

## A taxonomic revision of the *Tragul* mouse-deer (Artiodactyla)

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*Received October 2002; accepted for publication July 2003*

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The taxonomy of South-East Asian mouse-deer (*Tragulus*) is complex, and after some 120 years of considerable taxonomic revisions of the genus a clear key is still lacking for the determination of species and subspecies. Through craniometrical analysis of 338 skulls of *Tragulus* and some study of coat coloration patterns we have come to a better understanding of mouse-deer taxonomy. Our results show that there are three species groups: the *T. javanicus*-group, the *T. napu*-group, and *T. versicolor*. Within the *T. javanicus*-group we recognize three species: *T. javanicus* (from Java), *T. williamsoni* (from northern Thailand and possibly southern China), and *T. kanchil* (from the rest of the range), and within these species we provisionally recognize 16 subspecies. Within the *T. napu*-group we recognize two species: *T. nigricans* (from Balabac), and *T. napu* (from the rest of the range); within these species we provisionally recognize eight subspecies. *T. versicolor* from Nhatrang, south-east Vietnam, is distinct from the two previous groups; it is, however, unclear whether this species is still extant. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **140**, 63–102.

**ADDITIONAL KEYWORDS:** chevrotain – coat colours – craniometrics – island fauna – South-East Asia – taxonomy – *Tragulidae*.

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### INTRODUCTION

The chevrotains or mouse-deer (*Tragulidae*) are an ancient group of ungulates, with a shared history dating back to the Miocene. They are considered the sister-group of the remaining living Ruminantia (Groves & Grubb, 1982). In southern Asia, they are found in fossil assemblages dated at 18 million years before present (Myr), although they reached their highest diversity with five named and 52 unnamed species at around 11.5 Myr (Barry *et al.*, 1991). Between 16 and 14 Myr, they were also common in the area that is now northern Thailand, although species diversity may have been low (Ducrocq *et al.*, 1994). After 9 Myr, the tragulid family declined significantly in diversity in southern Asia (Barry *et al.*, 1991), which may have been caused by the evolution of more open vegetation types. Presently there are three genera left, of which two, *Moschiola* and *Tragulus*, occur in the South and South-East Asian region.

Smit-van Dort (1989) studied the morphological differences between the four conventionally recognized species of tragulids, i.e. the African *Hyemoschus aquaticus*, *Moschiola meminna*, *Tragulus javanicus*, and *T. napu*. She could separate the two *Tragulus* species only by using metrical characters in the skeleton, i.e. the greater mouse-deer *T. napu* has stronger and broader feet than the lesser mouse-deer *T. javanicus*. Skull dimensions of *T. napu* and *T. javanicus*, especially in specimens from small islands, converged to such an extent that the two species could not be reliably separated using skull characters (also see van Dort, 1988). Skin patterns do differ between the two species, with *T. napu* having mottled fur and light superciliary lines on the head, whereas *T. javanicus* normally has three strong white lines on the throat and has uniformly coloured upperparts (Smit-van Dort, 1989). There is, however, considerable variation within each species in the coloration and striping patterns, especially on the many islands where the species occur, and in several instances it is nearly impossible to determine whether a taxon is more closely related to *T. napu* or to *T. javanicus*. In fact,

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Groves (1989) considered the two to be sibling species. Based on this geographical variation, Chasen (1940), the first major reviser of *Tragulus*, recorded 27 subspecies for *T. napu* and 26 for *T. javanicus* (some of which he had reallocated from one to the other) for the Malayan region, and at least ten more subspecies, primarily from mainland Asia, have been described in other publications. The determination of this plethora of subspecies has been based primarily on variation in skin patterns, but when, during preliminary research, we investigated skins of *Tragulus* we realized that the characteristics of the subspecies reported by Chasen (1940) and others were not always consistent, and there appeared to be considerable morphological overlap between subspecies. Also, some taxa that Chasen had assigned to subspecies appeared to be distinct enough to qualify as species. We therefore decided to focus on a craniometrical analysis, because the taxonomists who worked on the genus had paid relatively little attention to skull form.

