

RESULTS OF THE ARCHBOLD
EXPEDITIONS. NO. 102.
THE SPECIES OF *CHIROPDOMYS*,
ARBOREAL MICE
OF INDOCHINA AND THE MALAY
ARCHIPELAGO

GUY G. MUSSER

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 162 : ARTICLE 6 NEW YORK : 1979

RESULTS OF THE ARCHBOLD
EXPEDITIONS. NO. 102.
THE SPECIES OF *CHIROPDOMYS*,
ARBOREAL MICE
OF INDOCHINA AND THE MALAY
ARCHIPELAGO

GUY G. MUSSER

*Archbold Curator, Department of Mammalogy
The American Museum of Natural History*

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 162 : ARTICLE 6
NEW YORK : 1979

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 162, article 6, pages 377-445, figures 1-16, tables 1-7

Issued April 3, 1979

Price. \$4.65 a copy

This article completes Volume 162.

ISBN 0003-0090

Copyright © The American Museum of Natural History 1979

CONTENTS

Abstract	381
Introduction	381
Abbreviations and Methods	383
Acknowledgments	387
The Species of <i>Chiropodomys</i>	388
<i>Chiropodomys karlkoopmani</i> , New Species	389
<i>Chiropodomys major</i>	395
<i>Chiropodomys calamianensis</i>	400
<i>Chiropodomys muroides</i>	403
<i>Chiropodomys gliroides</i>	406
Summary of the Species	427
Morphological Similarities Among the Species of <i>Chiropodomys</i>	428
Discussion	433
The Genus <i>Chiropodomys</i>	433
Possible Relatives of <i>Chiropodomys</i>	436
Other Questions and Speculations	438
Literature Cited	441

ABSTRACT

Chiropodomys is an Asian genus of arboreal mice that contains five species. One, *C. karlkoopmani*, is new and described here; it is represented by a specimen from North Pagai Island in the Mentawai islands off the west coast of Sumatra. Another, *C. major*, is found in Sarawak and Sabah. A third, *C. calamianensis*, occurs in the Palawan area and is known by specimens from the islands of Balabac, Palawan, and Busuanga. The fourth, *C. muroides*, the smallest in body size within the genus, is represented by a few specimens from Sabah and northern Kalimantan and occurs together with *C. major* and *C. gliroides*, the fifth species. The latter has the most extensive geographic range of the five. It is found throughout Indochina (Assam, Burma, south-

ern China, Laos, Vietnam, and Thailand), the Malay Peninsula, and on the Sunda Shelf (Sumatra, Borneo, Java, Bali, Nias and Tjujuh islands, and the Natuna islands). The morphological and geographic limits of the five species of *Chiropodomys* are outlined, some of the geographic variation is described, the available information about their natural histories is summarized, and their taxonomies are revised. Defining characteristics of each species within *Chiropodomys* is important in order to determine their place in the pattern of zoogeographic alliances among species of murid rodents which occur throughout the Far East, from Indochina to Australia.

INTRODUCTION

In 1855, Mr. F. Skipwith Esq. C.S. obtained a few mammals and invertebrates from Cherrapunji in the Khasi Hills of Assam. He donated his small collection to the Indian Museum at Calcutta. In the lot were samples of three kinds of mice which Edward Blyth, who was then curator of zoological collections at the Indian Museum, described in the published report (1856) for the October Meeting, 1855, of the Asiatic Society of Bengal. Blyth named one of the mice *Mus gliroides* because the structure of its body, tail, and feet reminded him of the British dormouse, *Muscardinus avellanarius*. Thirteen years later, Peters (1869) described a rodent very similar to *Mus gliroides*. The morphology of his specimen indicated special adaptations and habits to Peters and he named it *Chiropodomys penicillatus*, the hand-footed mouse with a tufted tail. Blyth's allusion to a dormouse and Peters's to an animal with feet that are like hands previewed the information on morphology and natural history that in later years would describe more completely the characteristics of mice in the genus *Chiropodomys*.

We now know there are several species in Peters's genus of hand-footed mice. Distinctive features common to all of them are a short head and a small body clothed in dense fur,

large eyes, long vibrissae on the muzzle and above the eye, a long tufted tail, and specialized feet. Both front and hind feet are short and broad. The first digit of each foot bears a nail; the other digits end in large pads adorned by short, sharp claws. All the species are arboreal and live in tropical forests of western India, Burma, Thailand, Laos, Vietnam, southern China, the Malay Peninsula, the large islands of Sumatra, Java, and Borneo, and several smaller islands on the Sunda Shelf. They are not known to occur on any islands forming the backbone of the Philippine chain, from Luzon to Mindanao, or anywhere in the Indonesian Archipelago east of Borneo and Bali. No fossils have been found.

During the years which followed Blyth's report, biologists learned little about how many species were in *Chiropodomys*, their morphological and geographic limits, or their natural histories. By 1940, there was still scanty information on natural history, but several new forms had been named and described. In 1940, Chasen's handlist of Malaysian Mammals was published, and in it he summarized the taxonomy of *Chiropodomys*. Seven species were listed: *C. gliroides*, with one subspecies (*C. g. gliroides*) in Indochina and another (*C. g.*

peguensis) from the Malay States, Sumatra, Bunguran Island, and North Natuna islands; *C. niadis* from Nias Island off the coast of West Sumatra; *C. anna* on Java; and *C. major*, *C. legatus*, *C. pictor*, and *C. pusillus*, all occurring on Borneo. There were few specimens of any of these forms and Chasen's entries were not so much an indication of the real number of species as they were a list of how many scientific names had been applied to single specimens and small samples during the period from 1855 to 1940, a fact Chasen (1940, p. 184) himself recognized: "I have seen so few examples of this genus from Malaysia, that no reconstruction of the genus is here attempted."

A year later, in a monograph on the families and genera of living rodents, Ellerman (1941) recognized the same seven species of *Chiropodomys* listed by Chasen; included an eighth one, *C. calamianensis*, from Busuanga Island in the Calamianes Group of the Philippines; and a ninth, *C. fulvus*, a Chinese mouse which Ellerman had not seen. Tate (1936) had earlier noted that *C. fulvus* should be excluded from *Chiropodomys*. Anthony (1941) later allocated *fulvus* to *Vernaya*, a new genus he described and also compared with both *Vandeleuria* and *Chiropodomys*.

By the 1960s, there were enough specimens in collections of museums so Ellerman (1961) could conclude that only one species, *C. gliroides*, occurred in Indochina; Sody (1941) could ally the populations on Java with *C. gliroides* and report its presence on Bali as well; Harrison (1966) and Medway (1969) could write that there was only one species, *C. gliroides*, from the Malay Peninsula; Medway (1965) could show that three species lived in Borneo, two of them, *C. major* and *C. muroides*, known only from northern Borneo, and the third, *C. gliroides*, more widespread and apparently the Bornean representative of the species that was known from Malaya and Indochina; and Sanborn (1952) could amplify the geographic distribution of *C. calamianensis*, writing about specimens from Palawan. These reports still did not clarify either the number of species in *Chiropodomys* or their morphological and geographic limits. The samples that had been included in *C. gliroides*, *C. muroides*, *C. ma-*

ajor, and *C. calamianensis* were considered valid species, and the mouse from Nias Island, *C. niadis*, was regarded as distinctive. The change in content of *Chiropodomys* from the seven species in Chasen's list to the five recorded in the literature during the next 30 years was still an estimate; for example, by the late 1960s Walker (1968) stated there were eight species in the genus but Misonne (1969), at the other extreme, claimed there was but one.

I am interested in the species of *Chiropodomys* because they are part of that rich fauna of rats and mice found in tropical forests of the Indochinese region and the Malay Archipelago, a fauna containing species that are diverse in morphology and habitus. Several years ago while sorting through a batch of unidentified rodents, which had been collected from islands on the Sunda Shelf, I found a specimen of *Chiropodomys* from North Pagai Island, one of the Mentawai group west of Sumatra. The specimen was the first example of *Chiropodomys* I had seen from an island in the Mentawai group, islands separated from the rim of the Sunda Shelf by deep water and populated by a unique assemblage of mammals. The specimen was distinctive in size and color and seemed to represent an undescribed species. To describe the animal and compare it with other species in the genus could be done only after I had looked at many samples of *Chiropodomys* so as to define the morphological and distributional limits of the species which occurred elsewhere. The specimen from North Pagai Island contained new information: from it I could extend the geographic distribution of *Chiropodomys*, expand the morphological and specific diversity of the genus, and glean additional zoogeographic data about relationships between mammal faunas from the Mentawai islands and those from nearby Sumatra and other islands on the Sunda Shelf.

A revised taxonomic assessment of *Chiropodomys* with the attendant changes in the morphological and distributional scope of the genus will provide general information about murid rodents of Indochina and the Sunda Shelf, and also help answer questions asked in the larger context of zoogeographic relationships among faunas from those areas and the

endemic groups on the Philippines and the islands scattered east of Wallace's Line, from Celebes to New Guinea. If species of *Chiropodomys* do not occur on the main islands of the Philippines or east of Borneo, then are there relatives or ecological counterparts within the rodent assemblages in those archipelagos? There is, for example, a group of small arboreal rats in the genus *Pogonomys* which lives in forests on New Guinea. In structure of body, skull, and teeth the species resemble those in *Chiropodomys*. Are they phylogenetically closely related to that Malayan genus (Misonne, 1969) or do their morphologies reflect convergence rather than close alliance (Tate, 1936)? If the two groups are related, then other populations of a similar type of arboreal animal may occur on islands located between the eastern margin of the Sunda Shelf and New Guinea; Celebes is such an island.

Separated from Borneo by the deep Makassar Strait, Celebes is the first large land area east of the Sunda Shelf. Most of its mammals are unique. Almost 30 percent of the fauna consists of rats and mice in the family Muridae: more than 30 species are endemic and live in tropical evergreen forests; six are associated with habitats made and maintained by humans and may have been inadvertently brought to Celebes through human transport (Musser, 1977). The endemic rats and mice are interesting not only because they are morphologically and ecologically diverse—some species are terrestrial, others are scansorial, and a few are arboreal—but because they are also a composite of zoogeographic alliances with rats and mice of the Sunda Shelf and Indochina to the west, the Philippine Islands to the north, and the Moluccas to the east. Certain species and small groups of species on Celebes are clearly related to rats and mice in each of those places. Some forest species on Celebes appear to be relicts related to similar relictual groups scattered from the Philippines to New Guinea. Other species are unique, isolated not only in the mountain forests of Celebes but in the pattern of zoogeographic relationships formed by rodent faunas in the Malayan and Indonesian archipelagos. To understand the diversity and origins of the Celebesian fauna requires accu-

rate information about the groups of rats and mice from places to the west, north, and east of that large island.

Before determining the nature of the relationships of species on Celebes with faunas elsewhere, I have had to learn the characteristics of the rats and mice from New Guinea, from the Philippines, and especially those from Indochina and the Malay Archipelago: their morphologies, habitats, and geographic ranges; the kind of geographic variation within each, if any; and something about their life histories. The species of *Chiropodomys* are part of the Indochinese and Malayan fauna and may be morphologically and phylogenetically related to two groups of arboreal rats and mice on Celebes, or may be only unrelated ecological counterparts of them. For that reason, and because the climbing mice of Southeast Asia and the Sunda Shelf are of interest by themselves, I have tried to answer questions about the species in *Chiropodomys* by evaluating older information and collecting new data; I report the results here.

ABBREVIATIONS AND METHODS

Most specimens I examined consisted of study skins with skulls; a few were preserved in alcohol. In the discussions that follow each specimen is referred to by catalogue number and an abbreviation of the institution in which it is stored. Names of those museums and the persons who lent me specimens are listed below.

AMNH, the American Museum of Natural History, New York
 BM, British Museum (Natural History), London; Mr. John E. Hill and Ms. Paula Jenkins
 BZM, Zoologisches Museum, an der Humboldt-Universität zu Berlin; Dr. Renate Angerman
 FMNH, Field Museum of Natural History, Chicago; Dr. Patricia W. Freeman
 MNHN, Museum National d'Histoire Naturelle, Paris; Dr. Francis Petter
 MCZ, Museum of Comparative Zoology at Harvard College, Cambridge; Ms. M. Edith Rutzmoser
 MZB, Museum Zoologicum Bogoriense, Bogor; Dr. Sampurno Kadarsan and Mr. Boedi
 NMS, National Museum (formerly Raffles Museum), Singapore; Mr. Eric Alfred
 RMNH, Rijksmuseum van Natuurlijke Historie, Leiden (includes the collections of the late Max

Bartels, Jr. and H.J.V. Sody); Dr. Chris Smeenk SMT, Staatliches Museum für Tierkunde, Dresden; Dr. Alfred Feiler USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Dr. Richard W. Thorington, Jr. ZMA, Zoological Museum of the University of Amsterdam, Amsterdam; Dr. P.J.H. van Bree

Measurements of the skin, skull, and teeth of each specimen are in millimeters. Values for the standard skin measurements of total length, length of tail, length of hind foot, and length of ear were recorded by the collectors on labels attached to the skins; I used most of those values. I subtracted length of tail from total length to obtain length of head and body for each specimen. I have assumed that each collector measured the length of tail from its base to its tip and not to the end of the tail brush, which extends well beyond the tip of the tail. I measured the hind feet, including claws, of most specimens; I used my values whenever they differed from those recorded on the skin labels. Length of ear was probably measured from the notch by most collectors but may have been measured from the base of the external pinna in some specimens; values for this measurement are less reliable than those for other dimensions of the skin. I have listed them in some tables to provide an estimate of length of ear, but I did not use these data in comparisons among samples. Because the skins were measured by many different persons and because I am unsure of the limits of the dimensions, I have been careful about interpreting the significance of differences in values for external measurements between some samples and caution readers to do the same.

Cranial and dental measurements were taken with either Anderson's (1968) craniometer attached to a Wild M5 Stereo-microscope or with dial calipers graduated to tenths of millimeters. I originally took 27 cranial and dental measurements but finally used only 23. The limits of those measurements are illustrated in figure 1 and defined below.

BB, breadth of braincase: Measured just above the squamosal roots of each zygomatic arch.

BIF, breadth across incisive foramina: The greatest distance across both foramina.

BIT, breadth across incisor tips: The distance across the tips of the incisors.

BM¹, breadth of palatal bridge at first molars: The least distance between the lingual edge of the alveolus of the first molar and the lingual edge of the alveolus of the opposite molar.

BM³, breadth of palatal bridge at third molars: The least distance between the lingual edge of the alveolus of the third molar and the lingual edge of the alveolus of the opposite molar.

BMF, breadth of mesopterygoid fossa: The distance from one edge of the mesopterygoid fossa to the other.

BR, breadth of rostrum: The greatest breadth across the rostrum, including the bony capsules enclosing the nasolacrimal canals.

BZP, breadth of zygomatic plate: The least distance between the anterior and posterior edges of the zygomatic plate.

HB, height of bulla: The distance from the dorsal surface of the bulla to its ventral surface.

HBC, height of braincase: From the top of the braincase to the ventral surface of the basisphenoid bone.

IB, interorbital breadth: The least distance, as viewed dorsally, across the frontal bones between the orbital fossae.

IF-M¹, incisive foramina to M¹: The distance from the posterior margins of the incisive foramina to the anterior alveolar margins of the first molars.

LB, length of bulla: The length of the bulla, excluding the bony eustachian tube.

LD, length of diastema: The distance from the posterior alveolar margins of the upper incisors to the anterior alveolar margins of the first upper molars.

LIF, length of incisive foramina: The distance from the anterior edge of one of the foramina to its posterior edge.

LM¹⁻³, alveolar length of maxillary toothrow: The distance from the anterior edge of the alveolus of the first molar to the posterior edge of the alveolus of the third molar.

LN, length of nasals: The distance from the anterior tip of the nasal bones to the most posterior suture between the nasal and frontal bones, measured parallel to the surface of the nasals.

LPB, length of palatal bridge: The distance from the posterior edge of the incisive foramina to the posterior margin of the bony palate.

LR, length of rostrum: From the tip of the nasal bones to the posterior margin of the zygomatic notch (the anterior edge of the dorsal maxillary root of the zygomatic plate).

ONL, occipitonasal length: The distance from the

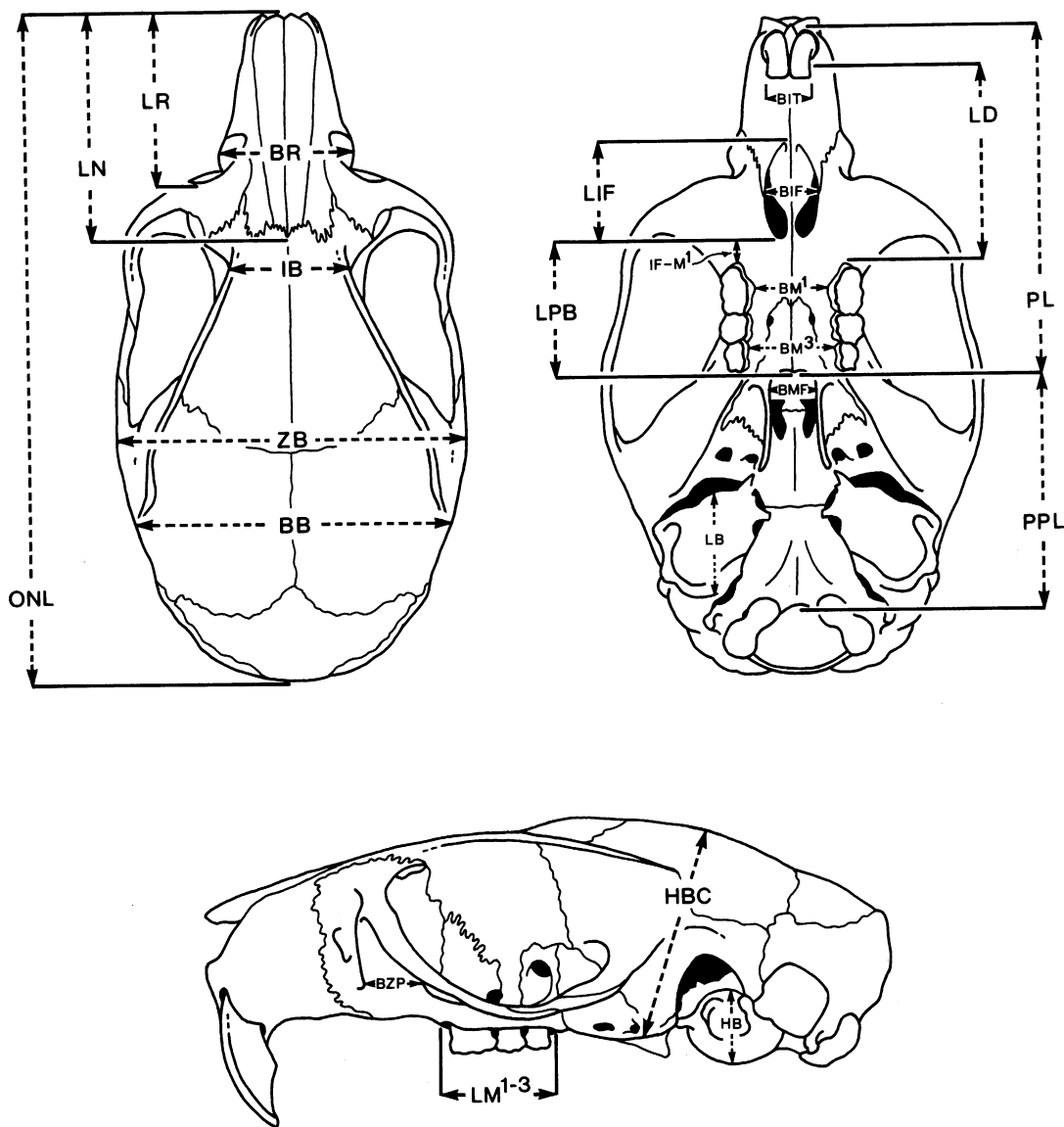


FIG. 1. Views of cranium and teeth of an adult *Chiropodomys gliroides* showing limits of cranial and dental measurements which are defined in the text. Abbreviations, listed alphabetically, are as follows:

BB, breadth of braincase
 BIF, breadth across incisive foramina
 BIT, breadth across incisor tips
 BM¹, breadth of palatal bridge at M¹
 BM³, breadth of palatal bridge at M³
 BMF, breadth of mesopterygoid fossa
 BR, breadth of rostrum
 BZP, breadth of zygomatic plate
 HB, height of bulla
 HBC, height of braincase
 IB, interorbital breadth
 IF-M¹, incisive foramina to M¹

LB, length of bulla
 LD, length of diastema
 LIF, length of incisive foramina
 LM¹-³, length of maxillary tooththrow
 LN, length of nasals
 LPB, length of palatal bridge
 LR, length of rostrum
 ONL, occipitonasal length
 PL, palatal length
 PPL, postpalatal length
 ZB, zygomatic breadth

tip of the nasals to the posterior margin of the occiput.

PL, palatal length: The distance from the anterior alveolar margins of the incisors to the posterior edge of the palatal bridge.

PPL, postpalatal length: The distance from the posterior margin of the palatal bridge to the posterior edge of the basioccipital bone—the ventral lip of the foramen magnum.

ZB, zygomatic breadth: The greatest breadth across the zygomatic arches.

The four measurements I excluded were the greatest length of the skull, palatilar length, distance from the posterior alveolar margin of the third molar to the back edge of the palatal bridge, and breadth of bulla (defined in Musser, 1970). I used the values for occipitonasal length to estimate size of the skull instead of greatest length. Greatest length of the skull and occipitonasal length are measurements of the same dimension in most species of murid rodents. These may or may not be the same for specimens of *Chiropodomys*. In any sample of the genus there are some individuals in which the anterior margins of the nasals terminate a few tenths of a millimeter behind the front edges of the premaxillary bones which form the sides of the rostrum. The composition of the pooled sample from the Malay Peninsula is a good example of this variation in length of nasals. Out of 23 specimens there are three in which greatest length of the skull (from anterior margins of the premaxillary bones to posterior margin of the occiput) is the same as occipitonasal length (from the tip of the nasals to the back of the occiput); nine which have a longer occipitonasal length, indicating that the nasals extend beyond the sides of the rostrum; and 11 in which the values for greatest length of skull are higher than those for occipitonasal length, pointing to nasals that are shorter than the rostrum in those specimens.

Of the other three measurements which I excluded, the variation in palatilar length is correlated with that in palatal length and I used the latter; the extension of the bony palate beyond the third molars was not helpful in discriminating among samples; and breadth of the bulla was difficult to measure and the results too variable to use in the analyses—limits

defining length and height of bullae are clear and values from those measurements are more reliable for estimating bullar size.

Depth of the zygomatic notch is another measurement I usually take from most skulls but did not from crania of *Chiropodomys*. This measurement indicates the extension of the front margin of each zygomatic plate beyond the anterior edge of the dorsal maxillary root of the plate. Terrestrial species of murids have wide zygomatic plates which project well beyond the front margins of the zygomatic arches. In most species of arboreal rats and mice, however, the plates either barely extend beyond, are even with the tops of the arches, or their edges are concave, each curving back behind the front part of the arch. In specimens of *Chiropodomys* the plate either does not extend forward beyond the front edge of the top of the zygomatic arch or barely projects beyond, not far enough to measure.

Most of the cranial and dental data I used in the analyses are from crania and upper teeth. I examined mandibles and lower tooththrows but did not measure them. The shapes of the mandibles and configurations of cusps on the teeth are similar among all species of *Chiropodomys*; size constitutes the primary difference and I used values from measurements taken from crania and upper tooththrows to quantify this distinction among the samples.

Samples, which form the basis of my comparisons among species and among geographic variants within a single species, are composed of adults. I examined juveniles to learn the kinds of differences between juveniles and adults and to determine if any of the species went through an intermediate molt between the juvenile and adult stages. Although collections contain mostly adults, I found enough juveniles to determine that immature animals molt from juvenile into adult pelage and apparently do not pass through a subadult transition. I defined adults as those specimens in full adult pelage. I did not separate the adults into different relative age groups based on criteria such as wear of teeth but grouped all adults together. A large sample, therefore, will contain young adults (specimens that have just completed the molt from juvenile to adult pelage), very old adults

(examples with teeth worn to the point where their occlusal patterns are no longer evident), and adults of intermediate ages.

I pooled males and females to increase the size of each sample and so obtain a better estimate of the range of variation in the dimensions I measured than would have resulted from smaller samples. Were there large series available from each locality, I would have separated them into males and females and within each sexual group would have divided them into relative ages, then compared samples of the same sex and similar relative age. Such comparisons would have allowed finer resolution of the patterns formed by individual, sexual, geographic, and interspecific variation within *Chiropodomys*. More refined discrimination among the samples may reveal more details in the patterns of variation but will probably not significantly alter the results I present here.

My statistical analyses of the samples are not elaborate. For each sample that was large enough to treat in a statistical way I computed the mean and standard deviation, standard error of the mean, recorded the observed range of values, and sample size. To test for significant differences between sample means I employed Student's *t*-test. When I refer to differences that are significant in the sections to follow, I mean that the differences between means of two samples are significant at the .05 level of statistical significance or lower.

Throughout the text I have usually used older names of places; below is a list of those names and their currently used counterparts.

INDOCHINA: Assam, Burma, Thailand, Laos, southern China, Vietnam, Cambodia (Democratic Kampuchea)

CEYLON: Sri Lanka

MALAYA: West Malaysia

SUMATRA: Sumatera

JAVA: Jawa

BORNEO: Sarawak, Sabah, Brunei (East Malaysia); Kalimantan (Indonesian Borneo)

NATUNA ISLANDS: Kepulauan Bunguran

CELEBES: Sulawesi

MOLUCCAS: Maluku

NEW GUINEA: Irian Jaya (Indonesian New Guinea); Papua New Guinea

I have also used *sungai* (stream or small

river); *gunong*, the Malay spelling, and *gunung*, the Indonesian form (mountain); and *pulau* (island) to designate some localities.

ACKNOWLEDGMENTS

Reports like this one are conceived and written alone but between conception and completed manuscript the paper reflects the work and interest of many people. The contributions begin with the persons who supervise museum collections from which I borrowed specimens. They, whose names are listed above, and their supporting technical staffs took time and effort to look for and send me specimens I requested. Two persons went to extra trouble: Dr. P.J.H. van Bree examined specimens in Bogor and sent me information I did not have; Ms. Paula Jenkins studied and measured a large series in the British Museum for me. Gathering and analyzing data is usually a solitary chore but I was helped by Ms. Margareta Becker who carefully measured much of the material at the National Museum of Natural History in Washington, D.C. Good illustrations are critical to communicating results, and much about the species of *Chiropodomys* is conveyed to readers by the superb drawings of Ms. Fran Stiles, and the excellent photographs made by Mr. Arthur Singer, Chief Photographer at the American Museum of Natural History. My rough manuscript pages were transformed into typescript by Ms. Helen M. Ellis. The completed manuscript was read, criticized, and evaluated by the following persons: Dr. Sydney Anderson, Ms. Margareta Becker, Mr. Michael D. Carleton, Ms. Mary Evensen, Mr. Lawrence R. Haeney, Dr. David Klingener, Dr. Karl F. Koopman, Ms. Marie A. Lawrence, Dr. Emily C. Oaks, Ms. Nancy Olds, Ms. Katherine Rabenau, Ms. R. Jean Stout, and Dr. Richard G. Van Gelder. I am grateful to all for their excellent contributions to this paper.

The results I report here are part of a larger study of the rats and mice from the Indo-Malayan region. My work in the past has been generously supported by the late Mr. Richard Archbold of Archbold Expeditions Inc. and that commitment has been unselfishly and graciously continued by Mrs. Frances A. Hufty.

During the period from 1973 to 1976 I lived and worked in Indonesia. There I saw some places where specimens of *Chiropodomys* had been collected, and I studied examples of the genus in the museum at Bogor. The Celebes Fund of the American Museum of Natural History provided money for my travels in Indonesia and for my work there. The Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences) and the Museum Zoologicum Bogoriense sponsored my research. I could not have pursued my studies without the assistance and cooperation of personnel in those two institutions. Dr. Sampurno Kadarsan, for-

mer Director of the Museum Zoologicum Bogoriense, aided me in many ways and is largely responsible for making the time that I spent in his country both very pleasant and productive. While I lived in Indonesia I sometimes used facilities in the laboratories of the U.S. Naval Medical Research Unit No. 2 in Jakarta and Tomado. The various officers in charge of that post over the three years—first Dr. P.F.D. Van Peenen, then Dr. Kurt Sorenson, finally Dr. David T. Dennis—always welcomed me to the laboratories and helped me in many ways; I appreciate their interest and thank them for their help and hospitality.

THE SPECIES OF *CHIROPDOMYS*

I have examined 379 specimens of *Chiropodomys*, obtained from localities shown in figures 5 and 8. In the last decade much more material has been available for study than was accessible to taxonomists working from the late 1800s into the 1940s. During that early period most samples came from Indochina, the Malay Peninsula, and Java. The bulk of today's material still derives from those places. At an earlier time the species of *Chiropodomys* from Borneo and Sumatra, and a few smaller islands on the Sunda Shelf were represented by a handful of specimens. Present-day samples from those areas are still meager; collectors have gathered additional specimens only from northern Borneo.

