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Identification of Bandicoot Rats from Thailand (*Bandicota,* Muridae, Rodentia)

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ABSTRACT

In 1989, Boonsong and Felten documented the occurrence of five species of *Bandicota* in Thailand: "*B. bengalensis,*" "*B. varius,*" "*B. savilei,*" "*B. indica,*" and "*B. bangchakensis*"; the first four names were already available in the literature; *bangchakensis* was described by Boonsong and Felten as a new species. Previously only *B. savilei* and *B. indica* had been recorded from Thailand. Those two species, along with *B. bengalensis,* had long been considered the only species contained in the genus *Bandicota* (Corbet and Hill, 1992; Musser and Carleton, 1993). The different opinions are resolved by examination of the material studied by Boonsong and Felten, which is in the Senckenberg Museum. Those specimens have been compared to reference samples of the three species. Results indicate that only two species of *Bandicota* do occur in Thailand; *B. bengalensis* has yet to be recorded from there. The samples identified by Boonsong and Felten as "*B. bengalensis,*" "*B. varius,*" and "*B. bangchakensis*" are actually examples of *B. savilei*; *bangchakensis* is listed as one of several synonyms under *B. savilei.* Those series determined by Boonsong and Felten to be "*B. savilei*" and "*B. indica*" represent the large bandicoot, *B. indica.* Our identifications are documented. Notes are provided on phylogenetic relationships between *Bandicota* and other murine rodents.

INTRODUCTION

More than 260 species of mammals are recorded from Thailand (Lekagul and McNeely, 1977). Among these are species of rats in the genus *Bandicota.* Until the late 1980s three species of bandicoots were recognized in the literature and only two of these had been found in Thailand: *Bandicota indica* and *B. savilei* (Marshall, 1977). Thailand is only a segment of the geographical distribution of *B. indica,* which extends from India

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east to Taiwan and southern China south to scattered regions on the Sunda Shelf (Musser and Carleton, 1993). *Bandicota savilei* has a much smaller range and has been recorded only from a central Burma, Thailand, and Vietnam (fig. 1) although it probably occurs elsewhere in the Indochinese region. The third species, *B. bengalensis,* had not been reported from Thailand. It has been found from eastern Pakistan through the Indian subcontinent to central and peninsular Burma, on various islands on the Sunda Shelf, and in Saudi Arabia (Musser and Carleton, 1993).

In 1989, Boonsong and Felten reported on 128 specimens of *Bandicota* they had collected from Thailand during 1977–81. In the process of identifying the material, they encountered "unexpected taxonomic difficulties" and exclaimed that "this fact is astonishing all the more as the animals of the different species of this genus are very numerous and widespread in S- and SE-Asia. They are of great importance in agriculture by damaging rice fields; but they play also an important part in human nutrition as suppliers of animal protein."

Using measurements of skulls and molars, Boonsong and Felten separated their material into five groups, each treated as a species. Four were identified by names already proposed in the literature: "*B. bengalensis,*" "*B. varius,*" "*B. savilei,*" and "*B. indica.*" A fifth sample did not seem to fit any previously recognized form and they described it as a new species, "*B. bangchakensis.*"

If Boonsong and Felten were astonished at the difficulties they experienced identifying their material, researchers working with rodent faunas in Southeast Asia were even more surprised with Boonsong and Felten's results. Five species of *Bandicota* apparently occurred in Thailand, all existed sympatrically, and one had not been detected by previous taxonomists working with Asian faunas in general and Thai mammals in particular.

This view of *Bandicota* diversity in Thailand clashed with that provided in *Mammals of Thailand,* published in 1977, the only comprehensive compendium of the Thai mammal fauna available (it was reprinted in 1988, without changes in the accounts). Boonsong and Felten had consulted this work, did not find it to be useful, and incorrectly credited the bandicoot accounts to Lekagul and McNeely, the editors. The chapter on murid rodents, which contains accounts of the Thai bandicoots, was actually written by Joe T. Marshall, Jr., and is based on his extensive field surveys in Thailand and comparisons of specimens he collected with those housed in various museums. Marshall could identify only *B. indica* and *B. savilei* in Thailand, and claimed that *B. bengalensis* did not occur there. During the same time Marshall was working in Thailand, Musser had independently obtained the same results by studying specimens in museum collections as part of a review, still unpublished, of bandicoot taxonomy. These research results were condensed into checklist accounts by Musser and Carleton (1993) who acknowledged only two species of *Bandicota* from Thailand and just three in the genus. Corbet and Hill (1992), in their accounts of Indomalayan mammals, recognized the same three species but could not assess the status of Boonsong and Felten's *B. bangchakensis.*

Marshall's contribution to systematics of Thai bandicoots was largely derived from specimens which he and his colleagues had obtained in Thailand. Collections made by Boonsong and Felten were the basis for their interpretation of Thai bandicoot species diversity. The disparity between the views of these two groups of researchers inspired us to provide a resolution of the conflict.

Dr. Gerhard Storch provided the opportunity to assess the identifications defended by Boonsong and Felten. In the summer of 1992, Storch invited Musser to study the material from Asia in the collection of the Senckenberg Museum, particularly series from Thailand, and especially the samples of *Bandicota,* examined by Boonsong and Felten, upon which their results are constructed.

We have studied the specimens in Senckenberg and compared data gathered from them with information previously obtained by Musser. We also reexamined material stored in museums other than Senckenberg. Our study includes nearly all of the specimens used by Marshall for his chapter on bandicoots in the *Mammals of Thailand.*

Our results are reported here within the context of hypothesis-testing and curiosity about evolutionary diversity in nature. The identification of a specimen is a hypothesis. Determining the number of species within a

particular genus, which is an estimate of evolutionary diversity within a monophyletic group, is also a hypothesis. Boonsong and Felten provided hypotheses of identification and species diversity that gave us an unexpected perspective about the number of species of *Bandicota* occurring in Thailand, their morphologies, and their geographic ranges. The picture Boonsong and Felten showed us was drawn from analyses based on data derived from primary sources—the specimens they had collected. Each skin and skull was carefully documented, identified, and stored safely in a museum where it could be examined by other researchers who might want to use the same material to determine whether or not the specimens mirrored the same picture framed by Boonsong and Felten. We went to these primary sources not with the intent to criticize the work of our colleagues but to test their hypotheses.

In the following pages, we first present the three species of *Bandicota* recognized in recent checklists. This tripartite composition of *Bandicota* is based on our survey of specimens in institutions other than the Senckenberg Museum. The discussion takes the form of synonymies, geographic distributions, and taxonomic problems associated with each species. We then outline the distinctive morphological contrasts among them. Following this section comes our identification of the Senckenberg material and justification for our allocations of specimens to only two species rather than five.

Finally, we comment on the possible phylogenetic relationships of *Bandicota*. This has little relevance to our original intent, but while we were examining characters to help us answer our primary question, we surveyed morphological features that might be useful in assessing the relationship between *Bandicota* and other murines, particularly *Nesokia*. *Bandicota* has always been thought to be closely related to *Nesokia* but the phylogenetic alliances of the two genera within the Murinae (as defined by Carleton and Musser, 1984) have been obscure.

Materials and Methods

Abbreviations, Institutions, and Specimens: The 1056 specimens we examined, most of them conventional museum study skins with associated skulls, are in collections of the following institutions (identified throughout this report by the appropriate acronym):

AMNH	American Museum of Natural History, New York City
ANSP	Philadelphia Academy of Natural Sciences, Philadelphia
ASRCT	Applied Scientific Research Corporation of Thailand, Centre for Thai National Reference Collections, Bangkok
BMNH	British Museum of Natural History, London
BS	Private Collection of Dr. Boonsong Lekagul, Bangkok
FMNH	Field Museum of Natural History, Chicago
FTM	Faculty of Tropical Medicine, Bangkok
LACM	Los Angeles County Museum, Los Angeles
MNHN	Museum National d'Histoire Naturelle, Paris
NUS	Zoological Reference Collection, National University of Singapore, Singapore
RFD	Royal Forest Department of Thailand Mammal Collection, Bangkok
RPRC	Rice Protection Research Center, Bangkok
SMF	Senckenberg Museum, Frankfurt am Main
SMRL	SEATO Medical Research Laboratory, Bangkok
USNM	National Museum of Natural History, Washington, DC.

The localities from which the specimens were obtained, along with the institutional acronym and catalog number of each rat, are provided in two lists. One constitutes Appendix 1 and contains material we studied from localities that were not mapped; most of these specimens are from areas outside the Indochinese region. The other list is in Appendix 2; it consists of specimens examined from Indochinese localities that are plotted on the map in figure 1. Measured specimens from which summary statistics were derived (Tables 2–4) are identified in table footnotes; they include specimens from both lists.

Measurements: Four external measure-

ments were used in the analyses: length of tail (LT), length of hind foot (LHF), length of ear (LE), and length of head and body (LHB). Values for the first three were taken from labels attached to skins; subtracting length of tail from total length gave us length of head and body.

We used dial calipers (graduated to hundredths of millimeters) to obtain measurements of the following cranial and dental dimensions (listed in the sequence they appear in the tables):

GLS	greatest length of skull
ONL	occipitonasal length
ZB	zygomatic breadth
IB	interorbital breadth
LN	length of nasals
BR	breadth of rostrum
BBC	breadth of braincase
HBC	height of braincase
BZP	breadth of zygomatic plate
DZN	depth of zygomatic notch
LD	length of diastema
LIF	length of incisive foramina
BIF	breadth of incisive foramina
LBP	length of bony palate
BBPM1	breadth of bony palate at first molar
BBPM3	breadth of bony palate at third molar
BMF	breadth of mesopterygoid fossa
LB	length of auditory bulla
ALMI-3	alveolar length of maxillary molar row
CBM1	crown breadth of first upper molar

Dimensions are defined in Musser (1979) and Musser and Newcomb (1983); their limits are illustrated in Musser (1979) and Musser and Holden (1991). Values are given in millimeters.

DENTAL TERMINOLOGY: The names used throughout the text for cusps and cusplets of upper and lower molars are presented in figure 27.

STATISTICS: We employed descriptive statistics to calculate the mean, standard deviation, and observed range for each measurement. The significance of the difference between two sample means was determined by a *t*-test. Wherever we refer to the differences between sample means as being significant, we are rejecting the null hypothesis using the 0.05 level of significance.

ACKNOWLEDGMENTS

Persons in charge of the institutions listed above allowed us to study material for which they were responsible. We appreciate the access they allowed us to the collections and their efforts in loaning us specimens. We especially thank Dr. Gerhard Storch for allowing Musser unhindered access to the Senckenberg collections and for facilitating the loan of specimens to the American Museum of Natural History.

Photographs (figs. 5, 6, 9, 10, 15, 16, 17, 18, 20–25) are the work of Peter Goldberg. Figures 4, 7, 8, 19, 26, and 27 were completed by Patricia Wynne; Eric Brothers did the map, scatterplots, and histograms. By their talents, these three people allow readers to clearly visualize the comparisons we discuss in the text. Figures 2 and 3 were taken by the late Dr. Boonsong Lekagul and sent to Musser as a gift, delivered by Joe Marshall.

Drs. Gerhard Storch, Joe T. Marshall, Jr., and Mary Ellen Holden reviewed the manuscript; we appreciate their time and contributions to the final product. Musser is especially grateful to Marshall, who took him into Thai cornfields where they trapped *B. savilei* in its agricultural habitat.

THE SPECIES OF *BANDICOTA*

We hypothesize that only three species of *Bandicota* can be diagnosed at the present time—*B. bengalensis, B. savilei,* and *B. indica*—the same three currently recognized in recent faunal checklists (Corbet and Hill, 1992; Musser and Carleton, 1993). We defend this hypothesis because we can allocate each of the several hundred specimens examined from institutions (other than the Senckenberg Museum; those specimens we discuss later), along with holotypes, to one of these three entities. Each group is diagnosable, and represents a distinct biological entity, indicating an evolutionary history separate from each of the other two.

Throughout our present report we refer to our reference samples of these three species (formed from the individuals listed in Ap-

pendices 1 and 2). They comprise a large portion of all the specimens in museum collections, contain most of the relevant holotypes, and constitute the material to which we compared the specimens of the Senckenberg Museum.

Our exposition does not constitute a revision. There is appreciable morphological variation associated with sex, age, individuals, and geography that we have seen in the samples. The significance of the geographic variation in certain external and cranial qualitative traits and in dimensions is unclear, despite the few attempts to taxonomically revise the groups (see our discussions farther along in this section) and won't be resolved until a thorough systematic revision is undertaken. We also are aware of the range in definitions of species currently being debated in the literature (for example, see the following and references cited therein: Otte and Endler, 1989; Patton and Smith, 1994; O'Hara, 1994) and the consequences of accepting any particular one to express the exposition of morphological and geographic diversity within *Bandicota.*

It is within this framework that we examined the Thai bandicoot rats in the Senckenberg Museum that were studied by Boonsong and Felten (1989) and tested their hypotheses of identification and the validity of the new species they described.

We introduce the bandicoots by listing the scientific names associated first with the genus and then with each of the three species, elucidate the geographic range of each species with special attention to the distribution in Indochina (fig. 1), discuss some of the taxonomic problems that can only be resolved by careful systematic revision of each species, and then provide morphological and metric distinctions among the three kinds of bandicoots. We devote more attention to the taxonomy and distribution of *B. savilei* because at one time it was considered only a subspecies of *B. indica,* because specimens of it collected in Thailand and Vietnam have been misidentified as *B. bengalensis,* and because samples of "*B. bengalensis,*" "*B. varius,*" and "*B. bangchakensis,*" three out of five Thai species documented by Boonsong and Felten (1989), actually represent *B. savilei.*

Taxonomy and Geographic Distribution

The Genus *Bandicota*

Bandicota Gray 1873: 418.
Gunomys Thomas 1907: 203.

Many of the scientific names associated with the species of *Bandicota* were originally proposed as species of *Mus,* combinations reflected in the synonymies listed below for each of the three species we recognize. The first taxonomic revision of the group (Anderson, 1878) was reported under *Nesokia,* which at the time was considered to be a subgenus of *Mus.* This nomenclatural convention was later followed by Thomas (1881) in his monograph, "Indian Species of the Genus *Mus.*"

A few years later, Sclater (1890), in his report on "Some Indian Rats and Mice," treated *Nesokia* as a full genus. In the "Fauna of British India," Blanford (1891) also recognized the generic status of *Nesokia* (which he spelled "*Nesocia*"), but noted that "it is doubtful whether this should rank as more than a subgenus of *Mus*" (p. 421).

Although Gray proposed the generic name *Bandicota* in 1873, it was not associated with *Nesokia* until 1907, when Oldfield Thomas wrote that the "genus *Nesokia* contains three such very distinct and natural groups that in accordance with modern ideas they should be recognized as distinct genera" (p. 203). Thomas proposed *Gunomys* as a genus to contain the species *bengalensis* and listed *Nesokia* ("Skull short and broad. Palatal foramina short. Molars laminate, least *Mus*-like. Mammae 2−2=8"), *Gunomys* ("Skull broad. palatal foramina long. Mammae irregular, 14–18 in number"), and *Bandicota* ("Skull comparatively long and narrow. Palatal foramina long. Molars most *Mus*-like. Mammae 3−3=12") as full genera in that order. Thomas noted that "these three genera are specialized in the order given, *Nesokia* being the most extreme and the farthest from *Mus,* both in skull, tooth-structure, and external characters, and *Bandicota* the nearest, while *Gunomys* is intermediate between the other two" (p. 203). This tripartite generic view of bandicoots was retained by Wroughton (1908) in

his review of bandicoot rats, the only taxonomic synthesis of the group until Ellerman (1941) presented his classificatory outline four decades later.

In the period between the contributions by Wroughton in 1908 and Ellerman in 1941, the generic triad of bandicoot rats was questioned only by Kloss in 1921. He reported a collection of *Bandicota setifera* (= *indica*) from Java and described *sundavensis,* a new subspecies of *Gunomys bengalensis* based on four specimens from the Aceh region of northern Sumatra and one example from eastern Java. He tabulated what he thought the principal differences were between *Bandicota* and *Gunomys* (slightly narrower skull, fewer mammae, longer tail, and less constricted posterior portion of incisive foramina in *Bandicota*) and concluded that "the differences seem hardly of generic importance" (p. 117), In Ellerman's (1941) influential checklist of the families and genera of living rodents, *Gunomys* was treated as a synonym of *Bandicota,* which was listed as a genus separate from *Nesokia,* an arrangement accepted today (Corbet and Hill, 1992; Musser and Carleton, 1993). We follow the convention of retaining *Gunomys* within *Bandicota.* This does not mean that *bengalensis,* the type species of *Gunomys,* is not distinctive. It is and can be diagnosed by discrete traits, some not appreciated by earlier taxonomists. In a later section we will discuss the significance of the distinctions between *Gunomys* and *Bandicota* as well as their relationship with *Nesokia* and other murine genera.

Bandicota bengalensis

Arvicola bengalensis Gray 1835 (*in* 1830–1835): pl. 21.
Mus kok Gray 1837: 585.
Mus (*Neotoma*) *providens* Elliot 1839: 209.
Mus dubius Kelaart 1850: 217.
Mus daccaensis Tytler 1854: 173.
Mus tarayensis Hodgson, *in* Horsfield 1855: 112.
Mus plurimammis Hodgson, *in* Horsfield 1855: 112.
Mus morungensis Hodgson, in Horsfield 1855: 112.
Mus (*Nesokia*) *blythianus* Anderson 1878: 227.
Mus (*Nesokia*) *barclayanus* Anderson 1878: 229.
Nesokia gracilis Nehring 1902: 116.
Gunomys varius Thomas 1907: 204.
Gunomys varillus Thomas 1907: 205.
Gunomys wardi Wroughton 1908: 744.
Gunomys lordi Wroughton 1908: 745.
Gunomys sindicus Wroughton 1908: 746.
Gunomys bengalensis sundavensis Kloss 1921: 116.
Gunomys kok insularis Phillips 1936: 95.

GEOGRAPHIC DISTRIBUTION: The probable natural range extends from north and southeast Pakistan (the Punjab and Sind, respectively) through India (including lowland Kashmir and Assam), Sri Lanka, the southern lowlands of Nepal, and Bangladesh east to Burma (see fig. 1 for the Burmese portion of the range). Outside this region the species was probably introduced to Pinang (Penang) island off the west coast of the Malay Peninsula (Chasen, 1936), The Acaeh region of northern Sumatra, eastern Java (Kloss, 1921; Musser and Newcomb, 1983: 525), and Saudi Arabia (Kock et al., 1990). Corbet and Hill (1992: 354) noted a report of *B. bengalensis* from Patta Island in Kenya but were uncertain if the population was established.

Our delimitation of the possible natural range is speculative. We don't have information to accurately reconstruct what may have been the original distribution of *B. bengalensis* before the modification of pristine habitats by humans. Undoubtedly parts of its distribution in India and adjacent regions represents an expansion over the original range facilitated by unintentional human activities.

TAXONOMIC NOTES: No careful systematic study of morphological and geographic variation among all the samples now identified as *B. bengalensis* is available. Ellerman (1941) listed *Bandicota bengalensis* in his compendium on families and genera of living rodents, putting it in his "*bengalensis* Group," in which the subspecies *sundavensis, varillus, kok, insularis, wardi, sindicus, varius, and lordi* were regarded as valid. The taxon *gracilis* from Sri Lanka was listed as a separate species in its own "*gracilis* Group." Later, Ellerman and Morrison-Scott (1951) and Ellerman (1961) incorporated *gracilis* as a subspecies of *B. bengalensis.* The studies upon which these results were based lacked analytical rigor with a result that the subspecies were ambiguously defined.

Agrawal and Chakraborty (1976) attempted a taxonomic revision of *B. bengalensis,* based on variation in fur characteristics and

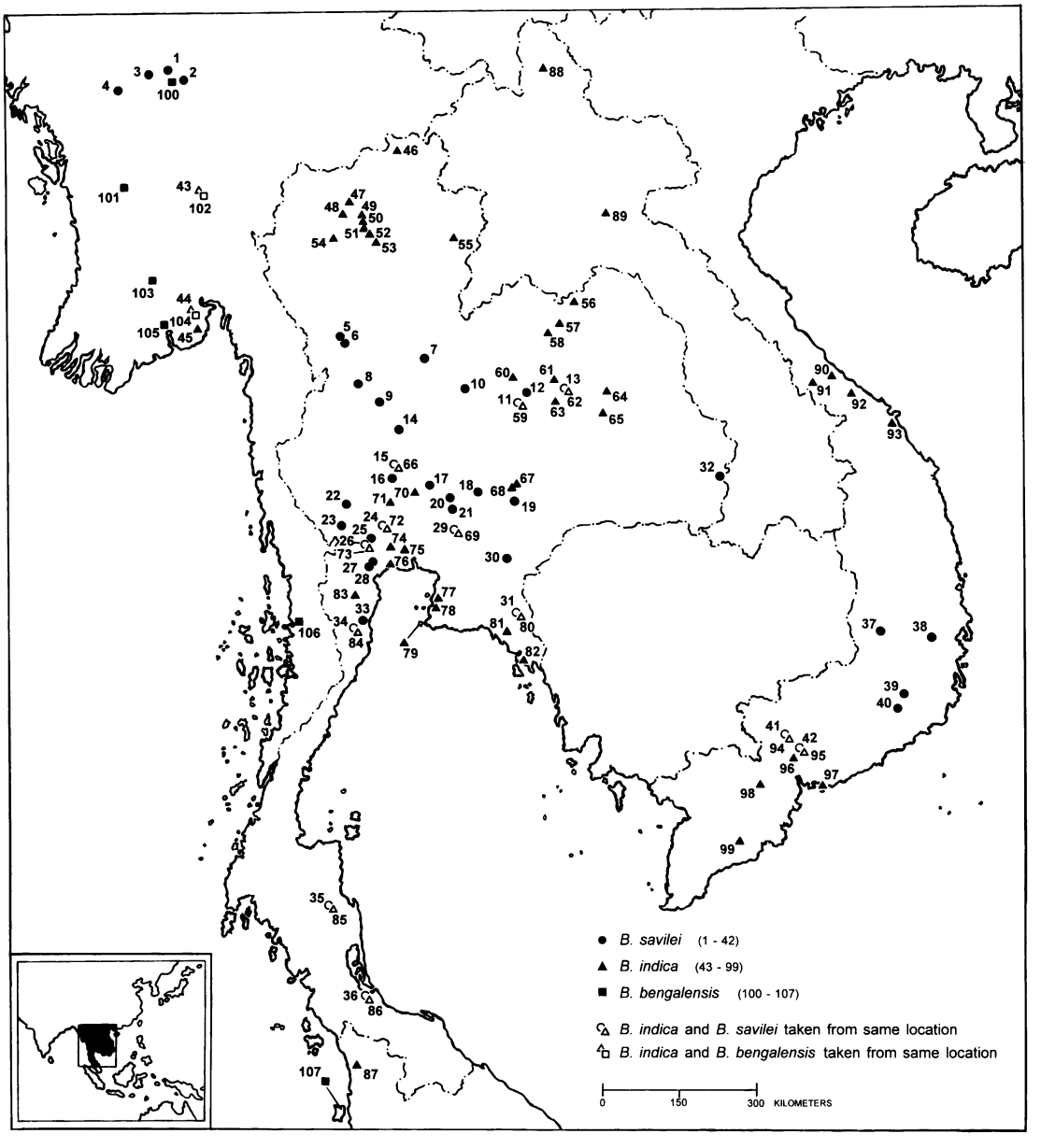


Fig. 1. Range of *Bandicota bengalensis, B. savilei,* and *B. indica* in Burma, Thailand, Laos, Vietnam, and northern Malay Peninsula. Number next to each symbol refers to each numbered locality and specimens (identified by institutional acronym and catalog number) collected at that place, which is listed in Appendix 2. The distribution shown here is based only on material we have examined; no literature records are represented. We focus on the entire known geographic range of *B. savilei* and the distributions of the other two species in the same region (*B. indica* and *B. bengalensis* are also found outside of the area). Both *B. savilei* and *B. indica* most certainly occur in Cambodia, Laos, northern Vietnam, and eastern Burma, areas that are blank on our map (the holotype of *hichensis,* for example is from northern Vietnam); we have simply not seen any specimens from those regions.

Note that *B. indica* has been collected together with either *B. bengalensis* or *B. savilei* at several places. The ranges of *B. savilei* and *B. bengalensis* are not sympatric but the species do occur close to each other in central Burma.

Fig. 2. Adult *Bandicota savilei* from Thailand.

measurements of museum skins, skulls, and teeth. Results of their analyses suggested that only three subspecies could be recognized: *B. b. bengalensis, B. b. wardi,* and *B. b. varius.* However, some of the geographic samples they used were small and there is no indication in the report that they compared specimens of approximately the same age. Corbet and Hill (1992: 354) validated the study by recognizing the three subspecies. But in the framework of the methodology used and uneven sample sizes, the conclusions presented by Agrawal and Chakraborty are equivocal and need to be tested by a more critical systematic review.

For example, Agrawal and Chakraborty recognized *B. b. wardi* based on samples from Kashmir and Himachal Pradesh because of their long and dense pelage. In an analysis of geographic variation between specimens from the Punjab in northern Pakistan and those from the Sind in the southern part of that country, Smiet et al. (1978) claimed the softness or harshness of the fur to vary seasonally. They also pointed out that the two populations differ significantly in length of tail. The latter result was substantiated by Lathiya and Akhtar (1981), who also discovered significant differences in means of some cranial and dental measurements between the samples from the Punjab and Sind. Again, however, it is difficult to evaluate the results presented in these two reports because the methods are unexplained and no indication is provided that comparisons among similar age groups were made.

Bandicota savilei

Bandicota savilei Thomas 1916: 641.
Bandicota savilei curtata Thomas 1929: 205.
Bandicota bengalensis hichensis Dao 1961: 305.
Bandicota bangchakensis Boonsong and Felten 1989: 202.
Bandicota bengalensis giaraiensis Dao and Cao 1990: 235.

GEOGRAPHIC DISTRIBUTION: Recorded from Central Burma, Thailand (throughout the country north of the Isthmus of Kra and south of the Isthmus to the southern end of peninsular Thailand), and southern and northern Vietnam (the northern record is based on the holotype of *hichensis* Dao, 1961, a specimen we have not seen); the entire distribution of the species as resolved from our study of specimens is shown in figure 1. The actual extent of *B. savilei*'s range is unknown; the species probably also occurs in Laos, Cam-

Fig. 3. Adult *Bandicota indica* collected in Thailand.

bodia, and parts of southern China bordering the countries from Burma to Vietman.