In this research we investigated skulls of *Tragulus* to obtain a more transparent and consistent taxonomy for the genus. In addition we studied some skins, but because many type specimens especially of small island taxa are located in the Smithsonian Museum, which we did not visit, we were unable to assess the validity of all taxa. We intend to address the variation between these island taxa, and also variation within *M. meminna* in future publications.

## TAXONOMIC HISTORY OF THE TRAGULIDAE

The earliest scientific name generally considered applicable to a tragulid is *Cervus javanicus* Osbeck (1757), described from Nieu Bay, Ujung Kulon, Java. We are not convinced that this name actually applies to a tragulid at all; he may have been describing a juvenile cervid, perhaps *Muntiacus muntjak*. As this will be the subject of a future application to the International Commission on Zoological Nomenclature, we will not argue the case here.

Pallas (1777) gave what we consider to be the first description of a specimen of a mouse-deer that he had obtained from Java; he did not name it, but Gmelin (1788) considered it a new species of musk-deer (*Moschus*), and on the basis of Pallas' description named it *Moschus javanicus* (see Appendix 1). Pallas' description not only clearly refers to a mouse-deer, but his mention of a grey nape confirms that the specimen was from Java, as no other mouse-deer species has this characteristic (e.g. Miller, 1903a). Pallas also cited Brisson's (1762) generic name *Tragulus*, which had been substituted for Linnaeus' *Moschus*; as Gentry (1994) showed, the type of this genus is *pygmaea*, but she proposed, following Ellerman & Morrison-Scott (1951), to designate *Cervus javanicus* Osbeck as type.

We propose instead to designate Gmelin's *Moschus javanicus* as type, which, with Pallas' *Tragulus*, would fix the name of the Javan mouse-deer as *Tragulus javanicus* (this will be part of our submission to the Commission).

Opinions as to the identity of *javanicus*, whether dated from Osbeck or Gmelin, have fluctuated between authors, from the large (*napu* group) to the small (*kanchil* group) and back. Raffles (1822), the first to mention the existence of two (or even three) species of South-East Asian mouse-deer, called the larger species *Moschus javanicus* Pallas and named the smaller *M. kanchil*, mentioning in addition a potential third species, 'the Pelandok', based on anecdotal information. His specimens were from the Bengkulu district of Sumatra. His descriptions of the two named species are accurate, and recognizably those of the two that occur today sympatrically on Sumatra. Hamilton-Smith (1827) named Raffles' Pelandok *Moschus pelandoc*, although his rather confused description suggests that he thought his specimen to be the same as Raffles' 'Napu'. Miller (1903b) finally rejected all descriptions of *M. javanicus*, *T. javanicus*, and *T. pelandoc*, and instead proposed a new species, *T. focalinus*, to designate the species from Java.

Gray (1836) recognized *Moschus javanicus* Gmelin (with *M. napu* F.Cuvier a synonym), *Moschus kanchil* Raffles, and two new species: *Moschus fulviventer* (which he thought is probably Raffles' 'pelandok') and *Moschus stanleyanus*. After these initial descriptions several intermediate revisions appeared. In a later publication, Gray (1843) dropped the genus *Moschus*, included it in the Bovidae, and referred the South-East Asian mouse-deer to *Tragulus*; he also introduced the name *Tragulus affinis* from Malacca. Blyth (1858) suggested that four (if not five) species of *Tragulus* were distinguishable. Milne-Edwards (1864) wrote a long review of the Tragulidae, recognizing *Tragulus javanicus*, *T. napu*, *T. kanchil* and *T. stanleyanus* (as well as South Asian *T. meminna*). Gray (1872) changed his species listing yet again and recognized *T. stanleyanus*, *T. javanicus* (of which he maintained that *T. napu* of Milne-Edwards was the adult, and his *T. javanicus* the young), *T. fulviventer* (= *Tragulus kanchil* Milne-Edwards, 1864), and *Tragulus pygmaeus*. One year later, Gray (1873) dropped the last species again.

The late 19th and early 20th centuries were a time of prolixity in the taxonomy of *Tragulus*, when zoologists such as Miller, Lyon, Lydekker, Kloss, Sody, Bonhote and Chasen described numerous species and subspecies. They differed in their opinions on how species and subspecies should be defined. For instance, Miller (1911) referred his new taxa to subspecies when there was some overlap in skin characteristics

between the specimens from two geographical groups, but when there was complete distinction he referred them to species; he was, however, not always consistent in this, and on occasion would nonetheless name a new form as a species despite acknowledging that there was some overlap with a closely related form. His approach resulted in naming a large number of taxa. Bonhote (1903) disagreed and suggested that most mouse-deer forms should be considered subspecies, especially the insular races.