I have sorted the specimens into five lots, each defined and distinguished from the others by a combination of features: color of pelage; size and proportions of the head and body, tail, hind feet, skull, incisors, and molars; and pattern of cusps on certain molars. I judge that each lot represents a species. I do not have data from breeding experiments, but the morphological evidence and geographic origins of the samples support the hypothesis that each group represents a genetic entity which is distinct and isolated from each of the others. The diagnostic characteristics of each set of samples are discrete and do not overlap those of another. And three of the lots come from the same locality on the lower slopes of Gunong

Kinabalu in Sabah. One consists of a small *Chiropodomys* with head and body less than 90 mm. long, brown upperparts and gray underparts, a small skull, and wide pale yellow incisors. The second contains a slightly larger mouse with a head and body less than 100 mm. long, reddish brown upperparts and white underparts, small skull, and narrow orange incisors. The third is composed of a large *Chiropodomys* with head and body over 100 mm. long, grayish brown upperparts and white underparts, large skull, and narrow orange incisors. The three lots have already been recognized as samples of three species (Medway, 1965). The smallest one, *C. muroides*, is known from Sabah and eastern Kalimantan. The next largest in body size is *C. gliroides*, and the sample of it from Borneo represents a geographic variant of a species that is also found on Java, Sumatra, smaller islands on the Sunda Shelf, the Malay Peninsula, and Indochina. The largest is *C. major*, a species sampled only from localities in Sabah and Sarawak.

The remaining two groups of samples are comprised of the largest mice in the genus. One set of specimens is from the Palawan region. The examples resemble those of *C. major* but their pelage is bright with buffy and orange hues. *Chiropodomys calamianensis* is the name for this morphological type. The fifth lot consists of one specimen from North Pagai Island

in the Menawai Group. If that specimen is a reliable sample of the kind of *Chiropodomys* living on North Pagai then it represents a species that in body size is the largest in the genus, in color of pelage is the most distinctive, and in geographic origin is the only one from an island off the fringe of the Sunda Shelf.

Some diagnostic features of the five kinds of *Chiropodomys* are summarized in table 1. I discuss these species in the following paragraphs, where I shall elaborate their morphological

characteristics; describe their diagnostic features, geographic distributions, and any geographic variation; and summarize information about their natural histories. I begin with the animal from North Pagai Island, which needs to be named and formally described.

***Chiropodomys karlkoopmani*, new species**

HOLOTYPE: A young adult female, AMNH 103305, from North Pagai Island (Pulau Pagai Utara), part of the Mentawai islands off the

TABLE 1
Contrasts in Size, Color, and Dental Features Among Species of *Chiropodomys*^a

	<i>karlkoopmani</i> North Pagai	<i>major</i> Sabah	<i>calamianensis</i> Palawan Area	<i>muroides</i> Sabah	<i>gliroides</i> Malaya
Head and body	107	105.3, 94-114 (17)	117.0, 109-122 (4)	71.0, 66-88 (3)	86.2, 69-102 (57)
Tail	171	128.4, 109-144 (17)	153.5, 140-171 (4)	88.7, 85-91 (3)	116.0, 94-143 (57)
<u>Tail</u> Head and body	160	122	131	125	135
Hind foot	29	24.1, 21-28 (17)	25.5, 25-26 (4)	16.0, 15-17 (3)	18.8, 15-22 (57)
Ear	17	16.8, 13-27 (17)	16.8, 15-19 (4)	17.0, 14-19 (3)	15.6, 13-19 (57)
Weight	—	37.5, 32-43 (4)	40.5	—	20.4, 15-32 (33)
Cranium	29.3	29.2, 27.5-30.2 (17)	28.7, 28.4-29.2 (3)	20.8, 19.9-21.6 (2)	25.3, 24.0-26.7 (23)
M ¹⁻³	4.6	4.7, 4.2-5.1 (17)	4.4, 4.2-4.6 (4)	3.0, 2.9-3.0 (3)	3.8, 3.3-4.2 (23)
Upperparts	Grayish brown	Grayish brown	Bright buffy brown or chestnut	Buffy brown	Pale chestnut
Underparts	Pale gray	White, cream, or buffy white	Orange-white to or- ange-red	Buffy dark gray	White
Strip between back and belly	None	None	Buffy orange	None	Ochraceous
Cheeks	Grayish brown	White	Buffy	Gray	Buffy
Tail	Basal 1/3 brown, rest white	Brown; mono- color or mottled be- neath	Brown or blackish brown; mono- color	Brown; mono- color	Brown; mono- color
Incisors	Orange	Orange	Orange	Pale Yellow	Orange
Cusp t7 (fig. 4)	Round and wide	Round and wide	Round and wide	Long and thin	Long and thin

^aThe mean, observed range, and size of sample (in parentheses) are listed for each measurement. Lengths are in millimeters, ratios are in percentages, and weights are in grams.

coast of southwestern Sumatra. The specimen was collected in primary forest on flat lowlands, probably near the coast, on January 18, 1935. It was sent to the American Museum of Natural History by J. J. Menden (original field no. 235).

The holotype consists of a study skin, cranium, and mandibles. The skin was prepared well and is in good condition; unfortunately, the distal 25 mm. of the tail are missing (fig. 3). The cranium is complete except for a missing left jugal (fig. 6). The angular process and posterior margin of each mandible were broken off and are now lost.

DISTRIBUTION: Known only from North Pagai Island.

MEASUREMENTS: See the values listed in tables 1 and 2.

DEFINITION AND DIAGNOSIS: *Chiropodomys karlkoopmani* is a large, arboreal mouse (fig. 2). It has dark grayish brown upperparts, pale gray underparts, dark brown feet, and a long, densely haired and bicolored tail. The basal third of the tail is dark brown and the distal two-thirds is white, resembling a slender, feathery plume. (I assume that the missing 25 mm. of the tail were white. This pattern is usual in the species of rats and mice from the Indo-Malayan and Australian regions that have bicolored tails in which the basal portion is brown and the rest is white.)

The combination of large size, grayish head and body, and long, bicolored tail is unique in the genus *Chiropodomys* and distinguishes *C. karlkoopmani* from the four other known species in the genus: *C. muroides*, *C. gliroides*, *C. major*, and *C. calamianensis* (table 1). No examples of the other species are as large and long-tailed as *C. karlkoopmani*, none of them has a bicolored tail, and none is known to occur on any of the Mentawai islands; all samples of the other four are from large and small islands on the Sunda Shelf, from the Malay Peninsula, or from Indochina.

DESCRIPTION OF THE HOLOTYPE: The holotype, a female, is the only sample of *C. karlkoopmani*. The nature of the pelage, configuration of the cranium, and amount of wear on the molars indicate to me that the

specimen is adult but still young. The animal is clothed in what appears to be fresh adult pelage. There are spots on top of the head, back, and rump where new hairs are proliferating through the skin. The cranium has mostly attained an adult configuration, although the braincase is still a bit globular and slightly oversized relative to the rostrum. All the molars are slightly worn, and patterns of their occlusal surfaces are clear. Although the female had mostly completed the molt into fresh adult pelage, it was probably sexually immature when caught. The two pairs of inguinal mammae on the skin are small and do not look as if they were functional.

Upperparts of the holotype are covered by short, dense, and soft pelage. The coat is 8 to 10 mm. thick; short, inconspicuous guard hairs extend up to 5 mm. beyond the thick layer of overhairs. Overall color of the upperparts is grayish brown and in this feature *C. karlkoopmani* resembles *C. major*. The hairs are dark gray for most of their lengths and tipped with brown or pale tawny hues. Sides of the body are gray and the top of the head, back, and rump are darker and distinguished by a mixture of dark brown and brownish tawny hues that provide highlights to the top of the head and body, highlights the sides do not have. Each eye is encircled by a conspicuous dark brown ring. The tip of the nose is also dark brown. The cheeks are grayish brown. Facial vibrissae on the muzzle and over the eyes are abundant and long, some of which reach 60 mm., whereas most others extend to more than half the length of the head and body. The ears are thin, dark brown, and scantily haired.

The demarcation between color of upperparts and underparts is gradual and subtle. The chin and throat are white. The rest of the ventral surface is pale gray; the short hairs, 3 to 4 mm. long, have gray bases and either pale gray or white tips. The underparts are paler and more somber than the buffy dark gray venter of *C. muroides*, the only other species of *Chiropodomys* with gray over the chest and abdomen (table 1).

The front and hind feet are large and appear robust. Not only are they actually larger than



FIG. 2. *Chiropodomys karlkoopmani*. Drawn by Fran Stiles.

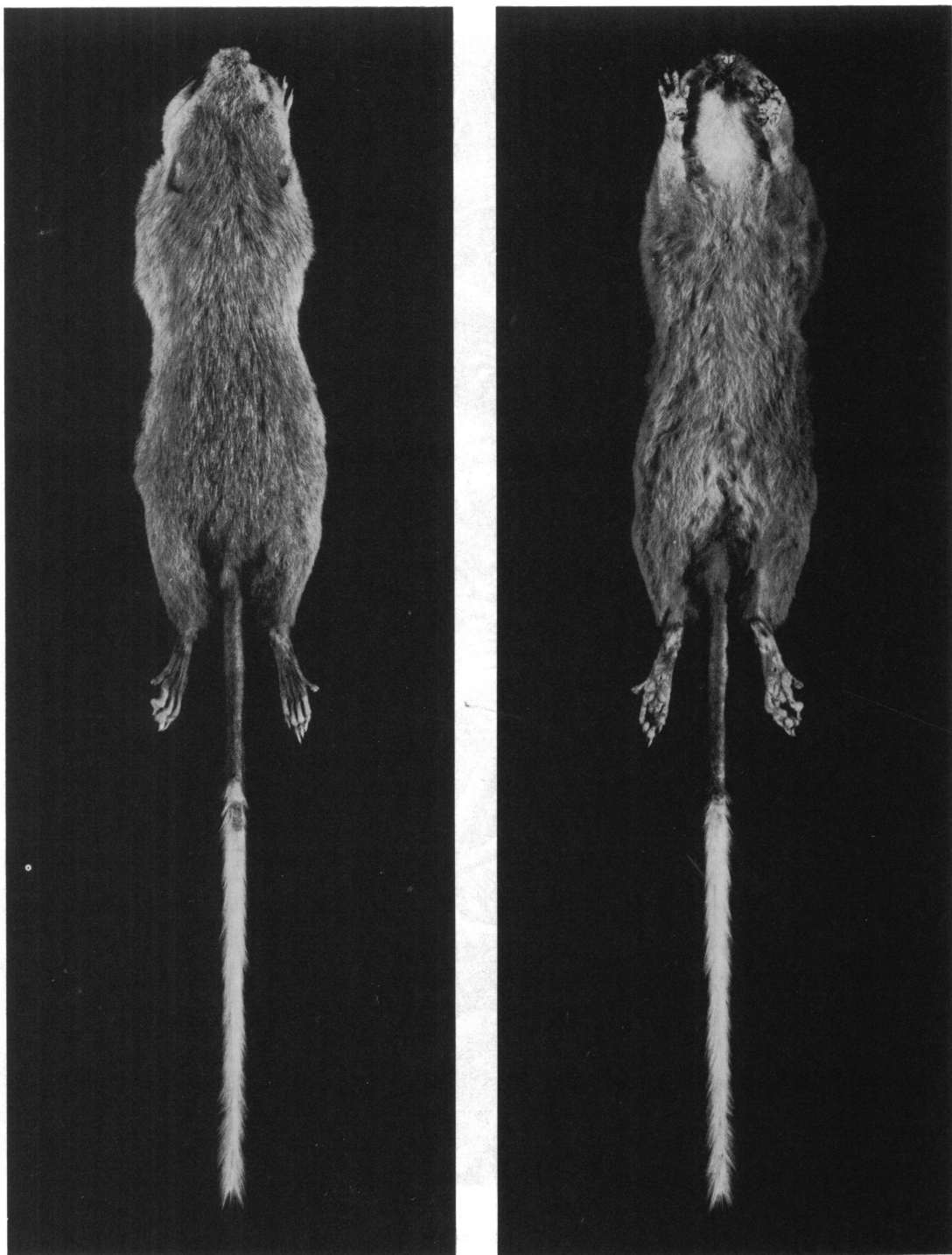


FIG. 3. *Chiropodomys karlkoopmani*. Dorsal and ventral views of the holotype (AMNH 103305). The tail is incomplete. Photographed by Arthur Singer.

those in all other species of *Chiropodomys*, but the feet are much longer relative to length of head and body. Their upper surfaces are densely covered with dark brown fur which extends onto some of the digits. The stumpy first digit of each front foot and the longer first digit of each hind foot bear flat nails; the other digits terminate in short, sharp claws. Palmar and plantar surfaces are naked.

The tail is long, both in actuality and relative to length of head and body. It is covered with long hair, longer than in any other species of *Chiropodomys*. Hairs near the base of the tail are 2 mm. long. From the base to the distal portion of the tail the hairs gradually increase in length until those at the end of the tail are 10 mm. long; hairs at the tip, which are now missing, were probably even longer. In samples of the other kinds of *Chiropodomys* the hairs near the tip of the tail are usually 5 mm. long, rarely longer than 7.

The cranium of *C. karlkoopmani* is illustrated in figure 6 and is compared with crania from older adults of *C. major*, *C. calamianensis*, *C. gliroides*, and *C. muroides*. Its basic shape is like those of the other species: a short and broad rostrum, nearly as wide as long, behind which is a long braincase that in side view arches up from the rostrum and down sharply to the occiput. In dorsal view the interorbital area is wide, the braincase broad and round. High, prominent bony ridges extend from the back edges of the orbits along the margins of the frontal bones and onto the sides of the braincase. The front margins of the zygomatic arches come off the skull at nearly right angles. The zygomatic plates are narrow and do not project in front of the anterior parts of the zygomatic arches. In ventral view the incisive foramina are short and very wide; they occupy less than half the distance from the incisors to the front margins of the first molars and end well in front of those teeth. The bony palatal bridge is very long and ends 0.1 mm. behind the posterior margins of the third molars. The mesopterygoid and ectopterygoid fossae are broad. The bullae are small and globular.

I did not measure the mandibles or lower tooththrows of *C. karlkoopmani*. The mandibles are larger than those in the other species but

their shapes are closely similar; otherwise, there are no other important differences. Patterns formed by cusps and ridges on the occlusal surfaces of the lower molars are like the patterns in *C. gliroides* (fig. 15) and the other species of *Chiropodomys*.

Shape and proportions of the incisors of *C. karlkoopmani* resemble those in samples of the other two large species of *Chiropodomys* and the smaller *C. gliroides* but are different from those in *C. muroides*. The enamel fronts of the upper incisors are bright orange, the lowers are yellowish orange. Their size and color contrast with the relatively wider and heavier incisors of *C. muroides*, which have pale yellow enamel.

The upper molars of *C. karlkoopmani* are small relative to the size of its skull, and the patterns formed by the arrangements of cusps and ridges on the occlusal surfaces of the teeth are similar to those of *C. gliroides* (fig. 15) and the other kinds of *Chiropodomys*. There is one cusp configuration that *C. karlkoopmani* shares with *C. major* and *C. calamianensis* and not with either *C. gliroides* or *C. muroides*. In each species the occlusal surfaces of the first and second molars consist of three rows of cusps which, with an exception, are similar in position and shape among all the species. The exception is each lingual cusp of the third row on the first and second molars (designated cusp t7 by Miller, 1912). In samples of *C. karlkoopmani*, *C. major*, and *C. calamianensis*, the species with large bodies, these cusps are large and round (fig. 4). In examples of the two species with small bodies, *C. gliroides* and *C. muroides*, the cusps are small and narrow, appearing elongate rather than round.

Similarities and differences in body and cranial proportions between *C. karlkoopmani* and the other species are based on comparisons between the holotype, a young adult, and a series of each of the other species in which each sample is larger and the ages of the specimens range from young to old adults. Hence some of the proportional features I record here may not characterize larger samples of *C. karlkoopmani*. Body and cranial proportions of that species are closely similar to proportions of the other two species of large *Chiropodomys*, *C. major* and *C. calamianensis* (fig. 7). The exceptions include the tail, hind feet, and parts of the cra-

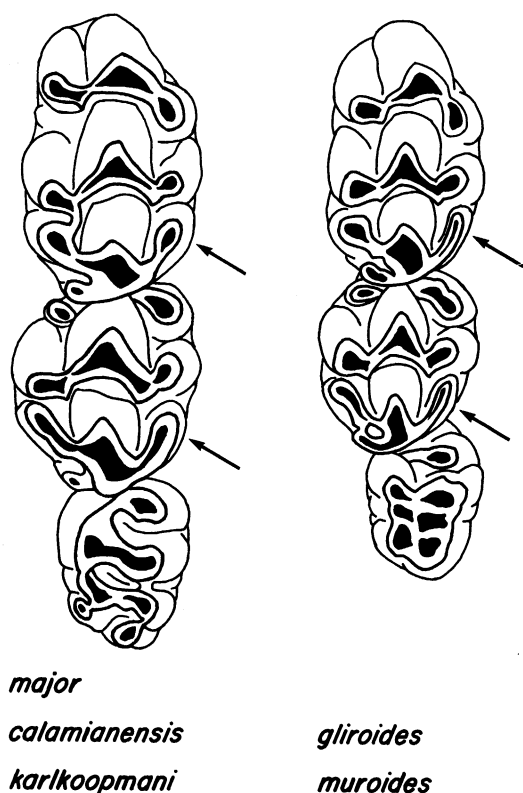


FIG. 4. Diagrammatic occlusal views of the right upper tooththrows in *Chiropodomys*. Arrows point to the posterior lingual cusps (designated cusp t7 by Miller, 1912) of the first and second molars. At the left is the shape of each cusp in the three species with large bodies; on the right is the configuration in the two species which are small in size of body.

nium. The tail and hind feet are longer relative to length of head and body than in either *C. major* or *C. calamianensis*, and also relatively longer than in samples of the two species of smaller mice, *C. gliroides* and *C. muroides*. Compared with the two larger species of *Chiropodomys*, *C. karlkoopmani* has a wider interorbital region relative to zygomatic breadth or breadth of braincase, and larger bullae relative to size of cranium. The incisive foramina are very short and broad in *C. karlkoopmani*, as they are in *C. muroides*, and the size of these openings accounts for the proportional differences in the palatal region between *C. karl-*

koopmani and *C. muroides* and the other three species (fig. 9). The palatal bridge is longer relative to either palatal length or occipitonasal length than in *C. major*, *C. calamianensis*, or *C. gliroides*, and the incisive foramina are shorter relative to palatal length. In both these proportional characteristics the specimen of *C. karlkoopmani* resembles the small *C. muroides* and differs conspicuously from samples of all the other species.

The specimen from North Pagai Island represents a distinctive species of *Chiropodomys*. Coloration of its pelage and the pattern of its tail are unique within the genus. It is also the largest of the known species. This feature may not be apparent from the values listed in table 1 where I have compared body measurements of the holotype of *C. karlkoopmani* with samples of the two other large-bodied species, *C. major* and *C. calamianensis*, samples which contain specimens that range in age from young to old adults. When the specimen of *C. karlkoopmani* is compared with young adults of *C. major* and *C. calamianensis* of similar age—determined by configuration of cranium and wear of teeth—its larger size is conspicuous: *C. karlkoopmani* has a larger body, longer tail—both actually longer and longer relative to length of head and body—and much larger front and hind feet. If more and older adults of *C. karlkoopmani* are ever collected from North Pagai Island, the values for body measurements of the holotype should fall within the small end of the range of variation in such a series.

A rendering of how *C. karlkoopmani* probably looks in life is depicted in figure 2. Morphological features of the skin and skull point to an arboreal animal. The terse note written on a tag tied to the skin indicates only that the specimen was obtained from primary forest in lowlands. I have no other information about the natural history of the species.

ETYMOLOGY: I am pleased to name *C. karlkoopmani* after Dr. Karl F. Koopman, a colleague in the Department of Mammalogy at the American Museum of Natural History. A student of evolutionary biology in general, the Mammalia in particular, and the Chiroptera in detail, the breadth of Koopman's interest in biology is reflected in his conversations, lec-

tures, and published reports; I think it appropriate to name the species in his honor.

Chiropodomys karlkoopmani is one of the three kinds of *Chiropodomys* that is characterized by grayish upperparts and large body size. The gray-backed and white-bellied mouse from northern Borneo is another large member of *Chiropodomys*, a species represented by more material than is the animal from the Mentawai islands.

Chiropodomys major

From November 1854, until January 1856, Alfred Russel Wallace traveled and collected in southern Sarawak, the only place he stopped in Borneo during his wanderings through the Malay Archipelago. In Sarawak he studied the spectacular Bornean animals and the forests, focusing on insects and orangutans, and also managed to pursue his curiosity about life and language of the Dyaks. Always the geographer as well as the naturalist, he journeyed for more than a month up the Sungei Sadong to its sources. During that trip he obtained specimens of a large, long-tailed tree-mouse, an animal with a grayish brown back and a white belly. Wallace eventually shipped the mice to the British Museum in London; apparently they were the first examples of that kind of Bornean mouse to be received by any European museum. Oldfield Thomas (1893a) described Wallace's specimens under the name *Chiropodomys major*. In that publication he compared *C. major* with *C. gliroides*, the only other species of *Chiropodomys* known at the time: "Colour and proportions very much as in *Ch. gliroides*, but size conspicuously greater, especially so far as the skull is concerned. . . . Upper surface fawn, the bases of the hairs slate-coloured; whole of lower surface pure white. Ears large, naked. Tail long, hairy, and pencilled as usual; uniformly brown above and below. . . . Skull with a flatter profile than in *Ch. gliroides*; anterior palatine foramina very short, ending half their own length in front of the molars. Molars broad and rounded."

Eighteen years after the description of *C. major* was published, Thomas (1911) named and described two other species of large *Chi-*

ropodomys from northern Borneo, *C. legatus* and *C. pictor*. The specimens were collected by A. Everett from the slopes of Gunong Kinabalu in Sabah. The holotype of *C. legatus* is an adult male, obtained in October 1892. Everett collected the holotype of *C. pictor* during January 1894; it is young and smaller than the example of *C. legatus*. Both represent a large *Chiropodomys* with grayish brown upperparts and white underparts. Thomas's description of *C. pictor* is similar to the one he wrote for *C. legatus*, the smaller size of the former was the only feature that distinguished the two. And Thomas thought that both *C. legatus* and *C. pictor* were different animals from *C. major*, although even he noted the close similarity in external features between *C. legatus* and *C. major*.

Before 1965, the names *major*, *legatus*, and *pictor* were three of four that had been applied to samples of *Chiropodomys* from northern Borneo; *pusillus* was the fourth, a name given to a small mouse with reddish brown upperparts and white underparts. Chasen (1940) listed all four as species in his list of Malaysian mammals because he had not seen enough specimens to evaluate their taxonomic status. Ellerman (1949) thought there were at least two distinct kinds of *Chiropodomys* in northern Borneo, a large one, which he called *C. major*, and a small one he recognized as *C. pusillus*. Later, Ellerman and Morrison-Scott (1955) associated *pictor* with *C. gliroides*—as a subspecies—and this allocation was followed by Hill in 1960. In 1965 Medway pointed out that the holotypes of *C. major*, *C. legatus*, and *C. pictor* were really samples of one species and that *major* was the earliest scientific name for this large *Chiropodomys* from Borneo. I have examined those three holotypes and I agree with Medway's conclusion. The holotypes of *legatus* and *pictor* are from Gunong Kinabalu, that of *major* is from southern Sarawak; the holotype of *legatus* is an old adult, those of *pictor* and *major* are young adults; the morphological differences between the specimens are those associated with age, not those indicative of different species.

There are many more examples of *C. major* in collections of museums than of the other

kinds of *Chiropodomys* which are known from Borneo. My knowledge of that large species comes from 31 specimens. Most were collected on Gunong Kinabalu, a few were taken in Sarawak; these specimens and localities are listed below (the localities are arranged from north to south) and indicated on the map in figure 5.

SABAH

Gunong Kinabalu: BM 94.7.2.43 (holotype of *C. pictor*), 94.7.2.44, 95.11.6.4, 16.5.9.2, and 16.5.9.3; "above Pinokok," BM 93.4.1.21 (holotype of *C. legatus*); Tenompok, 4900 feet, USNM 268764 (for-

merly MCZ 36536), MCZ 36535, 36537, and 36538 (these four were originally reported by Allen and Coolidge, 1940); Tenompok, 4000 feet, USNM 301098 and 301099; Bundu Tuhan, about 4000 feet, USNM 292879-292884, BM 71.3058 and 71.3059.

Ranau Area: Seven miles west of Ranau, USNM 301097; Poring, Mount Kinabalu National Park, 1600 feet, USNM 489361-489365.

SARAWAK

Sungai Baram, Marudi: unregistered specimen in BM.

Sadong: BM 56.9.19.11 (holotype of *C. major*) and 56.9.19.12

Bukar, Samarahan: BM 55.999 and 55.1000.

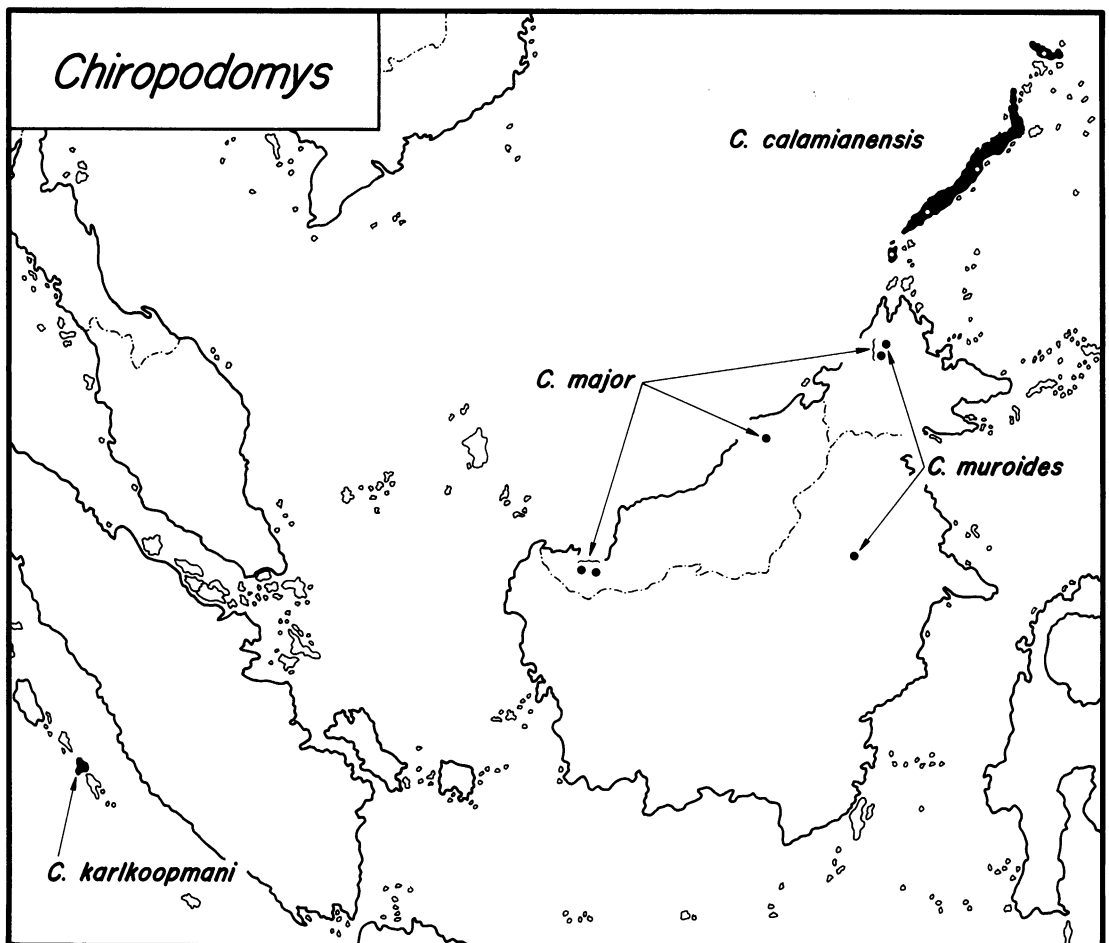


FIG. 5. Geographic distributions, based on specimens examined of four species of *Chiropodomys*. Localities are arranged from north to south for *C. calamianensis* (circles), *C. major* (dots), and *C. muroides* (dots). The localities and information about specimens from each place are discussed in the text in the account of that species.

Chiropodomys major is a large, handsome mouse, the largest kind of *Chiropodomys* known from Borneo. Its pelage, like that in other species of the genus, is short (5 to 8 mm. thick), dense, and woolly. Inconspicuous black guard hairs are scattered through the coat and extend only a few millimeters beyond it. Pelage over the upperparts is grayish brown or grayish tawny. The tawny or brown tints are concentrated on top of the head and back, the sides are mostly gray. The underparts are white (12 out of 19 specimens), cream (5 out of 19), or pale buffy white (2 out of 19) and contrast sharply with the soft grays and browns of the head and back. No ochraceous strip separates colors of the upperparts and underparts. The cheeks are usually white, like the underparts (14 out of 19 specimens), a few are gray (4 out of 19), or rarely buffy (1 out of 19). The ears are thin and dark brown. The front and hind feet are white. There is a thin brown strip down the center of the top of each hind foot, from the ankle to the base of the digits. The tail is long-haired and tipped with a thin brush 4 to 6 mm. long. Ten out of 19 specimens have brown, monocolored tails. In the other nine the tails are brown on their tops and sides but mottled beneath. The extent of mottling is variable and ranges from a condition in which all but the last 20 mm. of the tail is unpigmented, appearing white or cream, to a pattern where the underside is mostly brown but broken up by small unpigmented areas.

Juveniles have very short, soft, and fine pelage. The upperparts are dark gray with a brown wash over the top of head and back; the underparts are white or cream. Tails are either brown all over or mottled on their undersurfaces in patterns similar to those of adults.