How much of the range of *B. savilei*—as documented by specimens—is the result of expansion into areas deforested by humans and converted to agricultural or fallow fields is also unknown. If grassland ecosystems were its original habitat, *Bandicota savilei* has made a successful shift to cultivated crops and scrubby fallow fields—grassland counterparts—and conceivably could have spread to farming regions that were once covered with forest. In Thailand, for example, the specimens were reported by Boonsong and Felten (1989; under the names "*varius,*" "*bengalensis,*" and "*bangchakensis*") were all taken from rice fields. Marshall (1977: 427) found that a "wild, indigenous population lives in grass beneath teak forest in Tak Province" but that everywhere else the species "is known from recently cleared foothill areas where it lives in cornfields and the tall grass in and around vegetable gardens and orchards."

Examples of *Bandicota savilei* and the much larger *B. indica* have been collected at the same place in Thailand and Vietnam (fig. 1; Marshall, 1977) but *B. savilei* has yet to be obtained together with *B. bengalensis.* The closest they are recorded is in central Burma (fig. 1) where specimens of *B. savilei* were taken in fields at Myingyan and examples of *B. bengalensis* were caught in houses 30 km away at Taungtha (Marshall, in letter).

TAXONOMIC NOTES: Named and contrasted with other forms of *Bandicota* by Thomas in 1916, *B. savilei* was originally known only from the type locality, Mount Popa at about 2500 ft in central Burma. Thomas compared the new species with the larger *B. nemorivaga,* which was the name he used for what is now called *B. indica* (Musser and Carleton, 1993: 579). Thomas noted that *savilei* could easily be separated from other *Bandicota* by its smaller size and that, although in this respect it resembled forms of *Gunomys* (a category he erected to contain the small-bodied *bengalensis* and its relatives [Thomas, 1907]), its cranial morphology ("less fossorial type than those of *Gunomys,* as indicated by the longer nasals and normally set incisors . . . as compared with the shortened nasals and forwardly projected incisors of the latter genus,"

p. 642) closely resembled that of the larger forms of *Bandicota.* By the late 1920s, the species was collected from Thailand and morphology of the specimens differed sufficiently from those in the type series for Thomas (1929) to describe them as a new subspecies, *B. savilei curtata.*

The species status of *savilei* was preserved until the 1940s when it was relegated to *B. indica* as a subspecies and its morphological and geographical distinctness lost. In his checklist of families and genera of living rodents, Ellerman (1941: 279) followed Thomas and recognized *B. savilei* as a member of his "*indica* Group," but by 1949 thought his classification of *Bandicota* to be "oversplit" and arranged *savilei* as a subspecies of *B. indica,* an allocation also followed in later reports (Ellerman, 1961: 844; Ellerman and Morrison-Scott, 1951: 618). To Ellerman, *savilei* simply represented the small end of a spectrum in body size that culminated in such forms as *malabarica* and *gigantea,* which were the largest forms of *Bandicota* that had been described.

Ellerman's treatises were so pervasive that the uniqueness of *savilei* became obscured in the literature as did the identifications of *Bandicota* from Thailand. Harrison (1956), for example, in reporting on samples of *Bandicota,* identified series of *B. indica* and *B. bengalensis* from Thailand, noting that the latter had not been recorded there. Measurements of the Thai *bengalensis* listed in his table, however, are clearly those of *B. savilei* and not *B. bengalensis.*

One mammalogist working with Indomalayan faunas disagreed with Ellerman but his work was unpublished and reference to it obscure. Hoogstraal and Kohls (1965: 466) described a new species of tick obtained from hosts they identified as *Bandicota* sp. collected in Taiwan, Thailand, and Burma. Noting that "taxonomy of the genus *Bandicota* is unsettled," they cited a letter written by Dr. David H. Johnson (formly Curator of Mammals at the National Museum of Natural History in Washington, DC) who apparently had been asked to identify the hosts. Johnson remarked that some of the Thai specimens were *B. savilei curtata* and noted that "contrary to some of the current literature led by Ellerman and Morrison-Scott's 'Checklist of Palaearctic and Indian Mammals,' *B. savilei* is a quite distinct species from the common large bandicoot, *Bandicota indica,* which also occurs in Thailand."

Johnson's astute observations were verified independently by Musser, working with museum specimens, and Dr. Joe T. Marshall Jr., who collected *Bandicota* in Thailand as part of a study on the rats and mice native to that country. Marshall, with his colleagues, presented their results in the 1970s (Markvong et al., 1973; Marshall, 1977) and from that time until now *Bandicota savilei* has regained and maintained its identity as a species native to Indochina (Musser and Carleton, 1993; Corbet and Hill, 1992).

We now appreciate *B. savilei* as a component of the Indochinese fauna but we know little else about it, aside from the general ecological observations offered by Marshall (1977) and gross characteristics of its chromosomal morphology (see references in Rickart and Musser, 1993: 17). Studies seeking to determine the significance of variation in pelage, skeletal, dental, chromosomal, and biochemical features associated with geography have yet to be done. Without results from such an endeavor it is difficult to evaluate the relevance of three of the four scientific names that have been proposed in the literature, either intentionally or unwittingly, for different geographic samples of *B. savilei.*

Two of the names, *curtata* and *bangchakensis,* apply to examples of *B. savilei* from Thailand. Described as a subspecies of *B. savilei* by Thomas (1929: 205), and based on a few specimens from west-central Thailand, *curtata* was characterized by shorter tail and paler incisors than typical *savilei* from central Burma. Judging from the material of *B. savilei* we have studied, incisor pigmentation is geographically variable and undiagnostic, but average size may discriminate geographic entities. Means of the external and cranial measurements reflecting overall size in samples from Thailand average smaller than those from the few specimens available to us from Burma (table 2). The significance of this observation will have to be tested by contrasting larger samples from Burma with additional series from east of there in which there are more critical comparisons between groups of the same age and sex. Our grossly constituted

samples, in which sexes and ages from young adult to old individuals were combined, precludes such critical analyses to detect any possibly significant geographic variation.

We will justify the identity of *bangchakensis* with *B. savilei* in another section of our report.

The other two names, *hichensis* and *giaraiensis,* are based on samples from Vietnam. Corbet and Hill (1992: 354) listed each of them as a subspecies of *B. bengalensis,* but both names apply to samples of *B. savilei* (Musser and Carleton, 1993: 579). Measurement values alone support these allocations. Dao (1961: 305) described *hichensis,* represented by the holotype from northern Vietnam, as a subspecies of *B. bengalensis.* However, some of Dao's values for measurements reflecting size—lengths of head and body (215 mm), tail (175 mm), hind foot (43 mm), and nasals (15.4 mm)—fall within the range of variation we recorded in samples of *B. savilei* from Thailand and are outside the ranges in samples of *B. bengalensis,* which is a smaller animal (table 2). Values for the diagnostic measurements of the southern Vietnamese *giaraiensis,* named by Dao and Cao (1990: 235) as a subspecies of *B. bengalensis* and based on several specimens, also point to *B. savilei* and not *B. bengalensis.* For example, their values for lengths of nasals (14.0 and 15.6 mm) and molar row (9.0, 9.4, and 9.6) are within the range of variation associated with *B. savilei* rather than the smaller *B. bengalensis* (tables 2 and 3).

Geographic distribution also supports the assignment of *hichensis* and *giaraiensis* to *B. savilei* rather than to *B. bengalensis.* Despite its recorded occurrences on eastern Java, northern Sumatra, and Pinang Island off the west coast of the Malay Peninsula, which probably reflect introductions, *B. bengalensis* is apparently not a member of the indigenous Indochinese or Sundaic faunas. The bulk of its range lies to the west of Thailand and Vietnam (Corbet and Hill, 1992: 353; Musser and Carleton, 1993: 578) and central Burma represents its easternmost extension into Indochina (fig. 1). Although some museum specimens from Indochina have been identified as *B. bengalensis,* and its occurrence in that region is documented in the literature, all that material has, after our examinations, turned out to be either young examples of *B. indica* or samples of *B. savilei*; in all the institutional collections in which we worked, we have not seen specimens of *B. bengalensis* taken in Indochina east of about central and peninsular Burma.

The few specimens of *savilei* from Vietnam we have seen differ from Thai samples in that the bullae are slightly smaller, and the posterior margins of the incisive foramina are constricted (resembling the shape in *B. bengalensis,* rather than parallel or only slightly constricted as in most Thai *savilei,* but the difference is subtle).

Bandicota indica

Mus indicus Bechstein 1800: 497.
Mus bandicota Bechstein 1800: 498.
Mus malabaricus Shaw 1801: 54.
Mus perchal Shaw 1801: 55.
Mus giganteus Hardwicke 1804: 306.
Mus setifer Horsfield 1824.
Mus (*Rattus*) *nemorivagus* Hodgson 1836: 234.
Mus macropus Hodgson 1845: 268.
Mus (*Nesokia*) *elliotanus* Anderson 1878: 231.
Bandicota mordax Thomas 1916: 642.
Bandicota siamensis Kloss 1919: 382
Rattus eloquens Kishida 1926: 144.
Bandicota jabouilei Thomas 1927: 54.
Nesokia nemorivaga taiwanus Tokuda 1941: 74.
Bandicota indica sonlaensis Dao 1972 or 1975.

GEOGRAPHIC DISTRIBUTION: The bulk of the range extends from India, Sri Lanka, Bangladesh, lowlands of Nepal through Burma, southern China (Guangdong, Gangxi, Fujian, Yunnan, Guizhou, Sichuan, Jiangxi; see Qin, 1985), Hong Kong, Thailand, Laos, and Vietnam; also recorded from the Kedah and Perlis regions of the Malay Peninsula (Harrison, 1956; Marshall, 1977), Taiwan, and Java. Occurrences in Java and on the Malay Peninsula probably represent introductions (Musser and Newcomb, 1983), as does possibly the population on Taiwan (Thomas, 1916: 642). Corbet and Hill (1992: 352) included Pakistan within the range of *B. indica* but we have not seen any Pakistan specimens and Roberts (1977) did not record it from that country.

Bandicota indica, like the other two species, may have expanded its range beyond original boundaries. This species is regularly collected in habitats modified from pristine

TABLE 1
Contrasts among Adult *Bandicota* in Traits Associated with Head and Body, Tail, Hind Feet, Fur Color and Texture[a]

	B. bengalensis	*B. savilei*	*B. indica*
Body size	Smallest of the three species (estimated by length of head and body or greatest length of skull; table 2)	Averages larger than *B. bengalensis,* much smaller than *B. indica* (table 2)	Much larger than other two species (table 2)
Upperparts	Variegated dark brownish gray (due to mixture of buff and dark brown overhairs) with moderately long guard hairs over back and rump; fur harsh and short	Similar brown and buff variegation as in *B. bengalensis* but overall paler, brown to brownish gray instead of dark brown; pelage softer than in other two species	Blackish brown from head to rump, dark brownish gray along sides; black guard hairs relatively longer, forming mantle over rump; entire dorsum appears blackish contrasted with other two species
Underparts	Dark gray in most specimens	Similar to *B. bengalensis* but paler (pale grayish buff)	Darker (dark brownish gray) than other two species
Tail	Shorter than head and body (table 2), 10–12 scales/cm, monocolor brown	Similar to *B. bengalensis* in proportion relative to head and body (table 2; fig. 4) and in scalation; paler in some individuals (brown to grayish brown)	Actually shorter than head and body but significantly longer relative to body compared with *B. bengalensis* and *B. savilei* (table 2; fig. 4); fewer scales (8/cm is usual); tone darker
Feet	Brown or brownish gray	Similar to *B. bengalensis*	Significantly longer relative to head and body than in other two species (fig. 4); much darker (dark brown to blackish)
Mammae	10-20 (one pectoral, 1 postaxillary, 1 abdominal, and 2 inguinal pairs is pattern of minimal number); higher counts due to additional postaxillary pair and variation in number of abdominal mammae (see text)	12 (1 pectoral pair, 2 postaxillary pairs, 1 abdominal pair, and 2 inguinal pairs); no variation from this number seen in our samples	12 (positions of each pair as in *B. savilei*); no variation from this number seen in our samples

[a] Contrasts are based on our sample of *B. bengalensis* from India, and series of *B. savilei* and *B. indica* collected in Thailand. Measurements and catalog numbers of these specimens are listed in table 2.

formations. For example, most of the specimens reported by Boonsong and Felten (1989: 209) were caught "in rice fields, a few in plots with grass, herbaceous vegetation and sweet potatoes." Marshall (1977: 429) did not find *B. indica* "in any purely natural habitat in Thailand."

TAXONOMIC NOTES: In addition to *Bandicota savilei,* Ellerman's (1941) conception of the large-bodied bandicoots consisted of three species he placed in an *indica* group (*B. indica, B. nemorivaga,* and *B. siamensis*) and two species contained in the *gigantea* group (*B. gigantea* and *B. malabarica*). By 1961 Ellerman recognized only one species, *B. indica,* an arrangement previously formulated by Ellerman and Morrison-Scott (1951) and one accepted today by most authors (Corbet and Hill, 1992, for example).

Whether all the named forms represent just one or more than one species has yet to be determined. No critical study of morphology related to sex, age, and geography in all available samples within a systematic context has ever been made. The few published attempts have been based on small regional samples

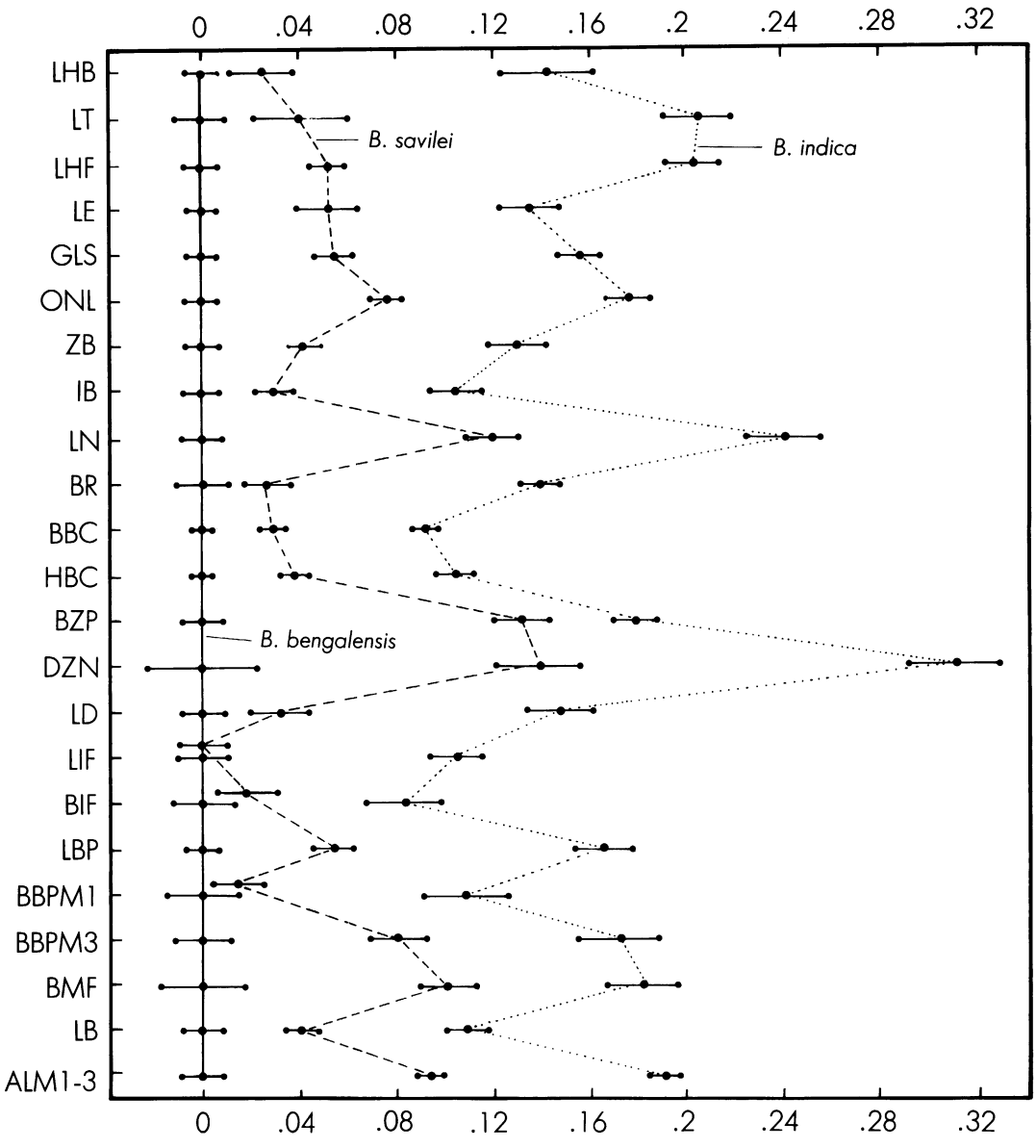


Fig. 4. Ratio diagram indicating some proportional relationships among species of *Bandicota*. Dimensions are compared among samples of *Bandicota bengalensis* (the standard) from India, *B. savilei* from Burma and Thailand, and *B. indica* from Thailand and Vietnam. For each measurement, the absolute value of the mean, and plus or minus two standard errors of the mean, were converted to logarithms. For each dimension, the logarithm of the mean of the standard (*B. bengalensis*) was subtracted from the logarithm of the mean of each sample to be compared with the standard, and the logarithms of plus or minus two standard errors of the mean of the standard were subtracted from the logarithms of plus or minus two standard errors of the mean of each comparative sample. Measurements larger than the standard are represented by positive values, those smaller by negative values. In each sample, the solid or dashed lines connect the means of measurements, the horizontal bars represent plus or minus two standard errors of the mean. A sample with the same proportions as the standard will be represented by mean values on a line parallel to that of the standard regardless of absolute size (for example, lengths of hind foot, ear, and skull of *B. savilei* as compared with the standard, *B. bengalensis*). Also, if values for the samples being compared with the standard are similar in absolute size, they will be close together on the diagram. If proportions between any of the measured dimensions are similar, the positions of their points relative to each other on the horizontal scale will be similar. Data are derived from values for mean, standard deviation, and sample size of variates listed in table 2.

TABLE 2

Comparisons of Measurements (mm) Among Selected Samples of the Reference Species of *Bandicota*

(Mean ± SD, range [in parentheses], and number of specimens are listed for each measurement. Sexes are combined. Samples consist of a range from young to old adults, identified by institutional acronyms and catalog numbers in the footnotes.)

	B. bengalensis[a]	*B. savilei*[b]		*B. indica*[c]
	West Bengal, India	Burma	Thailand	Thailand and Vietnam
LHB	185.1 ± 9.70 (161–208) 39	229.0 ± 9.25 (216–240) 7	194.8 ± 16.60 (145–225) 33	255.8 ± 30.55 (188–328) 32
LT	143.3 ± 9.70 (112–163) 35	209.9 ± 16.20 (189–230) 7	156.4 ± 18.75 (75–178) 32	229.7 ± 21.80 (190–280) 32
LHF	33.3 ± 1.80 (27–38) 39	41.7 ± 1.65 (39–44) 7	37.4 ± 1.70 (33–40) 33	53.0 ± 3.60 (46–60) 33
LE	21.8 ± 1.00 (20–24) 39	26.2 ± 0.65 (25–28) 7	24.5 ± 2.00 (20–30) 33	29.7 ± 2.15 (25–33) 28
GLS	39.8 ± 1.59 (36.0–43.9) 37	49.1 ± 1.20 (46.7–51.6) 7	44.9 ± 1.96 (41.8–50.1) 29	56.8 ± 3.11 (48.6–63.6) 34
ONL	37.8 ± 1.56 (33.4–41.3) 37	48.9 ± 1.13 (46.5–51.5) 7	44.9 ± 1.88 (42.0–47.8) 31	56.6 ± 3.30 (49.0–64.2) 30
ZB	22.4 ± 0.90 (20.6–25.2) 37	27.0 ± 1.05 (25.3–28.3) 5	24.6 ± 1.04 (22.4–26.5) 31	30.2 ± 2.09 (26.1–33.6) 32
IB	6.0 ± 0.31 (5.3–6.6) 39	6.7 ± 0.31 (6.3–7.1) 7	6.4 ± 0.28 (5.8–6.9) 33	7.6 ± 0.48 (6.7–8.7) 34
LN	11.8 ± 0.70 (9.8–13.3) 38	18.2 ± 0.78 (16.7–18.5) 7	15.5 ± 0.98 (13.8–17.6) 32	20.5 ± 1.96 (17.0–24.3) 32
BR	8.5 ± 0.61 (7.3–9.9) 39	9.7 ± 0.56 (8.8–10.6) 7	9.0 ± 0.58 (8.1–10.2) 32	11.7 ± 0.61 (9.7–13.5) 35
BBC	16.4 ± 0.48 (15.2–17.5) 39	18.0 ± 0.41 (17.3–18.7) 7	17.5 ± 0.46 (16.6–18.3) 33	20.2 ± 0.64 (18.7–21.4) 35
HBC	12.3 ± 0.44 (11.1–13.0) 39	14.7 ± 0.38 (13.7–15.7) 6	13.4 ± 0.51 (12.3–14.4) 33	15.6 ± 0.81 (13.9–17.6) 33
BZP	5.1 ± 0.30 (4.5–5.6) 38	7.5 ± 0.46 (6.1–8.0) 7	6.9 ± 0.52 (6.2–7.9) 33	7.7 ± 0.48 (6.6–8.9) 35
DZN	2.4 ± 0.40 (1.6–3.1) 38	—	3.3 ± 0.34 (2.5–4.0) 31	4.9 ± 0.63 (3.5–6.5) 35
LD	12.2 ± 0.81 (10.5–13.8) 38	15.0 ± 0.54 (13.6–16.1) 7	13.1 ± 1.04 (11.5–15.5) 33	17.1 ± 1.46 (14.6–20.1) 35
LIF	8.1 ± 0.46 (7.0–9.3) 29	8.7 ± 0.28 (8.1–9.3) 7	8.1 ± 0.53 (7.3–9.5) 33	10.3 ± 0.70 (8.8–11.5) 35
BIF	2.4 ± 0.23 (1.9–2.8) 39	2.8 ± 0.23 (2.5–3.2) 7	2.5 ± 0.20 (2.1–3.0) 33	2.9 ± 0.29 (2.6–3.5) 35
LBP	8.4 ± 0.37 (7.6–9.4) 39	10.3 ± 0.39 (9.8–11.3) 7	9.5 ± 0.49 (8.6–10.5) 33	12.3 ± 0.96 (10.7–14.5) 35
BBPM1	3.2 ± 0.33 (2.3–3.6) 39	3.9 ± 0.16 (3.4–4.2) 7	3.3 ± 0.22 (3.1–4.1) 33	4.1 ± 0.48 (2.8–5.0) 35
BBPM3	3.9 ± 0.31 (3.3–4.8) 39	4.8 ± 0.22 (4.5–5.0) 7	4.7 ± 0.35 (4.0–5.4) 33	5.8 ± 0.64 (4.2–6.9) 35

TABLE 2—(*Continued*)

	B. bengalensis[a] West Bengal, India	*B. savilei*[b] Burma	*B. savilei*[b] Thailand	*B. indica*[c] Thailand and Vietnam
BMF	2.3 ± 0.30 (1.8–3.0) 38	2.9 ± 0.35 (2.3–3.2) 4	2.9 ± 0.20 (2.6–3.4) 35	3.5 ± 0.34 (2.7–4.2) 35
LB	8.1 ± 0.44 (7.3–9.0) 38	9.0 ± 0.29 (8.6–9.3) 7	8.9 ± 0.34 (8.1–9.5) 33	10.4 ± 0.61 (9.3–12.2) 34
ALM1-3	7.2 ± 0.39 (6.6–8.3) 39	9.4 ± 0.37 (8.8–10.0) 7	9.2 ± 0.29 (8.6–9.7) 33	11.5 ± 0.43 (10.7–12.4) 35

[a] AMNH 215639–215641, 215643–215677, 215703.

[b] BURMA: AMNH 163695; BMNH 14.7.19.211–14.7.19.216.

THAILAND: AMNH 239619–239623; BMNH 28.5.3.2; USNM 253590, 253599, 533935–533937.

[c] THAILAND: AMNH 167929–167932, 239625–239628; USNM 260636, 294953, 296547, 296548, 297165, 300166, 300165, 355313, 355316–355318, 355320, 315322, 315325.

VIETNAM: USNM 355550, 355551, 356817, 356565–356569, 356927, 356928, 357567–357570.

and were uncritical in methodology and analyses. One example is the report by Tiwari et al. (1971) on a collection of mammals from Western Ghats (India) which, using only on a few specimens, reinstated *malabarica* as a distinctive subspecies of *B. indica* based on its larger body size; Ellerman and Morrison-Scott (1951) and Ellerman (1961) had included *malabarica* as a synonym of *B. i. indica.* Another is the account by Pradhan et al (1989) who recognized *B. gigantea* as occurring in India and Burma and distinguished it from *B. indica,* which they claimed is sympatric with *B. gigantea,* based on larger body size.

With few exceptions (Kock et al., 1990, for example), *gigantea* has not been recognized as a species of *Bandicota* (Corbet and Hill, 1992; Musser and Carleton, 1993). Pradhan et al. (1989) did study large series but gave no indication that they separated their samples into age groups which they then contrasted. Furthermore, Corbet and Hill (1990: 352) noted that some of the reputed cranial differences reported by Pradhan et al. between means from the two kinds were not significant and that the "authors did not demonstrate that these characters showed a bimodal distribution generally or at any one locality, and the distinction remains dubious. . . . If there is a specific difference, it is more likely to be between two allopatric species: *B. indica s.s.* in peninsular India and Sri Lanka [skull greater than 58 mm, nasals greater than 21 mm] and *B. nemorivaga* in Bengal, Nepal, Assam and eastwards [skull less than 58 m, nasals less than 21 mm]."

This last suggestion about species boundaries within the *indica* group is not supported by our data. Among 30 or more specimens from Thailand and Vietnam that we measured, the range in occipitonasal length reaches 64.2 mm, that in length of nasals extends to 24.3 mm (table 2). If more than one species is represented among the samples now identified as *B. indica,* it has not been demonstrated in the literature and can only be revealed by critical systematic revisionary studies that compare large samples composed of similar sex and relatively similar ages.