Finally, in the 1930s and 1940s, Chasen, in collaboration with his colleague Kloss, revised the genus and reunited all taxa of *Tragulus* under the two species *T. javanicus* (greater mouse-deer) and *T. kanchil* (lesser mouse-deer). Since then most authors have followed this two-species plan, except that the nomenclature has had to be changed: van Bemmelen (1949) pointed out that the greater mouse-deer does not occur on Java, so the name *T. javanicus* actually applies to the lesser mouse-deer, the next available name for the greater mouse-deer being *T. napu*.

## MATERIAL AND METHODS

### SKULLS

One of us (E.M.) measured 338 skulls of *Tragulus* in the following museums: Zoological Museum Cibinong (ZMC), Indonesia; Sarawak Museum (SM), Kuching, Malaysia; Zoological Reference Collection (ZRC), Singapore; National Museum of Natural History (NMHM), Leiden, the Netherlands; Zoological Museum Amsterdam (ZMA), the Netherlands; the Field Museum (FMNH), Chicago, USA; and the British Natural History Museum (BNHM), London, UK (see Appendix 2 for the specimens list). Initially, E.M. measured 45 different dental and cranial characters on 17 *Tragulus* skulls in the Zoological Museum in Cibinong, Indonesia (formally Museum Zoologicum Bogoriense). These measurements were analysed to see which showed the most inter-, and intraspecific variation, and from the original 45 we selected 18 for detailed analysis (see Fig. 1 for measurement details). These were (letters refer to those in Fig. 1): condylo-basal length (CBL) = A–A'; basal–palatal length (BPL) = B–B'; zygomatic width (ZW) = C–C'; width of auditory bullae (BW) = D–D'; length of auditory bullae (BL) = E–E'; interbullae distance (IB) = F; canine width (CAW) = G–G'; least width across maxilla (LWM) = H–H'; condylar width (CW) = I–I'; width of braincase (WB) = K–K'; width across orbits (WAO) = L–L'; nasal length (NL) = M–M'; occipital height from basion (OHB) = B–N; occipital height from opisthion (OHO) = J–N; mandible height (MH) = O; mandible length (ML) = P; distance mandibular condyle – coronoid process = Q; width across

paraoccipital processes (PPW) (not shown in Fig. 1); and shape coronoid process (the only observational character, not shown in Fig. 1).

All measurements were made with an accuracy of 0.1 mm with a pair of Vernier callipers (precision 0.05 mm). Because of the often poor quality of the bone material (e.g. skulls shattered or fractured by lead shot), and/or the difficulty of measuring repeatedly between exactly the same two spots on a skull, there was potential for considerable inaccuracy in some of the measurements. To investigate this, ten skulls were measured twice, with at least one day between the measurements. Measuring error within characters varied from 0.1 mm to 3.8 mm, or when averaged over all measurements of one character, between 0.09 mm and 1.06 mm. This equals between 1% and 66% of the standard error. Based on this, the following measurements were omitted from the analysis: distance mandibular condyle – coronoid process (in which the average error was 66% of the standard error of the measurement); width across orbits (32%); and nasal length (25%). Also, the shape of the coronoid process was omitted from the analysis as it had not been consistently characterized.