The cranium of *C. major* is fundamentally like crania of the other species, basically a larger version of *C. gliroides* and about the same size as *C. calamianensis* (fig. 6). *Chiropodomys major* has orange incisors and their widths relative to the cranium are like incisors of *C. gliroides*, *C. calamianensis*, and *C. karlkoopmani*, but unlike *C. muroides*, a species with relatively wider and paler incisors. The arrangement and relative sizes of the cusps on the molars are also like those in the other species, with the small difference in shapes of the

lingual cusps on the first and second upper molars that I pointed out in the account of *C. karlkoopmani*.

No other species of *Chiropodomys* is quite like *C. major*; the combination of large body, grayish brown back, white belly, and mottled tail is unique. It is a much larger mouse than either *C. muroides* or *C. gliroides* (table 1) and is further unlike *C. muroides* in color and relative size of incisors and many cranial proportions. Of the two species of small *Chiropodomys*, *C. major* looks more like a differently colored and larger version of *C. gliroides*, but it differs from that species in certain dental details (fig. 4) and in some proportions of the body, cranium, and teeth (fig. 7). Compared with samples of *C. gliroides* from the Malay Peninsula, for example, *C. major* has a shorter tail and longer hind foot relative to length of head and body; a narrower interorbital region relative to occipitonasal length, zygomatic breadth, or breadth of braincase; a longer rostrum relative to its breadth or to occipitonasal length; a narrower braincase relative to occipitonasal length; a much wider zygomatic plate relative to all other cranial dimensions; a longer palatal bridge relative to length of diastema, palatal length, or occipitonasal length; a wider palate at the level of the first upper molars relative to length of the palatal bridge; narrower incisive foramina relative to their lengths; longer bullae relative to their breadths or heights or to occipitonasal length; and a conspicuously longer toothrow relative to occipitonasal or palatal length.

Chiropodomys major is similar to *C. calamianensis* and *C. karlkoopmani* in body size (table 2), differs from each of them in color of pelage, and of the two is more like *C. calamianensis* in absolute size and proportions of most cranial and dental dimensions. The only conspicuous difference between *C. major* and *C. calamianensis* in the samples of each I have examined are those of pelage coloration and body dimensions. *Chiropodomys major* is a grayish brown mouse with white or cream undersides and a brown, usually mottled tail; *C. calamianensis* is a bright, buffy brown animal with orange-white to orange-red underparts, and a dark brown, monocolored tail. If the values I have for measurements of head and

TABLE 2
Measurements of Adults from Samples of Three Species of Large *Chiropodomys*^a

	<i>karlkoopmani</i> (North Pagai) AMNH 103305 ^b	<i>major</i> (Sabah)	<i>calamianensis</i> (Samarahan)		(Palawan)
			BM55.999	BM55.1000	
Length of head and body	107	105.3 ± 5.5, 17 102.5-108.1 (94-114)	84	85	117.0 ± 5.9, 4 114.0-120.0 (109-122)
Length of tail	171	128.4 ± 11.1, 17 123.0-133.8 (109-144)	95	104	153.5 ± 15.5, 4 138.1-168.9 (140-171)
Length of hind foot	29	24.1 ± 1.5, 17 23.3-24.9 (21-28)	20	20	25.5 ± 0.6, 4 25.2-25.8 (25-26)
Length of ear	17	16.8 ± 2.9, 17 15.4-18.2 (13-27)	15	14	16.8 ± 1.7, 4 15.0-18.6 (15-19)
Occipitonasal length	29.3	29.27 ± .80, 17 28.89-29.65 (27.5-30.2)	26.9	26.8	28.73 ± .42, 3 28.25-29.21 (28.4-29.2)
Zygomatic breadth	15.7	16.59 ± .49, 16 16.35-16.83 (15.5-17.4)	15.5	15.6	16.40 ± .40, 3 15.94-16.86 (16.0-16.8)
Interorbital breadth	5.7	5.21 ± .13, 17 5.15-5.27 (4.9-5.4)	5.0	5.1	5.33 ± .24, 4 5.21-5.45 (5.0-5.5)
Length of nasals	9.4	9.75 ± .73, 17 9.39-10.11 (8.6-11.1)			9.75 ± .19, 4 9.55-9.95 (9.6-10.0)
Length of rostrum	6.7	7.10 ± .46, 17 6.88-7.32 (6.5-8.0)			7.05 ± .33, 4 6.71-7.39 (6.6-7.4)
Breadth of rostrum	5.9	5.61 ± .24, 17 5.49-5.73 (5.3-6.0)			5.78 ± .21, 4 5.58-5.98 (5.5-6.0)
Breadth of braincase	14.0	13.96 ± .26, 17 13.84-14.08 (13.3-14.4)	13.2	13.2	13.55 ± .64, 2 12.65-14.45 (13.1-14.0)
Height of braincase	9.1	9.33 ± .33, 17 9.17-9.49 (8.8-10.2)	8.5	8.6	9.30 ± .00, 2
Breadth of incisor tips	1.7	1.75 ± .17, 17 1.67-1.83 (1.4-2.0)			1.78 ± .17, 4 1.60-1.96 (1.6-2.0)
Breadth of zygomatic plate	3.0	2.75 ± .18, 17 2.67-2.83 (2.4-3.0)			3.10 ± .16, 4 2.94-3.26 (2.9-3.3)

TABLE 2 — (Continued)

	<i>karlkoopmani</i> (North Pagai) AMNH 103305 ^b	<i>major</i> (Sabah)	<i>calamianensis</i> (Samarahan)		(Palawan)
			BM55.999	BM55.1000	
Length of diastema	8.1	7.84 ± .38, 17 7.66-8.02 (7.2-8.7)	7.6	7.4	7.60 ± .14, 4 7.46-7.74 (7.4-7.7)
Palatal length	14.5	14.92 ± .57, 17 14.64-15.20 (13.9-15.7)	13.5	13.9	14.17 ± .32, 3 13.79-14.55 (13.8-14.3)
Postpalatal length	10.1	10.11 ± .57, 17 9.83-10.39 (9.3-11.4)	9.4	10.1	10.15 ± .35, 2 9.65-10.65 (9.9-10.4)
Length of palatal bridge	6.7	6.12 ± .29, 17 5.98-6.26 (5.7-6.7)			5.87 ± .40, 3 5.41-6.33 (5.5-6.3)
Breadth of bridge at M ¹	3.3	3.15 ± .14, 17 3.09-3.21 (2.9-3.4)			3.20 ± .10, 3 3.08-3.32 (3.1-3.3)
Breadth of bridge at M ³	3.9	3.48 ± .14, 17 3.42-3.54 (3.2-3.7)			3.20 ± .20, 3 2.96-3.44 (3.0-3.4)
Length of incisive foramina	3.3	4.16 ± .27, 17 4.02-4.30 (3.5-4.6)	4.0	3.3	4.33 ± .21, 4 4.13-4.53 (4.1-4.5)
Breadth of incisive foramina	2.3	2.24 ± .12, 17 2.18-2.30 (2.0-2.4)			2.28 ± .17, 4 2.10-2.46 (2.1-2.5)
Incisive foramina to M ¹	2.0	1.09 ± .24, 17 .97-1.21 (.6-1.5)			1.08 ± .36, 4 .72-1.44 (.8-1.6)
Breadth of mesopterygoid fossa	1.9	2.05 ± .23, 17 1.93-2.17 (1.7-2.4)			2.07 ± .06, 3 2.01-2.13 (2.0-2.1)
Length of bulla	4.1	4.02 ± .11, 17 3.96-4.08 (3.8-4.2)			4.15 ± .35, 2 3.65-4.65 (3.9-4.4)
Height of bulla	3.8	3.36 ± .11, 17 3.30-3.42 (3.2-3.5)			3.45 ± .07, 2 3.35-3.55 (3.4-3.5)
Alveolar length of M ¹⁻³	4.6	4.72 ± .25, 17 4.60-4.84 (4.2-5.1)	4.1	4.2	4.38 ± .17, 4 4.00-4.76 (4.2-4.6)

^aThe mean and standard deviation, size of sample after comma, plus and minus two times the standard error of the mean, and the observed range in parentheses are listed, in that order, for each measurement. Measurements are in millimeters.

^bHolotype.

body, tail, and hind feet are reliable, then adult examples of *C. major* in my samples have significantly shorter heads and bodies, shorter tails (both actually and relative to length of head and body), and shorter hind feet than do adults of *C. calamianensis*.

Crania and teeth of the two species are similar and there are only a few differences between the samples. Compared with the sample of *C. calamianensis*, *C. major* has a significantly narrower zygomatic plate (both actually and relative to most other cranial dimensions), longer diastema, greater palatal length, and longer maxillary toothrows. The toothrow is also longer relative to palatal length, length of palatal bridge, and occipitonasal length. The few cranial and dental differences I see between samples of *C. major* and *C. calamianensis*, along with the geographic distributions of these two kinds of mice, indicate to me that they are closely related, closer to each other than to any other species in *Chiropodomys*.

There are enough examples of *C. major* to delimit and distinguish it morphologically from other kinds of *Chiropodomys* but not enough to determine the real pattern of geographic variation within the species. Most specimens are from the upper slopes or foothills of Gunong Kinabalu in Sabah; the few others were collected in Sarawak. Mice from the two areas are closely similar to each other in the features of skins and skulls which I examined. The two specimens from Samarahan, BM 55.999 and 55.1000, may be exceptions. Both are adults, both are inseparable from other specimens in color of head, body, feet, and tail, but both are conspicuously smaller than specimens of comparable age in all other samples. Values for some measurements, which I selected to reflect size, fall at or outside the low end of the distribution of values for the same measurements from the large sample from Sabah (table 2). Possibly the mice represent only the small end of the range of variation within the species; they may, however, be a sample of a population in Sarawak that is distinguished by individuals of small size. Large series from more localities in Sarawak and elsewhere in Borneo are needed to test the significance of the differences I see between the two mice from Sa-

marahan and those from other places in Borneo.

The little information I have about elevations and habitats where the specimens of *C. major* were taken indicates that the species occurs from lowlands up to about 5000 feet, a range embracing both lowland evergreen and montane forest formations. Most of the specimens collected in Sabah were obtained from Highlands. On Gunong Kinabalu, for example, the lowest elevation where mice were collected is recorded at 1600 feet, the highest is 4900 feet. In Sarawak the species apparently occurs in the lowlands. The specimen from Marudi, for instance, was obtained by Charles Hose in 1894. On the tag attached to the skin is Hose's note that the mouse was "taken from a cat in my house at Marudi, Baram River." Marudi is below an elevation of 200 feet on the coastal plain. The specimens from Sadong and Samarahan may have come from the coastal plain or from mountain forest near sources of the rivers; there are no elevational data with the skins. Medway (1965) noted the records listed by Banks from Kuching and Balingian on the coast of Sarawak; likely those specimens were obtained on the coast.

There is much yet to learn about *C. major*—its actual distribution over Borneo and offshore islands, its elevational limits, its habitat and habits, and nearly all other aspects of its natural history. In that respect the species is not so different from the large *C. karlkoopmani* in the Mentawai islands or the other large kind that occurs in the Palawan chain between the northern tip of Borneo and the island of Mindoro in the backbone of the Philippines.

Chiropodomys calamianensis

On April 18, 1918, E. H. Taylor caught a long-tailed mouse in a tree stump on the seashore at Minuit, Busuanga Island, one of the islands in the Calamian Group between Palawan and Mindoro. The animal was an adult female and Taylor thought it might have young that were still nursing. He preserved the specimen in alcohol. Later it became the holotype of *Insulaemus calamianensis*, a new genus and species which Taylor named and described in

1934. Taylor did not know what other murids *Insulaemus* might be closely related to, but other persons did. Tate (1936), two years later, examined and figured the holotype, allied *Insulaemus* with *Chiropodomys*, and wrote that "A careful drawing of the skull has been prepared from which *Insulaemus* is seen to be very closely related to *Chiropodomys*, if not congeneric." Subsequently, Ellerman (1941) and Sanborn (1952) regarded *calamianensis* as a species of *Chiropodomys*. My own study confirms those observations: *calamianensis* is a type of *Chiropodomys* from the Palawan area; in size and structure of skin and skull it is most like *C. major* of northern Borneo.

Once known only from Busuanga Island, the geographic range of *C. calamianensis* now includes the islands of Balabac and Palawan. I have examined 11 specimens collected at the localities listed below (arranged from north to south) and shown on the map in figure 5.

BUSUANGA ISLAND

Minuit, sea level: holotype, originally no. 104 in E. H. Taylor's personal collection, but now no. 33391 in the collection of the University of Illinois Museum of Natural History.

PALAWAN ISLAND

Puerto Princesa, sea level: FMNH 63122, 63124-63127, and 63129-63131.

Macagua, Brooke's Point, 250 feet: USNM 478268.

BALABAC ISLAND

Minagas Point, Dabwan Bay, sea level: USNM 478269.

Large size and brightly colored pelage (tables 1 and 2) characterize *C. calamianensis*. Next to *C. karlkoopmani*, it is the largest in body size of all known species of *Chiropodomys*. Adults from Palawan have bright, dark buffy brown to orange-brown upperparts. The underparts range from pale cream to pale orange. In those examples with darker underparts, the throat, chest, and inguinal area are usually paler, sometimes white. The underparts are separated from the upperparts by a wide, buffy orange strip. The cheeks are this same color. Dorsal surfaces of the front feet are either white or pale brown. The hind feet are white with a pale to dark brown strip over the

inner third of each foot. The tails are long, range in color from tan to dark brown, and are penicillate with terminal tufts 6 to 7 mm. long.

Juvenile pelage is shorter and finer, grayish brown over the upperparts, and cream on the underparts.

The adult and only specimen I have seen from Balabac Island is darker and redder than those from Palawan. Its upperparts are rich chestnut, the underparts are bright orange-red, the cheeks are the same color as the rest of the upperparts, the front and hind feet are dark brown, the ears and tail are blackish brown, and there is no bright strip between back and belly.

The holotype and only specimen from Busuanga Island was preserved in alcohol and the original colors have altered. Judged from Taylor's (1934) description, the color of its pelage was like that of the series from Palawan.

The skull and teeth of *C. calamianensis* resemble those of *C. major*, both in size, shape, and many proportions (tables 1 and 2; fig. 6). The cranial differences between samples of the two species available to me are neither as conspicuous nor of the same magnitude as some of the differences among geographic samples of *C. gliroides*. If I had examined only skulls and teeth, I might consider the samples from Balabac, Palawan, and Busuanga islands to the insular variants of *C. major*. However, the samples from the islands have in common a large body with bright orange-brown back and belly, a long hind foot, and a long and monocolored tail, features which distinguish them from samples of *C. major* of northern Borneo.

Although my samples of *C. calamianensis* are small, they may reflect geographic variation within the species. All adults from the three islands are similar in sizes and shapes of skins, skulls, and teeth, and I have been unable to detect any significant geographic variation in features associated with those structures. The samples do differ in color of pelage, and the difference may be significant. It is certainly striking. The specimen from Balabac Island is much darker with a deep red tone over the head and body, and has darker feet and tail than any specimen from Palawan or Busuanga, an over-

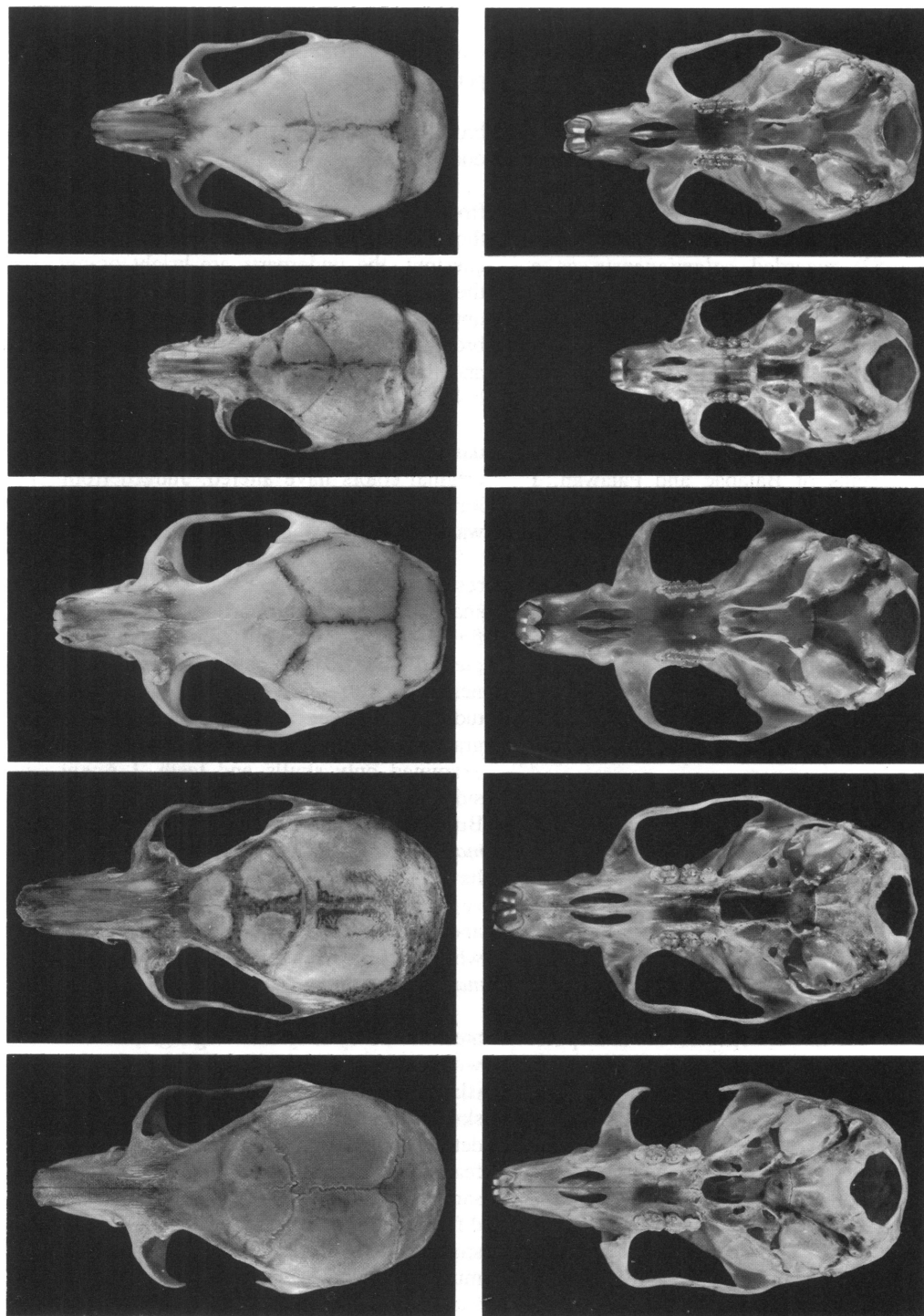


FIG. 6. Dorsal (top) and ventral (bottom) views of adult crania of five species of *Chiropodomys*. From left to right: *C. karlkoopmani* (AMNH 103305), *C. major* (USNM 301098), *C. calamanianensis* (USNM 478269), *C. muroides* (USNM 292885), and *C. gliroides* (USNM 283692). X2. Photographed by Arthur Singer.

all coloration well outside the range of variation in the last two samples. If the example from Balabac does not represent just an erythrocytic morph that occurs at a certain frequency in the population along with a paler morph, but accurately reflects coloration in the entire adult population, then those mice are a conspicuous island variant of *C. calamianensis*.

Our knowledge of the biology and habitat of *C. calamianensis* is as scanty as it is for most other species of *Chiropodomys*. The data that are available come from labels attached to skins and from Sanborn's (1952) records. The examples of *C. calamianensis* from Palawan, at Puerto Princesa, were trapped in the rafters of a building within a coconut grove on a beach and on a log in the grove; one was caught by hand in bamboo. Other specimens are without habitat data. I do not know if the mice have ever been taken in primary forest, but evidently that type of forest is not necessary to the animals, for most specimens were collected from habitats made and maintained by humans (coconut groves and buildings) or from disturbed places in the forest (bamboo). Perhaps naturally formed light gaps or other natural disturbances in primary forest, indicated usually by bamboo, scrub, or tall secondary growth, are the usual habitat of this large, brightly colored tree mouse.

Chiropodomys muroides

Chiropodomys karlkoopmani from North Pagai Island, the species with the largest body size in the genus, and the two kinds of large *Chiropodomys* from the Palawan area and Borneo contrast strikingly with *C. muroides*, the smallest of the *Chiropodomys*. That small mouse was not named and described until recently (Medway, 1965, p. 133) although examples of it had been collected during the late 1920s and early 1950s. Medway based his description on three specimens (USNM 292885, 301100, and 301101) obtained from Bundu Tuhan at 4000 feet on the slopes of Gunong Kinabalu in Sabah, one in July 1951, the other two in August 1953. Medway also allocated a fourth specimen to *C. muroides*. It originally had been recorded by Chasen and Kloss in

1928 as "*Chiropodomys* sp." and was collected at Long Petak (1° 43' N) in highlands along the Sungai Telen, the upper part of the first large tributary to enter the Sungai Mahakam from the north (fig. 5). Chasen and Kloss recognized that their specimen was distinct from all forms of *Chiropodomys* then known from Borneo, but they were reluctant to name and describe a new species with only one specimen. That example (unregistered in the British Museum) and the three from Sabah are adults. I have seen no other material.

Small size, bright buffy brown upperparts, and dark gray underparts washed with buff are the body features distinguishing *C. muroides* from all other known kinds of *Chiropodomys* (table 1). The dorsal surfaces of its front feet are white, the hind feet are either white or have a thin brown strip down the middle of each one. The tail is hairy; it is tipped with a brush 6 mm. long.

The cranium of *C. muroides* is small (fig. 6), but is not just a miniature version (table 3) of the larger species of *Chiropodomys*, differing significantly from them in proportions of the rostrum, interorbital area, zygomatic plates, palatal region, bullae, and incisors (fig. 7). The interorbital region and rostrum of *C. muroides* are wider relative to either zygomatic breadth or breadth of braincase than those of all other species. Each zygomatic plate is narrower relative to all other cranial dimensions except length of incisive foramina—a proportion similar to *C. major*, which also has relatively narrow zygomatic plates. The incisive foramina are short and wide. They are conspicuously shorter relative to palatal length and length of diastema than in other species; the distance from the back edges of the foramina to the anterior margins of the first upper molars is correspondingly relatively longer than in any of the other species except *C. karlkoopmani*, which also has short and wide incisive foramina. Along with short incisive foramina goes a relatively longer palatal bridge, which is a feature of both *C. muroides* and *C. karlkoopmani*. Finally, the bullae of *C. muroides* are smaller relative to occipitonasal length than in the other samples of *Chiropodomys*.

The incisors of *C. muroides* are unique in

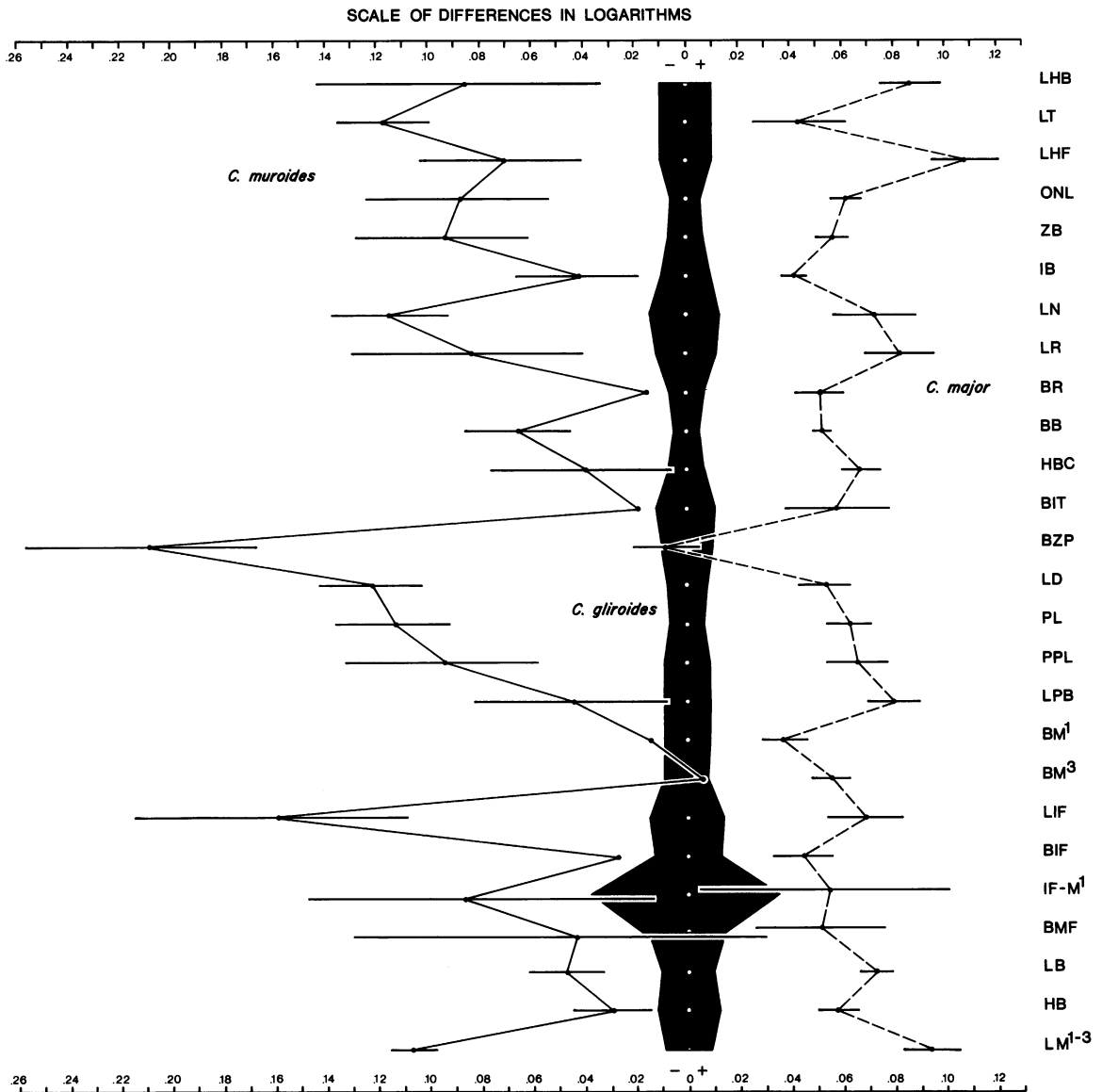


FIG. 7. Ratio Diagram. Twenty-six dimensions are compared in samples of *Chiropodomys gliroides* (the standard), *C. major*, and *C. muroides*. The patterns of *C. karlkoopmani* and *C. calamanensis*, which are not illustrated here, are similar to that of *C. major*, with the exceptions discussed in the text. See Musser (1970) for an explanation of the diagram. Abbreviations from top to bottom are as follows: length of head and body (LHB), length of tail (LT), length of hind foot (LHF), occipitonasal length (ONL), zygomatic breadth (ZB), interorbital breadth (IB), length of nasals (LN), length of rostrum (LR), breadth of rostrum (BR), breadth of braincase (BB), height of braincase (HBC), breadth across incisor tips (BIT), breadth of zygomatic plate (BZP), length of diastema (LD), palatal length (PL), postpalatal length (PPL), length of palatal bridge (LPB), breadth of palatal bridge at M¹ (BM¹), breadth of palatal bridge at M³ (BM³), length of incisive foramina (LIF), breadth across incisive foramina (BIF), incisive foramina to first molars (IF-M¹), breadth of mesopterygoid fossa (BMF), length of bulla (LB), height of bulla (HB), and alveolar length of maxillary toothrow (LM¹⁻³).

their enamel pigmentation and size. The enameled faces of the uppers are pale yellow, those surfaces of the lowers are cream. In all other samples of *Chiropodomys*, the upper incisors have bright, deep orange front surfaces and the lowers are pale orange. The incisors of *C. muroides* also appear strong and robust, more so than in other species because they are actually wide and significantly wider relative to either zygomatic breadth or breadth of braincase than in any other sample of *Chiropodomys*.

Chiropodomys muroides has small molars, but relative to the rest of the cranium they are proportionally similar in size to those of other samples of *Chiropodomys*. The patterns formed by the cusps are more like the patterns in *C.*

gliroides than in *C. major*, *C. calamianensis*, or *C. karlkoopmani* (fig. 4).

Like the other species of *Chiropodomys*, the small *C. muroides* is likely arboreal and is associated with forests, I have no firsthand information about its habits or specific habitat and there is nothing recorded in the literature. Most specimens come from mountain forest at elevations that Medway (1965, p. 134) referred to as "submontane localities." Lim and Heyne-man (1968) described the forest in the vicinity of Bundu Tuhan as "Low oak montane forest intermixed with hill dipterocarp forest." On the slopes of Gunong Kinabalu the species occurs together with *C. gliroides* and the larger *C. major*, but how the three utilize the forest resources and how the three may interact are

TABLE 3
Measurements of Adult *Chiropodomys muroides* from Sabah^a

	301101 female	292885 male	301100 female	Mean \pm S.D.
Length of head and body	66	80	67	71.0 \pm 7.8
Length of tail	91	85	90	88.7 \pm 3.2
Length of hind foot	15	17	16	16.0 \pm 1.0
Length of ear	14	18	19	17.0 \pm 2.6
Occipitonasal length	19.9	21.6	—	20.75 \pm 1.20
Zygomatic breadth	11.3	12.2	—	11.75 \pm .64
Interorbital breadth	4.1	4.5	4.3	4.30 \pm .20
Length of nasals	6.0	6.5	6.5	6.33 \pm .29
Length of rostrum	4.6	5.1	—	4.85 \pm .35
Breadth of rostrum	4.8	4.8	—	4.80
Breadth of braincase	10.4	10.9	—	10.65 \pm .35
Height of braincase	7.0	7.6	—	7.30 \pm .42
Breadth of incisor tips	1.6	1.6	—	1.60
Breadth of zygomatic plate	1.6	1.7	1.9	1.73 \pm .15
Length of diastema	5.0	5.4	5.3	5.23 \pm .21
Palatal length	9.7	10.2	—	9.95 \pm .35
Postpalatal length	6.7	7.3	—	7.00 \pm .42
Length of palatal bridge	4.4	4.8	—	4.60 \pm .28
Breadth of bridge at M ¹	2.8	2.8	—	2.80
Breadth of bridge at M ³	3.1	3.1	—	3.10
Length of incisive foramina	2.7	2.5	2.2	2.47 \pm .25
Breadth of incisive foramina	1.9	1.9	—	1.90
Incisive foramina to M ¹	1.0	1.3	1.2	1.67 \pm .15
Breadth of Mesopterygoid fossa	1.8	1.5	—	1.65 \pm .21
Length of bulla	3.1	3.0	—	3.05 \pm .07
Height of bulla	2.7	2.8	—	2.75 \pm .07
Alveolar length of M ¹⁻³	3.0	2.9	3.0	2.97 \pm .06

^aAll three specimens are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; 301101 is the holotype. Measurements are in millimeters.

unknown. Judged from the small body size of *C. muroides* and its wide and pale yellow incisors, I suspect the mouse can utilize smaller spaces for nests than are available to the other species and probably eats different foods than do the other kinds of *Chiropodomys*. We need to learn more about the biology of this mouse and its place in the tropical forest ecosystem.