Discrimination Among Species of *Bandicota*

Because we are primarily interested in the Thai bandicoots, our comparisons are based on those portions of the reference samples of *B. indica* and *B. savilei* that are from Thailand. The comparative sample of *Bandicota bengalensis* we employ here comes from West Bengal, India. We have relied on this sample because the species does not occur in Thailand. *Bandicota bengalensis* is found closer to Thailand in central Burma but we have few specimens at hand for comparison.

Contrasts among the three species in features associated with size and proportions of head and body, tail, and hind feet, as well as

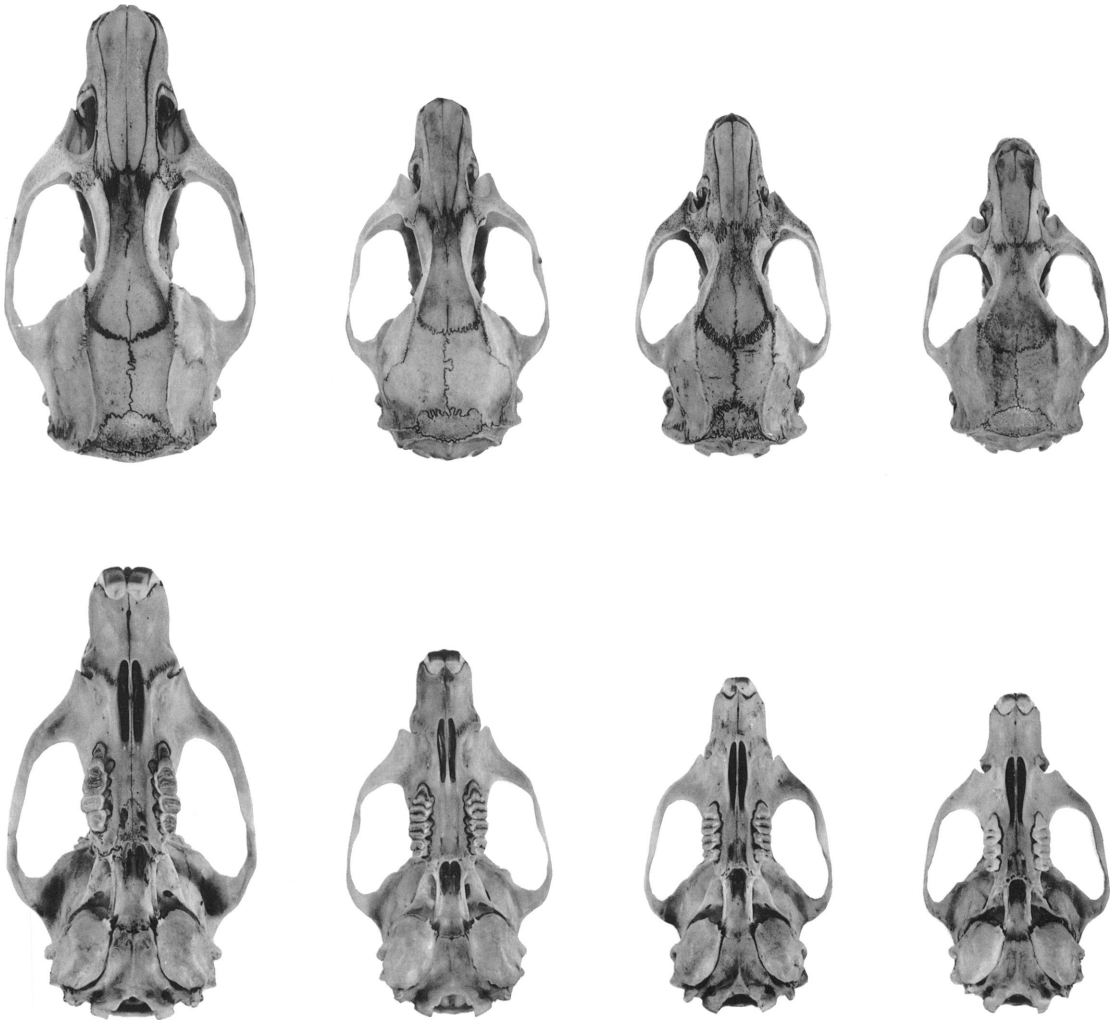


Fig. 5. Crania of adult *Bandicota* (×1) as viewed from dorsal (top row) and ventral perspectives (bottom row). From left to right: *B. indica* (AMNH 239628), Thailand; *B. savilei* (AMNH 241645), Thailand; *B. bengalensis* (AMNH 267632), central Burma; and *B. bengalensis* (AMNH 215674), eastern India. Among traits distinguishing species that can be seen here is size; the differences illustrated are typical of the samples we studied. *Bandicota indica* has a much larger cranium than any of the other species. *Bandicota bengalensis,* from lowlands of the Indian subcontinent, has the smallest skull, the individuals from central Burma average larger. Crania of *B. savilei* are somewhat larger than those of *B. bengalensis.*

texture and coloration of fur, are summarized in table 1. Thai *savilei* (fig. 2) and *indica* (fig. 3) are easily distinguished from each other by the larger body size of the latter, its darker fur and feet, and its longer tail and hind feet relative to head and body length (fig. 4). Contrasts in body size and fur color between *B. savilei* and *B. bengalensis,* however, are not as marked and it is not surprising that samples of *B. savilei* from Thailand were so often misidentified as *B. bengalensis.*

Other characters form a different pattern of contrasts among the three species. In conformation of the cranium and mandible, pro-

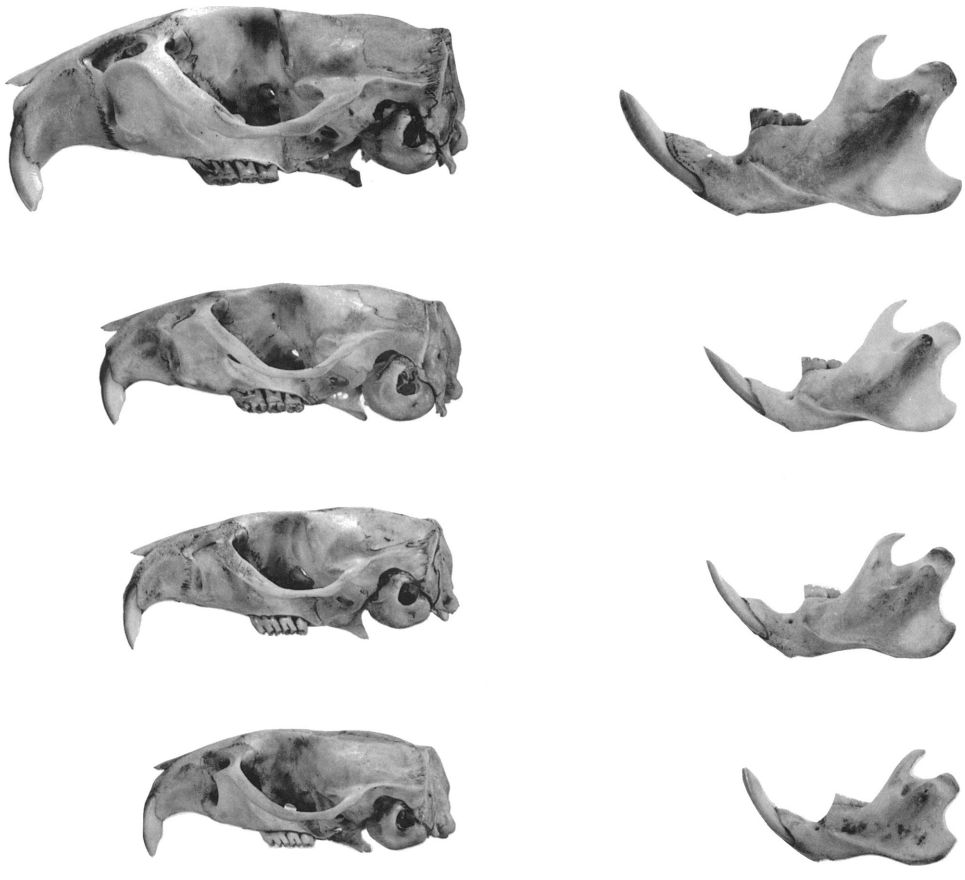


Fig. 6. Lateral views (× 1) of crania and left dentaries from the specimens in figure 5. From top to bottom: *B. indica, B. savilei, B. bengalensis* (Burma), and *B. bengalensis* (India).

portions of most dimensions, and dental traits, *B. savilei* and *B. indica* are very similar and differ primarily in absolute size (table 2; figs. 5 and 6) and a few proportions. *Bandicota indica,* for example, has a much deeper zygomatic notch relative to breadth of zygomatic plate and a significantly wider rostrum relative to breadth of braincase (fig. 4); *B. savilei* has a wider zygomatic plate relative to occipitonasal length compared to these proportions in *B. indica* (fig. 4). *Bandicota bengalensis* is unlike the other two species not only in proportions but in the other characters discussed below.

Number of mammae is an external feature that can be used to separate most specimens of *B. bengalensis* from samples of *B. savilei,* as well as *B. indica* (table 1). Females of the latter two species have 12 mammae. The count varies from 10 to 20 in *B. bengalensis,* but the range from 14 to 17 is most frequent in samples (Walton et al., 1978; Begg et al., 1981; Niethammer, 1984).

Chromosomal complement of *B. bengalensis* differs from that of the other two species in diploid and fundamental numbers (see references in Rickart and Musser, 1993, and Gadi and Sharma, 1983). Matthey (1956) earlier had presented the karyotypes of *B. bengalensis* and *B. indica* and was so impressed with the differences between them that he concluded the species could not be related; the few similarities present reflected convergence. Gadi and Sharma (1983: 34), however, demonstrated "a remarkable similarity in G-band patterns" in the chromo-

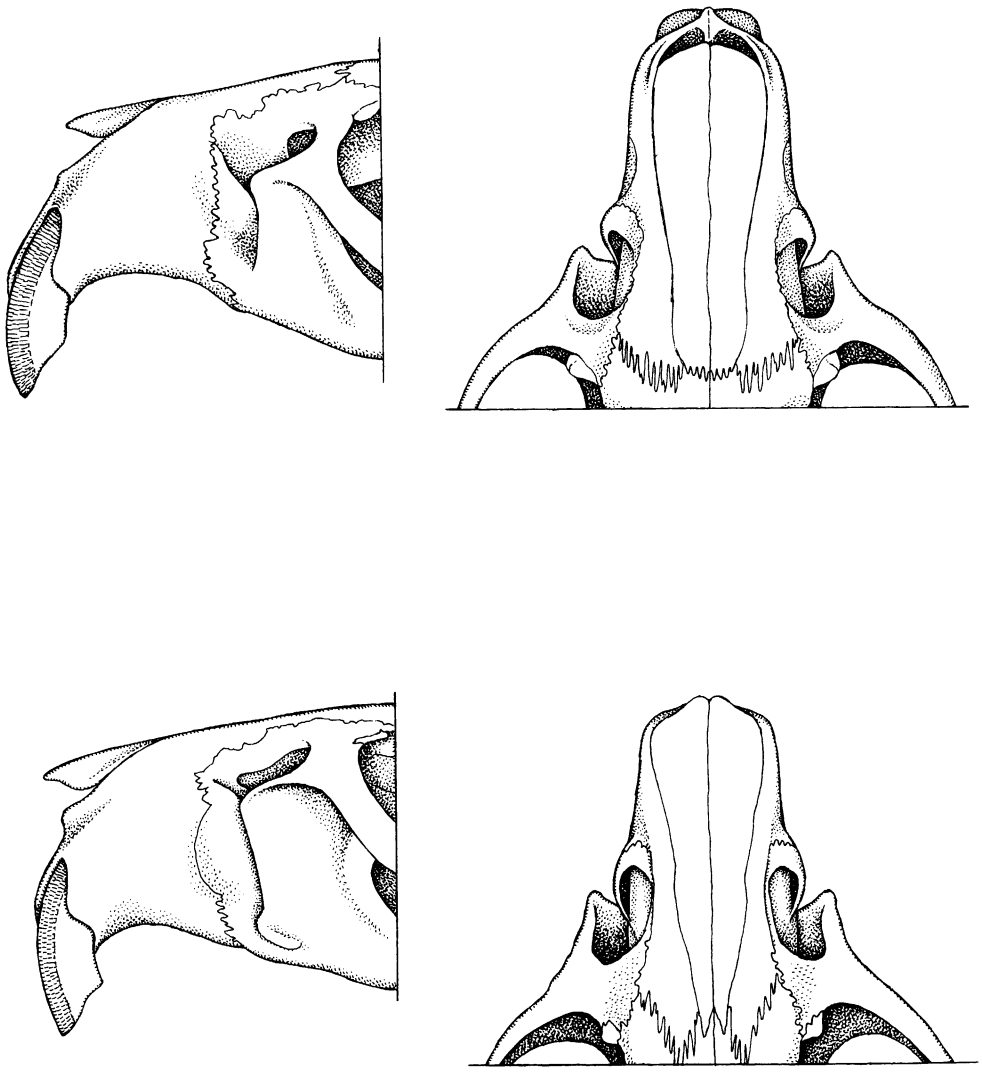


Fig. 7. Rostral views of adult *Bandicota*. **Top**: *B. bengalensis* (AMNH 215674). **Bottom**: *B. savilei* (AMNH 241645). The short nasals and procumbent incisors of *B. bengalensis* contrast with the longer nasals and opisthodont (recurved) incisors of *B. savilei*. In dorsal perspective (right side of each set), the nasals of *B. bengalensis* are shorter than the premaxillaries and do not conceal the nasal opening or incisors. The relatively longer nasals of *B. savilei* conceal the nasal orifice and the incisors. The conformation of the incisors and rostrum of *B. indica* resembles that in *B. savilei*.

somal complements of the two species. They also provided an excellent discussion of the chromosomal variation recorded in all three species of *Bandicota* and its significance for phylogenetic inferences.

Bandicota bengalensis has the smallest skull of the three species, much smaller than for *B. indica*, and somewhat smaller than that of *B. savilei* (table 2; figs. 5 and 6).

The two larger species of bandicoots are similar in most cranial and dental proportions but differ strikingly from *B. bengalensis* (fig. 4). For example, compared with the smaller bandicoot, both *B. indica* and *B. savi-*

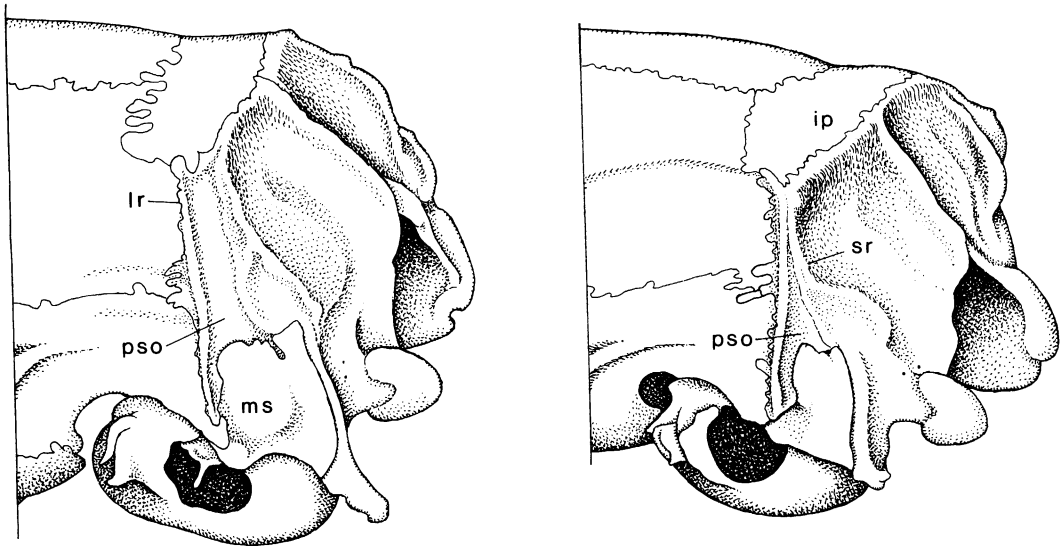


Fig. 8. Occipital views of adult *Bandicota.* **Left**: *B. savilei* (AMNH 241645). **Right**: *B. bengalensis* (AMNH 215674). In the latter species, the posterolateral surface of the supraoccipital (**pso**) is a narrow and short wedge because a supraoccipital ridge (**sr**) has fused with the dorsal third of the lambdoidal ridge (**lr**); the fusion extends nearly to the mastoid in some individuals). In *B. savilei,* the posterolateral surface is wide, extending from the dorsal margin of the mastoid (**ms**) to the posterolateral border of the interparietal (**ip**); there is a significant gap between the supraoccipital and lambdoidal ridges.

lei have (1) a longer occipitonasal length and longer nasals relative to greatest length of skull, (2) a narrower rostrum and wider zygomatic plate relative to greatest skull length, (3) a shorter diastema relative to occipitonasal length, (4) narrow and shorter incisive foramina relative to length of diastema, (5) shorter distance between first molars relative to length of bony palate, (6) smaller auditory bullae relative to greatest length of skull, (7) and longer maxillary tooth rows relative to length of bony palate and greatest length of skull. Other proportional differences can be seen in Figure 4.

One set of proportional differences reflects contrasts in rostral configuration between *B. bengalensis* and the other two species (figs. 5, 6, 7). In examples of *B. bengalensis,* the nasals are shorter than the premaxillaries so that the ventral rim of the nasal orifice and anterior margins of the incisors can be seen from dorsal perspective (seen clearly in fig. 7); occipitonasal length is shorter than greatest length of skull (table 2), remarkably shorter in some specimens. The nasals of *B. indica* and *B. savilei* are as long as the premaxillaries, completely form a roof over the nasal opening, and conceal the incisors; in these two species, with very few exceptions, the occipitonasal length is the same as greatest skull length (table 2); however, occipitonasal and nasal lengths are longer relative to overall skull length (fig. 4).

Coupled with the rostral difference are the positions of the upper incisors relative to the rostrum (fig. 7). Those of *B. bengalensis* are procumbent; the incisors of the other two species are usually opisthodont (recurved).

These contrasts in nasal length and configuration of upper incisors were described earlier by Thomas (1916) as trenchant differences that allied *savilei* with the larger bandicoot and separated them from *bengalensis,* which Thomas had placed in the genus *Gunomys.*

Although incisive foramina of *B. savilei* and *B. indica* are either the same absolute length or longer than in *B. bengalensis,* they are shorter relative to diastemal length (fig. 4). This proportional difference reflects the de-

Fig. 9. Occlusal views (×10) of right upper molar rows in three species of *Bandicota*. **Left**, *B. indica* (AMNH 101558), Java. **Middle**, *B. savilei* (AMNH 239621), Thailand. **Right**, *B. bengalensis* (AMNH 241644), eastern India. Arrows point to cusplike structure on each first and second molar that has been identified as a cusp t7 (Misonne, 1969: 116) but is probably not homologous to that cusp and is simply a wide ridge on the lingual margin of cusp t8. We cannot confidently identify a comparable structure on each third molar.

gree to which the incisive foramina penetrate the bony palate between first molars (fig. 5), another useful feature which can be used to separate skulls of *B. bengalensis* from those of the two other species. The penetration of the foramina are greatest in the small *B. bengalensis,* extending past the large anterior root to about the level of each small anterolingual root of each first upper molar. In the two species of larger *Bandicota,* the incisive foramina extend either to the front face of the large anterior root or only slightly beyond it, but not as far as the anterolingual root.

The shape of the incisive foramina has been mentioned in the literature as a trait useful in separating *B. bengalensis* from the other species of *Bandicota* (Kloss, 1921, for example). The posterior portions of the incisive foramina are constricted in most specimens of *B. bengalensis* but not most examples of the other two species. We found this trait to be variable; it is useful only if applied in combination with other discriminatory characters. The incisive foramina in specimens of *B. savilei* from Vietnam, for example, are constricted posteriorly and closely resemble the conformation of the foramina typical of *B. bengalensis.*

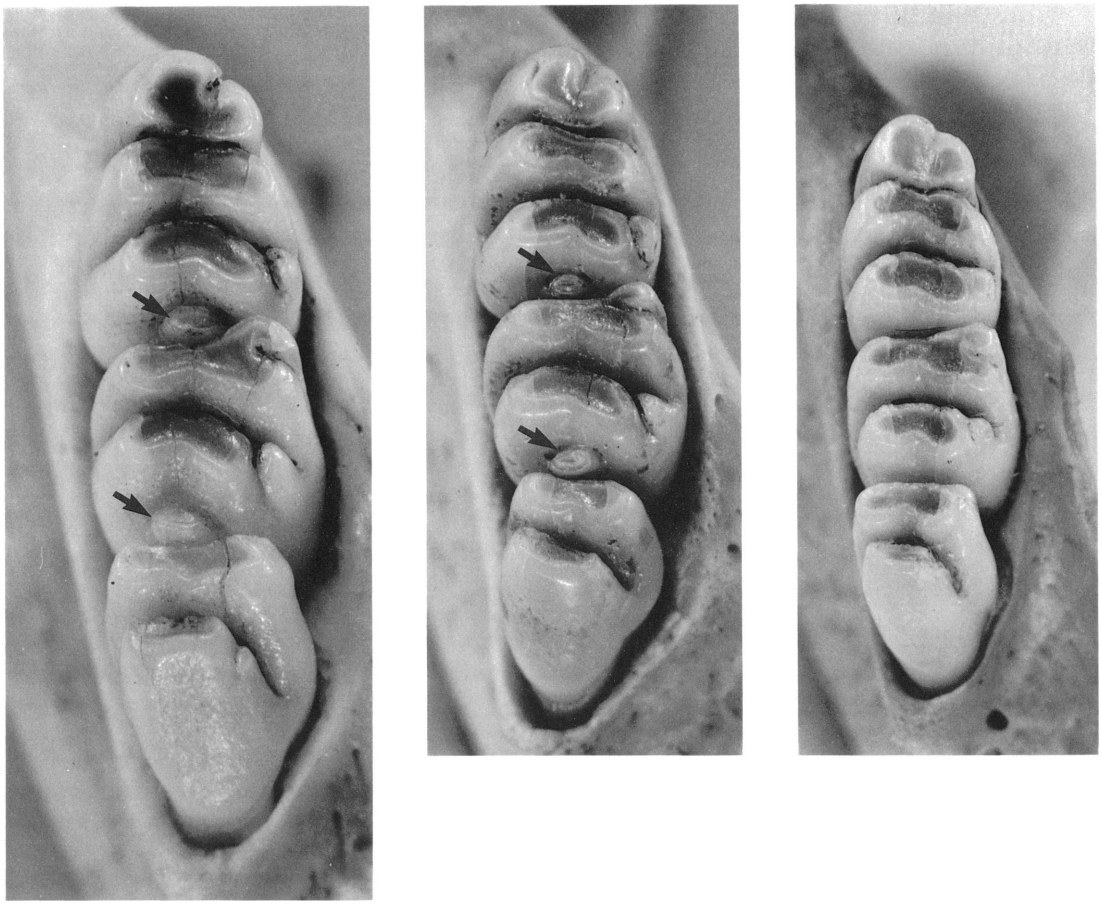


Fig. 10. Occlusal views (×10) of right lower molar rows from the same specimens of *Bandicota* portrayed in figure 9 on the opposite page. **Left**, *B. indica*; **middle**, *B. savilei*; **right**, *B. bengalensis*. Arrows identify posterior cingula on the first and second molars of *B. indica* and *B. savilei*; *B. bengalensis* does not have these cusps.

Specimens of *B. savilei* and *B. bengalensis* are often misidentified in the literature and in collections of museums, but the two are easily distinguished by the traits discussed above. The shape of another cranial area, the occipital region, also can be used to separate adults of *B. savilei* from those of *B. bengalensis* (fig. 8).

In *B. bengalensis*, the occiput forms a nearly vertical surface pressed against the braincase so that the back of the cranium seems truncated. This configuration exists because the posterolateral side of the supraoccipital (the area between the lambdoidal ridge in front of the mastoid and a supraoccipital ridge extending from the posterodorsal corner of the mastoid up to the posterolateral edge of the interparietal) has essentially disappeared beneath the posterior wall of the supraoccipital. The supraoccipital ridge is fused not only with the posterolateral border of the interparietal but also with the lambdoidal crest nearly all the way down to the top of the mastoid; the side of the occiput is represented only by a narrow wedge or sliver of bone above the mastoid.

The occiput is deeper (anterior-posterior) in specimens of *B. savilei* (fig. 8) and posterolateral surface of the supraoccipital is an elongate triangular area between lambdoidal ridge and supraoccipital ridges, an area extending from the entire dorsal margin of the

TABLE 3

Measurements (mm) of Alveolar Length of Maxillary Toothrow (ALM1-3) and Crown Breadth of First Upper Molar (CBM1) in the Three Reference Species of *Bandicota* from Southeast Asian Samples

(Mean ± SD and observed range [in parentheses] are listed for each measurement; N = size of sample. Sexes and ages, from juveniles [in which all molars are erupted] to old adults, are combined. Specimens from which the measurements were obtained are identified in the footnotes by institutional acronym and catalog number.)

Species	N	ALM1-3	CBM1
B. bengalensis[a]	101	7.29 ± 0.46 (6.52–8.46)	2.41 ± 0.13 (2.13–2.75)
B. savilei[b]	95	9.13 ± 0.37 (7.98–10.00)	2.81 ± 0.13 (2.52–3.16)
B. indica[c]	216	11.14 ± 0.54 (9.49–12.72)	3.38 ± 0.12 (3.02–3.65)

[a] INDIA: West Bengal (AMNH 215630–215641, 215644–215649, 215651–215713, 215715, 215717, 215719–215726); NE Assam (AMNH 163126–163131, 163165); Maharashtra (AMNH 208171, 208172); Madras (AMNH 171145).

SRI LANKA: Central Province (AMNH 240905, 240906); North Western Province (AMNN 240907, 240908); Western Province (AMNH 240909).

BANGLADESH: Kasimpur (AMNH 249889, 249890).

BURMA: Mandalay Division (AMNH 267631, 267632).

[b] BURMA: AMNH 163695, 163696, 267633, 267634; BMNH 14.7.19.211–14.7.19.216.