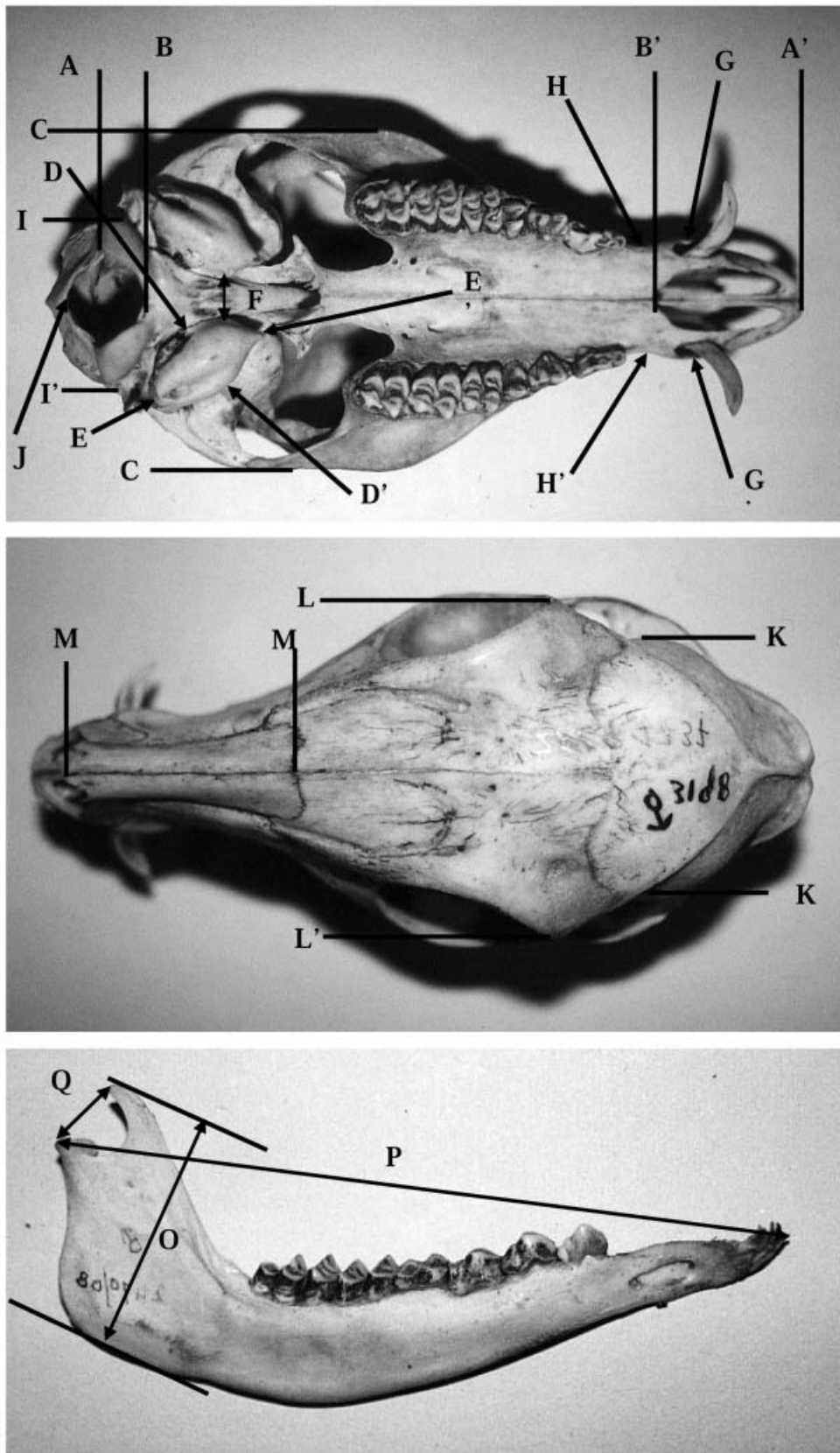
For all skulls, we determined the age-class as follows: Adult = M<sup>3</sup> erupted and basilar suture (= spheno-occipital synchondrosis, which fuses with increasing age) fused; Young Adult–Adult = M<sup>3</sup> erupted and basilar suture fusing; Young Adult = M<sup>3</sup> erupted and basilar suture open; Juvenile 2 = M<sup>2</sup> erupted, but not M<sup>3</sup>; Juvenile 1 = M<sup>1</sup> erupted, but not M<sup>2</sup> or M<sup>3</sup>; and Infant = no permanent teeth erupted. Additional skull measurements of 160 individuals were obtained from the literature. These measurements included ZW, and the maxillary tooth row. Lyon's 'maxillary tooth row' measurements were found to be the same as measurements for upper molar tooth row, not tooth row as such.