Chiropodomys gliroides

Of the species in *Chiropodomys*, *C. gliroides* was the first to be described (Blyth, 1856), its morphological features have provided the basis for most descriptions and diagnoses of the genus (Sclater, 1890; Allen, 1940; and Ellerman, 1941 and 1961, for example), and it is the best known to biologists. In contrast to the other four which are represented by either a single specimen or small series that were collected from small islands on the Sunda Shelf or from parts of the large island of Borneo, specimens of *C. gliroides* have been gathered from extensive areas of Indochina and the Malay Archipelago. Whereas there is little geographic variation within each of the other species of *Chiropodomys*, there is significant morphological variation from place to place within *C. gliroides*. And while knowledge about natural histories and habitats of the other four kinds is scanty, much information has been published about the biology and habitats of *C. gliroides*. To present this large amount of data, I have partitioned it into seven sections: localities and specimens, description and comparisons, geographic variation, taxonomy, habitats, habits and life history, and parasites.

LOCALITIES AND SPECIMENS: I have studied more than 330 specimens of *C. gliroides* which were obtained from the localities that are listed below and shown on the map in figure 8. I have also placed published records on that map but only those provided by persons whose identifications I considered to be reliable.

Chiropodomys gliroides gliroides
(Indochinese Form)

INDIA, ASSAM

1. Khasi Hills, Cherrapunji: FMNH 76438 and 76439; holotype of *Mus gliroides*, which I

have not seen. It was in the Indian Museum at Calcutta but by 1890 had disappeared from the collection (Sclater, 1890).

2. Jaintia Hills, Khonsandng, 3000 feet; FMNH 82928, BM 21.1.6.78.

I also examined FMNH 76435 and 76437 from Karong, Manipur, but did not place the locality on the map in figure 8.

BURMA

3. Kachin Province, Nam Tamai Valley (27° 42' N, 97° 54' E), 3000 and 3500 feet: FMNH 40954, BM 32.11.1.163 and 50.679-50.681.
- 3a. Kachin Province, Hkinlum, Triangle (26° 53' N, 98° 11' E), 5000 feet: BM 50.582.
- 3b. Kachin Province, Htingnan (26° 36' N, 97° 52' E), 3200 feet: BM 50.671-50.678, 76.1322, and 76.1323.
4. Dalu, 626 feet: AMNH 113040.
5. Gora, 2600 feet: AMNH 113037-113039.
6. Kakhyen (also spelled Kakhien) Hills, Bhamo: specimens from here are recorded by Doria (1887) and Thomas (1891).
7. Yado and Thao, Carin Hills (also on maps as the Karennee or Karenni area), northeast of Tounghoo: examples recorded by Thomas (1891).
8. Schwegyin, in the valley of the Sittang River: holotype of *Mus peguensis*, in the collection of the Indian Museum at Calcutta. I have not seen this specimen.
9. Northern Tenasserim, Thagata (also spelled Thaget or Thagyet), east of Moulmein and near Mount Mooleyit: BM 88.12.1.46.
10. Southern Tenasserim, 5 miles south of Karathuri: AMNH 54988 and 54989.
11. Southern Tenasserim, Bankachon: BM 14.12.8.148-14.12.8.163; FMNH 82929.

THAILAND

12. Mae Hong Son Province, Mae Sariang District, 23 kilometers northeast of Mae Sariang, 1000 meters: USNM 522981.
13. Mae Hong Son Province, Mae Sariang District, near Mae Sariang: USNM 522982.
14. Chaing Mai Province, Doi Suthep: USNM 260618.
15. Lampang Province, Doi Khun Tan: AMNH 240134.
16. Sukhothai Province, Ban San To: USNM 261088.

LAOS

17. Phong Saly, 4400 feet: FMNH 32461 and 32462.

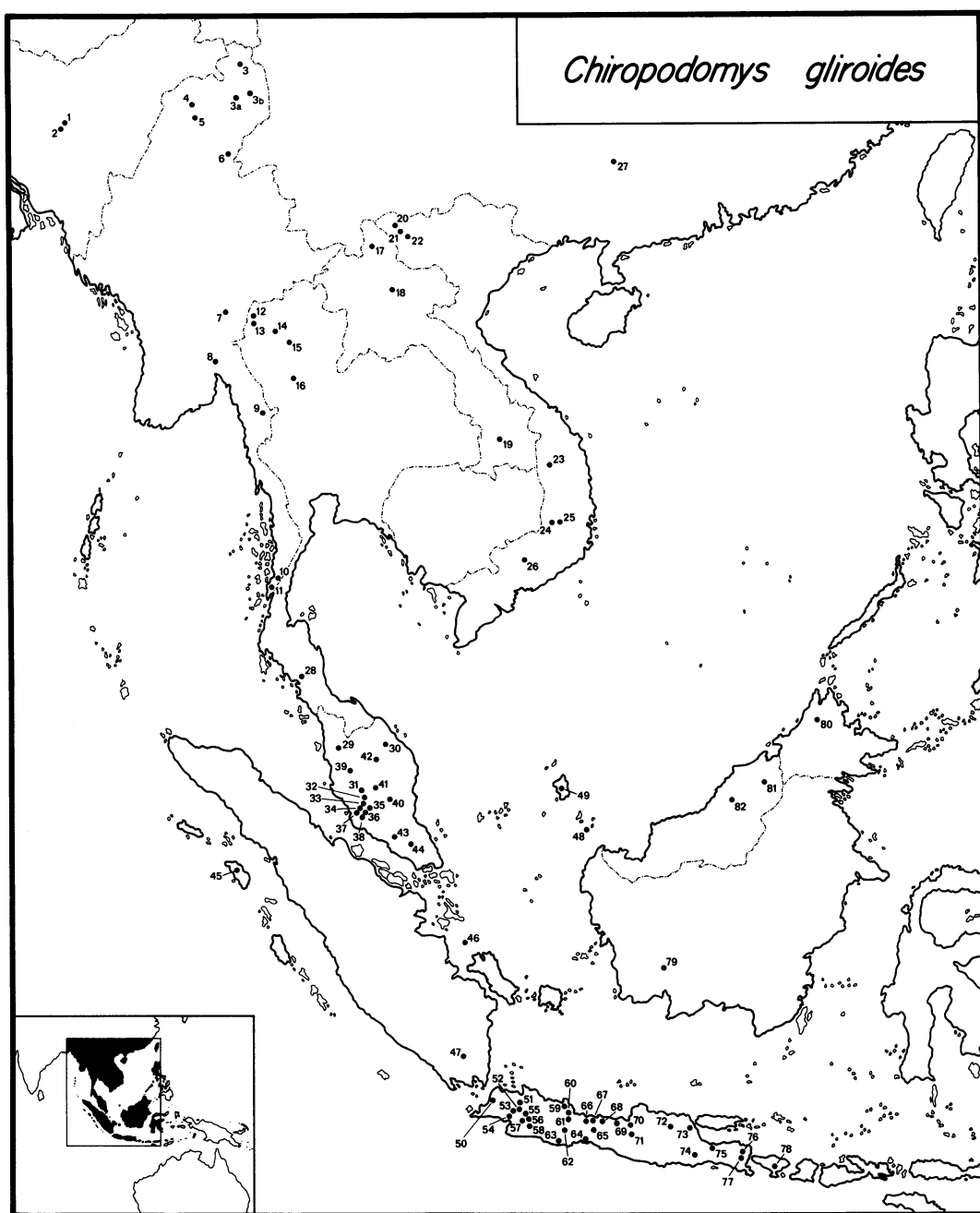


FIG. 8. Geographic distribution of *Chiropodomys gliroides* based on specimens I examined and reliable published records. Each dot represents a locality. The number beside the dot refers to the numbered localities in the text where I have given the name of each place, the number of specimens from there, and either their catalogue numbers or a reference to the source of the record.

18. Col de Taloun: MCZ 38233.
19. Plateau Bolovens: AMNH 87548 and 87549.

VIETNAM

20. Muong Boum: FMNH 32456.
21. Muong Mo, 750 feet ("On the Mo River, a branch of the Riviere Noire" according to Bangs and Van Tyne, 1931): FMNH 32453-32455.
22. Muong Moun, south of Lai Chau, 1200 feet: FMNH 32457-32459, MCZ 27058 (formerly FMNH 32460).
23. Kontum Province, Dakto (also spelled Dak-To), 500-600 meters: MNHN 1929-327 to 1929-329, BM 26.10.4.168 and 26.10.4.169.
24. Darlac Province, Ban Me Thout, 400-500 meters: FMNH 46720-46732.
25. Darlac Province, 10 km. east of Ban Me Thout, 1900 feet: USNM 355555.
26. Long Khanh Province, Caryu Danar, 200 meters: USNM 321516.

CHINA

27. Kwangsi Province, Yao Shan Mountains: MCZ 27105.

Chiropodomys gliroides penicillatus
(Malayan Form)

PENINSULAR THAILAND

28. Trang Province, Trang: USNM 84400.

MALAYA

29. Kedah, Kedah Peak, 3000 feet: BM 55.3192-55.3195.
30. Trengganu, Gunong Tebu, 350 feet: USNM 311448.
31. Selangor, Bukit Kutu, 3400 feet: BM 55.3196.
32. Selangor, Satapak, Ulu Gombak, 1000-3000 feet: USNM 489313, 489317, and 489318; BM 61.1261 and 61.1262. Batu, Ulu Sungai Tua, 0-250 feet: USNM 489332.
33. Selangor, Batu, Bukit Lagong, 1000-3000 feet: USNM 489314-489316, 489319, 489325, 489328-489330, 489343, and 489344; AMNH 240325-240347; BM 61.12.64.
34. Selangor, Pahang Road, 16 miles north of Kuala Lumpur: USNM 283515-283520, 283681, 283682, 283692, 283697, 290239-290245; FMNH 65889; AMNH 135029; BM 49.224-49.231.

35. Selangor, Ulu Langat: USMN 291332 and 291333; AMNH 240348; BM 61.1263.
36. Selangor, Klang, Tanjong Rabok: USNM 489347-489355 and 489357-489359.
37. Selangor, Kepong Forest Reserve, 3 miles north of Kepong: FMNH 98646.
38. Selangor, Bukit Mandol, 0-250 feet: USNM 489320-489324, 489337, 489338, 489345, and 489360.
39. Pahang, Semangko Pass: BM 55.3199, 55.3200, and 55.3201.
40. Pahang, Teku Plateau, Gunong Tahan, 5300 feet: BM 55.3191. K. Teku, BM 55.3190.
41. Pahang, Gunong Benom, 5000 feet: BM 55.3198. Gunong Benom, Jerantut, Krau Game Preserve, 4000-4500 feet: USNM 489309.
42. Pahang, Bentong, Bentong Forest Reserve, Janda Baik, 1-3000 feet: FMNH 98645; USNM 489346.
43. Johore, Bekok, foot of Gunong Ledang, 1000 feet: USNM 489310.
44. Johore, Kluang, Bekok, Labis Forest Preserve, Tamok 250-500 feet: USNM 489311 and 489312; Segamat, Labis, Lais Forest Preserve, Kampong Juaseh, 500-1000 feet: USNM 489333-489336 and 489339-489341.

I also examined specimens from Ulu Setiu (BM 75.1342) and Gunong Lawit (BM 75.1343) in Trengganu, Jaram (BM 85.8.1.327) in Selangor, and Telom River (BM 34.7.18.150-34.7.18.160) in Pahang, but omitted the localities from figure 8.

Chiropodomys gliroides niadis

45. Nias Island: La Fau, USNM 12187, holotype of *C. niadis*; Soliga, MCZ 35968 and 35969; Lelewean, BM 23.1.2.39.

UNALLOCATED TO SUBSPECIES

46. Tujuh islands, between Kepulauan Lingga and Pulau Banka, off the southeastern coast of Sumatra: MZB 4839.
47. Southern Sumatra, Lampung Province, Sungai Langka: RMNH 23874. I could not locate Sungai Langka on maps and merely placed a dot in the middle of the province.

NATUNA ISLANDS

48. Serasan Island, in the southern Natuna islands: MZB 4838. Sody (1941) examined another specimen from Serasan.

49. Bunguran Island, northern Natuna islands. This record is based on Chasen's (1940) footnote.

Chiropodomys gliroides anna

JAVA

50. West Java Carita (6° 50' E): USNM 496976.
 51. West Java, Depok: USNM 155307.
 52. West Java, Bogor (Buitenzorg on old maps and labels of specimens collected before about 1945): BM 12.4.12.24. Sody (1941) examined specimens from Bogor. These mice, as well as those from the other localities in Java that Sody listed in his report are in the collection of the Museum Zoologicum Bogoriense. I have studied the same specimens, but will not list them separately here.
 53. West Java, Gunung Salak: Sody No. A-172 (in the RMNH).
 54. West Java, Palaboean (also spelled Palabuhan): Sody (1941) looked at examples from here; also RMNH 13836, a specimen collected by Max Bartels from the coast near Wijnkoops-Baai (now Teluk Pelabuhan Ratu).
 55. West Java, Southwest slopes of Pangrango-Gede Mountains: RMNH 13925, 14072, 14016, 14128, 14048, 14007, 14049, 14036, and 14139. The following localities are on the southwest slopes of Pangrango-Gede: Tjibodas, 900-1200 meters (RMNH 14000, 13921, 14002, 13923, 13924, and 13894); Tjiparaj, 900-1000 meters (RMNH 13789, 14001, 13567, and 14004); Tjimahi, 900-1200 meters (RMNH 14003, 14005, and 14006); Pasir Datar, 1000 meters (RMNH 13953, 14138, and 14047).
 56. West Java, Sukabumi: Sody's (1941) records; BM 9.1.5.752 and 9.1.5.753 from Kat-tamanah, Sukabumi.
 57. West Java, Legokoray (6° 50' S 106° 55' E): AMNH 198654 and 198655.
 58. West Java, Gunung Tjimerang: record from Sody (1941, P. 302).
 59. West Java, Indramaju: Sody's (1941, p. 302) records.
 60. West Java, Cheribon, sea level and 500 meters: AMNH 101901, 101902, 101904, 101999-102001, 102119, 102227, 102228, 102694, 106681-106689, and 101535; (SMT 12165 and 12166) also Sody (1941) and Tien (1966).
 61. Tjareme, 600 and 800 meters: AMNH 106680 and 101903.
 62. West Java, Tasikmalaya, Preanger: BM 9.1.5.758-9.1.5.763, 9.1.5.1127.
 63. West Java, Tjipatuja, south coast: recorded by Sody (1941).
 64. Central Java, Tjilatjap: BM 9.1.5.757 (holotype of *Chiropodomys anna*), BM 9.1.5.754 and 9.1.5.756.
 65. Central Java, Gunung Slamet, Baturadan: FMNH 4741, USNM 257630, and 257636-257638; Sody Collection nos. C-38, C-44, C-73, C-82, C-84-88, and C-163 (in the RMNH).
 66. Central Java, Brebes: Sody's (1941) record.
 67. Central Java, Tegal: Sody's (1941) record.
 68. Central Java, Pemalang: recorded by Sody (1941).
 69. Central Java, Siluwok Sawangan, near Weleri: another record from Sody (1941).
 70. Central Java, Semarang: Sody Collection nos. 9 and 10 (in the RMNH); also recorded by Sody in 1941.
 71. Central Java, Salatiga: ZMA G-28 and G-29; BM 23.1.2.37 and 23.1.2.38.
 72. East Java, Bojonegoro: listed by Sody (1941).
 73. East Java, Surabaya: another record from Sody (1941).
 74. East Java, Malang: seven specimens in ZMA, unregistered at the time I examined them.
 75. East Java, Probolinggo: a Sody (1941) record.
 76. East Java, Blawan: recorded by Sody (1941).
 77. East Java, Idjen: from Sody (1941).

BALI

78. Oeboed (also spelled Ubud on new maps), 250-300 meters: AMNH 107987, 107546, and 107547; MZB 4833-4837.

Chiropodomys gliroides pusillus

KALIMANTAN (SOUTHERN BORNEO)

79. Korawaringin, Riam, 300 meters: AMNH 106112.

SABAH (NORTH BORNEO)

80. Gunong Kinabalu, 1000 feet: BM 95.10.4.38 (holotype of *C. pusillus*); Kiau, 3000 and 3100 feet: SNM 3637 and MCZ 36540. Sody (1941) recorded a specimen from "North Borneo" (MZB 2450) that was obtained in 1912. He identified it as *C. pusillus* and listed some measurements; I have not seen this example.

SARAWAK (NORTH BORNEO)

81. Gunong Mulu: BM 94.9.29.20 and 94.9.29.21.
82. Gunong Dulit: recorded by Hose (1893). Medway (1965) also recorded *C. gliroides pusillus* from the Kelabit highlands, based on specimens in collections at the Field Museum of Natural History and the Singapore National Museum. I have not seen the material at Singapore, but the specimen in Chicago (FMNH 8447) is an example of *Haeromys pusillus*, not *Chiropodomys*.

DESCRIPTION AND COMPARISONS: The specimens I have listed above represent a small species of *Chiropodomys* with a head and body usually no longer than 100 mm., a skull about 25 mm. long, maxillary toothrows usually under 4 mm., and weight from 15 to 32 grams (tables 1 and 4). Pelage over upperparts of the head and body is thick (6 to 8 mm.) and dense. The fur is bright, pale chestnut or reddish brown in most samples, paler in others. Under-side of the head and body is usually white, rarely cream. On specimens in some samples a narrow, ochraceous strip separates the white underparts from the pale chestnut above. The cheeks are ochraceous or buffy. The tail is long, hairy, and tipped with a brush 4 to 5 mm. long. The tail ranges in color from grayish brown to dark brown, and all surfaces are solidly pigmented—I have never seen any mottling like that on tails of *C. major* nor any tendency toward the bicolored pattern of *C. karlkoopmani*. The facial vibrissae are long, most are longer than half the length of the head and body. The ears are thin, brown, and finely haired. Upper surfaces of the front feet are white. Dorsal surfaces of the hind feet may be white or brown, but most specimens are white with a V-shaped brown area over half of the foot or a thin brown strip extending from the ankle to the bases of the digits.

The cranium is shaped as shown in figure 6. The incisors are narrow relative to width of the rostrum and pigmented a deep orange. The occlusal patterns of the upper and lower molars are shown in figure 15; teeth have also been figured by Sclater (1890), Tate (1936), and Misonne (1969).

No other species of *Chiropodomys* has the same combination of size, pelage coloration,

and dental features as in *C. gliroides*. *Chiropodomys major*, the only other kind with whitish underparts, has grayish brown upperparts, either a monocolored or a mottled tail, slightly different configurations of cusps on the first and second molars, and is much larger than *C. gliroides* (table 1). *Chiropodomys calamianensis* has bright reddish brown upperparts and a monocolored tail. These features are similar to those of *C. gliroides*, but in contrast to that species *C. calamianensis* has a brightly pigmented throat and belly and is the size of *C. major*. The other species of large body size, *C. karlkoopmani*, is grayish brown above and gray below and has a bicolored tail; *C. gliroides* is unlike that large mouse in color, size, and shapes of some cusps on the first and second molars. *Chiropodomys muroides* is smaller than *C. gliroides* in body size, has buffy dark gray underparts, and wide pale yellow incisors.

Chiropodomys gliroides is the only *Chiropodomys* that is known from Sumatra, Java, Bali, some small islands on the Sunda Shelf, the Malay Peninsula, and Indochina. The species also lives on Borneo where it apparently occurs together with *C. major* and *C. muroides* in Sabah. *Chiropodomys gliroides* has never been recorded from the islands of Balabac, Palawan, or Busuanga, places where the large *C. calamianensis* is from; nor is *C. gliroides* known to occur on any of the Mentawai islands—*C. karlkoopmani* is the only species of *Chiropodomys* now recorded from an island in the Mentawai group.

GEOGRAPHIC VARIATION: As might be expected of a species with an extensive distribution over continent and archipelago, there is conspicuous and significant geographic variation within *C. gliroides*. I have been able to sort samples of that species into two primary groups, each distinguished by differences in actual and relative sizes of certain dimensions of bodies, skulls, and teeth; by contrasts in tone of pelage, and by geographic origins. I first thought these two sets of samples represented different species but rejected that hypothesis after some testing. One set comprises specimens from the mainland of Southeast Asia (Assam, Burma, Thailand, Laos, southern China, and Vietnam) south to about the latitude of the

TABLE 4
Measurements of Adults in Samples of *Chiropodomys gliroides* from Indochina, Malaya, and Java^a

	Indochina (Laos, Vietnam, Thailand)	P_1	Malay Peninsula (Pahang, Selangor, Johore)	P_2	West Java
Length of head and body	90.0 \pm 6.3, 21 87.2-92.7 (81-101)	.05-.02	86.2 \pm 7.4, 57 84.2-88.2 (69-102)	.5-.4	84.5 \pm 7.5, 18 80.9-88.1 (65-98)
Length of tail	115.3 \pm 6.8, 21 112.3-118.3 (105-134)	.8-.7	116.0 \pm 10.1, 57 113.4-118.6 (94-143)	.2-.1	120.0 \pm 9.7, 18 115.4-124.6 (98-135)
Length of hind foot	19.7 \pm 1.1, 21 19.2-20.2 (18-22)	.05-.02	18.8 \pm 1.6, 57 18.4-19.2 (15-22)	.9-.8	18.7 \pm 1.5, 18 17.9-19.5 (15-22)
Occipitonasal length	24.73 \pm .64, 18 24.43-25.03 (23.6-25.9)	.02-.01	25.37 \pm .83, 23 25.03-25.71 (24.0-26.7)	<.001	24.36 \pm .70, 18 24.04-24.68 (22.9-25.6)
Zygomatic breadth	14.37 \pm .33, 17 14.21-14.53 (13.8-15.1)	.4-.3	14.56 \pm .83, 23 14.34-14.78 (13.7-15.5)	.01-.001	14.01 \pm .60, 18 13.73-14.29 (12.8-14.9)
Interorbital breadth	4.52 \pm .18, 21 4.44-4.60 (4.1-4.8)	.01-.001	4.73 \pm .25, 23 4.63-4.83 (4.2-5.2)	<.001	4.48 \pm .11, 19 4.44-4.52 (4.2-4.7)
Length of nasals	7.47 \pm .34, 21 7.31-7.63 (6.9-8.1)	<.001	8.24 \pm .62, 23 7.98-8.50 (7.0-9.4)	.01-.001	7.72 \pm .38, 18 7.54-7.90 (6.8-8.3)
Length of rostrum	5.76 \pm .31, 21 5.62-5.90 (5.2-6.3)	.4-.3	5.87 \pm .40, 23 5.71-6.03 (5.1-6.7)	.05-.02	5.56 \pm .39, 18 5.38-5.74 (4.8-6.1)
Breadth of rostrum	4.87 \pm .22, 21 4.77-4.97 (4.3-5.2)	.1-.05	4.98 \pm .19, 23 4.90-5.06 (4.6-5.3)	.01-.001	4.73-.27, 19 4.61-4.85 (4.3-5.5)
Breadth of braincase	12.22 \pm .23, 18 12.12-12.32 (11.9-12.7)	.2-.1	12.37 \pm .35, 23 12.23-12.51 (11.9-13.1)	.01-.001	12.00 \pm .29, 19 11.86-12.14 (11.3-12.6)
Height of braincase	7.94 \pm .29, 17 7.80-8.08 (7.4-8.5)	.6-.5	7.99 \pm .31, 22 7.87-8.11 (7.3-8.5)	.1-.05	7.82 \pm .25, 19 7.70-7.94 (7.4-8.3)
Breadth of incisor tips	1.49 \pm .10, 20 1.45-1.53 (1.3-1.6)	.2-.1	1.53 \pm .08, 23 1.49-1.57 (1.4-1.7)	1.0	1.53 \pm .15, 19 1.47-1.59 (1.3-1.8)
Breadth of zygomatic plate	2.51 \pm .17, 21 2.43-2.59 (2.3-3.0)	<.001	2.80 \pm .16, 23 2.74-2.86 (2.6-3.1)	<.001	2.49 \pm .17, 19 2.41-2.57 (2.2-2.9)
Length of diastema	6.46 \pm .31, 22 6.32-6.60 (5.9-7.0)	<.001	6.93 \pm .29, 23 6.81-7.05 (6.4-7.4)	<.001	6.50 \pm .31, 19 6.36-6.64 (6.0-7.2)
Palatal length	12.47 \pm .47, 21 12.27-12.67 (11.5-13.4)	.01-.001	12.91 \pm .50, 23 12.71-13.11 (12.2-13.8)	<.001	12.31 \pm .39, 19 12.13-12.49 (11.4-12.7)

TABLE 4 — (Continued)

	Indochina (Laos, Vietnam, Thailand)	P_1	Malay Peninsula (Pahang, Selangor, Johore)	P_2	West Java
Postpalatal length	8.69 ± .42, 19 8.49-8.89 (7.8-9.6)	1.0	8.69 ± .41, 22 8.51-8.87 (8.1-9.9)	.3-.2	8.54 ± .46, 18 8.32-8.76 (7.8-9.6)
Length of palatal bridge	4.58 ± .24, 21 4.48-4.68 (4.1-5.0)	<.001	5.09 ± .23, 23 4.99-5.19 (4.6-5.5)	<.001	4.77 ± .23, 19 4.67-4.87 (4.3-5.2)
Breadth of bridge at M ¹	3.00 ± .15, 21 2.92-3.08 (2.8-3.4)	.02-.01	2.89 ± .13, 23 2.83-2.95 (2.7-3.2)	.2-.1	2.83 ± .14, 19 2.77-2.89 (2.5-3.2)
Breadth of bridge at M ³	3.22 ± .20, 21 3.14-3.30 (3.0-3.7)	.01-.001	3.06 ± .16, 23 3.00-3.12 (2.8-3.4)	.8-.7	3.08 ± .17, 19 3.00-3.16 (2.8-3.4)
Length of incisive foramina	4.33 ± .28, 22 4.21-4.45 (3.8-4.9)	<.001	3.56 ± .30, 23 3.44-3.68 (3.0-4.2)	.9-.8	3.54 ± .18, 19 3.46-3.62 (3.1-4.0)
Breadth of incisive foramina	2.07 ± .10, 21 2.03-2.11 (1.8-2.2)	.2-.1	2.02 ± .14, 23 1.96-2.08 (1.8-2.3)	.01-.001	1.89 ± .11, 19 1.85-1.93 (1.7-2.1)
Incisive foramina to M ¹	.33 ± .18, 21 .25-.41 (.1-.7)	<.001	.96 ± .20, 23 .88-1.04 (.5-1.4)	<.001	.73 ± .19, 19 .65-.81 (.4-1.1)
Breadth of mesopterygoid fossa	1.79 ± .20, 21 1.71-1.87 (1.5-2.3)	.6-.5	1.82 ± .14, 23 1.76-1.88 (1.5-2.1)	.001	1.67 ± .12, 19 1.61-1.73 (1.4-1.9)
Length of bulla	3.63 ± .14, 19 3.57-3.69 (3.5-3.8)	.001	3.40 ± .17, 23 3.32-3.48 (3.1-3.8)	.01-.001	3.53 ± .10, 19 3.49-3.57 (3.3-3.7)
Height of bulla	3.05 ± .14, 19 2.99-3.11 (2.8-3.2)	.05-.02	2.94 ± .17, 23 2.86-3.02 (2.6-3.3)	.9-.8	2.95 ± .13, 19 2.89-3.01 (2.7-3.1)
Alveolar length of M ¹⁻³	3.92 ± .16, 22 3.86-3.98 (3.6-4.1)	.05-.02	3.80 ± .17, 23 3.72-3.88 (3.3-4.2)	.05-.02	3.69 ± .12, 19 3.63-3.75 (3.5-3.9)

^aMeasurements are in millimeters. The mean and standard deviation, size of sample after comma, plus and minus two times the standard error of the mean, and the observed range in parentheses are listed, in that order, for each measurement.

^b P refers to probabilities that means of the samples were drawn from the same population.

Isthmus of Kra (10° 30' N) in peninsular Thailand. These specimens represent a morphological type I refer to as the Indochinese form of *C. gliroides*. The other lot includes mice from the Malay Peninsula south of the Isthmus of Kra and animals from islands on the Sunda Shelf; I designate this kind of mouse as the Malayan form. It is a distinct type with its own

pattern of geographic variation. I shall contrast the two forms, describe how and where the distinctive morphological traits of each may intergrade, then discuss the nature of geographic variation within each.

