rats are *R. steini* (Taylor et al., 1982).

<sup>q</sup> Yosida (1973) counted seven pairs of small metacentric chromosomes in *Sundamys muelleri* but judged from his karyogram one of these pairs is clearly subtelocentric.

<sup>r</sup> Results represent our interpretation of the karyogram published by Duncan et al. (1970). Both Yong (1969a) and Cao and Tran (1984) presented different karyotypes for *Berylmys berdmorei*.

The genus *Rattus* is represented within the oceanic Philippines (excluding the Palawan region) by three native and six introduced species (Heaney et al., 1987; Musser and Heaney, 1992; Musser and Carleton, 1993). The indigenous *Rattus everetti* (2N = 42, FN = 64; fig. 7B) is karyotypically similar to a host of other species in the genus, including the introduced *R. exulans* and *R. tanezumi mindanensis*, in sharing a diploid number of 42, a fundamental number within the range 56–64, and a series of seven pairs of small metacentric chromosomes (Baverstock et al., 1977b; table 2). Tabuena (1977) reported a fundamental number of 70 for specimens of *Rattus everetti* from undisclosed Philippine localities. Although this difference between her and our (FN = 64) samples may represent geographic variation in the karyotype of the species, it most likely reflects differences in preparation quality and the inherent difficulties in differentiating telocentric and subtelocentric chromosomes.

Musser and Heaney (1992: 126) proposed two alternative phylogenetic hypotheses about relationships among the Philippine New Endemics: either they are more closely related to each other or instead are allied to New Endemics in regions outside the Philippines. Chromosomal data from samples of *Bullimus* and *Rattus everetti* are unhelpful in resolving this.

### CONCLUSIONS

Chromosomal data from Philippine murines support some hypotheses concerning the phylogenetic relationships of Philippine murids proposed by Musser and Heaney (1992), and have suggested others. Among the species we examined, seven distinct chromosomal groups can be identified: (1) *Phloeomys*, (2) *Batomys*, (3) *Apomys* sp. from Negros, (4) *Apomys littoralis*, (5) *Apomys musculus*, *Chrotomys*, and *Rhynchomys*, (6) *Archboldomys*, and (7) *Rattus* and *Bullimus*. *Phloeomys* and *Archboldomys* are karyotyp-

ically unique compared with the other Philippine species.

If our interpretation of polarity in chromosomal characters is correct, the species of *Batomys* possess the most primitive complement. Their similarity with other species may only reflect the shared retention of primitive features, and in our view the chromosomal data from *Batomys* are ambiguous in assessing phylogenetic alliances of this genus. Impressive variation in chromosomal traits characterizes the three species of *Apomys* sampled. Two of them are at opposite fringes of the cloud of Indo-Australian rodents depicting the relationship between diploid and fundamental number (fig. 8). *Apomys musculus* shares derived elements with species of *Chrotomys* and *Rhynchomys*, and the three taxa form the tightest cluster among the species we sampled (fig. 8); this contrasts with evidence provided by morphology (Musser and Heaney, 1992). Chromosomal traits characterizing *Bullimus* and *Rattus everetti* are consistent with their placement within the New Endemic cluster, a grouping also supported by morphology. Results from analyses of chromosomal data support the general hypothesis that the murine fauna of the Philippines is composed of separate clades that represent independent ancestral invasions of the archipelago (Heaney and Rickart, 1990; Musser and Heaney, 1992).

Several of the Philippine species are characterized by standard chromosomal complements composed of all or mostly telocentric elements. Similar karyotypes have been documented for murines native to Australia, New Guinea, Sulawesi, the Sundaic region, Indochina, and peninsular India. If such a chromosomal constitution is primitive, as we have hypothesized, its presence suggests the retention of primitive (and probably ancestral) chromosomal complements in different murine faunas scattered throughout the Indo-Australian region rather than phylogenetic alliance among them.

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