THAILAND: AMNH 239618–239624, 241645–241648, 251682; BMNH 28.5.3.2; USNM 253589, 253590, 294949–294952, 294954–294956, 296545, 296546, 297166–297168, 300168, 533935–533937; ASRCT 54-857–54-878; FTM 101, 168, 238, 239, 242, 244.

VIETNAM: USNM 321517–321522, 357563–357566.

[c] INDIA: AMNH 112973, 112974, 208179; USNM 154452, 154453, 355718, 355722.

SRI LANKA: AMNH 240911, 240912, 240964–240967; USNM 257418, 257419, 257971, 258239.

BANGLADESH: SMF 66460.

BURMA: USNM 279311, 279312.

THAILAND: AMNH 167929–167932, 239625–239628, 241649–241655; ASRCT 54-880, 54-889, 54-900, 54-16544; USNM 221559, 241070, 260636, 294953, 296547, 296548, 297165, 300165–300167, 300169, 355313, 355315–355318, 355320–355325, 355328, 533929–533934.

LAOS: USNM 355551.

VIETNAM: USNM 355550, 356565–356569, 356817, 356927, 356928, 357567–357570.

MALAYSIA (Malay Peninsula, Kedah State): USNM 489307, 489308.

mastoid to the corner of the interparietal. We have been able to separate every adult example of *B. savilei* from every adult *B. bengalensis* by using the conformation of the occiput. Very young adults and juveniles of each species are difficult to separate because the occiput is deeper in young *B. bengalensis* and has not achieved its nearly vertical conformation.

The shape of the occiput in adult *B. indica* resembles that in *B. bengalensis.*

Dental traits can also be used to distinguish the three kinds of bandicoots. All three species share a basically similar occlusal pattern in upper and lower molars (figs. 9, 10) but at the same time differ in a significant qualitative trait and in size. Examples of *B. bengalensis* lack a posterior cingulum at the back of each first and second lower molar (fig. 10). This cusp is present in samples of *B. indica* and *B. savilei* (fig. 10). Our survey revealed slight variation in presence or absence of this structure. After excluding specimens from the survey in which the molars were so worn we could not detect cusp outlines, we found that out of 80 specimens of *B. bengalensis,* all lack posterior cingula except one specimen which has small versions of those cusps on the right first and second molars. Out of 114 examples of *B. indica,* all have posterior cingula except three in which they were missing from all lower molars. Out of 41 mandibles of *B. savilei,* all have posterior cingula except one in which all were absent except for a very small posterior cingulum on the right first molar.

Presence or absence of a posterior cingulum can be used to separate all ages of *B. bengalensis* from similar ranges of age in samples of the other two species (provided that the first two molars have erupted in juveniles and the molars are not excessively worn in old adults). Size of maxillary molar

←

INDONESIA (Java): AMNH 101552–101561, 101707, 101709, 102173, 102174, 102222–102225, 229882, 229884; USNM 449947–449950, 449952–449954, 449956, 533925, 533926.

CHINA (Taiwan): AMNH 183137–183139, 183193, 184545–184547, 185126–185129; USNM 283758, 294283–294289, 297864, 311283, 313689–313711, 330249–330264, 330266–330285, 333150, 333151, 333153, 333155–333161, 355843, 358558–358566, 358637, 358638.

TABLE 4

Measurements (mm) of Alveolar Length of Maxillary Molar Row (ALM1-3) and Crown Breadth of First Upper Molar (CBM1) from Samples of the Five Species of Thai *Bandicota* identified by Boonsong and Felten (1989)

(Mean ± SD and observed range [in parentheses] are listed for each measurement; N = size of sample. Sexes and ages, from juveniles [in which all molars are erupted] to old adults, are combined. The two names in boldface and capital letters indicate our identifications of the samples constituting Boonsong and Felten's five taxa [each in quotes]. Specimens from which measurements were obtained are identified in the footnotes by institutional acronym and catalog numbers.)

Species	N	ALM1-3	CBM1
B. SAVILEI			
"*B. bangchakensis*" [a]	2	8.70 ± 0.52 (8.70–9.40)	2.60 ± 0.21 (2.60–2.90)
"*B. bengalensis*" [b]	13	8.78 ± 0.27 (8.43–9.22)	2.79 ± 0.08 (2.68–2.91)
"*B. varius*" [c]	13	9.02 ± 0.27 (8.51–9.48)	2.82 ± 0.08 (2.71–2.96)
"*bangchakensis*" + "*bengalensis*" + "*varius*"	28	8.91 ± 0.30 (8.43–9.48)	2.80 ± 0.09 (2.60–2.96)
B. INDICA			
"*B. savilei*" [d]	48	10.27 ± 0.24 (9.62–10.63)	3.30 ± 0.11 (3.04–3.48)
"*B. indica*" [e]	125	10.81 ± 0.47 (9.81–12.14)	3.34 ± 0.13 (2.97–3.64)
"*savilei*" + "*indica*"	173	10.66 ± 0.48 (9.62–12.14)	3.33 ± 0.12 (2.97–3.64)

[a] Pak Chong Province: SMF 60166. Nakhon Si Thammarat Province: SMF 67852 (holotype of "*Bandicota bangchakensis*").

[b] Chainat Province: SMF 67741–67744, 67854. Khok Samrong Province: SMF 67745, 67746. Songkhla Province: SMF 67858. Prachuap Khiri Khan Province: SMF 67747, 67748, 67855–67857.

[c] Nakhon Ratchasima Province: SMF 60165, 67749. Chainat Province: SMF 60167, 67750–67752, 67859. Lop Buri Province: SMF 67753–67755. Nakhon Pathom Province: SMF 67756. Nakhon Si Thammarat Province: SMF 67757. "Thailand:" SMF 67758.

[d] Nakhon Si Thammarat Province: SMF 67759, 67771, 67772, 67869–67880, 7200. Phatthalung Province: SMF 67768. Songkhla Province: SMF 67769, 67770, 67887–67890. Chainat Province: SMF 67860. Prachuap Khiri Khan Province: SMF 67861. Nakhon Pathom Province: SMF 67862–67868. Phetchaburi Province: SMF 67760–67767, 67881–67886. Chiang Mai Province: SMF 67891, 67892.

[e] Chiang Mai Province: SMF 60164. Nakhon Pathom Province: SMF 60176, 60177, 60180, 67774–67787, 67789–67798, 67835–67849, 67900, 67901, 67918. Ang Thong Province: SMF 67799. Chainat Province: SMF 60168, 60169, 67800–67803, 67893. Khon Kaen Province: SMF 67804, 67805. Maha Sarakham Province: SMF 67806. Trat Province: SMF 67807, 67808, 67916, 67917. Phetchaburi Province: SMF 67809–67830, 67902–67911, 67925. Chanthaburi Province: SMF 60170. Prachuap Khiri Khan Province: SMF 60172. "Thailand:" SMF 60171, 60173–60175, 60178, 60182–60186, 67850, 67851, 67919, 67921. Phatthalung Province: 67831, 67832, 67912, 67914. Songkhla Province: 67833, 67834, 67915, 67926, 67927. Nakhon Pathom Province: 67894–67899, 67920, 67924.

row, as measured by alveolar length of the tooth row and crown breadth of first upper molar is another discriminating feature that is independent of age. *Bandicota bengalensis* has the smallest molars, *B. indica* the largest, and *B. savilei* falls between these two (table 3). The very narrow overlap of specimens between the samples of *B. bengalensis* and *B. savilei*, and between the latter and the sample of *B. indica* is clearly illustrated by the scatterplot in figure 11.

Just one of these traits, alveolar length of maxillary molar row, separates the samples into three groups that barely overlap. This trimodal distribution is illustrated by the histograms in figure 13. That three discrete en-

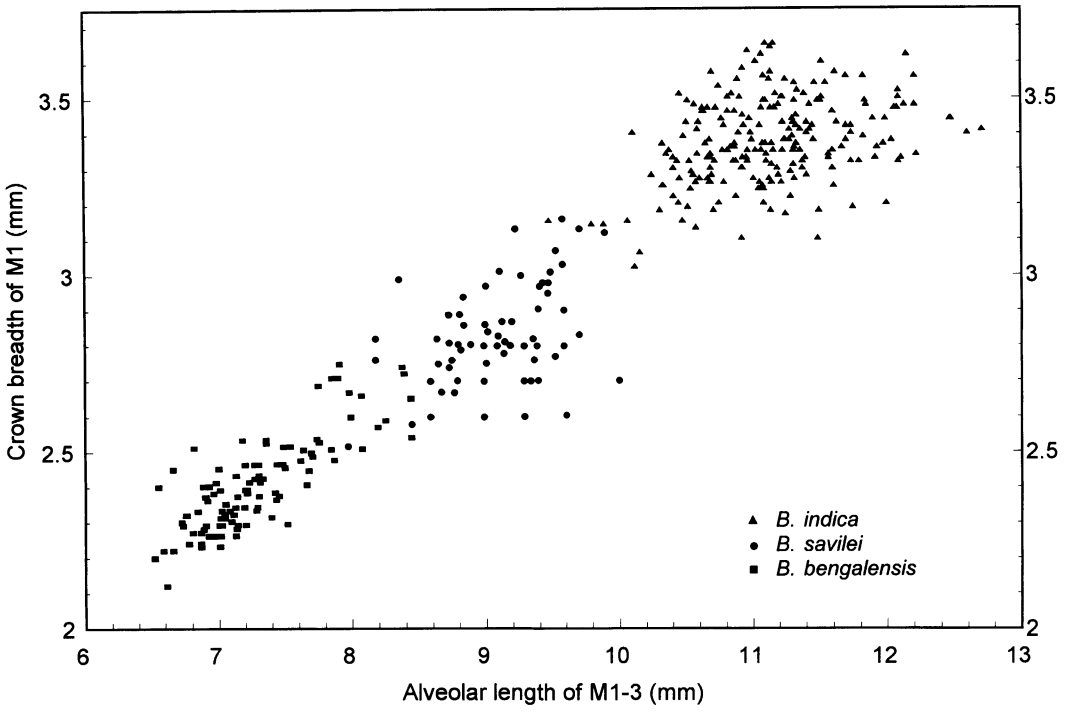


Fig. 11. Discrimination among *Bandicota bengalensis* (N = 101), *Bandicota savilei* (N = 95), and *Bandicota indica* (N = 216) by two measurements. The slight overlap between adjacent clusters reflects the highly significant differences in means of alveolar length of maxillary molar row between *B. bengalensis* and *B. savilei,* and between the latter and *B. indica* (table 5). Most specimens of *Bandicota* can be allocated to one of the three species by employing the two measurements, or even just alveolar length of maxillary molar row, which we used. Summary statistics for each cluster are listed in table 3; symbols represent the specimens we measured, which are also listed in table 3.

tities are represented among the samples is also indicated by probability values listed in table 5. The difference in means between samples of *B. bengalensis* and *B. savilei* is highly significant ($P = <.001$) as is the difference in means between samples of the latter species and *B. indica* ($P = <.001$).

Separating specimens into three species is not difficult. We found that individuals could be correctly identified as *B. bengalensis, B. savilei,* or *B. indica* by using the age-independent dental traits, the qualitative external and cranial features, and the measurements and proportions described above.

IDENTITIES OF BOONSONG AND FELTEN'S THAI *BANDICOTA*

Boonsong and Felten (1989) examined 128 specimens of *Bandicota* from Thailand and encountered "unexpected taxonomic difficulties" in their attempt to identify the species represented in their sample. They ignored data from skins (external dimensions, fur characteristics, and mammae counts) and studied only skulls from animals they judged to be adult. By employing certain length measurements (condylonasal, occipitonasal, condylobasal, nasals plus frontals, and rostrum), they sorted their material into four lots, graded in size from samples of small specimens to those containing larger individuals; the measurements did not overlap among the samples. Qualitative traits were not used—at least they were not mentioned—to distinguish among the groups.

The smallest individuals (occipitonasal length not exceeding 39.5 mm) were identified as *Bandicota bengalensis.* Specimens in the next largest size category (occipitonasal

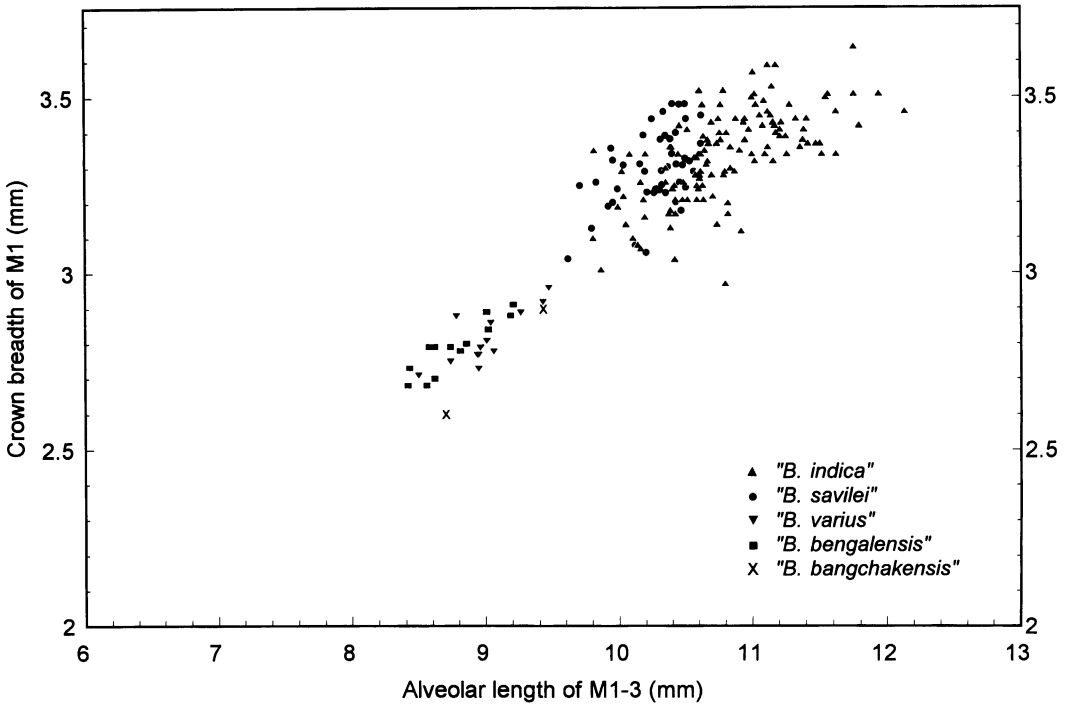


Fig. 12. Relationship between two measurements among samples of the five species of Thai *Bandicota* identified by Boonsong and Felten (1989): "*B. indica*" (N = 125), "*B. savilei*" (N = 48), "*B. bangchakensis*" (N = 2), "*B. varius*" (N = 13), and "*B. bengalensis*" (N = 13). Statistics for each sample are summarized in table 4; symbols represent the specimens we measured, which are also listed in table 4. Two clusters of symbols are evident. One consists of material identified by Boonsong and Felten as "*B. indica*" and "*B. savilei*"; the position of this scatter in the bivariate plot corresponds to the cloud of points derived from our standard sample of *B. indica* shown in figure 11 on opposite page. The other cluster of points indicates specimens identified by Boonsong and Felten as "*B. bangchakensis,*" "*B. varius,*" and "*B. bengalensis,*" and if superimposed on figure 11 would fall within the scatter derived from our standard sample of *B. savilei.*

The two clusters do not overlap; this lack of significant differences in alveolar length of maxillary molar row between means from the standard *B. indica* and Boonsong and Felten's "*indica-savilei,*" and between the standard *B. savilei* and Boonsong and Felten's "*bangchakensis, varius,* and *bengalensis*" (table 5) mirrors the results portrayed by the scatterplot.

Graph is empty on lower left, indicating that none of the specimens studied by Boonsong and Felten have narrow molars and short tooth rows, features characteristic of *B. bengalensis*; points derived from our standard sample of *B. bengalensis* form a cluster below the cloud representing *B. savilei* (see fig. 11 on opposite page).

length greater than 40.5 mm but less than 44.5 mm) were determined to be *B. varius.* The taxon *varius* is usually listed as a subspecies of *B. bengalensis* (Agrawal and Chakrabarty, 1976, for example), but Boonsong and Felten treated it as a species because in Thailand it existed "side by side with *B. bengalensis*" (p. 200). Individuals with an occipitonasal length greater than 44.5 mm but less than 49 mm defined the third group that was identified as *B. savilei.* The fourth cluster that contained the largest specimens (occipitonasal length greater than 49 mm) was treated as *B. indica.*

Boonsong and Felten used an additional measurement, "breadth across the upper molars (alv.)," to group the four samples into two larger lots. The samples of *B. bengalensis* and *B. varius* formed "the smaller bengalensis-group" and the series of *B. savilei* and *B.*

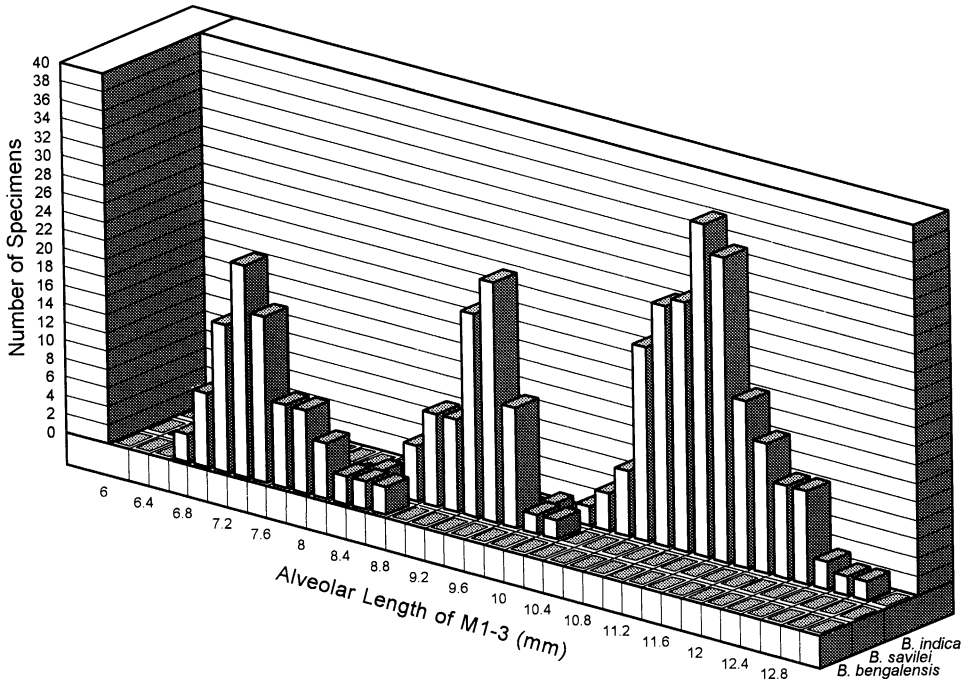
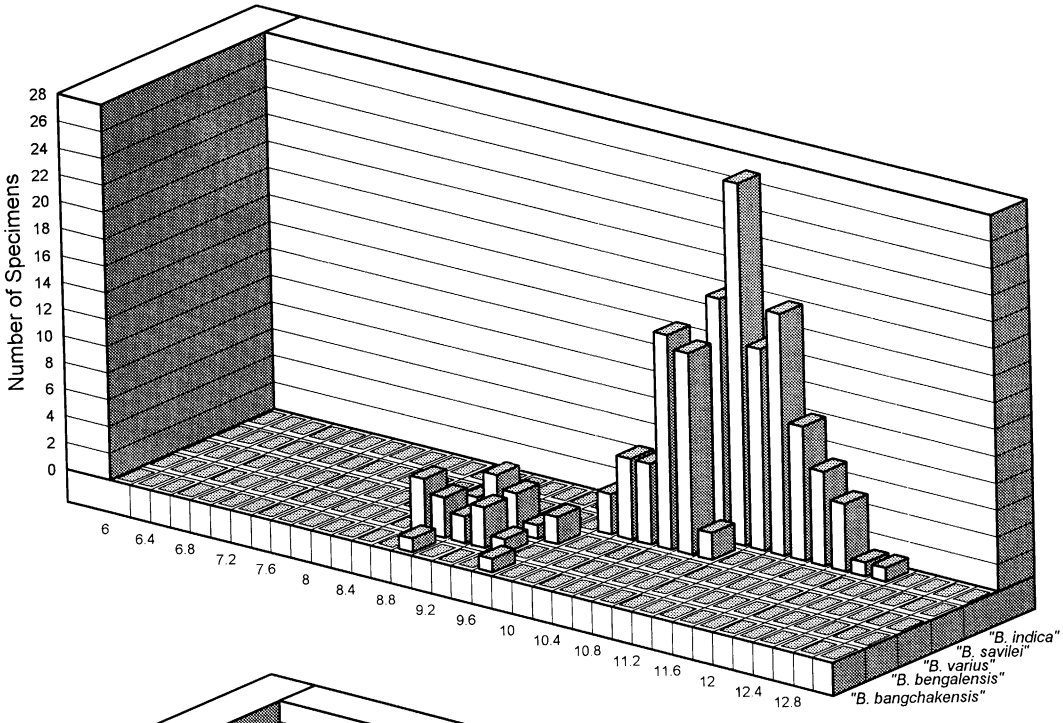


Fig. 13. Frequency distribution of values of alveolar length of maxillary molar row obtained from our reference samples of *Bandicota bengalensis* (N = 101), *Bandicota savilei* (N = 95), and *Bandicota indica* (N = 216). Summary statistics for the three samples and specimens from which the data were derived are listed in table 3. Like the scatterplots, the histograms for *B. bengalensis* and *B. indica* are widely separate, and that for *B. savilei* only slightly overlaps histograms for the other two species.

→

Fig. 14. Two sets of frequency distributions of values of alveolar length of maxillary molar row. **Top**: histograms were generated from values obtained from samples of the five Thai species identified by Boonsong and Felten (1989) as "*B. indica*" (N = 125), "*B. savilei*" (N = 48), "*B. bengalensis*" (N = 13), "*B. varius*" (N = 13), and "*B. bangchakensis*" (N = 2). Summary statistics for the five samples and specimens from which the data were obtained are listed in table 4. Like the scatterplot in figure 12, the histograms form two groups, reflecting two, not five, biological entities.

Bottom: combined histograms for "*B. indica*" and "*B. savilei*" form one distribution of values that in structure and statistical magnitude is similar to the histogram representing values derived from our standard samples of *B. indica.* The two distributions represent the same population since no significant difference in means of alveolar length of maxillary molar row exists between the standard *B. indica* and the combined sample of "*B. indica* and "*B. savilei*" (table 5). The combined distributions of values from "*B. bengalensis,*" '*B. varius,*" and "*B. bangchakensis*" form a different histogram that does not overlap the other and represents a population that is the same as that from which our standard sample of *B. savilei* was drawn; there are no significant differences in means of alveolar length of maxillary molar row between samples of our standard *B. savilei* and those combined samples of the three different species identified by Boonsong and Felten (table 5). The two histograms in the bottom chart are similar in position to the two histograms in figure 13 on this page representing the distribution of values in our reference samples of *B. indica* and *B. savilei.* None of the values are distributed in the left-hand portion of each chart; however, they would be if any of them were from examples of the small *B. bengalensis*; values from our reference sample of *B. bengalensis,* for example, form a histogram in that comparable space (see fig. 13 on this page).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8.4
8.8
9.2
9.6
10
10.4
10.8
11.2
11.6
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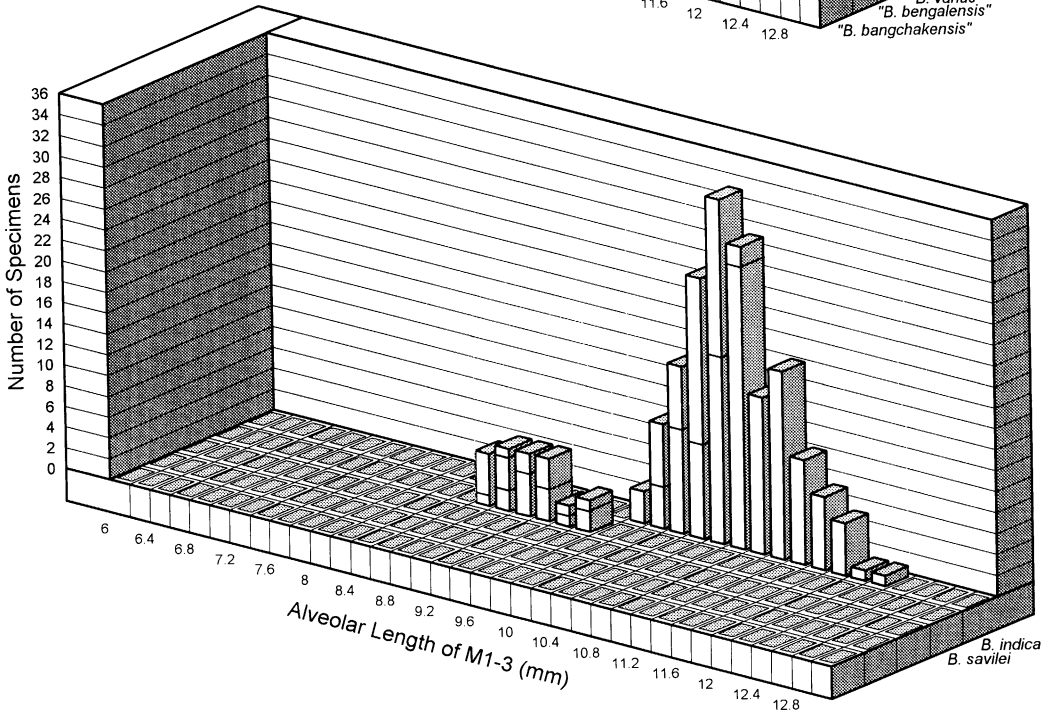
"B. savilei"
"B. varius"
"B. bengalensis"
"B. bangchakensis"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6
6.4
6.8
7.2
7.6
8
8.4
8.8
9.2
9.6
10
10.4
10.8
11.2
11.6
12
12.4
12.8
Alveolar Length of M1-3 (mm)
B. indica
B. savilei

TABLE 5

Combinations of Comparisons Between Samples of the Reference Species of *Bandicota* and the Thai Species Identified by Boonsong and Felten (1989)

(P is the significance probability derived from a table of cumulative Student's *t* distribution; values less than 0.05 were considered significant enough to reject the hypothesis that means of any two samples were drawn from the same population. Data from tables 3 and 4 were used to compute values of *t*. Names of the reference species are in boldface capital letters, those used by Boonsong and Felten are identified by quotation marks.)