My comparative sample of the Indochinese form of *C. gliroides* consists of specimens I grouped from localities in northern Thailand,

Laos, southern China, and Vietnam. I first compared series from those localities, then tested to determine if some of the differences I saw among them were significant, found they were not, and pooled the material into one large sample. I excluded series from Assam, northern Burma, and southern Tenasserim. Skulls of specimens from Assam and northern Burma were in poor condition and difficult to measure. The series from southern Tenasserim is a special one and I discuss it separately. It is the data from the pooled samples that are listed in table 4 and that I contrast with series from Malaya.

Samples of the Malayan kind from localities closest to Indochina are from the Malay Peninsula south of the Isthmus of Kra. I brought together specimens from Pahang, Selangor, and Johore to form the large sample which I compare with the Indochinese type.

The Malayan form of *C. gliroides* is a small, brightly colored mouse with a reddish brown body, buffy cheeks, and a white underside separated from the upperparts by narrow ochraceous strips. The type from Indochina has a longer head and body than the Malayan form, longer hind feet, and a shorter tail relative to head and body (table 4). Upperparts of mice in a few Indochinese samples are bright reddish brown, but in most samples the heads and backs are paler, with more brown and tan than red in the pelage; the underparts tend to be cream rather than white; the cheeks are buffy, and there are usually no ochraceous strips separating upperparts from the underparts—if present they are inconspicuous. The tail tends to be paler than the Malayan form, grayish brown instead of brown or dark brown.

For 15 out of 23 cranial and dental measurements, the means differ significantly between the Malayan and Indochinese samples (table 4), and the differences in actual values are accompanied by proportional dissimilarities. These statistics quantify the distinctions seen between the two types when skulls of each are viewed side by side: the Malayan form has a larger cranium, shorter incisive foramina, shorter maxillary toothrows, a narrower palatal bridge, and smaller bullae than the Indochinese form.

Differences between means for some of the measurements reflect a dissimilarity in configu-

ration of the diastemal and palatal regions in the two forms of *C. gliroides*. The diastema is long in the Malayan form and contrasts with short and wide incisive foramina. The lengths of those foramina vary in the sample, ranging from 39 to 61 percent of the length of the diastema. Accordingly, the distance between the posterior margins of the foramina and the front edges of the toothrows is long (table 4: incisive foramina to M^1), as is the palatal bridge (distance from the back edge of the incisive foramina to the end of the bony palate). Examples of *Chiropodomys karlkoopmani*, *C. calamianensis*, *C. major*, and *C. muroides* all have this configuration. The Indochinese form, in contrast, has long incisive foramina set in a short diastema (length of the foramina range from 55 to 73 percent of the length of the diastema) with a shorter distance between foramina and teeth, and a shorter palatal bridge. I have diagrammed the two configurations in figure 9 and for each sample portrayed the distribution of values obtained from the ratio: length of foramina to length of diastema. The distributions of the two configurations within the sample from Indochina north of the Isthmus of Kra and within that from the Malay Peninsula south of the Isthmus are nearly exclusive, overlapping each other by only a few specimens. This feature of each sample, along with the other differences between them in cranial and dental measurements and proportions, indicates two populations, each occupying a different geographic area.

As distinct as the two forms of *C. gliroides* are, the differences in cranial features that distinguish each kind apparently do not reflect complete genetic isolation. Bankachon (lat. $10^{\circ} 09' N$, long. $98^{\circ} 36' E$) in southern Tenasserim, the tip of Burma at the Isthmus of Kra, is the source of a sample containing evidence of intergradation between the two morphological types of *C. gliroides*. Bankachon is at the latitude where one would predict that either the two morphological types occur together, suggesting two species, or the diagnostic features of each intergrade, indicating partial genetic continuity between two distinctive geographic variants of a widespread species. Fifty mice were obtained from Bankachon by G. C. Shortridge in 1913. The specimens were identi-

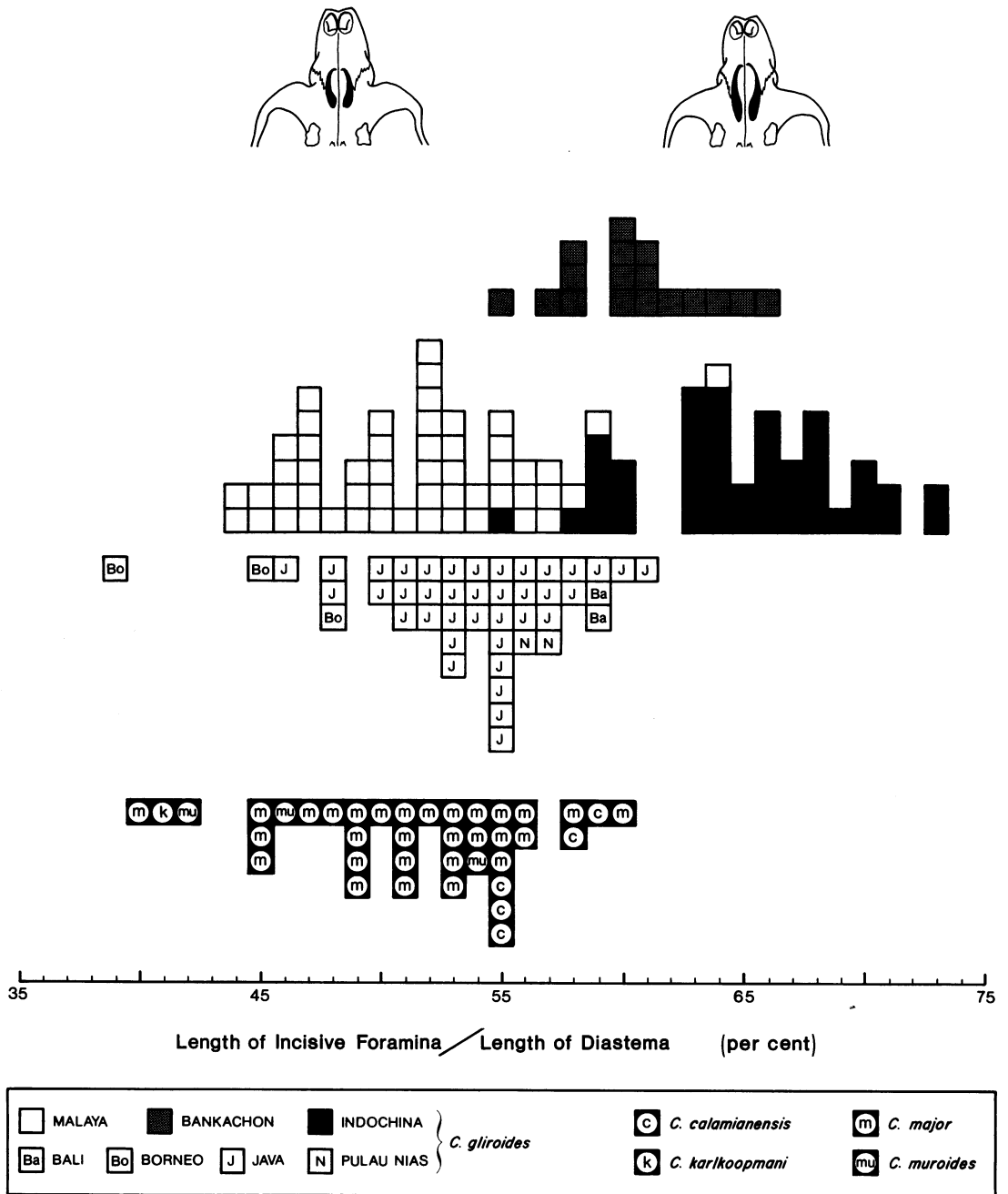


FIG. 9. Variation in length of incisive foramina relative to length of diastema in samples of *Chiropodomys gliroides* from Indochina and the Malay peninsula; and in samples of *C. karlkoopmani*, *C. major*, *C. calamianensis*, and *C. muroides* from throughout their known geographic ranges. Each square represents one adult.

fied as *C. peguensis* and discussed by Wroughton (1915, p. 714). I have examined 17 adults from Shortridge's series. Most features of the skins, skulls, and teeth of those animals are like specimens in the samples of the Indochinese type of *C. gliroides*. Values of some measurements and certain cranial configurations, however, suggest intergradation between the two types.

Mean values of the measurements from the 17 specimens from Bankachon fall into four categories (table 5). First, there are the six measurements (length of head and body, occipitonasal length, zygomatic breadth, breadth of braincase, breadth of palatal bridge at the level of first molars, and length of maxillary toothrows) in which the means do not differ significantly from means in either the Indochinese sample or the sample from the Malay Peninsula. Second, the mean values for five measurements (length of tail, breadth of rostrum, palatal length, length of incisive foramina, and incisive foramina to first molars) are significantly different from those in the other two samples; the values for four of those measurements lie between the means from the Indochinese and Malayan samples. Third, the means of six measurements (length of nasals, breadth of zygomatic plate, length of diastema, length of palatal bridge, length of bulla, and length of hind foot) do not differ significantly from means in the sample from Indochina. And fourth, values for two measurements (interorbital breadth and length of rostrum) do not differ significantly from means in the sample from the Malay Peninsula.

The percentages which express the length of incisive foramina relative to the length of diastema in specimens from Bankachon are not distributed equally between the two nearly discrete distributions of percentages from samples of the Indochinese and Malayan forms (fig. 9). Most values fall into the Indochinese cluster, a few extend over into the Malayan sample. The distribution of these percentages from the Bankachon sample, combined with values from the cranial and dental measurements, indicate that specimens in the series are like the Indochinese *C. gliroides* in most characteristics but

overlap the sample from the Malay Peninsula in a few features, enough to suggest that there is some morphological intergradation between the two forms in the narrow part of the Peninsula. I do not think the data support the other hypothesis, that there are two species in the sample from Bankachon; at least I have not been able to separate the specimens into two groups.

Eleven of the mice from Bankachon have bright upperparts that are like the Malayan form of *C. gliroides*; six have duller pelages. This composition may indicate that the population at Bankachon is a mixture of genes from the populations with bright pelage to the south and those with duller coats to the north and east. The variation in tone may, however, reflect another cause. Medway (1965), for example, observed individual *C. gliroides* in the laboratory whose pelages changed from grayish brown to rich golden brown, changes related to age and to periodicity of molting. All mice in the sample from Bankachon are adults and were collected on December 7, 10, 11, 14, 17, and 21; possibly the bright and dull tones indicate only fresh or worn pelages. Perhaps tone of pelage is linked with type of forest. Mice from Assam and northern Burma also have bright upperparts, but are like the Indochinese form in all other features of skin, skull, and teeth. Those samples and the series from Bankachon all come from areas that are, or at least were, covered by semi-evergreen rain forest (Whitmore, 1975). Tropical moist deciduous forest predominates in other parts of Burma, in Thailand, and in regions to the north and east, the geographic origins of specimens with pale pelages.

The Indochinese and Malayan forms of *C. gliroides* may also differ in morphology of chromosomes; the data, however, are incomplete. Yong (1973) obtained samples of chromosomes from three males and two females of *C. gliroides* which were collected from Gombak, Selangor State, on the Malay Peninsula. He determined the diploid number to be 42: the autosomes consisted of 18 telocentric pairs, one metacentric pair, and one submetacentric pair; a metacentric X and submetacentric Y constituted the sex chromosomes; the

TABLE 5
Measurements from Samples of *Chiropodomys gliroides* from Indochina, the Malay Peninsula, and Bankachon^a

	Indochina	P_1	Bankachon	P_2	Malay Peninsula
Length of head and body	90.0 ± 6.3 81-101 21	.4-.3	87.8 ± 7.3 76-103 17	.5-.4	86.2 ± 7.4 69-102 57
Occipitonasal length	24.73 ± .64 23.6-25.9 18	.7-.6	24.86 ± .53 24.3-25.8 9	.2-.1	25.37 ± .83 24.0-26.7 23
Zygomatic breadth	14.37 ± .33 13.8-15.1 17	.2-.1	14.09 ± .66 12.5-14.5 8	.2-.1	14.56 ± .83 13.7-15.5 23
Breadth of braincase	12.22 ± .23 11.9-12.7 18	.6-.5	12.30 ± .42 11.5-12.6 9	.7-.6	12.37 ± .35 11.9-13.1 23
Breadth of bridge at M ¹	3.00 ± .15 2.8-3.4 21	.2-.1	2.92 ± .14 2.7-3.2 15	.6-.5	2.89 ± .13 2.7-3.2 23
Alveolar length of M ¹⁻³	3.92 ± .16 3.6-4.1 22	.2-.1	3.85 ± .13 3.6-4.1 16	.4-.3	3.80 ± .17 3.3-4.2 23
Length of tail	115.3 ± 6.8 105-134 21	.05-.02	122.1 ± 11.9 100-148 17	.05-.02	116.0 ± 10.1 94-143 57
Breadth of rostrum	4.87 ± .22 4.3-5.2 21	.01-.001	4.63 ± .24 4.1-5.0 16	<.001	4.98 ± .19 4.6-5.3 23
Palatal length	12.47 ± .47 11.5-13.4 21	.02-.01	11.97 ± .70 10.7-13.2 15	<.001	12.91 ± .50 12.2-13.8 23
Length of incisive foramina	4.33 ± .28 3.8-4.9 23	<.001	3.87 3.4-4.2 15	.01-.001	3.56 ± .30 3.0-4.2 23
Incisive foramina to M ¹	.33 ± .18 .1-.7 21	.02-.01	.49 ± .16 .3-.8 16	<.001	.96 ± .20 .5-1.4 23
Length of hind foot	19.7 ± 1.1 18-22 21	.3-.2	20.1 ± .8 19-21 17	.01-.001	18.8 ± 1.6 15-22 57
Length of nasals	7.47 ± .34 6.9-8.1 21	.6-.5	7.38 ± .48 6.5-8.0 16	<.001	8.24 ± .62 7.0-9.4 23
Breadth of zygomatic plate	2.51 ± .17 2.3-3.0 21	.8-.7	2.53 ± .23 2.1-2.8 15	<.001	2.80 ± .16 2.6-3.1 23
Length of diastema	6.46 ± .31 5.9-7.0 22	.6-.5	6.39 ± .44 5.7-7.2 16	<.001	6.93 ± .29 6.4-7.4 23

TABLE 5 — (Continued)

	Indochina	P_1	Bankachon	P_2	Malay Peninsula
Length of palatal bridge	4.58 ± .24 4.1-5.0 21	.6-.5	4.53 ± .29 3.9-4.9 15	<.001	5.09 ± .23 4.6-5.5 23
Length of bulla	3.63 ± .14 3.5-3.8 19	.5-.4	3.58 ± .17 3.3-3.9 11	.01-.001	3.40 ± .17 3.1-3.8 23
Interorbital breadth	4.52 ± .18 4.1-4.8 21	<.001	4.79 ± .25 4.5-5.4 16	.5-.4	4.73 ± .25 4.2-5.2 23
Length of rostrum	5.76 ± .31 5.2-6.3 21	.01-.001	6.12 ± .37 5.4-6.8 16	.1-.05	5.87 ± .40 5.1-6.7 23

^aMeasurements are in millimeters and are from adults. The mean and one standard deviation, observed range, and size of sample are listed for each measurement.

P refers to probabilities that means of the samples were drawn from the same populations.

fundamental number was 48. A karyotype of the Indochinese form, from a Thai mouse, was reported by Marshall (1976) to consist of 42 telocentric chromosomes. He presented no further analysis of the sample and his published photograph of the chromosome spread is too murky to distinguish actual shapes of all the chromosomes. Marshall kindly sent me other photographs of spreads from the same mouse, a male, and there appear to be 42 telocentric chromosomes in one of the prints. Better samples must still be obtained from the Indochinese population to test Marshall's observation and to determine if there are differences in morphology of chromosomes between the two types, differences that might parallel those in the skins and skulls.

Both forms of *C. gliroides* display geographic variation, but the features involved and the magnitude of the variation within each form are not the same. With the exception of the series from Bankachon in which some characteristics of the specimens may reflect genetic intergradation with the Malayan type, mice in the samples from Indochina are much alike in dimensions and proportions of body, tail, skull, and teeth; I could not find significant geographic variation in those features over the mainland of Southeast Asia. A trait in the Indo-

chinese samples that does vary from place to place is color of the upperparts. Mice from Assam and northern Burma have bright, reddish brown upperparts which resemble the bright pelage of the Malayan form of *C. gliroides*. Specimens in the samples from Laos, southern China, Vietnam, Thailand, and southern Burma have much paler upperparts; the pelage has more browns and tans in it and is subdued in tone. The most southern sample of the Indochinese form, that from Bankachon, consists of specimens with bright upperparts and a few with the duller pelage.

While the Indochinese form of *C. gliroides* is known from the Asian mainland and peninsular Burma and Thailand and displays little variation from one place to another—a reflection of relatively unhindered gene flow over a wide area—populations of the Malayan type are scattered over a peninsula and across an archipelago; this disjunct distribution is paralleled by morphological variation, likely a reflection of past insular isolation and subsequent differentiation. I have recorded specimens from the Malay Peninsula, Sumatra, Nias and Tjjuh islands, the Natuna islands, Java, Bali, and Borneo (page 406). I did not personally examine examples from the Natuna and Tjjuh islands, but have looked at mice from all the

other places, and my analysis of geographic variation within the Malayan form of *C. gliroides* is based on data obtained from them. Many specimens are available from the Malay Peninsula, Java, and Bali, enough to characterize the populations there realistically. Samples from the other islands are small and the information they provide about their position in the pattern of geographic variation over the Malay Archipelago is incomplete. In the preceding pages I discussed mice from the Malay Peninsula when I used them as the examples of the Malayan type geographically closest to the Indochinese form. The color and pattern of pelage and the cranial configurations of specimens in the samples from the Malay Peninsula are also characteristic of mice from the Sunda islands, especially the size relations between the incisive foramina and diastema (fig. 9). There is some variation from island to island in intensity of pelage coloration, but most geographic variation is expressed as differences in certain body and cranial dimensions among island samples. Mice in the population from the Malay Peninsula are largest in body size, specimens from most of the Sunda islands are smaller, and the few examples from Borneo are the smallest. Outside of the Malay Peninsula, the sample with the most specimens comes from West Java. I shall discuss this series first, then the samples from other islands on the Sunda Shelf.

Samples from the Malay Peninsula and Java are similar in pelage coloration and dimensions of body, tail, and feet, but dissimilar in sizes of skulls and teeth (table 4). Means of 15 measurements from the Malayan sample are significantly greater and one is significantly smaller than means from the Javan series: mice on the Malay Peninsula have larger skulls and longer tooththrows but smaller bullae than do the mice living on Java. There are also a few significant proportional differences between the two samples. The Javan series has, on the average, a shorter postpalatal length relative to length of diastema or palatal length, narrower incisor tips relative to breadth of rostrum, narrower incisive foramina relative to their lengths, and longer bullae relative to length of skull or depth of bulla.

My samples of *Chiropodomys gliroides* from Java and the island of Bali appear to be drawn from the same population. I studied eight mice from Bali and could not detect any significant differences between them and the examples from Java. Sody (1941) examined five of these Balinese specimens and noted small differences in a few measurements between them and the Javan mice he had, but those differences are minute and indicate variation among individuals in one sample and not significant differences between populations. This similarity between samples of *C. gliroides* from Java and Bali contrasts with the relationship I found between samples of *Rattus cremoriventer*, a small arboreal rat, from those two islands (Musser, 1973b); the population on Bali comprises much larger individuals with conspicuously paler fur than the small and brightly colored mice in the Javanese population.

The mainland of Sumatra, Nias Island, and Borneo are the three other places represented by specimens. I have seen only one example of *C. gliroides* from Sumatra (RMNH 23874) and I know of no other specimens from that large island. The skin and skull is from Sungai Langka in the Lampung District of southern Sumatra. It is an adult female with moderately worn teeth. The skin is in poor shape and color of the pelage is altered. The mouse was probably preserved in alcohol and later made into a study skin. The skull and mandibles are incomplete; part of the right mandible and the right side of the cranium are all that can be measured, the rest of the parts are missing. The few external and cranial measurements I could obtain are listed in table 6. I cannot fully characterize the population of *C. gliroides* that lives on Sumatra from such an incomplete specimen, and I record only that it is more similar to specimens in samples from the Malay Peninsula and Java than to those from either Nias Island or Borneo. Two measurements from the Sumatran example, breadth of rostrum and length of tooththrow, fit best with the samples of large mice from the Malay Peninsula; breadth of zygomatic plate is like that in the Javan sample. Values for the other measurements are not helpful in assessing relationships of the Sumatran specimen. It also resembles the mice

from Nias Island, but the toothrow is much longer and again points to affinities with the Malay Peninsula. The mouse from Sumatra is larger than any of the small examples of *C. gliroides* from Borneo.

I know of four specimens from Nias Island, off the west coast of Sumatra. Thomas (1891) referred to one and Miller (1903) described another. I have studied those specimens and two others. Two of these are adults. I have listed their measurements in table 6. If the features of those specimens are a reliable estimate of the morphological characteristics of the population

on Nias Island then they represent an island form of *C. gliroides* that is more like the samples from the Malay Peninsula, Java, Bali, and probably Sumatra, than the small *C. gliroides* from Borneo. The two mice from Nias Island have bright, reddish brown upperparts and white bellies, like the other examples from the Sunda Shelf. They are distinct in a few measurements, resemble the Malayan series in some, and the Javan sample in others. Compared with those two large samples, the specimens from Nias have a shorter tail, narrower incisors, and longer incisive foramina. Means

TABLE 6
Measurements of Adult *Chiropodomys gliroides* from Borneo, Nias Island, and Sumatra^a

	MC36540	Borneo AMNH 106112	Mean	USNM 121867 ^b	Nias Island MCZ 35969	Mean	Sumatra RMNH 23874
Sex	M	M		F	F		F
Length of head and body	69	77	73.0	81	83	82.0	75
Length of tail	81	96	88.5	102	110	106.0	109
Length of hind foot	16	17	16.5	19	19	19.0	18
Length of ear	11	13	12.0	—	16		15
Occipitonasal length	22.3	19.7	21.0	23.6	25.7	24.7	—
Zygomatic breadth	—	12.1		13.6	14.5	14.1	—
Interorbital breadth	4.4	4.4	4.4	4.6	5.1	4.9	—
Length of nasals	7.2	6.1	6.6	7.6	8.5	8.1	7.7
Length of rostrum	5.7	4.9	5.3	5.4	6.2	5.8	7.0
Breadth of rostrum	5.2	4.3	4.8	4.8	5.1	5.0	5.6
Breadth of braincase	11.5	11.5	11.5	11.9	12.3	12.1	—
Height of braincase	8.0	7.3	7.7	7.9	8.4	8.2	—
Breadth of incisor tips	1.2	1.2	1.2	1.3	1.6	1.5	1.5
Breadth of zygomatic plate	—	2.1		2.2	2.8	2.5	2.4
Length of diastema	5.8	5.8	5.8	6.3	7.0	6.7	6.6
Palatal length	10.7	10.9	10.8	11.6	12.9	12.3	—
Postpalatal length	7.6	7.2	7.4	7.8	9.2	8.5	—
Length of palatal bridge	4.5	4.9	4.7	4.6	5.1	4.9	—
Breadth of bridge at M ¹	2.8	2.6	2.7	3.0	2.8	2.9	—
Breadth of bridge at M ³	3.0	3.0	3.0	3.2	2.9	3.1	—
Length of incisive foramina	2.8	2.6	2.7	3.5	4.0	3.8	—
Breadth of incisive foramina	1.8	1.7	1.8	1.9	2.3	2.1	—
Incisive foramina to M ¹	1.1	1.3	1.2	.8	.9	.9	—
Breadth of mesopterygoid fossa	—	1.5		1.7	1.8	1.8	—
Length of bulla	3.0	3.3	3.2	3.3	3.6	3.5	—
Height of bulla	2.5	2.5	2.5	3.0	2.9	3.0	—
Alveolar length of M ¹⁻³	3.3	3.3	3.3	3.5	3.7	3.6	4.0

^aMeasurements are in millimeters.

^bHolotype of *Chiropodomys niadis*.

of nine cranial measurements (interorbital breadth; lengths of bulla, nasals, and rostrum; height of braincase; breadths of rostrum and incisive foramina; and distance from incisive foramina to the first molars) do not differ significantly from the Malayan sample; and means of eight other measurements (occipitonasal length, zygomatic and braincase breadths, breadth of zygomatic plate, palatal length; lengths of diastema, palatal bridge, and maxillary toothrow) are smaller than the Malayan sample and do not differ from means of the Javan series. And the two specimens are much larger than any I measured from Borneo.

The sample from Borneo forms one segment of a semi-circular pattern of geographic variation in the Malayan form of *C. gliroides*: the largest mice live to the west on the Malay Peninsula, the smallest occur to the east on Borneo; animals of intermediate size are scattered over the southern arc of islands formed by Nias, Sumatra, Java, and Bali. I have looked at six examples from Borneo and measured two of them (table 6). Though the sample is small it contains animals from both northern and southern Borneo. The Bornean population, as represented by these few specimens, consists of small mice with bright reddish brown upperparts, white underparts, ochraceous cheeks and body strips, and white front and hind feet. Compared with the large mice in samples from the Malay Peninsula, means of all measurements except breadth across the palatal bridge and distance from incisive foramina to front of the toothrows are significantly smaller; width of the palatal bridge is the same, and the distance between incisive foramina and toothrows is greater, a reflection of the very short foramina in the Bornean specimens (fig. 9). Those mice are also smaller than the Javan series in all measurements except breadth of rostrum, interorbital breadth, and length and breadth of palatal bridge, which are the same in the two samples. The distance from incisive foramina to toothrows is also significantly greater in the Bornean mice than in Javan animals.

I have assumed the population on Borneo to be genetically part of a larger group which includes all the known morphological variants

of *C. gliroides* on each island of the Sunda Shelf and on the Malay Peninsula. I have no data from breeding tests—actual proof of genetic compatibility between the island forms—to support the assumption; I present it as a hypothesis that will have to be tested with data from additional samples and with information from other kinds of characters. Certainly all the samples that constitute what I have called the Malayan form of *C. gliroides* contain individuals basically similar in color and structure of head and body, tail, feet, ears, skull, and teeth. The distinctions among the samples are differences in average sizes of external, cranial, and dental dimensions. All the specimens cluster in a morphological group which is different from the form of *C. gliroides* occurring in Indochina, and all the specimens are unlike all the other morphological types which represent other species—*C. karlkoopmani*, *C. major*, *C. calamianensis*, and *C. muroides*. That the distinctive morphological features of the Indochinese type and the Malayan kind intergrade, pointing to incomplete genetic isolation, suggests strongly that the populations from the Peninsula and those from islands on the Sunda Shelf, all more alike than either is to any other kind of *Chiropodomys*, are potentially capable of interbreeding and are peninsular and insular subgroups of one species. Still, the difference in size among mice in some of those subgroups, between samples from the Malay Peninsula and Borneo, for example, is impressive, and the magnitude of such differences may reflect genetic divergence to a point where the populations are reproductively isolated from each other. Other kinds of data, especially from breeding experiments, are needed to resolve this aspect of the relationships among populations on the islands and those on the peninsula.

TAXONOMY: At various times in the past, six scientific names have been applied to the small *Chiropodomys* from Indochina and the Sunda Shelf. If we assume for now that the available samples represent a single species composed of discrete morphological and geographic groups, then some of the names can be used to identify particular groups as subspecies. Two names can be tied to the Indochinese form. The oldest, of

course, and the one I used for the species, is *C. gliroides*, proposed by Blyth in 1855 and published in 1856. Blyth, in 1859, also named and described *Mus peguensis* from a specimen obtained in southern Burma at Schwegyin, in the valley of the Sittang River. That specimen is an example of the Indochinese type of *C. gliroides*, and the name *peguensis* should be considered a synonym of *gliroides* as Ellerman (1961) relegated it. This statement is based not on my own comparisons of the holotypes of *gliroides* or *peguensis*—I have seen neither one—but on remarks in the literature and inferences based on specimens I examined which came from southern Burma where the holotype of *peguensis* was collected. The holotype of *peguensis* and a specimen from Cherrapunji, the type locality of *gliroides*, were examined and described by W.L. Sclater in 1890. Sclater at the time was Deputy Superintendent of the Indian Museum at Calcutta and he authored a report, "Notes on some Indian Rats and Mice," which "were written during the preparation of the catalogue of the specimens of Rats and Mice in the Indian Museum. . . ." There he described *Chiropodomys gliroides* in detail and illustrated its skull and teeth. He allocated Blyth's *peguensis* as a synonym of *gliroides* and included also, with a question mark, Peters's *Chiropodomys penicillatus*, published in 1869. His reasons for these inclusions were clear (1890, p. 532):

The unique type of *Mus gliroides* of Blyth has unfortunately disappeared from the Museum, so that it is not possible to be absolutely sure as to whether *Mus peguensis* is identical with it or not; there seems, however, to be no reasonable doubt on the subject since there is in the Museum a Mouse from Cherra Punji, whence the type originally came, which entirely agrees with the description of *Mus gliroides*, and this specimen is certainly conspecific with the type of *Mus peguensis*. Of *Chiropodomys penicillatus*, which is the type of the genus, it is not possible to be certain without a direct comparison of the types, but there is nothing in the description to prevent its being absolutely identical with *Mus gliroides* of Blyth.

All the specimens I have studied from southern Burma are clearly examples of the Indochi-

nese form of *C. gliroides*; there is no reason to think that the holotype of *peguensis* is not this same kind of mouse.