Taxon combinations	P
B. BENGALENSIS vs. ***B. SAVILEI***	**<.001**
B. BENGALENSIS vs. "*B. bengalensis*"	**.01-.001**
B. SAVILEI vs. ***B. INDICA***	**<.001**
B. SAVILEI vs. "*B. bengalensis*"	.4–.3
B. SAVILEI vs. "*B. varius*"	.8–.7
B. SAVILEI vs. "*B. bangchakensis*"	.9–.8
B. SAVILEI vs. "*B. bengalensis*" + "*B. varius*" + "*B. bangchakensis*"	.6–.5
"*B. bengalensis*" vs. "*B. varius*"	.6–.7
"*B. bengalensis*" vs. "*B. bangchakensis*"	.4–.3
B. SAVILEI vs. "*B. savilei*"	**<.001**
B. SAVILEI vs. "*B. indica*"	**<.001**
B. INDICA vs. "*B. savilei*"	.1
B. INDICA vs. "*B. indica*"	.6–.5
B. INDICA vs. "*B. savilei*" + "*B. indica*"	.4–.3
"*B. savilei*" vs. "*B. indica*"	.3–.2

indica constituted "the larger indica-group" (p. 198).

Two specimens from Nakhon Si Thammarat Province in the southern region of peninsular Thailand could not "be integrated within the four Thai species" (p. 202) and Boonsong and Felten designated them holotype and paratype of *B. bangchakensis,* a new species diagnosed as "similar to *Bandicota savilei,* but clearly separated by minor measurements, especially in molar breadth" (p. 202). A specimen from Nakhon Ratchasima Province (northeast of Bangkok) and another from "Thailand" were also identified as *B. bangchakensis.*

Boonsong and Felten used 128 specimens for their report, but the Senckenberg Museum has an additional 88 obtained through Boonsong and Felten's efforts in Thailand. We examined all 206 specimens, including the holotype of *B. bangchakensis.* We can distinguish only two specimens of *Bandicota* in the material, not five. Our determinations are the result of three surveys, taken at different times and focusing on separate aspects.

Musser made the first survey in the summer of 1992 in the Senckenberg Museum. There he examined skins and skulls of the *Bandicota* samples collected in Thailand. Based entirely on observations of qualitative characteristics and a few dental measurements, he determined that all the specimens identified as "*B. bengalensis*" by Boonsong and Felten (1989) were young examples of *B. savilei,* either very young adults in adult pelage, specimens in transitional coat from juvenile to adult, or individuals clothed in juvenile fur. The specimens identified as "*B. varius*" by Boonsong and Felten consisted of an old adult, several young adults, and many adults of small size; they too were judged by Musser to represent *B. savilei.* Boonsong and Felten's "*B. savilei*" were represented by young specimens, most of them juveniles in that pelage or in a transitional coat between juvenile and adult; to Musser they were clearly young *B. indica.* The specimens identified by Boonsong and Felten as "*B. indica*" ranged in age from very young to old adults; Musser agreed with their determination. Finally, he could not see any traits in the specimens labeled "*B. bangchakensis*" that would exclude

them from the other samples of *B. savilei.* These preliminary conclusions were reported, but not documented, by Musser and Carleton (1993).

We borrowed all the skulls. Because Boonsong and Felten had studied only cranial material, we wanted to test their identifications as well as the results from Musser's initial survey by analyzing data obtained only from the crania. Furthermore, by having the material at the American Museum of Natural History, we could compare the specimens with our reference samples of *B. bengalensis, B. savilei,* and *B. indica.* Some of the specimens in each of these three samples have been compared directly with relevant holotypes.

Eric Brothers conducted the second survey by measuring alveolar length of maxillary molar rows and crown breadths of first upper molars of all the Senckenberg Museum specimens. Before we examined Boonsong and Felten's material, we had already measured specimens in our large reference samples of *B. bengalensis, B. savilei,* and *B. indica* and had established that most individuals in each of the three samples could be identified to species by employing just these two measurements (fig. 11). Furthermore, nearly every one of our reference specimens could be identified simply by using alveolar length of maxillary molar row (fig. 13).

Values obtained from Thai Senckenberg specimens were summarized statistically (table 4), plotted on a scatter diagram (fig. 12), and their distributions illustrated by histograms (fig. 14). These quantitative results mirrored the qualitative results obtained from the first survey. Whether scatter diagram or frequency distributions, the measurement data fall into two groups. The specimens identified by Boonsong and Felten as "*B. indica*" and "*B. savilei*" form one group. The position of the cloud of points and the histogram correspond to the scatter cluster and histogram representing our reference sample of *B. indica* (compare fig. 11 with fig. 12, and fig. 13 with 14).

Furthermore, we tested the significance of the differences between samples in alveolar length of maxillary molar row. The difference is highly significant ($P = <.001$) between means of our reference samples of *B. indica* and *B. savilei* (table 5). The latter has a much shorter tooth row (and narrower molars); large samples of the two species barely overlap in these traits (figs. 11 and 13). We also found highly significant differences between means from samples of our reference *B. savilei* and their "*B. savilei*" ($P = .01–.001$) and between the reference *B. savilei* and their "*B. indica*" ($P = <.001$). However, no significant differences existed between means of Boonsong and Felten's "*B. savilei*" and their "*B. indica,*" or between the mean of our reference sample of *B. indica* and means of their samples of "*B. savilei,*" "*B. indica,*" or "*B. savilei*" combined with "*B. indica*" (table 5).

The other group contains the samples that Boonsong and Felten identified as "*B. bengalensis,*" "*B. varius,*" and "*B. bangchakensis.*" The position of the cluster of points in the scatter diagram (fig. 12) and the frequency distributions forming the histograms (fig. 14) correspond to the cluster and histogram derived from our reference sample of *B. savilei* (figs. 11 and 13).

Again we tested the significance of differences in alveolar length of maxillary tooth row among samples (table 5). The difference between means of our reference samples of *B. bengalensis* and *B. savilei* is highly significant ($P = <.001$; the latter has significantly longer molar rows. The difference between means of Boonsong and Felten's sample of "*B. bengalensis*" and our reference series of that species is also highly significant ($P = .01–.001$), indicating that their "*bengalensis*" also has tooth rows too long to be a part of real *B. bengalensis.*

In contrast, no significant differences exist between the means of Boonsong and Felten's samples of "*B. bengalensis*" and either "*B. varius*" or "*B. bangchakensis,*" or between means from our reference series of *B. savilei* and means from their samples of "*B. bengalensis,*" "*B. varius,*" and "*B. bangchakensis,*" or the mean from the combined sample of "*B. bengalensis,*" "*B. varius,*" and "*B. bangchakensis*" (table 5). All three of Boonsong and Felten's series cannot be distinguished from the reference sample of *B. savilei* by tooth-row length, but can be separated from the reference series of *B. bengalensis* by that trait.

In our third survey we reexamined each

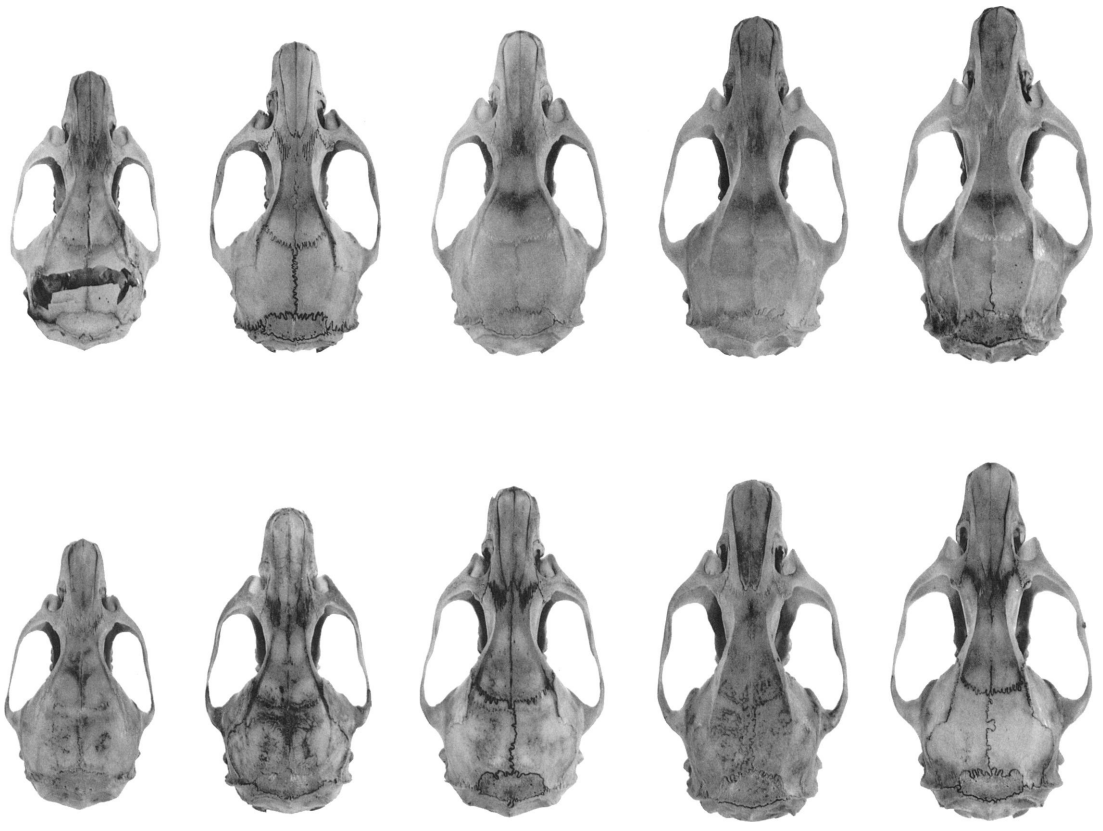

Fig. 15. Crania of *Bandicota* (×1) viewed from dorsal perspective (ventral views are portrayed in fig. 16 on opposite page). Specimens in bottom row come from our reference series of Thai *B. savilei* and are arranged by age from left to right: juvenile (AMNH 239624), very young adult (AMNH 239618), young adult (AMNH 239621), small adult (AMNH 239619), and larger adult (AMNH 241645). Individuals in top row are arranged in the same sequence of comparable ages (judged by wear of teeth along with size and conformation of skull). All are from Thai samples and were determined by Boonsong and Felten to represent three species. They identified the juvenile (SMF 67742) and very young adult (SMF 67856), the two crania on the left, as "*B. bengalensis*"; the young adult (SMF 67750) and small adult (SMF 67859), the two crania in the center, as "*B. varius*"; and the larger adult (SMF 60166), the cranium on the far right, as "*B. bangchakensis.*" The specimens illustrated here are good examples of those in the series determined by Boonsong and Felten to be "*bengalensis,*" "*varius,*" and "*bangchakensis*": their "*bengalensis*" invariably proved to be young *B. savilei,* their "*varius*" turned out to be mostly young and small adults of *B. savilei,* and their specimens of "*bangchakensis*" closely resemble the larger adults in our reference series of *B. savilei.*

Senckenberg individual to determine if the specimens in each of the two clusters we had identified by quantitative analyses also had the qualitative cranial features associated with our reference samples of *B. indica* and *B. savilei,* but not *B. bengalensis.* For example, could one or more of the specimens in the *savilei* cluster really be examples of *B. bengalensis* with unusually long molar rows?

Our results mirrored those obtained by Musser's initial survey: Boonsong and Felten's "*bengalensis*" are young examples of *B. savilei,* their "*varius*" and "*bangchakensis*" are adult *B. savilei,* represented by a range from young to old adults (figs. 15 and 16). In qualitative traits, none of the Senckenberg specimens, no matter what relative age, matched individuals of comparable ages in

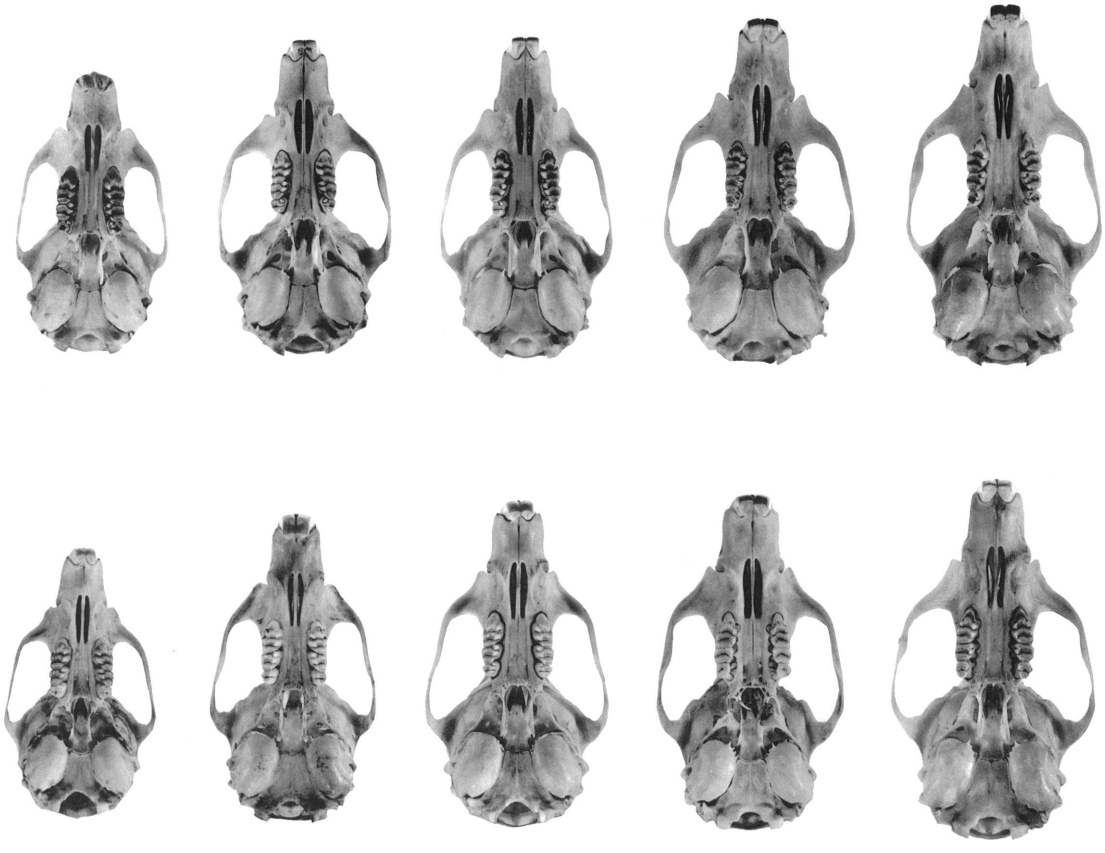

Fig. 16. Ventral views. (×1) of same crania portrayed in figure 15 on opposite page. The specimens are also arranged in the same age sequence.

our reference series of *B. bengalensis,* particularly those Boonsong and Felten determined to be "*B. bengalensis.*" For example, 12 out of the 13 in that series had a posterior cingulum on the back margin of each first and second lower molar; *B. bengalensis* lacks this cusp. Only SMF 67858 lacked such cusps except for a small posterior cingulum on the right first molar; in all other features the individual resembled young specimens of *B. savilei* and not those of *B. bengalensis.*

The sample Boonsong and Felten determined to be "*savilei*" actually consists of young *B. indica.* The only specimens correctly identified are those they referred to as "*B. indica*" (figs. 17 and 18).

We gave the holotype of *B. bangchakensis* additional scrutiny. A population of *B. bengalensis* occurs on Pinang Island (fig. 1, locality 107). The animals from Pinang have a larger average body size than do typical representatives of the species (Agrawal and Chakraborty, 1976), and conceivably the holotype of "*B. bangchakensis,*" because it was collected at the southern end of peninsular Thailand, not so far away from Pinang Island, could be an example of *B. bengalensis.* We had included the holotype of "*B. bangchakensis*" in our three surveys and were able to identify it as a representative of *B. savilei.* But, to be certain, we contrasted its proportions with those of a single male *B. bengalensis* of the same approximate age and compared the profiles with those derived from our three reference species.

Results are portrayed in the ratio diagram in figure 19 and reinforce our identification derived from the surveys. Configuration of the proportional profile of the holotype is very similar to those of *B. savilei* and *B. indica*

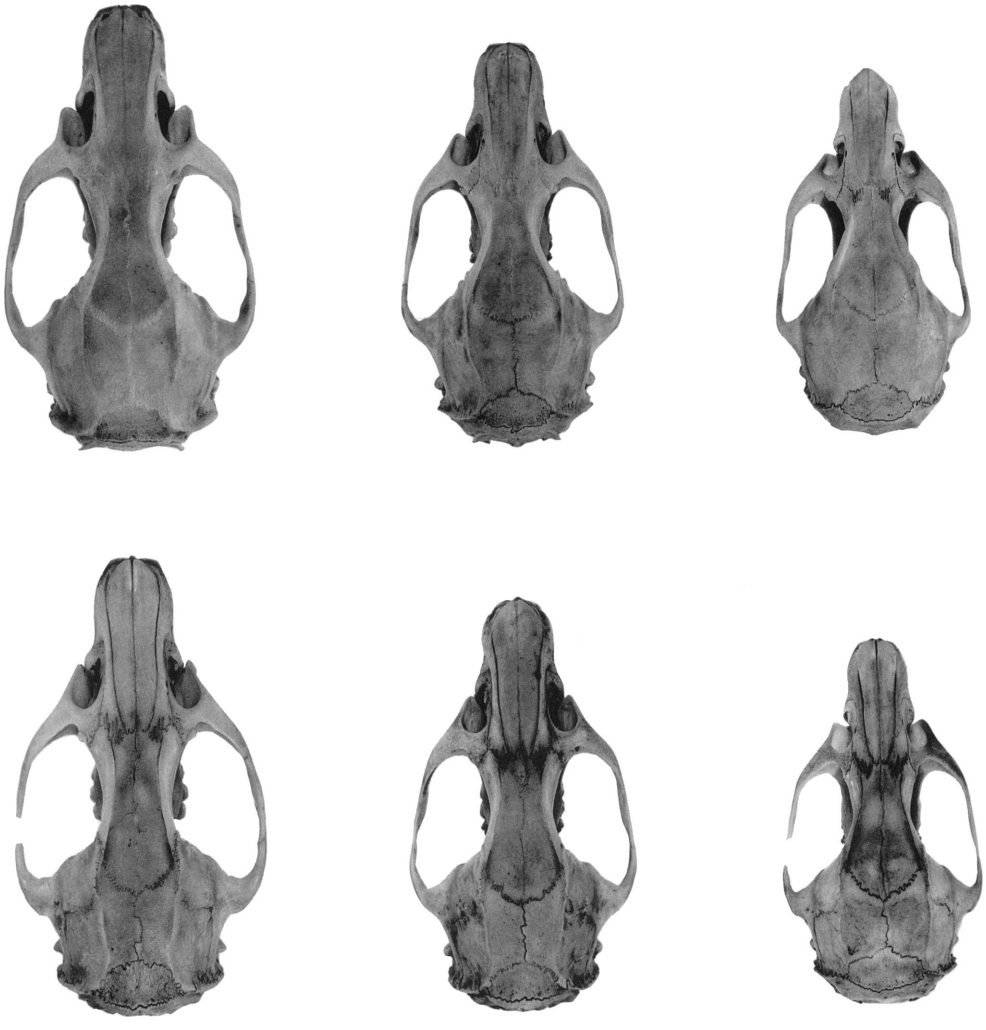

Fig. 17. Crania of *Bandicota* (×1) viewed from dorsal perspective (ventral views of the same individuals are shown in fig. 18 on opposite page). Bottom row portrays three individuals from Java that are part of our reference series representing *B. indica*: adult (AMNH 101554) on the left, young adult (AMNH 102224) in the center, and very young adult/old juvenile (AMNH 101559) on the right. Individuals of comparable age (judged by tooth wear as well as cranial size and conformation) from Thailand on top row. Left specimen (SMF 67813) and center specimen (SMF 67786) were correctly identified by Boonsong and Felten (1989) as *B. indica.* They determined the individual on the right (SMF 67771) to be an example of "*B. savilei.*" But its greater size compared with specimens of *B. savilei* in our reference series of comparable age (particularly the length of tooth row) excludes it from that species (also compare SMF 67771 with the adult *B. savilei* portrayed in fig. 5); its attributes closely resemble young specimens in our reference series of *B. indica,* and that is our determination of the specimen. All the specimens identified as "*B. savilei*" by Boonsong and Felten (table 4) proved to be young examples of *B. indica.*

and not that of *B. bengalensis.* The profile of the individual *B. bengalensis* is more closely aligned with the large sample of that species rather than with the other two species or the holotype of "*B. bangchakensis.*"

The distinctions between the holotype of "*B. bangchakensis*" and the specimen of *B. bengalensis* are those contrasting samples of the latter and *B. savilei,* differences we discussed previously. For example, the holotype

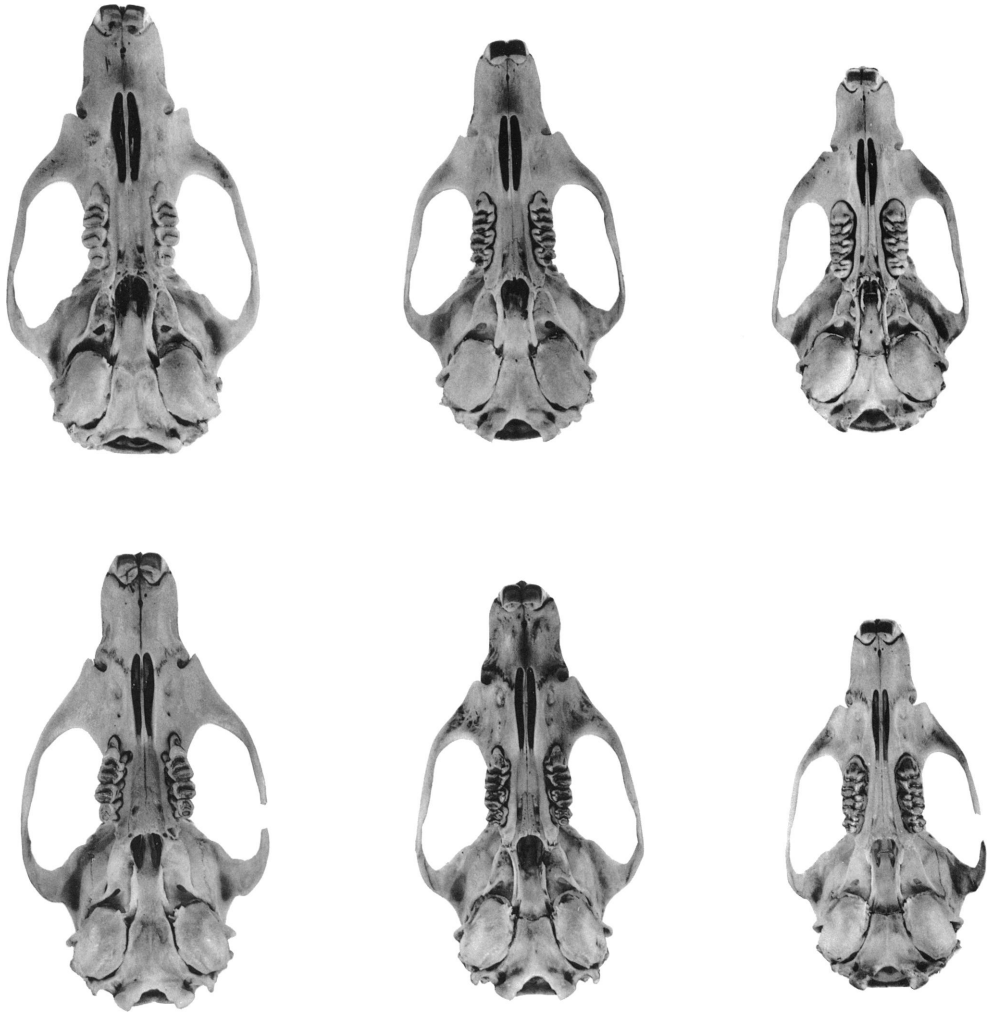

Fig. 18. Views (×1) from ventral perspective of specimens portrayed in figure 14.

of "*B. bangchakensis*" fits within the size range of *B. savilei* (compare tables 2 and 6). Its occipitonasal length is the same as greatest length of skull; its upper incisors are not procumbent; its incisive foramina barely extend past front margin of the anterior root on the first upper molar; and some of the lower molars, although very worn, retain evidence of posterior cingula. Based on our qualitative observations and quantitative analyses, we confidently identify the holotype as an example of *B. savilei.*

Boonsong and Felten apparently did not appreciate the significance of variation due to age that was present in their samples. They thought they were measuring adults, but the specimens actually represented a wide range in age, from juveniles to old adults. This may be why they assigned the individuals (which were very young) of smallest body size to "*B. bengalensis,*" which is the smallest of the familiar species of *Bandicota.* Assigning larger individuals (which were also older) to "*B. varius*" naturally followed because the measurements were similar to those Ellerman (1961) had provided for *varius* and because their "*varius*" specimens were not as large as those in the sample Boonsong and Felten assigned to "*B. savilei*" (which were young individuals of the large-bodied *B. indica*) but were larger than "*B. bengalensis*"; besides, their "*bengalensis*" and "*varius*" had been

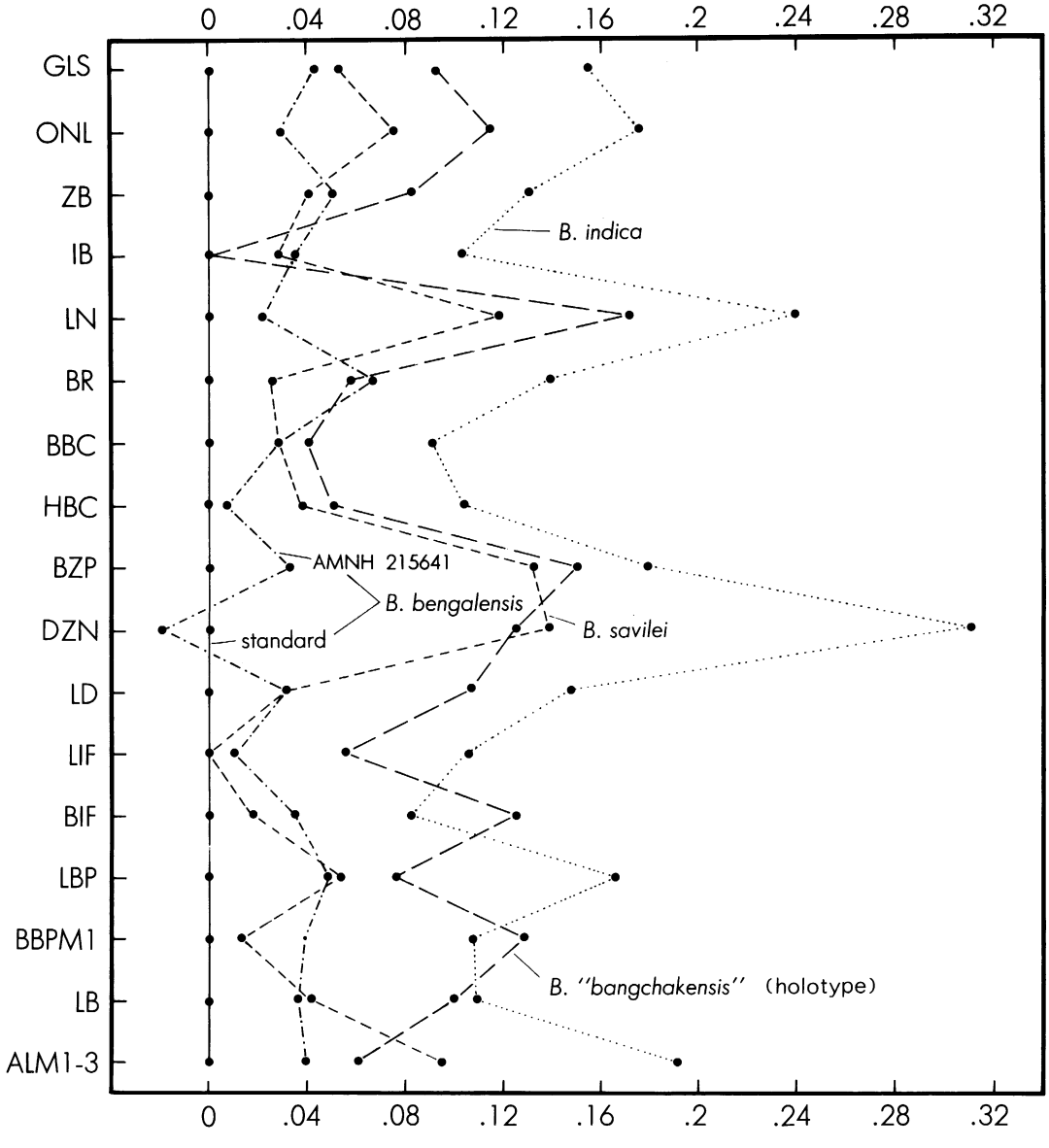

Fig. 19. Ratio diagram comparing some cranial and dental proportional relationships between individuals and larger samples of *Bandicota.* Dimensions of the holotype of "*B. bangchakensis*" (SMF 67852), an adult male, and an adult male *B. bengalensis* of comparable age (AMNH 215641, from West Bengal, India) are contrasted with those in samples of *B. bengalensis* (the standard), *B. savilei,* and *B. indica.* The profiles for the latter species are the same as those shown in figure 4 and were derived from the same data, but here only the means are plotted. The profile of the holotype of "*B. bangchakensis*" is similar to those of *B. savilei* and *B. indica* and unlike the configuration of the single *B. bengalensis,* which resembles the vertical line of the standard. Profiles for the holotype and specimen of *B. bengalensis* were derived from the data listed in table 6. See text for additional information and figure 4 for explanation of ratio diagram.

taken "side by side" and therefore had to be different species.

Boonsong and Felten did contribute additional specimens and localities of collection to our understanding of the magnitude in variation due to age and morphology, and in

the geographic ranges of the only two species of *Bandicota* known to occur in Thailand: *B. indica* and *B. savilei*. Although *B. bengalensis* has been found in nearby Burma, it has yet to be recorded from Thailand.

But, aside from this increase in specimens and the extension of the range of *B. savilei* into peninsular Thailand, Boonsong and Felten offered little to improve the accounts of *Bandicota* provided by Marshall in *Mammals of Thailand* (Lekagul and McNeely, 1977). They consulted this source, finding it of "no help" (p. 200). Boonsong and Felten also considered that Lekagul and McNeely (they did not realize Marshall authored the bandicoot accounts) "ignored the existence of *B. bengalensis* in Thailand. Apparently they were confusing specimens of *bengalensis* (or *varius*) with *savilei*" (p. 208); ironically it was Boonsong and Felten who confused examples of *B. savilei* with "*bengalensis*" and "*varius*."

NOTES ON RELATIONSHIPS OF *BANDICOTA*

Underlying our expositions on the distinctions between *indica, savilei,* and *bengalensis* and our identifications of the Thai *Bandicota* has been the assumption that the three species are part of the same monophyletic group to the exclusion of other murine species. Such an assumption, or hypothesis, has never been critically tested. The palearctic *Nesokia,* for example, has always been considered a close relative of *Bandicota* (Ellerman, 1941, 1961). While Marshall was preparing his accounts of Thai bandicoots (Marshall, 1977) he had studied examples of *Nesokia* and asked Musser why the two genera should not be united. Corbet and Hill (1992: 352) also suggested that perhaps the species of *Bandicota* should be included in *Nesokia.* But these impressions have been based on some morphological resemblances, not critical phylogenetic analyses; whether the shared likeness is phylogenetic or convergent is unknown. The affinities of these two genera relative to each other and to other murines has remained unclear. Views recorded in the literature suggest that either the two are close to one another and have no near relatives, especially not *Rattus* (Misonne, 1969), or that they are phylogenetically close to *Rattus* (Niethammer, 1977; Gadi and Sharma, 1983; Gemmeke and Niethammer, 1984).

TABLE 6

Comparisons of Measurements (mm) Between an Example of *Bandicota bengalensis* and the Holotype of "*Bandicota bangchakensis*"

(Both are adults of similar age, judged by wear of molars. The profiles in the ratio diagram [fig. 19] were obtained from these data.)

	B. bengalensis West Bengal, India (AMNH 215641)	"*B. bangchakensis*" Thailand (holotype, SMF 67852)
GLS	43.9	49.2
ONL	40.4	49.2
ZB	25.2	27.1
IB	6.5	6.0
LN	12.0	17.5
BR	9.9	9.7
BBC	17.5	18.0
HBC	12.5	13.8
BZP	5.5	7.2
DZN	2.3	3.2
LD	13.1	15.6
LIF	8.3	9.2
BIF	2.6	3.2
LBP	9.4	10.0
BBPM1	3.5	4.3
LB	8.8	10.2
ALM1-3	8.1	8.7

After we surveyed the morphological traits distinguishing species of *Bandicota,* we examined specimens of *Nesokia* to acquire a more informed grasp of the features separating that group from *Bandicota* and the possible phylogenetic significance of those characters. While we were inquisitive about any phylogenetic inferences, we also had an immediate practical goal. If the two genera were morphologically so similar to warrant merging, then the Thai animals should be referred to as species of *Nesokia,* not *Bandicota.* We cannot report results of a phylogenetic analysis but we are able to provide comments on the differences between these two genera, and an outline of the context in which a phylogenetic study should be undertaken.

Bandicota and *Nesokia*

The species now placed in *Bandicota* and *Nesokia* were originally brought together as a monophyletic group under *Nesokia* and either first treated as a subgenus of *Mus* (Anderson, 1878) or later as a full genus (Sclater,

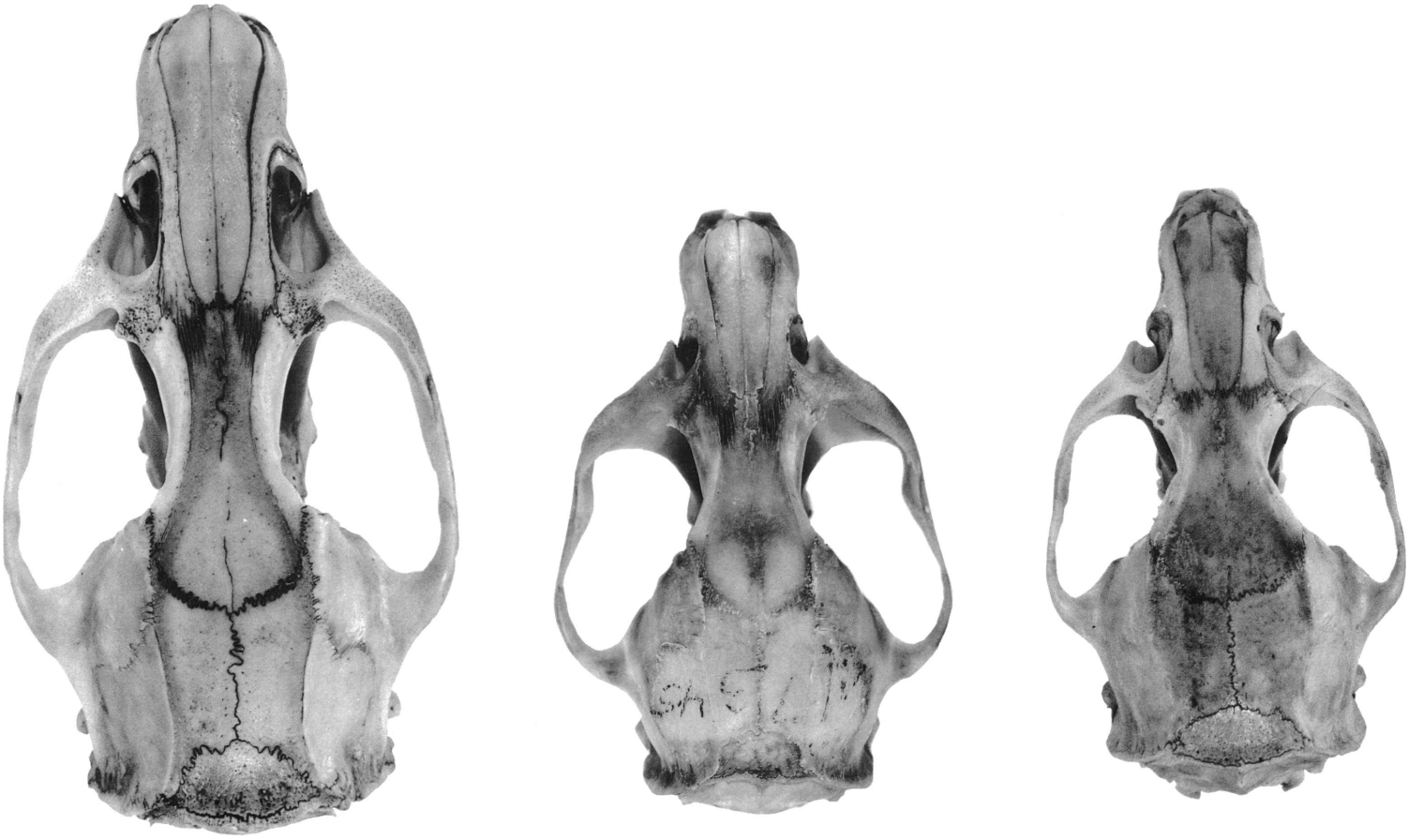

Fig. 20. Dorsal views of adult crania (×2). **Left**, *Bandicota indica* (AMNH 239628); **middle**, *Nesokia indica* (AMNH 217345); **right**, *Bandicota bengalensis* (AMNH 215674). In *Nesokia* and *B. bengalensis,* the nasals are shorter than the premaxillaries.

Fig. 21. Ventral views of crania in figure 20 (×2). **Left**, *Bandicota indica*; **middle**, *Nesokia indica*; **right**, *Bandicota bengalensis*. Note differences in length of incisive foramina and posterior position of bony palate.

Fig. 22. Lateral view of cranium and dentary (×2) from the *Bandicota indica* shown in figures 20 and 21. Contrast this view with those of *Nesokia indica* and *Bandicota bengalensis* in figure 23 on opposite page.

1890). It was Thomas in 1907 who separated the species into three generic groups, *Nesokia, Gunomys,* and *Bandicota.* By the 1940s, *Gunomys* was treated as a synonym of *Bandicota,* and *Nesokia* was recognized as a distinctive genus related to *Bandicota* (Ellerman, 1941), an arrangement accepted today (Corbet and Hill, 1992; Musser and Carleton, 1993). Ellerman (1961: 808) summarized this historical progression by noting that all the bandicoot rats had been referred to the genus *Nesokia* until Thomas' separation and exclaimed that "There is not the least excuse for retaining '*Gunomys,*' which is a pure synonym of *Bandicota,* but it is reasonable to restrict the name *Nesokia* to the highly specialized Palaearctic Bandicoot rats of the species *Nesokia indica* . . . and to use *Bandicota* for the more generalized Indo-Malayan species." Corbet and Hill (1992: 352) noted that *Bandicota* "is closely related to *Nesokia* (the prior name) but the lamination of the molars is much less extreme."

Other studies also support a close phylogenetic tie between *Nesokia* and *Bandicota.* Niethammer (1977) surveyed characters from the molars, soft palates, and chromosomes in selected species of *Rattus, Bandicota, Nesokia,* and *Niviventer* (he referred to this latter genus as *Maxomys* in his report) and used them to construct a dendrogram indicating *Nesokia* and *Bandicota* to be closely related to each other and to *Rattus,* and distant from *Niviventer.* An electrophoretic study by Radtke and Niethammer (1985) in which eight loci were compared among samples of *Bandicota, Nesokia,* and *Rattus* suggested that *Nesokia* groups with *Bandicota* and is most similar to *B. indica.* Chromosomal characteristics group *Bandicota* and *Nesokia* (Gadi and Sharma, 1983), and Dubey and Raman (1992: 275) noted that the "karyotypes of *Nesokia indica* and *Bandicota bengalensis* are identical except for their sex chromosomes, which are much larger in *Nesokia* due to additional constitutive heterochromatin."

Fig. 23. Lateral views of crania and dentaries (×2) from *Nesokia indica* (top) and *Bandicota bengalensis* (bottom) shown in figures 20 and 21.

The species of *Nesokia* that was used in all these comparisons is *N. indica,* sometimes called a bandicoot rat, but more often referred to as a mole rat, or the short-tailed mole rat. In contrast to the species of *Bandicota,* which occur at tropical latitudes, the geographic range of *N. indica* is basically Palearctic and extends from parts of Bangladesh through northeast and northwest India, central Nepal, Pakistan, Afghanistan, Iran, Iraq,

Fig. 24. Occlusal views (enlarged to same size) of right maxillary molar rows in young *Bandicota* and *Nesokia*. **Left**, *Bandicota indica* (SMF 67872, CLM1–3 = 9.8 mm). **Middle**, *Nesokia indica* (AMNH 88907, CLM1–3 = 7.6 mm). **Right**, *Bandicota bengalensis* (AMNH 215706, CLM1–3 = 6.9 mm). Coronal surfaces of the two bandicoots are similar and differ from that of *Nesokia*. A discrete lingual ridge (**lr**) on cusp t8 is part of each first and second molar in *B. indica* and *B. bengalensis*; in both species the ridge is larger and more conspicuous on the second molar. Both species also have a prominent anterolingual cusp (**t1**) on each second and third molar. The molars of *Nesokia* have a laminar coronal pattern. The individual cusps that form each plate are barely discernible in juveniles similar to the one illustrated here, but not evident in adults. Cusp t1 is present on the first molar but absent from the second and third molars. The lingual margin of the posterior lamina of each first and second molar may be comparable to the lingual ridges seen in *Bandicota*.

Syria, Saudi Arabia, Israel, northeast Egypt, northwest China, Turkmenistan, Uzbekistan, and Tadzhikistan (Roberts, 1977; Corbet and Hill, 1992; Musser and Carleton, 1993).

Only one kind of fossorial *Nesokia* is currently recognized throughout this vast region. We accept this proposition for the purposes of our report but at the same time point out that at least 17 scientific names have been applied to different geographic samples, reflecting the appreciable variation in body size and fur coloration evident among series of specimens from different places (Ellerman, 1961; Corbet and Hill, 1992; Musser and Carleton, 1993). Whether one or several species is represented in the complex has yet to be determined by critical systematic revision.

Fig. 25. Occlusal views (approximately ×10) of right mandibular tooth rows from specimens in figure 24. **Left**, *Bandicota indica* (clm1–3 = 9.9). **Middle**, *Nesokia indica* (clm1–3 = 8.2). **Right**, *Bandicota bengalensis* (clm1–3 = 7.1 mm). Arrows point to a posterior cingulum on each first and second molar in *Bandicota indica*; a comparable cusp does not occur on molars of either *Nesokia* or *B. bengalensis*. The laminar cusp rows of *Nesokia* still retain the posterior labial cusplet (**plc**) on the first molar, and an anterior labial cusplet (**alc**) as well as a posterior labial cusplet on the second molar; comparable cusps are also part of the occlusal surface of *Bandicota*.

All the samples contain animals of about the same body size and build as *B. bengalensis*, but with a shorter tail relative to length of head and body (Roberts, 1977). *Nesokia indica* is probably the most fossorial of all the species in the Murinae. Their burrows, according to Roberts (1977: 276), are the most extensive of any fossorial rodent of similar body size. "Generally they consist of tunnels quite close to the surface (15 cm) . . . which may ramify up to 24 m . . . in length. . . . Mounds of loose earth are pushed up to the surface at intervals along these tunnels. These mounds conceal the entrances or exits of these burrows and have earned *Nesokia* its trivial name Mole Rat. Some of the burrow systems may extend to a depth of 60 cm." The rats feed primarily on underground bulbs and succulent grass roots. Adults rarely emerge above ground surface. Roberts (1977) has provided a good description of *N. indica* and an excellent summary of its distribution and biology.

The morphologies of *Nesokia* and *Bandicota* are similar but the closest resemblance is between *Nesokia indica* and *Bandicota bengalensis*. Both are similar in body size, have short tails, have a robust cranium in

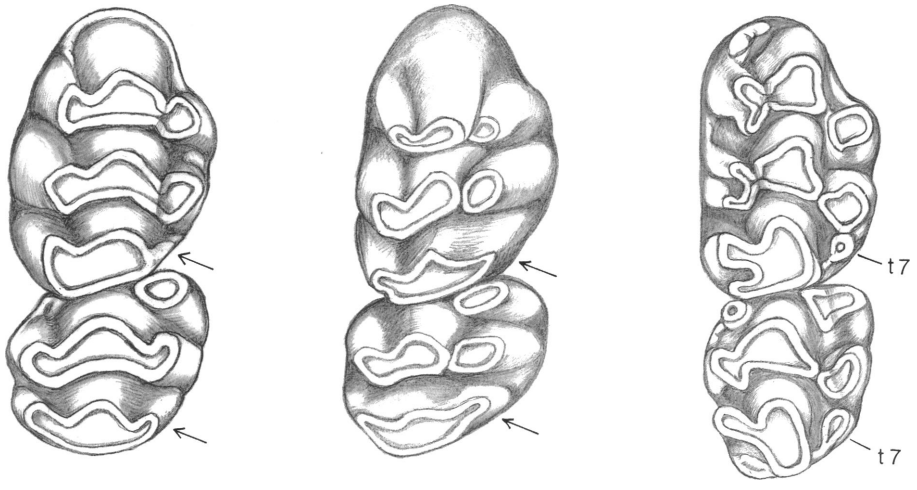

Fig. 26. The lingual ridge on cusp t8 contrasted with cusp t7 on first and second right maxillary molars. **Left**, *Rattus hoffmanni* (AMNH 224972); **middle**, *Bandicota indica* (SMF 67972); **right**, *Lenothrix canus* (USNM 488884). Arrows point to cusplike lingual margin of the large central cusp t8, which is part of the occlusal surfaces in all three species of *Bandicota,* and has been homologized with cusp t7 (Misonne, 1969; Niethammer, 1977). However, t7 is a discrete cusp on the posterolingual margin of the cingulum and not just a lingual ridgelike extension of the central cusp t8; its shape and placement relative to the adjacent cusp t8 and cusp t4 in front of it is exemplified by *Lenothrix.* We do not think the lingual ridge and cusp t7 are homologous. Although lingual ridges are characteristic of nearly all specimens of *Bandicota,* they are not peculiar to that genus. Comparable structures occur in low frequencies in most species of *Rattus,* and are common in *R. hoffmanni* (table 7). In many species, the lingual margin of cusp t8 is smooth and rounded, as shown by *Bunomys chrysocomus* on the opposite page (fig. 27). In others, such as species of *Bandicota* and some *Rattus,* the side of the cusp extends lingually in the form of a ridge, which increases the chewing surface.

which the nasals are shorter than the premaxillaries, have procumbent upper incisors, and lack posterior cingula on lower molars (figs. 20–25). These are some of the same features that separate *B. bengalensis* from the other species of *Bandicota.* The combination of chromosomal evidence, which suggests *B. bengalensis* to be more closely related to *N. indica* than to other species of *Bandicota* (Gadi and Sharma, 1983), and morphological data suggests that it is *B. bengalensis,* and not *B. indica* and *B. savilei,* that is the tropical counterpart of the Palearctic *N. indica.*

There are, however, features that separate *Nesokia indica* from all three species of *Bandicota.*

1. Claws on the front feet are longer, relative to size of the foot, than in any of the *Bandicota.*

2. Four pairs of mammae present (Begg et al., 1981); not less than five pairs and usually more in *Bandicota.*

3. Incisors are wider relative to rostral breadth and tend to be paler, sometimes only slightly pigmented.

4. Incisive foramina are very short and narrow, as contrasted with long and broad (fig. 21).

5. Bony palate ends anterior to the molar rows; the palate extends past the molars to form a narrow shelf in *Bandicota* (fig. 21).

6. Molars are much larger relative to size of dentaries and cranium (fig. 21), hypsodont, and their coronal surfaces consist of laminar rows in which the cusps are not evident in adults. In all species of *Bandicota,* the molars are relatively smaller, lower-crowned, and cuspidate, not laminar (figs. 24, 25).

7. Cusp t1 of the second and third molars is absent; this anterolingual cusp is a prominent part of the occlusal surface in all *Bandicota* (fig. 24).

8. The sex chromosomes are much larger (Gadi and Sharma, 1983). The sex chromo-

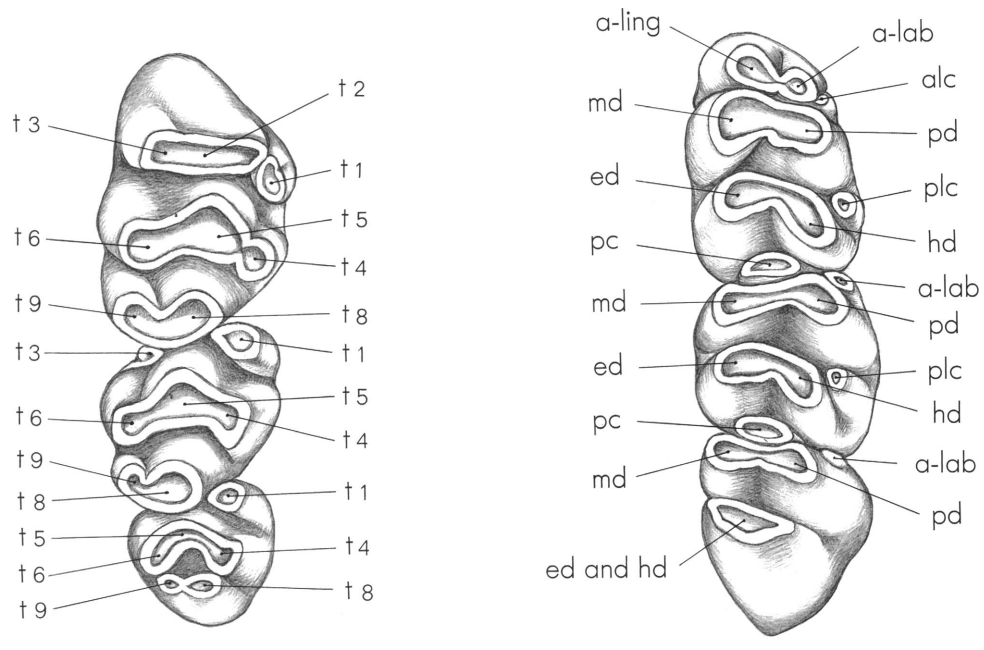

Fig. 27. Maxillary (left) and mandibular (right) molar rows from right side of *Bunomys chrysocomus* illustrating dental terminology. **Upper molars**: cusps are numbered according to Miller's scheme (see Musser and Newcomb, 1984) and referred to in the text with the prefix t. **Lower molars: a-lab**, anterolabial cusp; **a-ling**, anterolingual cusp; **hb**, hypoconid; **md**, metaconid; **ed**, entoconid; **pc**, posterior cingulum; **alc**, anterior labial cusplet; **plc**, posterior labial cusplet.

somes in *Bandicota* are larger than the sex chromosomes in most murines, but those of *Nesokia indica* are even greater in size.

All these are derived traits except length of incisive foramina and position of the back of the bony palate relative to the posterior margins of the molar rows (Musser and Newcomb, 1983).

Comparisons between *Bandicota* and *Nesokia* must now include another species of the latter than is not fossorial. A few specimens from the Basra Province of Iraq were described as *Erythronesokia bunnii,* a large animal about the size of *Bandicota indica* that, in addition to its unique features, also combined traits of *Nesokia* and *Bandicota* (Khajuria, 1981). This species contrasts with *Nesokia indica* not only by its much larger body size but in having a relatively longer tail covered with stiff white hairs, coarse reddish dorsal fur, and a whitish ventral coat. The skull and teeth resemble *Nesokia* except that the incisive foramina are relatively longer (but still very short compared with the configuration in *Bandicota*) and the upper incisors are recurved.

The very few specimens that have been collected of *Erythronesokia* were compared with examples of *Bandicota* and *Nesokia indica* by Al-Robaae and Felten (1990) who noted that most cranial proportions of *Erythronesokia* were closely similar to those of *Nesokia* and not *Bandicota.* While recognizing *bunnii* as very distinctive, they considered it to be a species of *Nesokia. Nesokia bunnii* is not fossorial. It apparently lives deep within swamps, is a good swimmer, and builds reed platforms above water level (Al-Robaae and Felten, 1990).