What now is the identity of *C. penicillatus*, the type species of the genus *Chiropodomys*? Peters defined the genus and described the type species in a report which was given July 16, 1868, during a monthly meeting of the Royal Prussian Academy of Science of Berlin. The report was not published until 1869.¹ Peters studied one specimen. His description of it is short but clear, and his illustration of it is excellent (fig. 10). My impression is that few if any of the persons who wrote about *C. gliroides* and who considered *penicillatus* to be a synonym of that species ever examined the holotype; all refer to Peters's illustration, which appears to be the same kind of mouse as *gliroides*. As fine as Peters's illustration is, I could not positively identify the specimen portrayed in it. The animal could be an example of *C. gliroides*, but it could also belong to one of the

¹The genus name, *Chiropodomys*, and its type species, *C. penicillatus*, dates from 1869, not 1868, as it is entrenched in the mammalogical literature (see, for example, Trouessart, 1881, 1897-1905; Sclater, 1891; Tate, 1936; Chasen, 1940; Allen, 1940; Simpson, 1941; Ellerman, 1940, 1961; Ellerman and Morrison-Scott, 1951, 1955; Arata, 1967; and Walker, 1968; and in bibliographic references which contain scientific names and citations to their dates and places of publication (Günther, 1869; Scudder, 1882; Palmer, 1904; Schulze, Kukenthal and Heider, 1929; and Neave, 1939, are some sources). I have before me the original volume in which Peters's report appears. The front page is titled: *Monatsberichte Der Königlich Preussischen Akademie Der Wissenschaften zu Berlin. Aus dem Jahre 1868*. Berlin. At the bottom of the page is the name and address of the publisher, "Buchdruckerei Der Königl. Akademie der Wissenschaften (G. Vogt) Universitätsstr. 8," and the date the volume was published, "1869." The entire volume contains reports which were given every month during the year, 1868, beginning with January 6 and ending with December 17. There is no evidence that any of the reports were published separately and distributed during 1868, and every indication that the papers were published together as one volume in 1869. Possibly biographers took "Aus dem Jahre 1868" to indicate the year of publication, but in context, the phrase clearly points only to the year in which the monthly meetings of the Royal Prussian Academy of Science of Berlin were held, not to the date the reports were published.

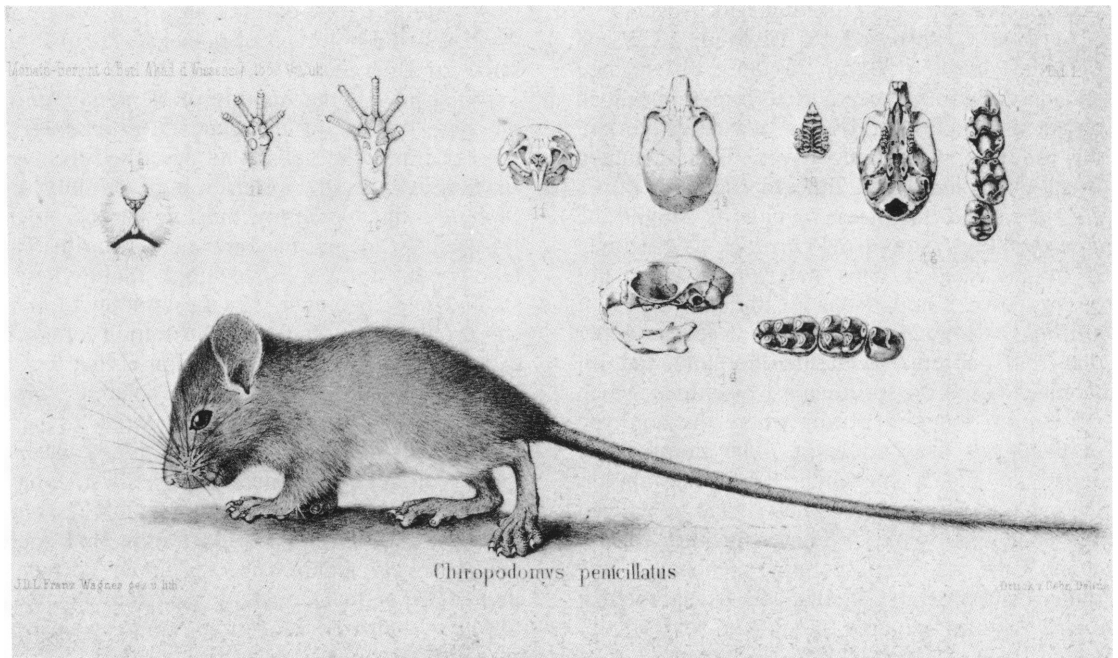


FIG. 10. The illustration of the holotype of *Chiropodomys penicillatus* which was included in Peter's (1869, pl. 1) original description. As reproduced here the drawings are slightly less than natural size.

other species of *Chiropodomys*. Peters had no information about where the mouse was collected; geographic origin, therefore, could not be used to help identify the animal. I had to examine the holotype before I could allocate the name with any certainty.

The holotype of *C. penicillatus* is in the Zoologisches Museum an der Humboldt-Universität zu Berlin; it was located and sent to me by Dr. Renate Angerman, a kindness I very much appreciate. The specimen, BZM 3476, is preserved in alcohol and its skull had been extracted and cleaned. The cranium and mandibles are complete. The animal is male and juvenile, facts that can easily be obtained by looking at Peters's illustration. The first and second upper and lower molars are fully erupted; the third molars had emerged just above the bone so that all of the crowns are now exposed. The head and body is brown above and white below; the tail is brown. Some measurements (in millimeters) I took from the

specimen are: length of head and body, 60; length of tail, 96; length of hind foot, 19; length of ear, 11; occipitonasal length, 21.0; zygomatic breadth, 12.5; interorbital breadth, 4.7; breadth of braincase, 11.4; length of diastema, 5.3; length of incisive foramina, 3.1; incisive foramina to first molar, .4; palatal length, 11.5; alveolar length of maxillary tooth-row, 4.1; and length of bulla, 3.3.

The holotype of *C. penicillatus* is a juvenile example of *C. gliroides*; it does not belong with any of the other four species of *Chiropodomys* I have discussed in this report. Furthermore, among the samples of *C. gliroides* that I have examined the specimen fits with the sample from the Malay Peninsula and only with that one. I have at hand one juvenile of about the same relative age from Selangor in the Malay Peninsula (USNM 283697), one from northern Burma (AMNH 113040), and two from Vietnam (FMNH 46720 and 46724). The skull of the holotype of *penicillatus* is larger

than those three from Southeast Asia, and about the same size as the one from Selangor; the difference in size between the juvenile from Selangor and those from Burma and Vietnam is of the same magnitude as the difference between skulls of adult *C. gliroides* in samples from Indochina and the Malay Peninsula. And although some of the cranial configurations of juveniles are distorted compared to those of adults, the differences in the region of the diastema are still evident when juveniles are compared to other juveniles. The juvenile from Selangor and the holotype of *penicillatus* have short incisive foramina relative to length of the diastema. The distance from the back of the incisive foramina to the fronts of the front molars is 0.4 mm. in both skulls. The ratio, length of incisive foramina to length of diastema, is 59 percent in the holotype and 58 percent in the specimen from Selangor. In the three specimens from Burma and Vietnam, the incisive foramina are long, ending at the fronts of the molars, and the percentages which express the relative size of incisive foramina to length of diastema are 64, 68, and 68.

Peters (1869, p. 449) did not know where the holotype of *penicillatus* came from and wrote that the species was probably to be found in Africa. *Chiropodomys* does not occur in Africa and Peters's specimen certainly did not come from there, but I do not know of any records, either published or sequestered in museums, which may reveal its geographic origin. Because BZM 3476 is closely similar in its external and cranial features to examples of *C. gliroides* from the Malay Peninsula south of the Isthmus of Kra and not to samples either from the mainland of Southeast Asia or from islands on the Sunda Shelf, I suggest we consider the specimen to have originated from somewhere on the Malay Peninsula.

My descriptive outline of the geographic variation in *C. gliroides* can be overlaid with subspecific notation in the following manner. Within the species there are two basic morphological types, an Indochinese kind and a Malayan form, which apparently intergrade in peninsular Burma and Thailand. Each type has its own pattern of geographic variation, gener-

ally continuous within the Indochinese form and discontinuous in the Malayan form. The name, *C. g. gliroides*, should be used to refer to the Indochinese mice from the Isthmus of Kra (including the series from Bankachon) and from north of there on the mainland of Southeast Asia (samples from localities 1-27). The animals which occur south of the Isthmus of Kra on the Malay Peninsula (the southern part of peninsular Thailand and West Malaysia) should be called *C. g. penicillatus* (localities 28-44). The name *peguensis* has always been used as the subspecific name of *C. gliroides* from the Malay Peninsula and other places on the Sunda Shelf but *peguensis* is a synonym of the Indochinese form of *C. gliroides*.

The subspecific names available for certain subgroups in the Malayan form of *C. gliroides* are *pusillus*, *niadis*, and *anna*. Thomas (1839a) described *C. pusillus*, and it is the name for the population of *C. gliroides* on Borneo (localities 79-82). Miller's (1903) *niadis*, originally described as a distinct species of *Chiropodomys*, designates the population on Nias Island off the west coast of Sumatra (locality 45). And *anna*, named and described by Thomas and Wroughton (1909a) as a separate species, is to be used for the mice from Java and Bali (localities 50-78).

I cannot apply subspecific names to the few specimens from Sumatra (locality 47), the Tuhuh islands (locality 46), or the Natuna islands (localities 48 and 49) until more material from those places is available for study.

HABITATS: Populations of *C. gliroides* occur in primary and secondary forests, especially where bamboo clumps are common, although the animal is apparently not confined to bamboo (Harrison, 1955; Medway, 1964, 1969); nor, judged from the geographic and altitudinal origins of the specimens, is the species restricted to a particular type of forest. Specimens have been obtained from tropical moist deciduous forest and evergreen and semi-evergreen rain forests on lowlands, coastal plains, and hills, and from the montane evergreen rain forests on mountains and plateaus (see Whitmore, 1975, for discussions of these types of forests and their distributions). The mice are

abundant in some localities; they are arboreal but also descend to the ground; they are more active at night than during the day; and they nest in hollow parts of trees or internodes of bamboo (Harrison and Lim, 1950; Harrison, 1955, 1957, 1966; Medway, 1969).

Most specimens of *C. gliroides*, from throughout its geographic range, are from lowlands and middle elevations; a few are from places above 5000 feet. In Indochina the highest records are the mice from 4400 feet at Phong Saly, Laos, and the specimen from Hkinlum Triangle, which was taken at 5000 feet. In Pahang, on the Malay Peninsula, specimens were taken on Gunong Benom at elevations from 4000 to 5000 feet, and one mouse was collected on the Teku Plateau, Gunong Tahan, at 5300 feet; these are the highest records I have for Malaya. Specimens were collected from sea level up to 1200 meters on Java, and all the mice I have studied from Bali come from 250 to 300 meters. The few specimens from Borneo were obtained at middle elevations: the one from Kalimantan is from 300 meters, and the three from Gunong Kinabalu were taken at 1000, 3000, and 3100 feet. The data on elevations are from notations on labels attached to the skins, and sometimes from notes recorded in the field.

I do not have specific firsthand observations about the habitats of *C. gliroides*, but I have data from specimen-labels and published reports which should be recorded here. For some specimens from northern Burma there is this information on labels attached to skins: an adult from Hkinlum Triangle, 5000 feet, was "caught in light forest"; at Htingnan, 3200 feet, two adults and two very young adults were "caught in a dry bamboo in thick jungle," two adults were taken together "in a dry bamboo in thick forest," a single adult was "caught in a dry bamboo in thick jungle," and two adults were "caught in undergrowth in moderate jungle"; and of the three specimens collected in the Nam Tamai Valley at 3000 feet, an adult was "caught by natives in dense hill jungle (bamboo clump)," a young adult was "caught by native under stone in maize field, dense hill jungle," and another was "trapped in field surrounded by light forest." There are also

specimens from Dalu and Gora; according to Carter (1943) the country at Dalu was "Paddy fields bordered by dense rain forests," and the terrain near Gora was covered with "Very dense jungle, chiefly bamboo."

The specimens from Bankachon, near the tip of southern Burma, were obtained by G. C. Shortridge, and he (recorded in Wroughton, 1915, p. 714) wrote that the mice were "Very plentiful around Bankachon wherever there were bamboos. They never got into traps, even when set among bamboos, but were easy to find as they hid by day, generally singly, occasionally a female and two young, inside the hollow joints of dead bamboos, through one side of which they had bored a circular entrance, about two inches in diameter."

In his report on the rats and mice of Thailand, Marshall (1976) wrote that one *C. gliroides* had been found during the day high in a flowering tree, two were caught in forest trees, and another was discovered after it had gnawed into a bureau in a cabin. The two which I examined from Mae Hong Son were taken in evergreen forest, one from a rock cliff. At Trang, in the southern part of peninsular Thailand, a juvenile was "killed in house," according to a notation on the skin label.

There are notes on labels attached to some specimens from Malaya that indicates the place in the forest where the mice were caught. An example from Kedah Peat at 3000 feet, for example, was caught "in bamboo" and a mouse was "trapped among moss" on Gunong Tahan at 5300 feet. The most reliable published observations on the habitat of *C. gliroides* in Malaya and the best that is now available for the entire species are those by Harrison and Lim (1950), Harrison (1955), and Medway (1964). According to Harrison and Lim (1950), the trapper's name for *C. gliroides* was "*tikus kending*" which referred to the holes made by the mice in stems of bamboo. The mice "lived in the internodes of bamboos. A hole is made near the top of an internode, several chambers are joined by biting through the nodes and a nest of leaves is made at the bottom of an internode." Harrison, in 1955, reported on reproduction of some Malayan mammals, results distilled from reproductive data obtained from

specimens collected in Selangor during the period 1948 to 1952 in connection with a study of the distribution of the trombiculid mites which are involved in the transmission of scrub typhus. Of the *C. gliroides* he examined, most "were obtained by the trappers plugging the exit holes of the lengths of bamboo in which they were hiding during the day, cutting down the bamboo, and sending the whole nest to the laboratory."

In an excellent paper about *Hapalomys longicaudatus*, Medway (1964) reported his observations of the *C. gliroides* he encountered with *H. longicaudatus* in the valley of the Sungai Blatop, Ulu Kelantan District, Malaya. There he obtained specimens of *H. longicaudatus* from clumps of the bamboo, *Gigantochloa scortechinii*, and noted that *C. gliroides* lived in the same clumps and was at least as common as *H. longicaudatus* if not more so. *Chiropodomys gliroides* nested in the bamboo stems. The holes they gnawed in the stems were 25 mm. in diameter (an average), and they occupied more slender stems (down to 200 mm. in circumference) than did *H. longicaudatus*. They also "utilise a variety of leaves to line their nests, including predominantly the leaves of woody dicotyledons." Medway (1969) elaborated on the nests of *C. gliroides* in his book about Malayan mammals: the mice

By day, retire to nests in hollow trees, or very frequently, the internodes of bamboo. Bamboo of all ages from standing green stems to old dead lengths lying on the ground may be occupied. To reach the internodal space of intact standing stems, a neat circular hole, 2½ cm in diameter, is gnawed in the side of an internode at any height from the ground. Once inside, nodal septa above and below the point of entry are pierced by a circular hole of the same diameter; sometimes a second entrance is made lower or higher on the same stem. Much nest material in the form of leaves of a variety of different plants is brought in, and the bottom of almost every occupied internode is more or less copiously lined.

Information about habitats of the specimens from Java comes from notes on labels attached to skins: an adult from Carita was taken in "scrub"; at Tjerimai, 800 meters, an adult was caught in a high tree in mixed forest; at sea level and 500 meters near Cheribon, one speci-

men was caught in a high tree, and 15 were obtained from the crowns of coconut palms. G. C. Shortridge (recorded in Thomas and Wroughton, 1909b) found the mice to be "very plentiful" at many localities in western Java. He noted that they were "arboreal; similar in habits to the dormouse, making small grass nests among bamboos or the heads of palm-trees."

HABITS AND LIFE HISTORY: The Malayan *C. gliroides* which have been studied in laboratories have been intractable (Harrison and Lim, 1950; Medway, 1969). Harrison and Lim wrote of *C. gliroides* that "Although so small they were remarkably fierce, and our specimens showed little sign of taming after as much as a year in captivity. When approached they would rear upright and chatter their teeth at the intruder. When un-friendly specimens were put together a furious fight would ensue and the loser was usually partly eaten. They were more active at night than during the day."

Very little is known about the predators of *C. gliroides*. The only published record I could find is Lim's (1956) report of the remains of a mouse found in the stomach of a Sumatran pit viper, *Trimeresurus sumatranus*, a ground snake whose habitat, according to Lim, is in forest.

Chiropodomys gliroides is a herbivore (Harrison, 1961); most of what is known about its food preferences comes from diets of captives in laboratories. Harrison and Lim (1950) and Medway (1967, 1969) have written that the mice thrive in captivity on mixed roots, sweet potato, grain, unhusked rice, green vegetables, and soft fruit (banana, papaya, and pineapple). With such a diet the mice do not require drinking water. Medway also reported supplementing the diet with fresh bones, raw meat, or mealworms. The only information of diet in wild populations of *C. gliroides* is reported by Harrison (1961) who examined the stomach of one specimen and recorded that it contained "nutty material."

Although data from the laboratory and from the scanty observations made in the field indicate that *C. gliroides* is probably primarily herbivorous, we need to know the actual composition of its diet in its natural habitats.

Such information would be of help in understanding the nature of the association between *C. gliroides* and the larger *Hapalomys longicaudatus*. Both rodents are associated with bamboo, and that monocot, in the forms of growing tips of twigs and fruits or flowers, apparently constitutes the diet of *H. longicaudatus* (Medway, 1964, 1967). I would like to know whether or not *C. gliroides* also eats the shoots, fruits, or inflorescences of bamboo; or if it feeds instead on fruits and seeds (or even buds and flowers) of trees, shrubs, woody vines, or palms. If the latter, then the bamboo clumps with stems of large and small diameters would provide excellent nesting sites for two kinds of arboreal rodents, that because of their different body sizes could utilize stems of different diameters; the clumps would furnish a close source of food for *H. longicaudatus*, and no competition would exist between it and *C. gliroides* for food. I also want to know if *H. delacouri*, smaller in body size than *H. longicaudatus* (Musser, 1972), also lives in clumps of bamboo with *C. gliroides*. Specimens of both rodents have been collected from Phong Saly and Col de Taloun in Laos, and from Dakto in Vietnam.

To know more about the natural foods of *C. gliroides* would add to the information about the tropical ecosystem of which it is a part and partly indicate how the food resources of the forest are divided among the species of murids that occur together at any given locality. We especially need these kinds of data from places like Gunong Kinabalu in Sabah where three species of *Chiropodomys* apparently live in the same forest. Do *C. major*, *C. gliroides*, and *C. muroides* nest in stems of bamboo, and are they able, because of their different body sizes, to nest in stems of different diameters in the same clump? Or does one or more of the three species nest in tree holes? Does one of them, the larger of the three, *C. major*, ecologically replace *Hapalomys*, which does not occur on Borneo (at least it has never been collected there)? If all three kinds of *Chiropodomys* live in the same clumps of bamboo, then is the utilizer of bamboo products for food reversed in regard to body size as compared with the

situation in Malaya where the large *H. longicaudatus* feeds on bamboo and the small *C. gliroides* does not? If so, the small *C. muroides* would then be the mouse that might make nests in the stems of small diameters and would feed on the shoots, fruits, or inflorescences of bamboo. This would partly explain the combination of small body size and wide incisors, teeth that appear robust and strong for such a small animal. A small mouse would be able to build nests in places that larger mice could not get into; strong incisors would be necessary to cope with the silaceous foods from bamboo, especially if the mouse had to strip away sheathing bases of the outer leaves to get at the meristematic parts; and a small mouse would need wide, robust incisors just to gnaw into the internodes of bamboo stems to nest. These are simply questions and speculations, but until the mice are studied in their natural habitats, that is all we have.

The only published information on breeding and reproduction in *C. gliroides* are the data gathered from Malayan animals and reported by Harrison (1955) and Medway (1967). Harrison's information comes from mice that were collected during the period 1948 to 1952 in Selangor State. Medway's results are based on two females kept in the laboratory. Harrison's sample consisted of 130 males and 143 females; the difference in numbers between sexes was not significant and indicated that in the wild, half the population consists of males and half of females. The sample is a good estimate of the sex ratio in the wild population because most of the mice were caught by trappers who brought sections of bamboo containing mice and nests into the laboratory. Out of the 143 females, 18 were pregnant: two had one embryo each, 10 had two embryos, and six had three; thus out of 18 potential litters the mean number of embryos per litter was 2.2. Harrison also recorded the distribution of embryos in the right and left horns of the uterus of each mouse and found no significant differences.

From the two females which Medway (1967) studied in the laboratory he determined that *C. gliroides* was polyestrous, with an estrus period of about one day, and an estrus cycle which

lasted a minimum of seven days. One of the females bred successfully and produced four litters of five young on September 2, 1963, and January 4, May 15, and June 23, 1964, during a period of 10 months. One of the gestation periods was 19 to 21 days. Medway reported a neonatal weight for only one of the young, a mouse born on June 23 which weighed 2.8 grams. Medway reported that the mice were naked at birth and that their eyes were closed. By the second day their skins had darkened; fur could be seen by the fifth day. They were partly independent and were apparently being weaned by the seventeenth day and had been completely weaned by one month. By about 17 days of age, when the young were being weaned, their weights ranged from 9 to 11 grams. All of them reached a plateau of adult weight, 14 to 22 grams, and apparently sexual maturity, within 100 days.

Newborn young cling firmly to the mother's nipples, and if she is disturbed she will run away, dragging the young with her (Harrison, 1966; Medway, 1969).

Medway (1967) correlated his data from laboratory studies with records of pregnancies in wild females that had been collected in Selangor during the period December 1948 to December 1961, data he extracted from the records of the Institute for Medical Research at Kuala Lumpur. During that period 169 females that weighed 15 grams or more were obtained. Medway assumed that all the females in this weight group were sexually mature. Pregnancies occurred in each month except June and July (see table 1 in Medway, 1967). He also noted, however, that juveniles less than 10 grams, and probably not yet weaned, were collected from the same area in all months except February, July, and November. By combining data from the Selangor sample and from the laboratory studies Medway reported that the young caught in the wild "can be calculated to represent pregnancies occurring in all months of the year, including June and July," and concluded "that in the wild population from which the experimental subjects originated there is a broad seasonal fluctuation in reproductive activity, with a higher proportion of

sexually mature females being pregnant in that half of the year during which the sun is south of the equator." He pointed out, however, that the fluctuation did not result in a restricted breeding season and that "there is probably in the wild no annually recurrent period during which pregnancies never occur."

Harrison (1956) calculated the mean length of life of *C. gliroides* in the wild to be 23.8 months; his data came from 272 specimens that had been collected during the years 1949 to 1952 in Selangor State. The maximum life span of captives in the London Zoo was 43 months (Jarvis and Morris, 1961).

PARASITES: Like most tropical rodents, examples of *C. gliroides* support ectoparasites, mostly mites, on their bodies and in their nests. Medway (1964) recorded these mites on specimens from the Blatop Valley: *Laelaps* (*Echinolaelaps*) sp. near *sculpturatus*, *Laelaps* (*Echinolaelaps*) *delta*, *Laelaps* (*Echinolaelaps*) *echidninus*, and *Laelaps* sp. near *turkestanicus*; two mites, *Laelaps* (*Echinolaelaps*) sp. near *echidninus* and *Haemolaelaps nadchatrami* were obtained from a nest. The same kinds of mites, along with several different species, were also gathered from nests and specimens of *Hapalomys longicaudatus* that lived in the same clumps of bamboo as *C. gliroides*.

The frequency of endoparasitic infection in populations of *C. gliroides* may be low. Dunn, Lim and Yap (1968) reported on the patterns of endoparasites in mammals living in the Malaysian rain forest. None of the 94 examples of *C. gliroides* they examined had blood parasites (trypanosomes, microfilariae, and the protozoan parasites of erythrocytes: *Plasmodium*, *Hepatocystis*, *Babesia*, *Hepatozoon*, and *Grahamella*). Out of the 145 mice which they examined for helminths (acanthocephalans, trematodes, nematodes, and cestodes), 18 were parasitized by nematodes and eight by cestodes.

SUMMARY OF THE SPECIES

The taxonomies and geographic distributions of the species which I have discussed in the preceding pages are summarized in the following list. I include the scientific names that

apply to each, either as the valid name of species or subspecies, or as synonym.

Chiropodomys gliroides gliroides
(Blyth), 1856

Mus gliroides Blyth, 1856, p. 721.

Mus peguensis Blyth, 1859, p. 295.

The form has been recorded from Assam, southern China, Laos, Vietnam, Thailand, and Burma south to the Isthmus of Kra in peninsular Thailand and the southern part of Tenasserim.

Chiropodomys gliroides penicillatus
Peters, 1869

Chiropodomys penicillatus Peters, 1869, p. 448.

The name applies to mice of the Malay Peninsula south of the Isthmus of Kra.

Chiropodomys gliroides pusillus Thomas, 1893

Chiropodomys pusillus Thomas, 1893a, p. 345.

A form known only from the mainland of Borneo.

Chiropodomys gliroides niadis Miller, 1903

Chiropodomys niadis Miller, 1903, p. 40.

The subspecies on Nias Island, off the west coast of Sumatra.

Chiropodomys gliroides anna
Thomas and Wroughton, 1909

Chiropodomys anna Thomas and Wroughton 1909a, p. 19.

The form from Java and Bali.

UNALLOCATED TO SUBSPECIES: Specimens of *C. gliroides* are also recorded from Sumatra, and the Natuna and Tujuh islands.

Chiropodomys major Thomas, 1893

Chiropodomys major Thomas, 1893a, p. 344.

Chiropodomys legatus Thomas, 1911, p. 206.

Chiropodomys pictor Thomas, 1911, p. 207.

A species known only from Sabah and Sarawak.

Chiropodomys calamianensis (Taylor), 1934

Insulaemus calamianensis Taylor, 1934, p. 470.

Records are from the islands of Balabac, Palawan, and Busuanga.

Chiropodomys muroides Medway, 1965

Chiropodomys muroides Medway, 1965, p. 133.

A species recorded from Sabah and northern Kalimantan.

Chiropodomys karlkoopmani Musser, 1979

Chiropodomys karlkoopmani Musser, this report, p. 389

Known from North Pagai Island, off the west coast of Sumatra.

MORPHOLOGICAL SIMILARITIES AMONG THE SPECIES OF *CHIROPDOMYS*

My conclusions about the morphological similarities among the species of *Chiropodomys* are based entirely on information from skins, skulls, and teeth. By themselves certain features are not helpful in grouping the species. Color of pelage is one of these, size of body is another, color pattern of the tail and shape of

cusps t7 are additional examples. Separating the species by color of underparts would result in one group with *C. gliroides* and *C. major*, which have white underparts, and another composed of *C. muroides*, *C. calamianensis*, and *C. karlkoopmani*, all with pigmented underparts. *Chiropodomys major* and *C. calamianen-*

sis are the only two that would cluster by using size of body; they would be part of a series graded from *C. muroides*, the smallest species, to *C. karlkoopmani*, the largest. If color pattern of the tail is used to sort the species then all those with a monocolored tail—*C. muroides*, *C. gliroides*, and *C. calamianensis*—would be brought together; *C. major*, in which the tail is either monocolored or mottled, would stand by itself but close to the group of three species, and *C. karlkoopmani*, with its distinctive brown and white tail, would be set well apart from all the others. Grouping the species by the shape of cusp t7 on the upper first and second molars would result in *C. muroides* and *C. gliroides*, the two species with small bodies, in one cluster, and *C. major*, *C. calamianensis*, and *C. karlkoopmani*, species with large bodies, in another. When the total similarities and differences among the species are considered there is a possibility that the shape of cusp t7 is related to size of the animal and not an indication of phylogenetic alliance. If a combination of characters are used, the species can be arranged in the following way.

Chiropodomys major, from Sarawak and Sabah, and *C. calamianensis*, from the islands of Balabac, Palawan, and Busuanga, differ conspicuously in color of pelage but otherwise resemble each other in size of body and in configurations of skulls and teeth. There are differences in a few external and cranial dimensions and proportions between the samples of each kind; still, the two species are clearly morphologically closer to each other than to any other known species of *Chiropodomys*. The degree of morphological similarity between them suggests that each one is an insular remnant of a species that was once spread over the northeastern part of the old Sundaland at a time in the past when sea levels were much lower and the Palawan area was either connected with northern Borneo by land, or separated only by narrow water gaps.

Chiropodomys karlkoopmani is distinctive and set apart from all the other species, but it is morphologically closer to the large *Chiropodomys*, *C. major* and *C. calamianensis*, than to the small ones, *C. gliroides* and *C. muroides*. The single specimen of *C. karlkoop-*

mani shares large size of body, similar external, cranial, and dental proportions, and a round cusp t7 with both *C. major* and *C. calamianensis*. It is the largest of the three and the only one with a tail in which the basal half is brown and the distal half is white. It is also the only species that is, at the present time, known from the Mentawai islands. My evaluation of the affinities of *C. karlkoopmani* will have to be tested with data from larger samples from the Mentawai islands, samples which will provide a better estimate of the range of morphological variation in the population.

Chiropodomys gliroides is small in body size. The labial cusp (t7) at the back of each upper first and second molar is elongate, like the cusp in *C. muroides*, rather than round as the cusps are in the three species of large *Chiropodomys*. Otherwise, *C. gliroides* is like those three large species in its configuration of skull and teeth, and also similar to them in most proportions.