We now perceive *Nesokia* to contain at least two very distinctive species that are Palearctic in distribution. As a monophyletic group, they can be distinguished from the species of *Bandicota* by (1) four pairs of mammae (in *N. indica*; the count in *N. bunnii* has not been recorded); (2) short incisive foramina, ending well in front of the molar rows; (3) chunky, hypsodont molars that are large relative to

sizes of cranium and dentaries; (4) laminar molar occlusal surfaces; (5) no cusp t1 on second and third upper molars; and (6) large sex chromosomes (in *N. indica*; chromosomal complement of *N. bunnii* is unknown).

At the present time it would be premature to consolidate *Nesokia* and *Bandicota* into one genus. Certain traits, from the few morphological systems that have been surveyed, define each cluster of species as a monophyletic group. We accept this hypothesis until results from additional study proves otherwise. No critical analysis of phylogenetic relationships between *Nesokia* and *Bandicota* is available. Those that are published are based on very few morphological systems and limited sampling of taxa. Molecular studies are also inadequate. For example, the one electrophoretic analysis (Radtke and Niethammer, 1985) used only eight loci and the results, as Corbet and Hill (1992: 352) realized, "needs to be reassessed on a larger sample."

The following alternative hypotheses deserve testing by critical phylogenetic analyses.

1. The species now placed in *Bandicota* form a monophyletic group separate from the one containing the two species of *Nesokia.* To accept this hypothesis would require evidence that the morphological and chromosomal derivations shared by *B. bengalensis* and *N. indica* represent independent acquisitions by each species.

2. The species of *Bandicota* and *Nesokia* are more closely related to each other than to any other known murine and form a single monophyletic group with Palearctic and tropical components. The oldest name for this cluster would then be *Nesokia.* Corbet and Hill (1992: 352) explained that such "a combination of genera would cause considerable nomenclatural confusion" because the large bandicoot rat (*Bandicota indica* [Bechstein]) would have the name *Nesokia indica* (Bechstein) and the present *Nesokia indica* (Gray), the short-tailed mole rat, would become *N. hardwickei* (Gray).

Bandicota and Other Murines

Outside its postulated tie to *Nesokia,* the phylogenetic relationship of *Bandicota* to other genera in the subfamily Murinae is obscure. Several studies suggest otherwise, but they are marred by inadequate sampling of morphological and biochemical systems as well as taxa. The few studies published argue that *Bandicota* either is or is not related to *Rattus* and its relatives. Based entirely on study of dentitions, Misonne (1969: 116) placed the species of *Bandicota,* along with *Nesokia indica,* after the groups he defined as the *Lenothrix-Parapodemus* Division and the *Arvicanthis* Division "because they are certainly not related to the *Rattus* Division." On the other hand, Niethammer (1977) concluded that *Bandicota* and *Nesokia* are very closely related to *Rattus,* judged by his survey of dental traits, characters of the soft palate, and chromosomal features. Later, Gemmeke and Niethammer (1984: 104) studied several taxa and suggested that the "degree of kinship with *Rattus rattus* decreases in the following order: *Rattus tiomanicus, R. argentiventer, R. exulans* or *R. norvegicus, R. berdmorei, Bandicota, Maxomys surifer.*" Results from their survey of several morphological features, as well as electrophoretic data, support this hypothesis. While Misonne surveyed all living murine taxa, he was studying only one morphological system: traits associated with molar size and occlusal pattern. Gemmeke and Niethammer were the first to use more than one set of characters. Although they surveyed more taxa than did Niethammer (1977), their sampling was still inadequate in view of the many genera recognized within the Murinae (see Musser and Carleton, 1993).

Chromosomes also suggest an affinity between *Bandicota* and *Rattus.* Gadi and Sharma (1983: 36), for example, report that "G-band comparisons show that karyologically bandicoot-rats are quite close to *R. rattus* (subgenus *Rattus*) given the occurrence of a few pericentric inversions."

One dental feature found in *Bandicota* has probably influenced the notion that the genus is not closely related to *Rattus.* In all species of *Bandicota* there is a cusplike structure at the posterolingual margin of the first and second molars (figs. 24, 26). It is usually coalesced with the adjacent cusp t8 and has been interpreted to be a separate cusp, t7 (Misonne, 1969; Niethammer, 1977; Gemmeke and Niethammer, 1984). Most of the species

in Misonne's *Lenothrix-Parademus* Division are characterized by a cusp t7 but *Rattus* and its allies are not.

We looked closely at this cusplike structure in *Bandicota* and compared it with species in other genera having a discrete cusp t7. In those forms, such as *Lenothrix* (fig. 26), cusp t7 is a conspicuous and discrete structure on the cingular margin between cusp t8 and cusp t4 (see fig. 27 for a diagram of cusps and their names). It is always separate in young rats but after wear it is more likely to coalesce with cusp t4 rather than with the adjacent cusp t8. In contrast, the comparable structure in the species of *Bandicota* appears to be a ridgelike lingual extension of the large central cusp t8 that is better developed on the second molar than on the first (fig. 24). On many specimens of *Bandicota* (including those examples of *B. indica* and *B. bengalensis* shown in fig. 24) the structure is clearly a simple low ridge and not a cusp.

Although characteristic of all *Bandicota,* the lingual ridge also occurs at different frequencies in some species of *Rattus* (table 7) and probably in other murines. Within *Rattus,* the structure was found most frequently in our sample of 104 *Rattus hoffmanni* (fig. 26). On the first molars, 31 specimens lacked the lingual ridge, 67 had the ridge but it extended only halfway from alveolar level to occlusal plane, and six specimens had a distinct ridge—closely resembling that configuration in species of *Bandicota*—extending all the way to the occlusal surface. On the second molars, 11 lacked a ridge (the sides were smooth), 44 had the partial ridge that ended below the occlusal plane, and 49 specimens had a complete ridge extending from cingulum to occlusal surface, just like the conformation in *Bandicota.*

We suggest that the cusplike structure in *Bandicota* is really a lingual ridgelike extension of cusp t8 and is not homologous to cusp t7 in other murines. If we are correct, then the occlusal patterns found in *Bandicota* are actually quite similar to those characterizing some species of *Rattus*—*R. hoffmanni,* for example (fig. 26). *Bandicota* and *Rattus* share other traits, some primitive (cephalic arterial pattern, for example), others derived. Among the derived features that are shared is lack of an alisphenoid strut, long incisive foramina that extend between the first upper molars, a bony palate ending posterior to the molar rows, and multirooted molars (see Niethammer, 1977, for data on molar roots).

TABLE 7

Development of Lingual Ridge on Cusp t8 of First and Second Upper Molars in Some Species of *Rattus*

		Expression of ridge relative to wear surface		
	N	absent	below occlusal surface	level with surface
R. rattus	50			
M1		46	4	0
M2		45	4	1
R. norvegicus	50			
M1		46	4	0
M2		45	4	1
R. exulans	50			
M1		50	0	0
M2		50	0	0
R. nitidus	50			
M1		46	4	0
M2		46	4	0
R. losea	50			
M1		48	2	0
M2		50	2	2
R. hoffmanni	104			
M1		31	67	6
M2		11	44	49

The significance of these shared derivations cannot be assessed outside of a critical phylogenetic study. Such an inquiry must include surveys of more characters from different systems—morphological to molecular. It must also incorporate a broad representation of murine taxa, not just a few species of *Rattus* and one or two other genera, and not just Asian groups. Finally, both species of *Nesokia* should be included, not just *N. indica.* Results would really test the hypothesis that *Bandicota,* as well as *Nesokia,* are phylogenetically closer to *Rattus* and the genera related to it (see Musser and Newcomb, 1983; Musser and Carleton, 1993) than to *Lenothrix* or any of the genera placed by Misonne (1969) in the *Lenothrix-Parapodemus* Division or *Arvicanthis* Division.

REFERENCES

Agrawal, V. C., and S. Chakraborty
1976. Revision of the subspecies of the lesser bandicoot rat *Bandicota bengalensis* (Gray) (Rodentia: Muridae). Rec. Zool. Surv. India 69: 267–274.

Al-Robaae, K., and H. Felten
1990. Was ist *Erythronesokia* Khajuria, 1981 (Mammalia: Rodentia: Muridae)? Z. Saugetierkunde 55: 253–259.

Anderson, J.
1878. On *Arvicola indica,* Gray, and its relations to the subgenus *Nesokia,* with a description of the species of *Nesokia.* J. Asiatic Soc. Bengal 47(2): 214–234.

Bechstein, J. M.
1799/1800. Thomas Pennant's allgemeine Uebersicht der vierfussiger Theire. Weimar.

Begg, M. A., N. Adeeb, and S. A. Rana
1981. Oservations on reproduction in *Bandicota bengalensis* and *Nesokia indica.* Biologia 27(1): 45–50.

Blanford, W. T.
1891. The fauna of British India, including Ceylon and Burma. Part II: 251–617. London: Taylor and Francis.

Boonsong, P., and H. Felten
1989. Remarks on the genus *Bandicota* in Thailand (Rodentia: Muridae). Thai J. Agric. Sci. 22: 197–211.

Carleton, M. D., and G. G. Musser
1984. Muroid rodents. *In* S. Anderson and J. K. Jones, Jr. (eds.), Orders and families of recent mammals of the world, pp. 289–379. New York: Wiley.

Chasen, F. N.
1936. A note on Malaysian *Gunomys.* Bull. Raffles Mus. Singapore, Straits Settlement 12: 135–136.

Corbet, G. B., and J. E. Hill
1992. The mammals of the Indomalayan Region: a systematic review. London: British Museum (Nat. Hist.), 488 pp.

Dao Van Tien
1961. Recherches zoologiques dans la région de Thai-Nguêyn (Nord-Vietnam). Zool. Anz. 166: 298–308.
1972 or 1975. Ve các dang chuot dúi lón (*Bandicota indica*) (Rodentia: Muridae) o Viet Nam và vùng lân cân, Thông báo khoa hoc, Sinh vât hoc, Dai hoc tòng hop Hà Nôi, 6: 43–51. [Not seen by us; taken from Dao, 1985: 322, which we have examined. 1975 is the publication date listed there for *Bandicota indica sonlaensis* Dao in the checklist on page 276, but the only paper on *Bandicota* by Dao in the references has 1972 as its year of publication (p. 322).]
1985. Scientific results of some mammal surveys in North Vietnam (1957–1971). Ha Noi: Scientific and Technical Publishing House, 330 pp.

Dao Van Tien, and Cao Van Sung
1990. Six new Vietnamese rodents. Mammalia 54: 233–238.

Dubey, D. D., and R. Raman
1992. Mammalian sex chromosomes. IV. Replication heterogeneity in the late replicating facultative- and constitutive-heterochromatic regions in the X chromosomes of the mole rats, *Bandicota bengalensis* and *Nesokia indica.* Hereditas 115: 275–282.

Ellerman, J. R.
1941. The families and genera of living rodents, vol. 2. London: British Museum (Nat. Hist.), 690 pp.
1949. The families and genera of living rodents, vol. 3, pt. 1. London: British Museum (Nat. Hist.), 210 pp.
1961. The fauna of India including Pakistan, Burma and Ceylon. Mammalia, vol. 3, pt. 2. Delhi: Manager of Publications, pp. 483–884.

Ellerman, J. R., and T. C. S. Morrison-Scott
1951. Checklist of Palaearctic and Indian mammals, 1759 to 1946. London: British Museum (Nat. Hist.), 810 pp.

Elliot, W.
1839. A catalogue of the species of Mammalia found in the southern Mahratta country; with their synonimes in the native languages in use there. Madras J. Litt. Sci. 10: 92–108, 205–233.

Gadi, I. K., and T. Sharma
1983. Cytogenetic relationships in *Rattus, Cremnomys, Millardia, Nesokia* and *Bandicota* (Rodentia: Muridae). Genetica 61: 21–40.

Gemmeke, H., and J. Niethammer
1984. Zur Taxonomie der Gattung *Rattus* (Rodentia, Muridae). Z. Saugetierkunde 49: 104–116.

Gray, J. E.
1830–35. Illustrations of Indian zoology chiefly selected from the collection of Major-General Hardwicke, FRS. London.
1837. Description of some new or little known Mammalia principally in the British Museum. Mag. Nat. Hist. 1: 577–587.
1873. Notes on the rats; with the description

of some new species from Panama and the Aru Islands. Ann. Mag. Nat. Hist., ser. 4, 12: 416–419.

Hardwicke, T.
1804. Description of a large species of rat, a native of the East Indies. Trans. Linn. Soc. London 7: 306–308.

Harrison, J. L.
1956. Records of bandicoot rats (*Bandicota*, Rodentia, Muridae) new to the fauna of Malaya and Thailand. Bull. Raffles Mus., Singapore 27: 27–31.

Hodgson, B. H.
1836. Synoptical description of sundry new animals, enumerated in the Catalogue of Nipalese Mammals. J. Asiatic Soc. Bengal 5: 231–238.
1845. On the rats, mice, and shrews of the central region of Nepal. Ann. Mag. Nat. Hist., ser. 1, 15: 266–270.

Hoogstraal, H., and G. M. Kohls
1965. Southeast Asian *Haemaphysalis* ticks (Ixodoidea, Ixodidae). *H. bandicota* sp. n. from bandicoot rats in Taiwan, Thailand, and Burma. J. Parasitol. 51: 460–466.

Horsfield, T.
1824. Zoological research in Java, and the neighbouring islands. London: Kingsbury, Parbury, & Allen.
1855. Brief notices of several new or little-known species of Mammalia, lately discovered and collected in Nepal. Ann. Mag. Nat. Hist., ser. 2, 16: 101–114.

Kelaart, E. F.
1850. Description of additional mammals. J. Ceylon Branch R. Asiatic Soc. 2: 216–217.

Khajuria, H.
1981. A new bandicoot rat, *Erythronesokia bunnii* gen. et sp. nov. (Rodentia: Muridae) from Iraq. Bull. Nat. Hist. Res. Cent. Univ. Baghdad 7(4): 157–165.

Kishida, K.
1926. [Nezumi (rats and mice).] Dobutsu Kyôzai no Konponteki Kenkyû, 139–150. [Not seen; taken from Corbet and Hill, 1992: 447).]

Kloss, C. Boden
1919. On mammals collected in Siam. J. Nat. Hist. Soc. Siam 3: 333–407.
1921. Some rats and mice of the Malay Archipelago. Treubia 2: 115–124.

Kock, D., I. A. Nader, and A. A. Banaja
1990. *Bandicota bengalensis* (Gray and Hardwicke, 1833) new to Saudi Arabia (Mammalia: Rodentia: Muridae). Fauna of Saudi Arabia 11: 323–328.

Lathiya, S. B., and M. T. Akhtar
1981. Morphological variation between two ecological populations of *Bandicota bengalensis* in Pakistan. Pakistan J. Zool. 13: 261–264.

Lekagul, B., and J. A. McNeely
1977. Mammals of Thailand. Bangkok: Association for the Conservation of Wildlife, Sahakarnbhat Co., 758 pp.

Markvong, A., J. Marshall, and A. Gropp
1973. Chromosomes of rats and mice of Thailand. Bull. Siam Soc. Nat. Hist. 25: 23–40.

Marshall, J. T., Jr.
1977. Family Muridae: rats and mice. Reprinted *in* B. Lekagul and J. A. McNeely (eds.), Mammals of Thailand, pp. 396–487. Bangkok, Thailand: Assoc. Conserv. of Wildlife.

Matthey, R.
1956. La formule chromosomique de quelques Murinae (Murida-Rodentia-Mammalia). Arch. Julius Klaus-Stift. Vererbungsforsch. Sozialanthropol. Rassenhyg. 31: 294–306.

Misonne, X.
1969. African and Indo-Australian Muridae. Evolutionary trends. Mus. R. l'Afrique Cent. Tervuren Belg. Ann. Sci. Zool. 172: 219 pp.

Musser, G. G.
1970. Species-limits of *Rattus brahma*, a murid rodent of northeastern India and northern Burma. Am. Mus. Novitates 2406: 27 pp.
1979. Results of the Archbold Expeditions. No. 102. The species of *Chiropodomys*, arboreal mice of Indochina and the Malay Archipelago. Bull. Am. Mus. Nat. Hist. 162: 377–445.

Musser, G. G., and M. D. Carleton
1993. Family Muridae. *In* D. E. Wilson and D. M. Reeder (eds.), Mammals species of the world. A taxonomic and geographic reference, 2nd ed., pp. 501–755. Washington DC: Smithsonian Inst. Press.

Musser, G. G., and M. E. Holden
1991. Sulawesi rodents (Muridae: Murinae): morphological and geographical boundaries of species in the *Rattus hoffmanni* group and a new species from Pulau Peleng. *In* T. A. Griffiths and D. Klingener (eds.), Contributions to mammalogy in honor of Karl F. Koopman, pp. 322–413. Bull. Am. Mus. Nat. Hist. 206.

Musser, G. G., and C. Newcomb
1983. Malaysian murids and the giant rat of

Sumatra. Bull. Am. Mus. Nat. Hist. 174: 327–598.

Nehring, A.
1902. Herr A. Nehring sprach uber *Nesokia gracilis,* n. sp., von der Insel Ceylon. Stiz.-Ber. Ges. Nat. Fr. Berlin. No. 5: 116–121.

Niethammer, J.
1977. Versuch der rekonstruktion der phylogenetischen beziehungen zwischen einigen zentralasiatischen Muriden. Bonn. Zool. Beit. 28: 236–247.
1984. Die Zahl der Zitzen der Kleinen Bandikutratte, *Bandicota bengalensis* Gray et Hardwicke, 1833. Z. Saugetierkunde 49: 377–378.

O'Hara, R. J.
1994. Evolutionary history and the species problem. Am. Zool. 34: 12–22.

Otte, D., and J. A. Endler
1989. Speciation and its consequences. Sunderland, MA: Sinauer, 679 pp.

Patton, J. L., and M. F. Smith
1994. Paraphyly, polyphyly, and the nature of species boundaries in pocket gophers (genus *Thomomys*). Syst. Biol. 43(1): 11–26.

Phillips, W. W. A.
1936. The mole-rats (*Gunomys*) of Ceylon; with the description of a new race from the Jaffna Peninsula. Ceylon J. Sci.(B) 20(1): 93–97.

Pradhan, M. S., A. Mondal, and V. C. Agrawal
1989. Proposal of an additional species in the genus *Bandicota* Gray (Order: Rodentia; Fam: Muridae) from India. Mammalia 53: 369–376.

Qin, Yao-Ling
1985. Faunal composition and distribution of rodents in south China. *In* T. Kawamichi (ed.), Contemporary mammalogy in China and Japan. Mammal. Soc. Japan, 1985: 194 pp.

Radtke, M., and J. Niethammer
1985. Zur stellung der pestratte (*Nesokia indica*) im system der Murinae. Saug. Mitt. 32: 13–16.

Rickart, E. A., and G. G. Musser
1993. Philippine rodents: chromosomal characteristics and their significance for phylogenetic inference among 13 species (Rodentia: Muridae: Murinae). Am. Mus. Novitates 3064: 34 pp.

Roberts, T. J.
1977. The mammals of Pakistan. London: Ernest Benn.

Sclater, W. L.
1890. Notes on some Indian rats and mice. Proc. Zool. Soc. London 1890: 522–539, 610–613.

Shaw, G.
1801. General zoology. Mammalia, vol. 2, pt. 1. London, 553: 226 pp.

Smiet, A. C., A. R. Khokhar, and G. W. Fulk
1978. Geographic distribution and variation of *Bandicota bengalensis* in Pakistan. Pakistan J. Zool. 10(1): 43–47.

Thomas, O.
1881. On the Indian species of the genus *Mus.* Proc. Zool. Soc. London 1881: 519–557.
1907. A subdivision of the old genus *Nesokia,* with descriptions of three new members of the group, and of a *Mus* from the Andamans. Ann. Mag. Nat. Hist., ser. 7, 20: 202–207.
1916. The bandicoot of Mount Popa, and its allies. J. Bombay Nat. Hist. Soc. 24: 640–643.
1927. The Delacour exploration of French Indo-China—mammals. Proc. Zool. Soc. London 1927: 41–58.
1929. A new bandicoot-rat from western Siam. Ann. Mag. Nat. Hist., ser. 10, 3: 205.

Tiwari, K. K., R. K. Ghose, and S. Chakraborty
1971. Notes on a collection of small mammals from western Ghats, with remarks on the status of *Rattus refuscens* (Gray) and *Bandicota indica malabarica* (Shaw). J. Bombay Nat. Hist. Soc. 68: 378–384.

Tokuda, M.
1941. A revised monograph of the Japanese and Manchou-Korean Muridae. Biogeographia 4: 155 pp.

Tytler, R. C.
1854. Miscellaneous notes on the fauna of Dacca, including remarks made on the line of march from Barrackpore to that station. Ann. Mag. Nat. Hist., ser. 2, 14: 168–177.

Walton, D. W., J. E. Brooks, U M. M. Tun, and U H. Naing
1978. Observations on reproductive activity among female *Bandicota bengalensis* in Rangoon. Acta Theriol. 23, 33: 489–501.

Wroughton, R. C.
1908. Notes on the classification of the bandicoots. J. Bombay Nat. Hist. Soc. 18: 736–752.

APPENDIX 1

List of specimens we studied, from localities not included on the map in figure 1. Each specimen is identified by institutional acronym and catalog number.

Bandicota savilei

THAILAND

1. **Khon Kaen Province, Amphoe Phu Wiang, Tamb. Nai Huang, Banttin kong:** SMF 68748 (identified as "*Bandicota indica*").
2. **Thailand:** SMF 67758, 60181 (identified as "*varius*" and "*bangchakensis,*" respectively.

VIETNAM

3. **Vietnam ("Cochinchine"):** MNHN 1876-713.

Bandicota bengalensis

PAKISTAN

4. **North-West Frontier Province, Malakand District, Malakand, Amandara:** USNM 354359.
5. **North-West Fronier Province, Hazara District, Abbottabad, Ilyasi area:** USNM 369304–369306.
6. **Islamabad Province, Rawalpindi District, Barrian, 6 mi north of Murree:** USNM 369303.
7. **Islamabad Province, Rawalpindi District, Rawalpindi, Ayub National Park:** USNM 326673, 327148, 327150, 327152, 327153, 327155, 327156.
8. **Punjab Province, Gujrat District, 1 mi southeast of Mangowal:** USNM 369227, 413701, 413705–413707.
9. **Punjab Province, Sialkot District, Charwa village area:** USNM 354357, 354358.
10. **Punjab Province, Sialkot District, Kalian, Bajwat area:** USNM 369299.
11. **Punjab Province, Shekhupura District, Dage Nallah Sultan, 25 mi west of Lahore:** USNM 369212.
12. **Sindh Province, central Sindh Desert, Pithoro:** BMNH 8.9.13.7 (holotype of *Gunomys sindicus*).

INDIA

13. **Jammu and Kashmir, Punch district, Wardwan:** AMNH 55691.
14. **Jammu and Kashmir, Pandritton,** 5500 ft: BMNH 8.7.6.34 (holotype of *Gunomys wardi*).
15. **Jammu and Kashmir, Valley of Kashmir:** USNM 63465–63467, 176136.
16. **Himchal Pradesh, Kangra District, Dhantal,** 2000 ft: FMNH 83044, 83045.
17. **Himchal Pradesh, Kullu Valley:** FMNH 34025, 34026.
18. **Uttar Pradesh, Mussoorie:** FMNH 65401, 65409, 65412, 65413.
19. **Bengal Presidency, Mangpu:** FMNH 34838, 34839, 35663, 35664.
20. **West Bengal, Darjeeling, Pashok,** 3500 ft: FMNH 35290.
21. **West Bengal, Koch Bihār district, Haldibari:** FMNH 34856.
22. **West Bengal, Hugli District, Singur:** USNM 355833; **Bandicoot Pen of Singur:** FMNH 104637–104648; **Ratanpur, 23 mi northwest of Calcutta:** USNM 355712–355720; **New Market, 23 mi northwest of Calcutta:** USNM 355721; **Open Market:** USNM 355834.
23. **West Bengal, Hāora:** FMNH 104623–104628, 104635, 104651; **#6 Mullick Ghat Road:** AMNH 215720–215722; FMNH 104629–104634, 104636, 104649, 104650, 104652–104656.
24. **West Bengal, Calcutta:** NUS 6000–6002, 6004–6007, 6010, 6011, 6084–6086, 9029, 9030, 9033, 9050, 9051; USNM 154428–154433; **#2 Canal East Road:** AMNH 215639–215677, 215703; **102 Maharshi Debendra Road:** AMNH 215678–215702, 215704–215711; **Ālipūr District, Zoo Hospital:** AMNH 215712–215719.
25. **West Bengal, Twenty-four Parganas District, 9 mi south of Calcutta:** AMNH 215723, 215725, 215726.
26. **Assam, Palasbari:** FMNH 76425.
27. **Assam, Golaghat, Komtai,** 300 ft: FMNH 83037, 83038.
28. **Assam, northeast Assam, Digrugarh, Mishmi Hills:** AMNH 163126–163131, 163165.

29. **Madyah Pradesh, Balaghat district:** FMNH 65734, 65735.
30. **Maharashtra, Bombay City:** AMNH 208171, 208172.
31. **Maharashtra, Konkan region, Kulāba district:** BMNH 8.9.13.1 (holotype of *Gunomys lordi*).
32. **Deccan [plateau]:** BMNH 79.11.21.427 (holotype of *Mus daccaensis*).
33. **Karnataka, Dhārwad district:** BMNH ("lectotype" of *Mus kok*); **South Mahratta,** 2300 ft: FMNH 83039, 83040.
34. **Tamil Nadu, Nilgiri district, Nilgiri Hills,** 7000 ft: AMNH 163143, 163148, 163150, 163151.
35. **Tamil Nadu, Salem:** AMNH 171145.
36. **Tamil Nadu, Chen Galpattu district, near Therkupattu:** USNM 448796–448804.

SRI LANKA

37. **Northern Province, Thinney, near Jaffna:** BMNH 35.10.6.2 (holotype of *Mus kok insularis*).
38. **North Western Province, Kurunegala:** AMNH 240907, 240908.
39. **Central Province, Kandy:** AMNH 240905, 240906, 241541–241545.
40. **Western Province, Gonapola:** AMNH 240909.
41. **Western Province, Labugama,** 1000 ft: AMNH 240910.
42. **Sri Lanka:** BMNH 52.5.9.22 (holotype of *Mus dubius*).

NEPAL

43. **Kathmandu:** AMNH 251666, 251667; USNM 290082.
44. **Hetauda (Hetauri),** 1700 ft: AMNH 251668–251670.
45. **Nepal:** BMNH 79.11.21.426 (holotype of *Mus tarayensis*); BMNH 79.11.21.408 (holotype of *Mus morungensis*); BMNH 79.11.21.409 (holotype of *Mus plurimammis*).

BHUTAN

46. **Gaylegphang:** USNM 564557.

BANGLADESH

47. **Kasimpur BADC, 30 km northwest of Dhaka:** AMNH 249889, 249890.
48. **Dhaka, Naya Kandi:** AMNH 249891.

INDONESIA

49. **Sumatra, Aceh, northern Sumatra:** NUS 7/23, 8/23.

Bandicota indica

INDIA

50. **Uttar Pradesh, Haridwar:** BMNH 60.5.4.84 (holotype of *Mus giganteus*).
51. **West Bengal, Singur, 23 mi northwest of Calcutta:** USNM 355718; **near Apurbapur:** USNM 355722.
52. **West Bengal, Calcutta:** BMNH 8.3.22.1, 8.3.22.2; USNM 154452, 154453.
53. **Assam, Meghalaya district, Khāsi Hills:** BMNH 91.10.7.114, 91.10.7.115; FMNH 76426–76430, 84880.
54. **Maharashtra, Chanda district:** FMNH 29781–29787.
55. **Maharashtra, Bombay City:** AMNH 208179.
56. **Andhra Pradesh, Madhavaram, Vontimitta Range:** FMNH 83051.
57. **Andhra Pradesh, Palkonda Hills:** FMNH 83046.
58. **Karnataka, Mysore, Billigrisangen Hills:** AMNH 112973, 112974.

SRI LANKA

59. **Northern Province, Kankesanturi:** AMNH 240912.
60. **North Western Province, Polgahawela:** USNM 257418, 257419, 258239.
61. **Central Province, Talawakele:** AMNH 240964, 240965.
62. **Central Province, Nuwara Eliya:** AMNH 240963; USNM 257971.
63. **Central Province, Boragas:** AMNH 240911.
64. **Western Province, Gonapola:** AMNH 249666; FMNH 95015, 95016.
65. **Western Province, Labugama:** AMNH 240967.
66. **Sri Lanka:** AMNH 241546.

NEPAL

67. **Balaju,** 4400 ft: FMNH 104383.
68. **Gorkhā:** BMNH 23.11.5.29.
69. **Kathmandu:** AMNH 251671–251676; BMNH 37.3.14.19; FMNH 104382.
70. **Nepal:** BMNH 10.4.15.1, 43.1.12.67

(lectotype of *Mus* (*Rattus*) *nemorivagus*), 43.1.12.68 (lectoparatype of *Mus* (*Rattus*) *nemorivagus*), 43.1.12.70, 43.1.12.128, 45.1.8.28b (holotype of *Mus macropus*).

BURMA

71. **Kachin State, Namti, 35 mi west Myitkyina:** LACM 10508.
72. **Kachin State, 8 mi north of Myitkyina:** USNM 279312.
73. **Kachin State, Myitkyina:** USNM 279311.

CHINA

74. **Yunnan Province:** BMNH 12.7.25.43; **Tengchong:** BMNH 12.7.15.4, 12.7.24.4, 13.12.8.22.
75. **Taiwan Province, Taibei (T'aipei) Hsien, Alilao [approximately 4.5 km west-southwest of Shih-men]:** AMNH 185126, 185127; USNM 330261–330264, 330265, 330273–330276, 330279–330282, 333151–333155, 333156.
76. **Taiwan Province, Taibei Hsien, Linkou:** USNM 358588.
77. **Taiwan Province, Taibei Hsien, Yung Foh Lee, 6 mi north of Taibei:** AMNH 183138, 183139, 184545–184547, 330286; USNM 330249, 330255, 330266–330269; **Grass Mountain:** USNM 313689, 313691–313696, 313698–313708, 313710, 313711; **Yang Min Shan:** USNM 333150.
78. **Taiwan Province, Taibei Hsien, Taibei, Sung Shan AFB:** USNM 358560, 358561.
79. **Taiwan Province, Taibei Hsien:** USNM 358601; **Mount Ro-cha-li:** USNM 283756; **Chu-ko:** USNM 283757.
80. **Taiwan Province, Taoyuan Hsien, Taoyuan:** USNM 333157.
81. **Taiwan Province, Miaoli Hsien, Dahu (Tahu):** USNM 358559, 358600.
82. **Taiwan Province, Taizhong (T'aichung) Hsien, Ma-an lio, 6 mi south of Dongshi (Tung Shi):** USNM 294283–294289.
83. **Taiwan Province, Nantou Hsien, Puli:** USNM 313709; **Mount Farming area:** AMNH 183137.
84. **Taiwan Province, Gaoxiong (Kao-hsiung) Hsien, Mei-nung:** USNM 333158–333161.
85. **Taiwan Province, Gaoxiong Hsien, Gaoxiong:** USNM 358562.
86. **Taiwan Province, Pingdong (P'ingtung) Hsien, Chao-chou:** AMNH 185128, 185129; USNM 313690, 313697, 330250–330254, 330256–330260, 330270–330272, 330277, 330278, 330283–330285; **Ssu-lin:** USNM 355843.
87. **Taiwan Province, Pingdong Hsien, S-tze:** USNM 358556.
88. **Taiwan Province, Pingdong Hsien, Hengchun:** USNM 358563, 358564; **San-Chiao li:** USNM 358565.
89. **Taiwan Province, Pingdong Hsien, Manzhou (Manchou):** USNM 358637.
90. **Taiwan Province:** BMNH 40.2.10.53, 40.2.10.55; USNM 283758, 297864, 358638; **Sun Moon Lake:** USNM 311283; **Teraso:** AMNH 31610, 31611, 31623.

THAILAND

91. **Songkhla Province, A. Sathing Phra, Bokhan:** SMF 67927; SMF 67889, 67890 (identified as "*Bandicota savilei*").
92. **Phatthalung Province, Amphoe Phatthalung, Khuan Kut:** SMF 67831, 67832, 67912-67914.
93. **Nakhon Si Thammarat Province, Amphoe Pak Phanang:** SMF 67846–67849, 67918.
94. **Chainat Province, Amphoe Chainat, Thammamun:** SMF 67893.
95. **Thailand:** USNM 300169; SMF 60171, 60173–60175, 60178, 60182–60186, 67850, 67851, 67919, 67921.

INDONESIA

96. **Java, Java Barat Province, Jakarta, Ancol:** AMNH 229880–229884; USNM 533925, 533926; **Sunter:** AMNH 229890–229895, 252273–252320; **near Jakarta:** USNM 449947–449959.
97. **Java, Java Barat Province, Cirebon:** AMNH 101552–101561, 101701, 101709, 102173, 102174, 102222–102225.
98. **Java:** BMNH (cotype of *Mus setifer*); **Rawasari:** AMNH 229885–229889.

APPENDIX 2

Specimens we examined (identified by institutional acronym and catalog number) from localities that are plotted on the map in figure 1. Number preceding each place corresponds to a numbered symbol on the map.

Bandicota savilei (localities 1–42)

BURMA

1. **Mandalay Division, Myingyan:** AMNH 267633 and 267634.
2. **Mandalay Division, 20 km north of Meiktila;** AMNH 163695 and 163696.
3. **Mandalay Division, Mount Popa,** 1500 m: BMNH 14.7.19.211 (holotype of *Bandicota savilei*), BMNH 14.7.19.212–14.7.19.215, 27.11.18.42; NUS 3765.
4. **Mandalay Division, Pagan:** BMNH 14.7.19.216.

THAILAND

5. **Tak Province, 40 mi northwest of Tak,** 137 m (16°52′N, 99°07′E): BMNH 28.5.3.2 (holotype of *Bandicota savilei curtata,* "Raheng"), 28.5.3.3; USNM 253589, 253590, 253592; NUS 17, 18, 22, 24.
6. **Tak Province, 20 mi northwest of Tak:** AMNH 239622, 239623, 240133.
7. **Phitsanulok Province, Wang Thong** (16°45′N, 100°35′E): uncataloged specimen in RPRC.
8. **Kamphaeng Phet Province, Ban Mae Na Rae, 4 km southwest of Na Bokham,** 200 m (16°25′N, 99°23′E): RFD 182, 183, 184.
9. **Kamphaeng Phet Province, Amphoe Khlong Khlung** (16°00′N, 99°40′E): USNM 297167.
10. **Phetchabun Province, Phetchabun** (16°25′N, 101°09′E): uncataloged specimen in RPRC.
11. **Chaiyaphum Province, Phu Khieo, Ban Lat** (16°24′N, 102°02′E): USNM 294949–294952.
12. **Chaiyaphum Province, Phu Khieo, Ban Non Khun** (16°30′N, 102°04′E): USNM 308220, 308221.
13. **Khon Kaen Province, Khon Khaen** (16°25′N, 102°50′E): uncataloged specimen in the RPRC.
14. **Nakhon Sawan Province, Nakhon Sawan** (15°42′N, 100°08′E): USNM 297166.
15. **Chai Nat Province, Amphoe Chai Nat, Muang Chai Nat** (15°11′N, 100°07′E): uncataloged specimen in RPRC; **Thammamun** (15°10′N, 100°05′E): SMF 677-41–67744 (identified as "*Bandicota bengalensis*" by Boonsong and Felten, 1989); SMF 60167, 67750–67752, 67859 (identified as "*Bandicota varius*" by Boonsong and Felten, 1989).
16. **Lop Buri Province, Khok Samrong** (15°05′N, 100°04′E): SMF 67745, 67746 (identified as "*Bandicota bengalensis*" by Boonsong and Felten, 1989); SMF 67753–67755 (identified as "*Bandicota varius*" by Boonsong and Felten, 1989).
17. **Lop Buri Province, Mount Erawan** (14°48′N, 100°40′E): USNM 297168.
18. **Nakhon Ratchasima Province, Pak Chong** (14°42′N, 101°25′E): AMNH 239624; ASRCT 54-857 to 54-868; FTM 101, 168, 170, 178, 179; NUS 6051–6053; (14°41′N, 101°25′E): SMF 60166 (identified as "*Bandicota bangchakensis*" by Boonsong and Felten, 1989); SMF 60165, 67749 (identified as "*Bandicota varius*" by Boonsong and Felten, 1989).
19. **Nakhon Ratchasima Province, Pak Thong Chai, Sakaerat District** (14°36′N, 102°02′E): SMRL 1144. **Ban Lum Ngoern** (14°35′N, 102°00′E): AMNH 241647, 241648. **Ban Ba Dan** (14°34′N, 101°59′E): AMNH 214645, 241646.
20. **Sara Buri Province, Kaeng Khoi District, Muek Lek** (14°39′N, 101°12′E): USNM 300168.
21. **Sara Buri Province, Kaeng Khoi District** (14°35′N, 101°00′E): ASRCT 54-1280 to 54-1282. **Phu Nam Tok Thap Kwang, 21 km east northeast of Sara Buri,** 130 m (14°35′N, 101°02′E): AMNH 239620, 239621, 240127–240131; USNM 533-935, 533937.
22. **Kanchanaburi Province, Bo Phloi** (14°19′N, 99°30′E): BS 506, 513.
23. **Kanchanaburi Province, Ban Kho Klang** (14°00′N, 99°33′E): AMNH 240126; USNM 533936.
24. **Nakhon Pathom Province, Amphoe Bang**

Len, Don Tum (14°02′N, 100°20′E): SMF 67756 (identified as "*Bandicota varius*" by Boonsong and Felten, 1989).

25. **Nakkon Pathom Province, Phrong Madua** (13°49′N, 99°59′E): ASRCT 54-855, 54-856.
26. **Ratchaburi Province, Ban Pong** (13°47′N, 99°45′E): BS M2, M3, and RE446; USNM 294954, 296545.
27. **Rachaburi Province, Pak Tho Khao Jeen** (13°23′N, 99°51′E): USNM 296546.
28. **Ratchaburi Province, Chom Bung, Thung Nok Ka Rien** 13°21′N, 99°46′E): BS Y114, 117, 124, 135, 151; USNM 294955, 294956.
29. **Nakhon Nayok Province, Sarika Falls** (14°16′N, 101°17′E): AMNH 239618; **Sangkha:** AMNH 239619; ASRCT 54-869 to 54-878; FTM 238, 242.
30. **Prachin Buri Province, Sa Kaeo** (13°55′N, 102°05′E): uncataloged specimen in RPRC.
31. **Chanthaburi Province, Pong Nam Ron, northeast base of Khao Soi Dao Tai,** 220 m (12°56′N, 102°13′E): ASRCT 54-884, KT nos. 2380, 2387.
32. **Ubon Ratchathani Province, Amphoe Phimun Mangsahan, Chong Mek** (15°08′N, 105°28′E): ASRCT 54-854.
33. **Prachuap Khiri Khan Province, Amphoe Pran Buri, Khao Rai** (13°04′N, 99°45′E): SMF 67856, 67857 (identified as "*Bandicota bengalensis*").
34. **Prachuap Khiri Khan Province, Amphoe Pran Buri, Tambon Silaloi, Ban Na Pum** (12°30′N, 99°00′E): SMF 67747, 67748, 67755 (identified as "*Bandicota bengalensis*" by Boonsong and Felten, 1989).
35. **Nakhon Si Thammarat Province, Amphoe Nakhon Si Thammarat, Bang Chak,** 2 m (08°30′N, 100°00′E): SMF 67757 (identified as "*Bandicota varius*" by Boonsong and Felten, 1989); SMF 67852 (holotype of "*Bandicota bangchakensis*").
36. **Songkhla Province, Amphoe Rattaphum, Kam Phaeng Phet** (7°08′N, 100°16′E): SMF 67858 (identified as "*Bandicota bengalensis*").

VIETNAM

37. **Dac Lac Province, Ban Me Thuot** (12°40′N, 108°03′E): FMNH 46808–46816.
38. **Dac Lac Province, Poste de Mdrak,** 400 m (Mdrak 12°42′N, 108°47′E): USNM 321519, 321520.
39. **Lam Dong Province, Ngoc So'n (Fyan),** 1200 m (11°53′N, 108°12′E): USNM 321521, 321522.
40. **Lam Dong Province, 3 km southwest of Kala,** 1300 m (11°34′N, 108°07′E): USNM 321517, 321518.
41. **Bin Thuan (Hau Giang) Province, Cu Chi** (10°58′N, 106°28′E): USNM 35763–35765.
42. **Dong Nai Province, Bien Hoa** (10°57′N, 106°49′E): USNM 357566.

Bandicota indica (localities 43–99)

BURMA

43. **Mon State, Toungoo (west),** 33 m: BMNH 27.11.18.41.
44. **Pegu Division, Vitkangale, 12 mi southeast of Pegu,** 9 m: BMNH 17.4.24.31, 27.11.18.39, 27.11.18.40; FMNH 83047, 83048.
45. **Pegu Division, Kyinigyuang, 30 mi southeast of Pegu,** 1.5 m: BMNH 17.4.24.32, 17.4.24.33.

THAILAND

46. **Chiang Rai Province, Mae Suai, Ban Huai Khrai** (20°21′N, 99°50′E): ASRCT 54-922.
47. **Chiang Mai Province, Amphoe Mae Taeng, Ban Khi Lek Noi** (19°07′N, 98°57′E): ASRCT 54-901 to 54-904; USNM 355315–355318; **Chiang Mai Province, Amphoe San Sai, Ban Pong, across river from Ban Khi Lek Noi:** USNM 355320–355324.
48. **Chiang Mai Province, Amphoe Mae Rim, Kilek:** USNM 533932.
49. **Chiang Mai Province Nong Han (Nam Muang Mae Nong Han), 20 km northnortheast of Chiang Mai** (18°53′N, 99°00′E): SMF 60164; SMF 67891, 67892 (identified as "*Bandicota savilei*").
50. **Chiang Mai Province, Amphoe Chiang Mai, Ban Chang Khien** (18°49′N, 99°00′E: USNM 355313, 355314; **"Chiang Mai" only:** ANSP 15329, 15330; BMNH 9.10.11.24 (holotype of *Bandicota mordax*); USNM 260636.
51. **Chiang Mai Province, Amphoe Saraphi**

(18°41′N, 99°02): **Champhu:** USNM 533931; **Ban Pak Muang (Ban Khua Mung)** (18°40′N, 99°05′E): ASRCT 54-905 to 54-907.

52. **Chiang Mai Province, Amphoe San Kamphaeng:** USNM 533934; **Ban Sai Mun** (18°40′N, 99°10′E): ASRCT 54-920.
53. **Lampang Province, Doi Khun Tan,** from near summit at 1220 m (18°30′N, 99°16′E): USNM 533929.
54. **Chiang Mai Province, Amphoe San Pa Tong** (approximately 18°40′N, 98°50′E): **Ban Hua Rin:** USNM 355319; **Pa Kwe:** AMNH 167929–167932; **Ban Mae Kung Bok:** ASRCT 54-908, 54-915; **Ban Tha Lo:** ASRCT 54-909 to 54-914, 54-917 to 54-919; **Ban Rong:** ASRCT 54-916.
55. **Nan Province, Muang Nan** (18°46′N, 100°41′E): ASRCT 54-921.
56. **Nong Khai Province, Nong Khai, Ban Non Sang** (17°53′N, 102°48′E): ASRCT 54-898.
57. **Udon Thani Province, Udon Thani** (17°24′N, 102°36′E): **Ban Nong Si:** USNM 355327; **Ban Makhaeng:** USNM 355328; **Ban Nong Bua:** ASCRT 54-924; USNM 355325, 355326.
58. **Udon Thani Province, Amphoe Nong Bua Lamphu, Nam Tok Thao To** (17°13′N, 102°47′E): ASRCT 54-923.
59. **Chaiyaphum Province, Phu Khieo, Ban Don Tao Lek** (16°24′N, 102°02′E): USNM 294953.
60. **Khon Kaen Province, Chum Phae** (16°40′N, 102°00′E): USNM 297165.
61. **Khon Kaen Province, Amphoe Khon Kaen, Don Kun** (16°30′N, 102°45′E): SMF 67804, 67805.
62. **Khon Kaen Province, Khon Kaen Muang** (16°25′N, 102°50′E): USNM 300165–300167.
63. **Khon Kaen Province, Khon Kaen Muang, Ban Nong Waeng** (16°21′N, 102°48′E): uncataloged specimen at ASRCT.
64. **Kalasin Province, Kalasin Muang** (16°25′N, 103°30′E); FTM SP no. 50.
65. **Maha Sarakham Province, Ban Khe Wha** (16°08′N, 103°20′E): ASRCT 54-925.
66. **Chai Nat Province, Amphoe Chai Nat, Thammamun** (15°10′N, 100°05′E): SMF 60168, 60169, 67800–67803; SMF 67860 (identified as "*Bandicota savilei*").
67. **Nakkon Ratchasima Province, Nakhon Ratchasima** (14°58′N, 102°06′E): FTM M no. 50; USNM 296547.
68. **Nakhon Ratchasima Province, Pak Thong Chai: Ban Po Daeng** (14°36.5′N, 102°01′E): AMNH 241652–241655; USNM 533933; **Ban Ba Dan** (14°34′N, 101°58.5′E): AMNH 241649, 241650, 241653–241655; **Ban Ba Yai** (14°33′N, 101°59′E): AMNH 241651.
69. **Nakhon Nayok Province, Sarika Falls** (14°16′N, 101°17′E): ASRCT 54-899, 54-900.
70. **Ang Thong Province, Amphoe Wiset Chai Chan** (14°45′N, 100°30′E): SMF 67799; SMF 67759 (identified as "*Bandicota savilei*" by Boonsong and Felten, 1989).
71. **Suphan Buri Province, (north of) Suphan Buri** (14°14′N, 100°07′E): ASRCT 54-885 to 54-897; FTM 215, 217, 222; USNM 533927.
72. **Nakhon Pathom Province, Amphoe Bang Len, Don Tum** (14°02′N, 100°20′E): SMF 60176, 60177, 60180, 67774–67787, 67789–67798, 67894–67899, 67920, 67924; SMF 67862–67868 (identified as "*Bandicota savilei*").
73. **Ratchaburi Province, Ban Pong, Ban Pak Rat** (13°47′N, 99°45′E): USNM 296548.
74. **Mahanakhon Krung Thep Province, Bang Khen** (13°47′N, 99°45′E): **Soi Thong Yoo:** ASRCT 54-16544; **Kasetsart University:** AMNH 215207, 215208, 239628.
75. **Mahanakhon Krung Thep Province, Bangkok:** NUS 26: USNM 241070, 533930; **Lumphini** (13°46′N, 100°29′E): ASRCT 54-879 (Wireless Road), ASRCT 54-880, 54-881; **vicinity of SEATO Laboratory:** AMNH 239625–239627, 240-125.
76. **Samut Sakhon Province, Samut Sakhon (Tachin)** (village of Pak Bu, in ricefields near mouth of Tachin River, about 20 mi west of Bangkok): USNM 221559 (holotype of *Bandicota siamensis*).
77. **Chon Buri Province, Ban Bang Lamung, Mab Huai Some** (12°58′N, 100°54′E): ASRCT 54-882.
78. **Chon Buri Province, Ban Phatthaya** (12°55′N, 100°52′E): ASRCT 54-883, 54-1642, 54-1643, KT nos. 5892, 5893;

Chotsan: ASRCT SP no. 92, S no. 279.

79. **Chon Buri Province, Amphoe Sattahip, Ko Kram** (12°42′N, 100°47′E): ASRCT KT nos. 2009–2011, 2013, 2014, 2043, 2044, 2199.
80. **Chanthaburi Province, Pong Nam Rong, northeast base of Khao Soi Dao Tai,** 220 m (12°56′N, 102°13′E): ASRCT KT no. 2379.
81. **Chanthaburi Province, Chanthaburi Muang, Phlui Horticultural Station** (12°32′N, 102°08′E): SMF 60170.
82. **Trat Province, Amphoe Laem Ngop** (12°05′N, 102°15′E): SMF 67807, 67808, 67916, 67917.
83. **Phetchaburi Province, Amphoe Phetchaburi, Ban Don Makham Chang** (13°05′N, 99°45′E): SMF 67809–67830, 67902–67911, 67925; SMF 67760–67767, 67881–67886 (most identified as "*Bandicota savilei*" by Boonsong and Felten, 1989).
84. **Prachuap Khiri Khan Province, Amphoe Pran Buri, Tambon Silaloi, Ban Na Pum** (12°30′N, 99°00′E): SMF 60172; SMF 67861 (identified as "*Bandicota savilei*").
85. **Nakhon Si Thammarat Province, Amphoe Nakhon Si Thammarat, Bang Chak** (08°30′N, 100°15′E): SMF 67835–67845, 67900, 67901; SMF 67768, 67771, 67772, 67869–67880, 72800 (most identified as "*Bandicota savilei*" by Boonsong and Felten, 1989).
86. **Songkhla Province, Amphoe Rattaphum, Kam Phaeng Phet** (07°08′N, 100°16′E): SMF 67833, 67834, 67915, 67926; SMF 67769, 67770 (identified as "*Bandicota savilei*" by Boonsong and Felten, 1989); SMF 67887, 67888, (identified as "*Bandicota savilei*").

MALAYSIA

87. **Malay Peninsula, Kedah State, Alur Setar, Kuala Jerlun:** USNM 489307, 489308.

LAOS

88. **Phong Saly Province, Phong Saly,** 1342 m. FMNH 31987, 31990.
89. **Xieng Khouang Province, Ban Theoung, 18 km northwest of Xieng Khouang:** USNM 355551.

VIETNAM

90. **Quang Tri Province, Quang Tri** (16°45′N, 107°13′E), 14 km southeast of Hue on Highway 1: USNM 356566.
91. **Quang Tri Province, Xom Cham,** 450m (16°39′N, 106°44′E): USNM 356927.
92. **Thua Thien Province, Hue** (16°28′N, 107°36′E): USNM 355550.
93. **Quang Nam-Da Nang Province, Da Nang** (16°04′N, 108°13′E): USNM 356565, 356928; **Naval Hospital:** USNM 358070; **Xom Da Me:** BMNH 26.10.4.143 (holotype of *Bandicota jabouillei*); USNM 356817.
94. **Bin Thuan (Hau Giang) Province, Cu Chi** (10°58′N, 106°28′E): USNM 357567.
95. **Dong Nai Province, Bien Hoa** (10°57′N, 106°49′E): USNM 357569, 357570.
96. **Ho Chi Minh Province, Gia Dinh, Thau Son Nhat Airport:** USNM 356569.
97. **Ba Ria-Vung Tau Province, Ap Phuoc Tuy** (10°21′N, 107°04′E): USNM 356567.
98. **Tien Giang Province, Dinh Tuong area, Dong Tam** (10°21′N, 106°21′E), northwest of My Tho: USNM 357568.
99. **Soc Trang Province, Soc Trang Airfield,** Rach Ba Xuyen [stream] (09°36′N, 105°58′E): USNM 356568.

Bandicota bengalensis
(localities 100–107)

BURMA

100. **Mandalay Division, Taungtha** (21°16′N, 95°25′E): AMNH 267631, 267632.
101. **Pegu Division, Pyè (Prome),** 133 m (18°50′N, 95°14′E): BMNH 27.11.18.43.
102. **Pegu Division, Toungoo (west),** 33 m: BMNH 27.11.18.28, 27.11.18.29, 27.11.18.44; **6 mi east of Toungoo:** FMNH 83043.
103. **Pegu Division, Tharawaddy,** 33 m: FMNH 83042.
104. **Pegu Division, Vitkangale, 12 mi south of Pegu,** 9 m: BMNH 17.4.24.7, 17.4.24.28, 17.4.24.29.
105. **Yangon (Rangoon) Division, Yangon (Rangoon):** NUS 19154, 19159, 19162.
106. **Tenasserim Division, Mergui:** BMNH 14.12.8.214, 23.11.11.3.

MALAYSIA

107. **Malay Peninsula, Pinang State, Pinang Island, George Town:** BMNH 98.8.3.3 (holotype of *Bandicota varius*), BMNH 98.8.3.5 (holotype of *Bandicota varillus*); NUS 19228, 19231–19234, 19236–19238, 19240, 19241, 19243–19246.

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