Chiropodomys gliroides is distinctive among all the species in that there is notable geographic variation within it. The morphological differences between samples of the Indochinese and Malayan forms of the species are conspicuous and significant. Most differences are in dimensions and proportions; that between the length of incisive foramina relative to length of the diastema (or the rostrum) seems fundamental and one that not only distinguishes the two forms of *C. gliroides* but also separates the Indochinese type from all the other species of *Chiropodomys*. I do not know what the functional significance of this feature is (dissection of the area in formalin-preserved specimens may provide answers) but it and the other characteristics of the Indochinese form indicates a geographic arm of *C. gliroides* north of the Isthmus of Kra that appears to have been isolated long enough to diverge widely from the populations south of the Isthmus. The little data available from samples taken at the Isthmus suggest the present contact between the two kinds is a secondary one, a contact representing the re-establishment of genetic continuity between two morphologically distinctive populations.

The different configuration of the diastema

and incisive foramina in the Indochinese form of *C. gliroides* and the similar proportions of these features in samples of all the species from south of the Isthmus of Kra may be important in providing information indicating the region from where *Chiropodomys* originally radiated. The morphological diversity of the genus is centered on the Sunda Shelf and Mentawai islands—peninsular and island remnants of what was once Sundaland, an extensive region covered with tropical forest and savanna, dissected by broad sinuous rivers, and spotted with mountains and plateaus of montane floras and faunas. If the number of extant species in an area is a clue that points to the place where the species in *Chiropodomys* evolved and diversified (and it may not; more species in one area and fewer in another may only indicate the extinction of species elsewhere), then Sundaland could have been the center of evolution of *Chiropodomys*. All five species occur there; only one, *C. gliroides*, extends north of the Isthmus of Kra on the mainland of Southeast Asia; and it is the only segment of *Chiropodomys* that is so different from the others in the diastemal region.

The fifth species, *C. muroides*, clusters with the other small *Chiropodomys*, *C. gliroides*, but is set apart from it and the other three by this combination of characteristics: small body; buffy, dark gray underparts; different proportions of the rostrum, interorbital area, zygomatic plates, palatal region, and bullae; and wide incisors (both absolutely and relative to size of the skull) which are pale yellow (the uppers) or cream (the lowers). *Chiropodomys muroides* and *pusillus*, the Bornean form of *C. gliroides*, are comprised of the smallest mice within *Chiropodomys*, and represent some of the smallest murids native to the Sunda islands. *Haeromys pusillus* is the only other murid on Borneo that is about the same size as *C. muroides* and *C. g. pusillus*.

After I had completed my manuscript I sent copies to several reviewers and two of them, Lawrence R. Haeney at the University of Kansas, and Michael D. Carleton, at the University of Michigan, suggested that I analyze the data with phenetic techniques which have become standard in dealing with the kinds of information I gathered from samples of *Chiropodomys*.

Carleton went ahead and summarized the phenetic relationships of selected samples of *Chiropodomys*, which represented all five species, by principal component and cluster analyses.¹ He standardized the features so that they had a mean of zero and a standard deviation of one.

TABLE 7
Results of Principal Component Analysis Using
26 Morphometric and 5 Qualitative
Characteristics for 9 Samples

Feature	Principal Component	
	I	II
Length of head and body	.96	.09
Length of tail	.93	-.10
Length of hind foot	.97	-.14
Occipitonasal length	.99	.11
Zygomatic breadth	.95	.28
Interorbital breadth	.95	-.17
Length of nasals	.97	.15
Length of rostrum	.96	.19
Breadth of rostrum	.95	-.23
Breadth of braincase	.98	.12
Height of braincase	.97	.05
Breadth across incisor tips	.79	-.20
Breadth across zygomatic plate	.89	.33
Length of diastema	.97	.13
Palatal length	.96	.21
Postpalatal length	.98	.18
Length of palatal bridge	.93	-.29
Breadth of bridge at M ¹	.97	-.12
Breadth of bridge at M ³	.79	-.44
Length of incisive foramina	.63	.69
Breadth of incisive foramina	.94	-.02
Incisive foramina to M ¹	.22	-.91
Breadth of mesopterygoid fossa	.91	.21
Length of bulla	.97	.12
Height of bulla	.94	-.22
Alveolar length of M ¹⁻³	.97	.13
Lateral body stripe	-.31	.79
Color of tail	.53	-.58
Color of incisors	-.47	-.69
Shape of cusp t7	-.92	.23
Color of underparts	.33	-.75
Percentage variation explained	75.4	13.9

¹I am grateful to Mr. Carleton, not only for his interest, but for his time and efforts. The principal components and cluster analyses were computed by the Michigan Interactive Data Analysis System (MIDAS), a series of computer programs formulated by the University of Michigan Statistical Research Laboratory.

The means of the 26 morphometric variables (except length of ear) served as character-states in the multivariate treatments. He also encoded character-states for five qualitative variables based on the presence or absence of a lateral stripe, color of the tail, color of the incisors, shape of cusp t7, and color of the underparts. He extracted principal components from a correlation matrix, and derived a phenogram from a distance matrix by the unweighted pair-group method using arithmetic averages (see Sneath and Sokal, 1973, for discussions). The lo-

calities and sizes of samples which were used are as follows:

- C. karlkoopmani*: North Pagai, 1.
- C. major*: Sabah, 17.
- C. calamianensis*: Palawan, 4.
- C. muroides*: Sabah, 3.
- C. gliroides*: Indochina, 21; Malay Peninsula, 23; West Java, 19; Borneo, 2; Pulau Nias, 2.

The results of Carleton's efforts are presented in table 7 and figures 11 and 12. I insert

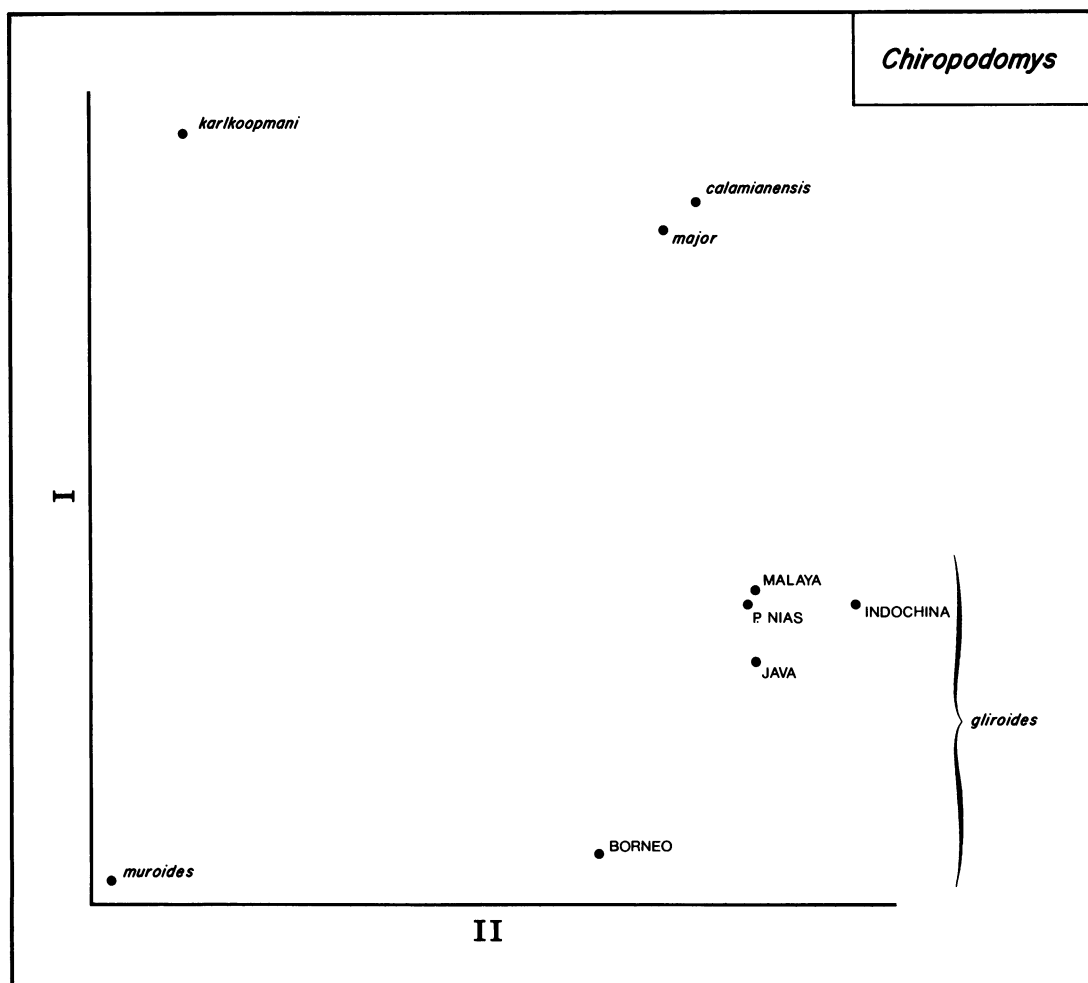


FIG. 11. Scatter plot of Principal Component I against II. The plot is based on nine samples of populations of *Chiropodomys* described by 31 characteristics (23 cranial and three external dimensions, and five qualitative features).

them at this place in the discussion because they provide a visual representation of the possible similarities among samples of the five species and because they illustrate how a different analytic technique yielded basically the same pattern as did my original treatment of the data. The dispersion of samples reinforces much of what I describe in the text. The samples representing *C. karlkoopmani*, *C. major*, and *C. gliroides* fall into one group, and those from *C. muroides* and *C. gliroides* fall into another, a basic dichotomy between the three large forms and the two smaller ones. Of the three large species, *C. karlkoopmani* is distinctive and set apart from *C. major* and *C. calamianensis*, the most similar pair of species. Of the small forms, the sample of *C. muroides* is located far from the samples of *C. gliroides*, an indication of its distinctive pelage coloration, cranial proportions, and size and color of incisors. And among the samples of *C. gliroides*, the one from Indochina is set apart from the samples from the Malay Peninsula, Pulau Nias, and West Java.

The only surprise to me is the separation of the Bornean sample of *C. gliroides (pusillus)* from the other samples of that species. The distance between it and the other lots of *C. gliroides* is greater than between the two large forms, *C. major* and *C. calamianensis*. If the population of *pusillus* is as morphologically distinct from the other samples of *C. gliroides* as the dispersions in figures 11 and 12 indicate, then perhaps that Bornean population is reproductively isolated from the others. But I am reluctant to recognize *pusillus* as a species because my sample of it is so small, because the specimens I have seen are small versions of *C. gliroides* from elsewhere on the Sunda Shelf (there are no pelage or other characteristics that mark it unique and size is the only feature which will distinguish it from specimens in the other samples), and because *pusillus* fits into a pattern of variation in body size over the Sunda Shelf where large mice are on the Malay Peninsula, small ones are on Borneo, and mice of intermediate size are on Java and Bali. Until larger samples of *pusillus* are available, and

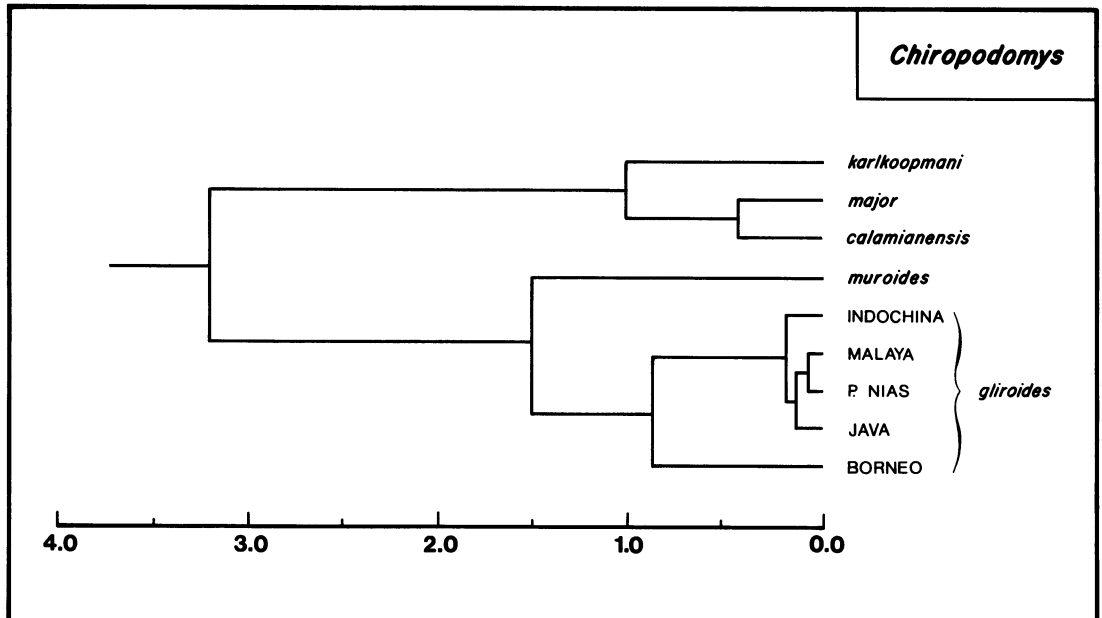


FIG. 12. Phenogram which was derived from a distance matrix by the unweighted pair-group method using arithmetic averages. The coefficient of cophenetic correlation equals 0.768. The results are from nine samples of populations of *Chiropodomys* listed in the text and described by 23 cranial and three external dimensions, and five qualitative features.

until other kinds of data can be gathered which can be used to test the genetic isolation or compatability of the Bornean mice, I prefer to retain that form as a subspecies of *C. gliroides*.

With the exceptions of *C. major* and *C. calamianensis*, two forms which seem to be closely allied, I do not yet know if the way I sorted out the species reflects phylogenetic alliances among them. I need information about other sets of characters; data, for example, that could be obtained from study of postcranial

morphology, internal and muscular anatomy, anatomy of the male and female reproductive tracts, chromosomes, spermatozoa, electrophoresis of proteins (blood sera and hemoglobin, for example), immunodiffusion, and parasites. I also have yet to determine which features are derived and which are primitive, something I cannot do until I compare the species of *Chiropodomys* with those in other genera thought to be phyletically allied with *Chiropodomys*.

DISCUSSION

THE GENUS *CHIROPODOMYS*

The five species I have defined and discussed in the preceding section are like one another in the structures of their bodies, skulls, and teeth. Taken together, these basic morphological similarities define the genus and distinguish it from any other known genus of murid rodent. The species in *Chiropodomys* are small, each stockily built and long-tailed (fig. 2; see also the photographs of live mice in Medway, 1964; Walker, 1968; and Marshall, 1976). The head is wide and the face short. Eyes are large and prominent, enclosed by dark rings and densely surrounded by thin lashes 1 to 4 mm. long. The mystacial vibrissae are long, reaching out 45 to 65 mm. Above each eye is one or two vibrissae, often as long as 40 mm. (these are clearly shown in the photographs in Medway, 1964). The ears are round, thin, and scantily haired. The pelage clothing the head and body is dense, short, and soft, appearing woolly in some species. Guard hairs are abundant but short, extending only a few millimeters beyond the dense coat. The tail is conspicuously longer than the head and body (table 1) and not prehensile. It is densely covered with hair, although the rows of scales are still visible (three hairs emerge from the base of each scale). The hairs are short near the base of the tail and longer along the distal half, giving it a brushy appearance; the tip is set off by a tuft that ranges from 4 to more than 10 mm., depending on the species.

The front and hind feet are short and broad

(figs. 13 and 14). The first digit of each front foot is thick, stumpy, and bears a wide nail; the other digits are short, and the sides of each one are flat; they end in thick pads adorned by claws which are thin and short, with sharp tips. The stubby first digit (hallux) of each hind foot is much shorter than the others and ends in a very large fleshy pad in which a nail is em-



FIG. 13. Front and hind feet of *Chiropodomys gliroides* (AMNH 240347, adult male). Ventral views of the palmar (left) and plantar (right) surfaces. Length of hind foot is 20 mm. Drawn by Fran Stiles.



FIG. 14. Front and hind feet of *Chiropodomys gliroides* (AMNH 240347). Tops and sides of the front foot (top) and hind foot (bottom). Drawn by Fran Stiles.

bedded; the other digits are slender and terminate in smaller pads which bear short, thin, sharp claws. The fifth toe appears to be always flexed and capable of being bent over toward the hallux. Both the palmar and plantar surfaces are naked and usually unpigmented. Most of the palm consists of large, fleshy interdigital and palmar pads. Large fleshy mounds at the bases of the digits and two large plantar pads form much of the topography of the bottom of each hind foot. The pads on both palmar and plantar surfaces are sculptured with transverse and semicircular striae (the ridges between striae have been called dermatoglyphic friction ridges; see Cartmill, 1974). In sum, the feet are highly specialized; their structure and palmar and plantar textures suggest adaptations for movement on supports above the ground where adhesion to surfaces may be more important than grasping supports.

Opposability of the halluces has always been included with the traits used to define the genus *Chiropodomys* (Tate, 1936; Ellerman, 1941, 1961; Harrison 1966; and Marshall, 1976). But I doubt that the hallux is opposable in species of *Chiropodomys*, at least not the type of opposability that is associated with the morphological adaptations in the divergent and

prehensile first toe found in arboreal marsupials (species of *Marmosa*, for example) and most species of extant primates (Haines, 1958; Cartmill, 1974). Cartmill stated that the first toe in *Chiropodomys* was "pseudo-opposable," but perhaps even that term cannot be used to describe the action of the hallux, which is stubby and short, not broadly divergent from the other digits, not prehensile, and can hardly be turned sideways and opposed to the other toes as was described by Harrison (1966). The fifth digit, in contrast, may be pseudo-opposable. It is long, apparently permanently flexed, and can be bent to the side against the first digit. But most semi-arboreal and arboreal murids have this type of structure—it is not unique to *Chiropodomys*. Except that the digital pads are slightly larger, the configuration of the hind foot in species of *Chiropodomys* is not much different from that in such arboreal rats as *Rattus cremoriventer* or *R. beccarii* (Musser, 1973b), for example.

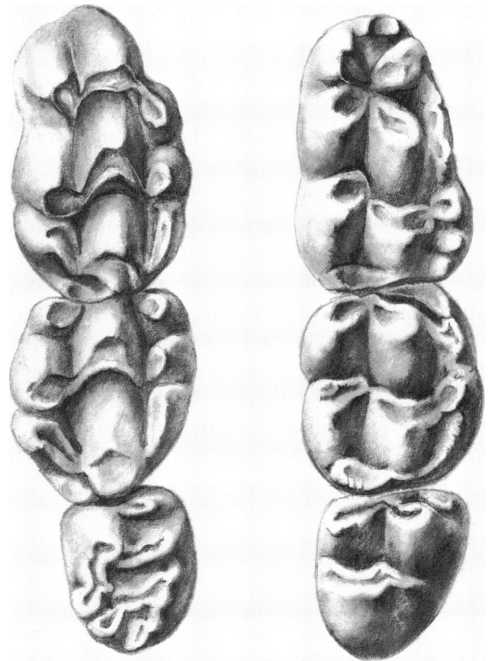


FIG. 15. Occlusal views of the right upper (left) and lower (right) molars of a young adult *Chiropodomys gliroides* (AMNH 113040) from Dalu, northern Burma. Length of M^{1-3} and M_{1-3} is each 3.7 m. Drawn by Fran Stiles.

The cranium of each species of *Chiropodomys* is wide and short (fig. 6). A short, broad rostrum is in front of a wide, rounded braincase that arches gently up from the rostrum and down sharply to the occiput. The nasals are short; their anterior margins usually end just behind the front edges of the premaxillaries forming the sides of the rostrum. The lacrimal bones are wide and prominent. The interorbital area is broad. Prominent supraorbital ridges extend onto the sides of the braincase. The zygomatic arches are wide and appear strong;

their front borders emerge from the sides of the skull at nearly right angles. The narrow zygomatic plates do not project in front of the anterior borders of the zygomatic arches, and their front edges are straight, not concave or convex. The incisive foramina are short and wide in most samples from the Malay Peninsula and islands on the Sunda Shelf, long and thin in samples from Indochina (fig. 9); they do not reach past the front margins of the toothrows. The palatal bridge is wide and long and ends about a millimeter behind the third mo-



FIG. 16. A summary of the geographic distribution of *Chiropodomys*. I have not seen material from Cambodia but *C. gliroides* probably occurs there.

lars. The mesopterygoid and ectopterygoid fossae are broad. The bullae are small and globular. The mandibles are short with small coronoid processes.

The incisors are either orange or pale yellow; their front and sides are smooth, not grooved. The upper incisors project down perpendicularly from the rostrum.

The upper and lower molars are small relative to the sizes of the cranium and mandibles (table 1; fig. 6). The first and third molars are long and narrow, the second molars are nearly as wide as they are long (fig. 15). The patterns formed by the cusps are similar to those in species of *Apodemus* but more complex, a reflection of the large cusp situated on the lingual and posterior part of each first and second upper molar (cusp t7) and the prominent crest on the back edge of each of those teeth (cusp t10, t12, or Z; see Missonne, 1969). The lower molars are also complex, with labial rows of large cusplets that give the appearance of three rows of cusps in young animals with slightly worn teeth. Each of the upper molars has three roots; there are two large roots on each of the lower molars.

Females of all the species have four mammae, two pairs in the inguinal region of the body.

The geographic distribution of *Chiropodomys* is summarized in figure 16. Members of the genus occur over the mainland of Southeast Asia, the Malay Peninsula, islands on the Sunda Shelf, and the Mentawai islands.

POSSIBLE RELATIVES OF *CHIROPODOMYS*

Chiropodomys is one of more than 60 extant genera of rats and mice from Southeast Asia and the Indo-Australian region. Its closest relatives among those genera may be *Micromys*, *Vandeleuria*, *Vernaya*, *Hapalomys*, and *Haeromys*. I introduce them here and summarize what is known about each in the following short accounts.

Micromys, according to Ellerman and Morrison-Scott (1951) and Corbet (1978), contains one species, *M. minutus*, the harvest mouse,

but their evaluations are not based on a critical systematic review of the genus and results of my own preliminary study suggest that the morphological and geographic variation is greater than indicated in the literature and may reflect the presence of more than one species. *Micromys minutus* is the smallest living rodent in Europe and is found in deciduous forest and the less arid steppes of the Palearctic from western Europe (including Britain) to China; northern Assam, Burma, and Vietnam; and Japan. Fossils are rare but there are records in Europe from the Upper Pliocene (Kretzoi, 1959) and Middle Pleistocene (Kürten, 1968) and apparently some Pleistocene material from China (Missone, 1969). Pelage coloration and length of tail vary geographically (Ellerman, 1961) but according to Král (1971) the number of chromosomes, $2n=68$, does not. The harvest mouse is specialized for climbing about in stems of herbaceous plants and uses its prehensile tail for support. It is often found in corn ricks during the winter, and is common in hedgerows, at least in Europe (Corbet, 1966). In northern Burma, Anthony (1941) encountered *M. minutus* on open hillsides among low shrubs, bracken, and tall grass, but not in primary forest. The mice build round grass nests above ground in stems of tall grass, reeds, or other plants. They feed on seeds, fruits, buds, and insects.

Vandeleuria has usually been considered to contain one species, *V. oleraceae* (Ellerman and Morrison-Scott, 1951; Ellerman, 1961), which occurs on Ceylon, on the Indian Peninsula north to Kumaon, then east to Nepal, Assam, Burma, Thailand, and Vietnam. No fossils have been found. There is conspicuous geographic variation in size of body and color of pelage (Ellerman, 1961), as well as number of chromosomes ($2n=29$ in India; $2n=26$ in Chiangmai, northern Thailand; and $2n=28$ in Nakhorn Phanom, northeastern Thailand; Gropp et al., 1972).

There is probably more than one species in the genus. I have looked at specimens in the British Museum, the Field Museum of Natural History, the National Museum of Natural History, and the American Museum of Natural History and can sort them into two groups

which appear to represent two species. One kind occurs on the Indian Peninsula and the mainland of Southeast Asia, from Nepal to Vietnam. It is a mouse with short and silky fur, a white belly, and upperparts which range from bright reddish brown to sandy. This animal is the *oleracea*-type. There are two kinds on Ceylon. One is a small, bright, white-bellied form that closely resembles *V. oleracea* on the continent and occurs at elevations below 4000 feet; in the early literature this type had been identified as *V. rubida* or *B. oleracea rubida*, but Ellerman (1961) stated that the specimens from Ceylon were more likely *V. o. nilagrica*. The other type is a larger mouse with long and dense fur, dark brown upperparts, and dark gray underparts that was collected from highlands at 6000 feet. Philips (1929) described this mouse and named it *V. nilagirica nolthenii*. The two morphological types seem to represent different species: *V. nolthenii* in the highlands of Ceylon, and *V. oleracea* in the lowlands of Ceylon and on the continent.

In Thailand, *V. oleracea* lives in tall canes or shrubs where it builds a globular nest of grass about 2 meters above the ground (Marshall, 1976). In Ceylon the highland form makes nests of dead leaves in hollow trees near the forest edge and the lowland type constructs nests of grass among slender branches of trees and shrubs or in tree-holes (Philips, 1928). The mice are nocturnal. They feed on fruits, shoots, and buds; in captivity they thrive on bread and milk and fruits (Philips, 1928).

*Vernaya*¹ was proposed by Anthony in 1941. The only species in the genus, *V. fulva*, was originally named and described by Allen (1927)

as a species of *Chiropodomys*, but later Allen (1940) regarded it as a synonym of *Vandeleuria dumeticola*. There are only a few specimens of *Vernaya fulva*: one from 9000 feet in Yunnan and two from above 7000 feet in northern Burma. No fossils of the species have been found. Anthony reported that of the two specimens from northern Burma, one was "trapped on an open hillside, covered by thickets of low shrubbery and a heavy growth of bracken. The trap line was set along a line of low cliffs and rocky outcrops," and the other was taken in a trap line "set just below the crest of a ridge on slopes from which the original forest had long been removed and its place taken by bracken and low shrubbery, tangled and difficult to penetrate in places." Nothing else is known about the natural history of this small, long-tailed mouse.

There are two species of *Hapalomys* (Musser, 1972). *Hapalomys longicaudatus* is a large animal found in Tenasserim, southern Thailand, and the Malay Peninsula. *Hapalomys delacouri* is a smaller rodent from Vietnam, Laos, and the island of Hainan off the coast of southern China. Neither species is represented by fossils. Nothing is known about the natural history of *H. delacouri* except that it is associated with tropical deciduous forests at elevations from 1200 to 1500 meters. *Hapalomys longicaudatus* also lives in highlands but it is tied to semi-evergreen and evergreen tropical rain forests where it is closely associated with stands of bamboo, both as places to nest and as sources of food. Medway's (1964) observations of the animals and his information about their natural history is the best and most complete that has yet been published; still, we know very little about the life history of the species.

Haeromys is a genus of small, long-tailed, arboreal mice. Two forms, *margarettae* (Thomas, 1893a) and *pusillus* (Thomas, 1893b), were described under the name *Mus* and later placed in *Haeromys* (Thomas, 1911); both are from Borneo and are currently regarded as two valid species (Medway, 1965). Thomas (1896) named and described a third form, *minahassae*, from Celebes, which, from my own observations, I judge to be a species distinct from the Bornean forms. Species of *Haeromys* have

¹Sody (1941, p. 261) proposed *Octopodomys* for *Chiropodomys fulvus*, based on the eight mammae possessed by *fulvus* as compared with the usual four found in each species of *Chiropodomys*. He was unaware that Anthony (1941) had proposed *Vernaya* for the same species; Anthony did not know of Sody's action. Ellerman pointed out the problem in 1949 (p. 188) and in 1961 he formally listed *Octopodomys* as a synonym of *Vernaya*, the correct course because *Vernaya*, in my opinion, has priority over *Octopodomys*. Anthony's article was published on December 8, 1941; the publication date of Sody's paper is indicated as simply, "December 1941." Furthermore, *Vernaya* was properly diagnosed and *Octopodomys* was not.

never been taken outside of Borneo and Celebes, and within the group which consists of *Micromys*, *Vandeleuria*, *Vernaya*, *Chiropodomys*, and *Hapalomys*, it is the only genus that is found both on the Sunda Shelf and off of it on a large island to the east of Wallace's Line.

Species of *Haeromys* inhabit tropical evergreen forests in both lowlands and mountains. They build globular nests in cavities in trees. The animals I observed in Celebes ate only small seeds, mostly from figs.

Micromys, *Vandeleuria*, *Vernaya*, *Hapalomys*, and *Haeromys* are the Recent genera that may cluster with *Chiropodomys*. Based on his examination of skins, skulls, and teeth, Ellerman (1941) considered *Vandeleuria* to be a close relative of *Chiropodomys*. Misonne (1969), whose phylogenetic conclusions were shaped by what he saw in dental patterns, stated that *Chiropodomys* and *Vernaya* were close, and that *Vandeleuria* was related to both *Chiropodomys* and *Micromys*. He summarized his view by writing that "*Chiropodomys*, *Vandeleuria* and *Micromys* are most certainly closely allied genera; *Chiropodomys* has kept more primitive characters, and *Vandeleuria* and *Micromys* are more advanced," and concluded that *Hapalomys* "has evidently followed its own line; its closest relative is probably *Chiropodomys*."

There is no consensus among workers on the alliances of *Haeromys*. Thomas compared the species with *Chiropodomys* when he described them but he did not state explicitly that they were closely related to species of *Chiropodomys*. Tate (1936) speculated that *Haeromys* was derived from an assemblage which he termed the *Rattus cremoriventer*-group. Ellerman (1941) originally allied *Haeromys* with *Rattus* but later (Ellerman, 1949) considered it to be nearest *Lorentzimys*, mice known only from New Guinea. To Misonne (1969) the genus was difficult to classify; he was uncertain of its closest relatives, although he did not think it was closely allied with *Chiropodomys*.

Except for the species of *Hapalomys*, those in the other genera discussed above are poorly defined; available information about their morphological, geographic, and ecological char-

acteristics is incomplete and inadequate for critical analyses of phylogenetic relationships among them. I have been looking at specimens of *Micromys*, *Vandeleuria*, *Vernaya*, and *Haeromys* to determine the morphological and distributional limits of the species in those four genera. After their taxonomic revisions are complete I plan to compare the data from those species with the information now available about the species in *Hapalomys* and *Chiropodomys* to estimate which of the many features are primitive and which are derived and to test the conclusions of Ellerman and those of Misonne regarding phylogenetic relationships among the species in this group of arboreal murids.

OTHER QUESTIONS AND SPECULATIONS

Much is yet to be learned about the species of *Chiropodomys*. One unstudied aspect is the nature of the opposability of the hallux, not only in species of *Chiropodomys* but in other arboreal rats and mice. Besides *Chiropodomys*, an opposable hallux has also been attributed to species in *Hapalomys* (Ellerman, 1941, 1961; Medway, 1964), *Vandeleuria* (Ellerman, 1941, 1961), *Vernaya* (described under the accounts of *Chiropodomys fulvus* by Allen, 1927, and Ellerman, 1941), *Chiromyscus* (Thomas, 1891, 1925; Ellerman, 1941, 1961), *Pithecheir* (Ellerman, 1941, 1961), and *Haeromys* (Thomas, 1893a, 1911; Ellerman, 1941). The halluces in species of *Hapalomys* and *Chiromyscus* have nails; the species of *Vandeleuria* bear nails on the halluces and nails on the fifth toes; all the toes of *Haeromys* and *Vernaya* are clawed (those on the halluces are smaller than on the other digits); and the halluces of the two kinds of *Pithecheir* bear claws—each is smaller with a slightly wider base than the claws on the other toes, but still a claw as Ellerman (1941) stated, and not a nail or scalelike claw as Medway (1969) indicated.

Because the hallux of some arboreal murids bears a nail instead of a claw, that hallux may be pseudo-opposable—certainly the pervading notion in the literature associates nailed halluces with opposability—but the association

may not exist for certain species. Nails are linked with pseudo-opposable halluces in some murids. Medway (1964), for example, observed the locomotion of a captive *Hapalomys longicaudatus* and described the actions of the first and fifth digits of the hind feet as opposable. Each hallux in that animal is long, diverges from the other digits, bears a nail, and is likely pseudo-opposable. Each hallux and fifth digit in species of *Vandeleuria* are slender, flexible, bear nails, and seem specialized for grasping with the first and fifth toes. In other species, however, claws occur on halluces which are pseudo-opposable. The best examples are the two species of *Pithecheir*: each hallux broadly diverges from the other digits; it is long and capable of opposing the other digits around a slender support; yet the digital pad supports a small claw, not a nail. Of all the arboreal rodents I have discussed here, the hind feet of *Pithecheir* are the most like primates or like species of *Marmosa*.

The types of opposability of the halluces in *Chiropodomys* and other arboreal rats and mice should be re-examined. We know very little about the internal specializations in the feet of species of *Chiropodomys*, *Vandeleuria*, *Vernaya*, *Chiromyscus*, and other arboreal, tropical murids. We do not know, for example, how the shapes and articular surfaces of the carpals and tarsals differ from those features in terrestrial rats; nor do we know the configurations of the extensor and flexor musculature in arboreal species, especially the arrangements of the contrahentes. And there are few observations of how different kinds of rats and mice use their feet as they move about on supports at levels above the ground.

Another, incompletely known, aspect of *Chiropodomys* is the geographical distributions of the species, especially over the Sunda Shelf and the Mentawai islands. Good samples of one species are available from Java and northern Borneo, but there is little material from the rest of Borneo and Sumatra, and no specimens yet from most of the hundreds of smaller islands on the Sunda Shelf. Sumatra, among the larger islands, needs to be explored for *Chiropodomys*. I have seen only one specimen

from there, an example of *C. gliroides*. I would like to know the distribution of *C. gliroides* over the entire island to determine if its pattern of geographic variation is similar to that for other rodents, such as *Rattus cremoriventer*, in which the samples from northern Sumatra fit with those from the Malay Peninsula and the mice from southeastern Sumatra are more like those occurring on Borneo (Musser, 1973b). I also suspect that more than one species of *Chiropodomys* lives on Sumatra. In mountain forests on Sumatra I would expect to find a counterpart of the large Bornean *C. major*, and perhaps even a relative of the smaller *C. muroides*, not an unreasonable expectation in view of the montane species which we know are common to both Borneo and Sumatra (Chasen, 1940), such murids as *Rattus infraluteus* and *R. baluensis*, for example.

I would also expect to find insular variants of *C. karlkoopmani* on the other Mentawai islands besides North Pagai, namely the islands of Simalur (Simeulue), Siberut, Sipora, South Pagai, and possibly Enggano (but not on Nias or the Batu islands which are on the Sunda Shelf). The rodents from those islands are morphologically more similar to one another than to any part of the fauna on the mainland of Sumatra or to rodents on islands off the west coast of Sumatra that are on the Sunda Shelf. For example, morphological variants of the rats *Rattus simalurensis*, *R. siporanus*, and *Maxomys pagensis*, as well as insular varieties of the squirrel *Callosciurus melanogaster* occur on the Mentawai islands (Chasen, 1940; and unpublished results of my research).

Sampling the hundreds of small islands on the Sunda Shelf for *C. gliroides*, a small-bodied mouse, is important not only to determine the insular distribution of the species but also to determine the relationship of body size to area of island. Haeney (1978), for example, has reported on this relationship in the large, tri-colored squirrel, *Callosciurus prevosti*, which occurs on the Sunda Shelf. He found that, "The body size of tri-colored squirrels is related to the size of the island on which they live; the smallest squirrels occur on the smallest islands and increase in body size on islands up

to about 10^4 km². On islands larger than this, body size decreases significantly as island area increases." Haeney also developed a model indicating "the major factors which affect the body size of tri-colored squirrels, the situations under which they are most important, and their effects." The model can be applied to other mammals under certain conditions: "equivalent climate on all of the islands, all islands connected to a continental land mass at approximately the same time in the past, little or no gene flow between islands, and no special selective pressure." The model also assumed "that the effects of food limitation are greater on large mammals than on small mammals, that interspecific competition is more important to small mammals than to large mammals, and that predation pressure may have substantial, though different, effects on mammals of any size."

According to Haeney's model, small mammals would be expected to show an increase in body size on small islands compared with mammals on the larger islands. I would like to know how *C. gliroides* would fit the model, since it is one of the smallest rodents on the Sunda Shelf, and likely occurs on many of the small islands. There is also the advantage that the mice are not limited to pristine tropical forest but can survive in secondary forest, coconut plantations, gardens, and even scrub and human dwellings if those habitats are near suitable nesting sites such as bamboo clumps, tall palms, and fruit trees. Hence, *C. gliroides* may be found on small islands where the original forest has been so altered that other small mammals which are tied to primary forest are no longer present.

The species of *Chiropodomys* will eventually have to be compared again with those in *Pogonomys*, a group of arboreal rats which form part of the endemic murid fauna of New Guinea (Tate, 1936; Laurie and Hill, 1954). The nature of any close relationships between species within those two genera can eventually be re-examined in the context of results from studies now in progress. The species of *Pogonomys* are being taxonomically revised by James Menzies and his colleagues. There are six or

seven species that can be separated into two morphological groups, each distinct at least at the subgeneric level and perhaps even at a generic level. When that study is complete there will be morphological and distributional definitions of the species and probably some information about their natural histories.

This potential information from taxonomic revision will supplement data from studies of chromosomes of Australian murids that have already been published (Baverstock, Watts and Hogarth, 1977; Baverstock et al., 1977) and studies of chromosomes of murids from New Guinea that are published (Dennis and Menzies, 1978) or being prepared. On the basis of number and morphology of chromosomes, Baverstock, Watts and Hogarth (1977) have challenged the earlier hypotheses which were proposed by Tate (1951) and Simpson (1961) that there are four major groups of Australian murids: one composed of *Uromys* and *Melomys*; a second consisting of species in the Pseudomyine cluster; a third containing the Hydromyines, *Hydromys* and *Xeromys*; and a fourth comprised of the endemic species of *Rattus*.¹ The data collected by Baverstock and his associates suggest that there are only two basic types of chromosomal patterns and from

¹These endemic groups contrast with a modern intrusive assemblage of murids that are closely tied to habitats made and maintained by humans. *Rattus rattus* (the European type, $2n = 38$), *R. norvegicus*, *R. exulans* (only on Adele, Mer, and Murray islands), and *Mus musculus* occur in Australia. Those four species are also found on New Guinea, along with the Asian form of *R. rattus* ($2n = 42$), *R. argentiventer*, and *R. nitidus*. This cluster of commensal species would be a fifth group in Australia, or a third, depending on whose hypothesis you consider. But as a group it is not comparable with any of the endemic assemblages because it consists of species from different lineages which originated and evolved in other parts of Asia and were likely brought inadvertently to Australia by humans at different times. Each of the endemic groups, on the other hand, is composed of species from the same lineage that probably evolved in Australia and New Guinea.

Some of the commensals which are found in Australia and New Guinea also occur throughout the Indonesian Archipelago and in the Philippines, a geographic pattern superimposed on distributions of the endemic murid faunas in those areas (Musser, 1973a, 1977).

this they infer the presence of two lineages; their working hypothesis is that the endemic murids of Australia belong to only two groups: the kinds of *Rattus* form one; the species in *Uromys*, *Melomys*, the Pseudomyines, and the Hydromyines comprise the other.

The hypothesis that the endemic rodents of New Guinea also represent only two lineages is being tested and some as yet unpublished results indicate that in number and morphology of chromosomes, the species of *Pogonomys* are closely similar to those in *Uromys*, *Melomys*, the Pseudomyines, and the Hydromyines. The implication is that the species in *Pogonomys* are part of an adaptive radiation from an ancestral stock that reached New Guinea very early, and not part of a group of *Chiropodomys*-like murids that got to New Guinea in a

separate wave, representing a different and discrete lineage.

Thus, old hypotheses are being tested with new data and our views of the relationships among species of rats and mice in that vast region of continents and archipelagos from Southeast Asia to Australia are being altered. Set against this context of recent inquiry—where biologists are gathering and analyzing different kinds of data, looking carefully again at skins and skulls and seeing more, and obtaining fresh insight into the phylogenetic relationships among species of rodents—we may eventually be able to better estimate the phylogenetic affinities of the species of *Chiropodomys* and their positions in the intricate and complex evolutionary pattern of that exceptional murid fauna of the Far East.

LITERATURE CITED

- Allen, Glover M.
1927. Murid rodents from the Asiatic expeditions. Amer. Mus. Novitates, no. 270, pp. 1-12.
1940. The mammals of China and Mongolia. Natural History of Central Asia, vol. 11, pt. 2. New York, The American Museum of Natural History, pp. i-xxvi, 621-1350, pls. 10-20.
- Allen, Glover M., and Harold J. Coolidge, Jr.
1940. Mammals. In Mammal and bird collections of the Asiatic Primate Expedition, Bull. Mus. Comp. Zool. Harvard College, vol. 87, no. 3, pp. 121-211, 3 maps.
- Anderson, Sydney
1968. A new craniometer and suggestions for craniometry. Jour. Mammal., vol. 49, no. 2, pp. 221-228, figs. 1-3.
- Anthony, Harold E.
1941. Mammals collected by the Vernay-Cutting Burma Expedition. Zool. Ser., Field Mus. Nat. Hist., vol. 27, pp. 37-123, 1 fig., 4 pls.
- Arata, Andrew A.
1967. Chapter 12. Muroid, gliroid, and dipodoid rodents. In Anderson, Sydney A., and J. Knox Jones, Jr. (eds.), Recent mammals of the world. A synopsis of families. New York, Ronald Press, pp. 226-253, figs. 34-38.
- Bangs, Outram, and Josselyn Van Tyne
1931. Birds of the Kelley-Roosevelts Expedition to French Indo-China, Field Mus. Nat. Hist., Publ. 290, Zool. Ser., vol. 18, no. 3, pp. 33-119, 1 map.
- Baverstock, P.R., C.H.S. Watts, and J.T. Hogarth
1977. Chromosome evolution in Australian rodents. I. The Pseudomyine, the Hydromyine and the *Uromys/Melomys* group. Chromosoma, vol. 61, no. 2, pp. 95-125, figs. 1-31.
- Baverstock, P.R., C.H.S. Watts, J.T. Hogarth, A.C. Robinson, and J.F. Robinson
1977. Chromosome evolution in Australian rodents. II. The *Rattus* group. *Ibid.*, vol. 61, no. 3, pp. 227-241, figs. 1-11.
- Blyth, Edward
1856. Report for October Meeting, 1855. Jour. Asiatic Soc. Bengal, vol. 24, no. 7, pp. 711-723.
1859. Proceedings of the Asiatic Society for the months of June, July, and August, 1859. *Ibid.*, no. 3, pp. 293-298.
- Carter, T. Donald
1943. The mammals of the Vernay-Hopwood Chindwin Expedition, northern Burma.

- Bull. Amer. Mus. Nat. Hist., vol. 82, art. 4, pp. 99-113, 1 map, 7 pls.
- Cartmill, Matt
1974. Pads and claws in arboreal locomotion, pp. 45-83, figs. 1-7. In F.A. Jenkins, Jr. (ed.), Primate locomotion, New York, Academic Press.
- Chasen, Frederick Nutter
1940. A handlist of Malaysian mammals (A systematic list of the mammals of the Malay Peninsula, Sumatra, Borneo and Java, including the adjacent small islands). Bull. Raffles Mus., Singapore, Straits Settlement, no. 15, pp. i-xx, 1-209, 1 map.
- Chasen, F.N., and C. Boden Kloss
1928. On some Carnivora, Rodentia and Insectivora principally from eastern Borneo. Malayan Branch Roy. Asiatic Soc., vol. 6, part 1, pp. 38-49, 1 map.
- Corbet, G. B.
1966. The terrestrial mammals of western Europe. Dufour Editions, Philadelphia, pp. i-xi, 1-265, figs. 1-23, frontispiece, pls. 1-15.
1978. The mammals of the Palaearctic Region. A taxonomic review. London, British Museum (Nat. Hist.), and Ithaca, Cornell Univ. Press, pp. 1-314, maps 1-104.
- Dennis, Elizabeth, and J. I. Menzies
1978. Systematics and chromosomes of New Guinea *Rattus*. Australian Jour. Zool., vol. 26, pp. 197-206, figs. 1-6.
- Doria, G.
1887. Nota intorno distribuzione geografica del *Chiropodomys penicillatus* Peters. Ann. del Mus Civ. di St. Nat. Genova, ser. 2, vol. 4, pp. 1-7.
- Dunn, F.J., B.L. Lim, and L. F. Yap
1968. Endoparasite patterns in mammals of the Malayan rain forest. Ecology, vol. 49, no. 6, pp. 1179-1184.
- Ellerman, J.R.
1941. The families and genera of living rodents. London, British Museum (Nat. Hist.), vol. 2, Family Muridae, pp. i-xii, 1-690, figs. 1-50.
1949. The families and genera of living rodents. *Ibid.*, vol. 3, pt. 1, pp. i-v, 1-210.
1961. The fauna of India including Pakistan, Burma and Ceylon. Mammalia. Delhi, Manager of Publications, vol. 3, pts. 2, pp. xxxi-xxxv, 483-884, and xxxvii-lii, 1 map, 29 figs.
- Ellerman, J.R., and T.C.S. Morrison-Scott
1951. Checklist of Palaearctic and Indian mammals, 1759 to 1946. London, British Museum (Nat. Hist.), pp. 1-810, 1 map.
1955. Supplement to Chasen (1940) a handlist of Malaysian mammals, containing a generic synonymy and a complete index. *Ibid.*, pp. 1-66.
- Gropp, A., A. Markwong, J. Marshall, Jr., and Y.J. Kim
1972. Robertsonian chromosomal variation in the longtailed tree mouse (*Vandeleuria*). Zeitschrift Zool. Syst. Evolut.-forsch., Band 10, heft 3, pp. 210-214, 1 fig.
- Günther, Albert C.L.G. (ED.)
1869. The record of zoological literature, 1868, vol. 5, i-ix, 1-592.
- Haeney, Lawrence R.
1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. Evolution, vol. 32, pp. 29-44, figs. 1-5.
- Haines, R. Wheeler
1958. Arboreal or terrestrial ancestry of placental mammals. Quart. Rev. Biol., vol. 33, no. 1, pp. 1-23, figs. 1-14.
- Harrison, John L.
1955. Data on reproduction of some Malayan mammals. Proc. Zool. Soc. London, vol. 125, pt. 2, pp. 445-460, figs. 1-3.
1956. Survival rates of Malayan rats. Bull. Raffles Mus., no. 27, pp. 5-26, figs. 1-9.
1957. Malayan parasites—XXXIII. The Hosts. Malaya, no. 28, pp. 409-426.
1961. The natural food of some Malayan mammals. Bull. Nat. Mus. Singapore, no. 30, pp. 5-18.
1966. An introduction to mammals of Singapore and Malaya. Singapore Branch, Malayan Nature Society, Singapore, pp. i-x, 1340, figs. 1-61.
- Harrison, John L., and Lim Boo Liat
1950. Notes on some small mammals of Malaya. Bull. Raffles Mus., no. 23, pp. 300-309.
- Hill, J.E.
1960. The Robinson collection of Malaysian mammals. Bull. Raffles Mus., Singapore, no. 29, pp. 1-112, figs. 1-4.
- Hose, Charles
1893. A descriptive account of the mammals of Borneo. Diss. Norfolk, London, pp. 1-78, 3 pls., 1 map.
- Javis, C., and D. Morris
1961. Longevity Survey. Length of life of mammals in captivity at the London Zoo and Whipsnade Park. The International Zoo

- Yearbook. Vol. 2 for 1960, pp. 288-299.
- Král, Bohumil
1971. Chromosome characteristics of certain Murine rodents (Muridae) of the Asiatic part of the USSR. *Zoologické Listy*, vol. 20, no. 4, pp. 331-347.
- Kretzoi, M.
1959. Insectivoren, Nagetiere und Lagomorphen der Jüngst-pliozänen Fauna von Csarnóta im Villányer Gebirge (Südungarn). *Vertebrata Hungarica* Budapest, vol. 1, fasc. 2, pp. 237-246.
- Kurtén, Björn
1968. Pleistocene mammals of Europe. Chicago, Aldine Publ. Co., viii + 317 pp., 111 figs.
- Laurie, E.M.O., and J.E. Hill
1954. List of land mammals of New Guinea, Celebes and adjacent islands, 1758-1952. London, British Museum (Nat. Hist.), pp. 1-175, pls. 1-2, 1 map.
- Lim, B.L.
1956. The natural food of some Malayan snakes. *Malayan Nature Jour.*, vol. 10, pp. 139-144.
- Lim, Boo Liat., and D. Heyneman
1968. A collection of small mammals from Tuaran and the southwest face of Mt. Kinabalu, Sabah. *Sarawak Mus. Jour.*, vol. 16, pp. 257-280, 1 fig., pls. 33-36.
- Marshall, Joe T., Jr.
1976. Family Muridae: rats and mice. Pp. 396-487. Reprinted from *Mammals of Thailand* (Boonsong Lekagul and J.A. McNeely), Assoc. Conserv. of Wildlife, Bangkok, Thailand.
- Medway, Lord
1964. The marmoset rat, *Hapalomys Longicaudatus* Blyth. *Malayan Nat. Jour.*, vol. 18, nos. 2 and 3, pp. 104-110, pls. XIII-XVIII.
1965. Mammals of Borneo. Field keys and an annotated checklist. Singapore, Malaysian Branch of the Royal Asiatic Society, Malaysia Printers, pp. i-xiv, 1-193, figs. 1-9, pls. 1-34, 1 map.
1967. Observations on breeding of the pencil-tailed tree mouse, *Chiropodomys gliroides*. *Jour. Mammal.*, vol. 48, no. 1, pp. 20-26, figs. 1-2.
1969. The wild mammals of Malaya and offshore islands including Singapore. Kuala Lumpur and Singapore, Oxford Univ. Press, xix + 127 pp., figs. 1-11, pls. 1-15.
- Miller, Gerrit S., Jr.
1903. Seventy new Malayan mammals. *Smithsonian Misc. Coll.*, vol. 45, pts. 1 and 2, pp. 1-73, pls. 1-19.
1912. Catalogue of the mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum. London, British Museum (Nat. Hist.), pp. i-xv, 1-1019, figs. 1-213.
- Misonne, Xavier
1969. African and Indo-Australian Muridae. Evolutionary trends. *Mus. Roy. l'Afrique Cent., Tervuren, Zool.*, no. 172, pp. 1-219, figs. A-K, pls. 1-27.
- Musser, Guy G.
1970. Species-limits of *Rattus brahma*, a murid rodent of northeastern India and northern Burma. *Amer. Mus. Novitates*, no. 2406, pp. 1-27, figs. 1-6.
1972. The species of *Hapalomys* (Rodentia, Muridae). *Ibid.*, no. 2503, pp. 1-27, figs. 1-12.
1973a. Zoogeographical significance of the ricefield rat, *Rattus argentiventer*, on Celebes and New Guinea and the identity of *Rattus pestivulus*. *Ibid.*, no. 2511, pp. 1-30, figs. 1-5.
1973b. Species-limits of *Rattus cremoriventer* and *Rattus langbianis*, murid rodents of Southeast Asia and the Greater Sunda islands. *Ibid.*, no. 2525, pp. 1-65, figs. 1-9.
1977. *Epimys benguetensis*, a composite, and one zoogeographic view of rat and mouse faunas in the Philippines and Celebes. *Ibid.*, no. 2624, pp. 1-15, figs. 1-4.
- Neave, Sheffield Airey
1939. Nomenclator Zoologicus. A list of the names of genera and subgenera in zoology from the tenth edition of Linnaeus 1758 to the end of 1935. Vol. 1, i-xiv, 1-957. Zoological Society of London.
- Palmer, T.S.
1904. Index generum mammalium: a list of the genera and families of mammals. *North American Fauna* no. 23, pp. 1-984.
- Peters, W.
1869. Hr. W. Peters machte eine Mittheilung über eine neue Nagergattung, *Chiropodomys penicillatus*, so wie über einige neue oder weniger bekannte Amphibien und Fische. *Monatsberichte der Königlich Preuss. Akad. der Wiss. zu Berlin*. Aus dem Jahre 1868, pp. 448-461, pls. 1-2.
- Philips, W.W.A.
1928. Guide to the mammals of Ceylon, Part

- VIII, Rodentia. *Spolia Zeylanica*, vol. 14, pp. 209-293, 2 pls.
1929. Two new rodents from the highlands of Ceylon. *Ceylon Jour. Sci.*, Sec. B, 15, pp. 165-168.
- Sanborn, Colin Campbell
1952. Philippine Zoological Expedition 1946-1947. *Mammals. Fieldiana: Zool.*, vol. 33, no. 2, pp. 89-158, figs. 8-22.
- Schulze, F.E., W. Kukenthal, and K. Heider
1929. *Nomenclator animalium generum et subgenerum im auftrage der Preufischen Akademie der Wissenschaften zu Berlin. Preuf. Akad. Wiss.*, Berlin, Band 2, C-E, pp. 477-1298.
- Sclater, W.L.
1890. Notes on some Indian rats and mice. *Proc. Zool. Soc. London*, pp. 522-530, 2 pls.
1891. Catalogue of Mammalia in the Indian Museum, Calcutta. Part II. Rodentia, Ungulata, Proboscidae, Hyracoidea, Carnivora, Cetacea, Sirenia, Marsupialia, Monotremata. Calcutta, Indian Museum, pp. i-xxix, 1-375.
- Scudder, Samuel H.
1882. *Nomenclator Zoologicus*. An alphabetical list of all generic names that have been employed by naturalists for recent and fossil animals from the earliest times to the close of the year 1879. *Bull. U.S. Natl. Mus.*, no. 19, pp. i-xxi, 1-340.
- Simpson, George Gaylord
1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, vol. 85, pp. i-xvi, 1-350.
1961. Historical zoogeography of Australian mammals. *Evolution*, vol. 15, no. 4, pp. 431-446, 1 fig.
- Sody, H.J.V.
1941. On a collection of rats from the Indo-Malayan and Indo-Australian regions (with descriptions of 43 new genera, species, and subspecies). *Treubia*, vol. 18, pp. 255-325.
- Tate, G.H.H.
1936. Results of the Archbold Expeditions. No. 13. Some Muridae of the Indo-Australian region. *Bull. Amer. Mus. Nat. Hist.*, vol. 72, pp. 501-728, figs. 1-32.
1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. *Ibid.*, vol. 97, pp. 187-430, figs. 1-4.
- Taylor, Edward H.
1934. Philippine land mammals. Monograph Bureau Science (Manila), no. 30, pp. 1-548, figs. 1-12, pls. 1-25.
- Tien Dao Van
1966. Sur une collection de rongeurs au sud-est de L'Asia. *Miss. Zool. Mus. Berlin*, Band 42, heft 2, pp. 219-228.
- Thomas, Oldfield
1891. On the Mammalia collected by Signor Leonardo Fea in Burma and Tenasserim. *Annali Del Museo.*, Civico di Storia Naturale Di Genova, ser. 2, vol. 10, pp. 913-949, 2 pls.
1893a. On some new Bornean Mammalia. *Ann. Mag. Nat. Hist.*, vol. 11, ser. 6, pp. 341-347.
1893b. Descriptions of two new North-Bornean mammals. *Ibid.*, vol. 12, ser. 6, pp. 230-232, 1 pl.
1896. On mammals from Celebes, Borneo, and the Philippines recently received at the British Museum. *Ibid.*, vol. 18, ser. 6, pp. 241-250.
1911. New Asiatic Muridae. *Ibid.*, vol. 7, ser. 8, pp. 205-209.
1925. The mammals obtained by Mr. Herbert Stevens on the Sladen-Godman Expedition to Tonkin. *Proc. Zool. Soc. London*, pp. 495-506.
- Thomas, O., and R. C. Wroughton
1909a. Abstract of the Proceedings of the Zoological Society of London. No. 68, pp. 17-19.
1909b. On a collection of mammals from western Java presented to the National Museum by Mr. W.E. Balston. *Proc. Zool. Soc. London*, 1909, pp. 371-392.
- Trouessart, E.L.
1881. Catalogue des mammifères vivants et fossiles. *Ordre des Rongeurs. Bull. Soc. Études Sci. Angers*, 10th ann., pt. 2, pp. 58-212.
1897-1905. Catalogue mammalium tam viventium quam fossilium. Nova edito (prima completa). Berlin, R. Friedlander und Sohn, pt. 1 (1897), pp. 1-218; pt. 2 (1897), pp. 219-452; pt. 3 (1897), pp. 453-664; pt. 4 (1898), pp. 665-998; pt. 5 (1898), pp. 999-1264; pt. 6 (1899), pp. 1265-1469; suppl., pts. 1, 2 (1904), pp. 1-546; pts. 3, 4 (1905), pp. 547-929.
- Yong, Hoi-Sen
1973. Chromosomes of the pencil-tailed tree-

- mouse, *Chiropodomys gliroides* (Rodentia, Muridae). Malay Nat. Jour., vol. 26, pp. 159-162, figs. 1-2.
- Walker, Ernest P.
1968. Mammals of the World. Second Edition. Volume II. PP. i-viii, 647-1500, numerous photographs.
- Whitmore, T.C.
1975. Tropical rain forests of the Far East. Clarendon Press, Oxford, i-xiv, 1-282 pp., many figs. and maps.
- Wroughton, R.C.
1915. Bombay Natural History Society's mammal survey of India, Burma and Ceylon. Report No. 17. Jour. Bombay Nat. Hist. Soc., vol. 23, pp. 695-720.

BULLETIN OF
THE AMERICAN MUSEUM
OF NATURAL HISTORY



Volume 162
1978-1979

PUBLISHED BY ORDER OF THE TRUSTEES
NEW YORK : 1979

Edited by
FLORENCE BRAUNER

CONTENTS OF VOLUME 162

- Article 1. The Ecology and Migrations of Sea Turtles, 7. The West Caribbean Green Turtle Colony. By Archie Carr, Marjorie Harris Carr, and Anne Barkau Meylan. Pages 1-46, figures 1-19, tables 1-13. December 4, 1978Price \$2.90
- Article 2. The Distribution of Birds in Venezuelan Páramos. By François Vuilleumier and David N. Ewert. Pages 47-90, figures 1-10, tables 1-6. December 27, 1978Price \$2.95
- Article 3. The Jurassic Turtles of North America. By Eugene S. Gaffney. Pages 91-136, figures 1-31, tables 1-4. January 22, 1979Price \$3.00
- Article 4. The Biology of Blister Beetles of the Vittata Group of the Genus *Epicauta* (Coleoptera, Meloidae). By Cheryl Lynn Adams and Richard B. Selander. Pages 137-266, figures 1-63, tables 1-63. March 16, 1979Price \$9.00
- Article 5. Fishes from the Uplands and Intermontane Basins of Guatemala: Revisionary Studies and Comparative Geography. By Donn E. Rosen. Pages 267-376, figures 1-50, tables 1-15 March 30, 1979Price \$8.30
- Article 6. Results of the Archbold Expeditions. No. 102. The Species of *Chiropodomys*, Arboreal Mice of Indochina and the Malay Archipelago. By Guy G. Musser. Pages 377-445, figures 1-16, tables 1-7. April 3, 1979Price \$4.65