### SKINS

E.M. described 36 selected skins from the Zoological Reference Collection in Singapore, two from the Field Museum, and three from the British Natural History Museum, took photographs of the ventral and dorsal sides of the studied skins, and described the following characteristics: mottling of upperparts; colour code of upperparts; colour code of the side of the neck; visibility of the neck line; the number of visible light throat lines; the degree to which the underparts were clearly separated in dark and light areas; colour code of the light underparts; colour code of the dark underparts; colour code of the throat–neck line; and colour code of the median flanking lines.

Colour codes of parts of photographed skins were described using the charts and codes in Ridgway





**Figure 1.** Measurement details of *Tragulus* skulls and mandibles (letters refer to text).

(1912). After ascribing colour codes to the various skin parts, the codes were transformed into ranked categories. This was done because the total number of colours used was 44, which was too high in relation to the number of specimens and the number of variables. Also, the colour codes did not indicate any ranking. We developed a system to rank the codes across a spectrum from dark and red to light and yellow. For this, we weighted the primary Ridgway colours (in this case R-O, OR-O, Orange, OY-O, Y-O, and O-Y) by 6, 5, 4, 3, 2, and 1, respectively. These we multiplied by a factor between 1 and 4.5 depending on the percentage white and black in the colour, according to the scale of tints and shades in Ridgway (1912). This number was multiplied by a factor between 1 and 3 depending on the dullness of the colour (see Ridgway, 1912: 18). This numerical system provided a satisfactory classification of the skin parts in terms of levels of melanism, albinism, and erythrism. The resulting transformed, numerical colour codes were grouped into four groups per variable on an equal percentage basis (25% of the specimens in each group). For the statistical analysis both grouped and ungrouped transformed colour codes were used. The coat variables other than colour were scored either as binary data (absent/present), for instance in mottling of upperparts, or as counts, for instance in number of necklines.

In order to test the consistency of the skin descriptions, we described six skins twice, and transformed their descriptions as described above. Based on that assessment we omitted from the further analysis the descriptions for colour code of the median flanking lines, and the colour code of the side of the neck. In addition to the museum specimens, we used skin descriptions from the literature.

#### STATISTICAL AND BIOGEOGRAPHICAL ANALYSIS

We analysed the skull measurements and skin descriptions with SPSS 11.0 software (Data Theory Scaling System Group (DTSS), 1999). Firstly, we determined for each species whether there was a significant difference between measurements for males and females within each age class, using an analysis of variance (ANOVA) test. Secondly, we determined whether there were significant differences between the age classes, again using an ANOVA. Subsequently, we made classifications between and within the species using the following multivariate techniques: principal component analysis (PCA), categorical principal component analysis (CATPCA), and discriminant analysis (DA). The goal of principal components analysis is to reduce an original set of variables into a smaller set of uncorrelated components that represent most of the information found in the original variables. The technique is most useful when a large num-

ber of variables prohibits effective interpretation of the relationships between objects. Discriminant analysis is useful for situations in which we want to build a predictive model of group membership based on observed characteristics of each case. The procedure generates a set of discriminant functions based on linear combinations of the predictor variables that provide the best discrimination between the groups. These techniques allowed us to analyse our large data set.

For the biogeographical analysis and mapping we plotted the specimens' localities on maps using ArcView GIS 3.2a software. We also added species presence records from other literature sources.

#### TAXONOMIC DEFINITIONS AND CONCEPTS

To resolve the confused taxonomy within the genus *Tragulus* an objective understanding is needed of what constitutes a species and what a subspecies. To achieve this we use the phylogenetic species concept: a species is a diagnosable entity, meaning that it differs absolutely from all other species, implying fixed heritable differences (Cracraft, 1983, 1997). This species concept is similar to the one used, if not entirely consistently, by Miller (1901b, 1902b, 1903a, 1903c, 1911) in his description of mouse-deer taxa. The more generally used 'biological species concept', whereby species are reproductively isolated, is impossible to apply in the case of mouse-deer, in which most of the described taxa are totally allopatric. We therefore assign taxa to distinct species if all specimens can at once be referred to one sample or the other (Groves, 1989).

We will follow the 75% rule rules for naming a subspecies: 75% of the individuals classified in one subspecies are distinguishable from 100% of the individuals belonging to the other subspecies of the same species, which is statistically equivalent to 90% joint non-overlap (Mayr, Linsley & Usinger, 1953).

## RESULTS

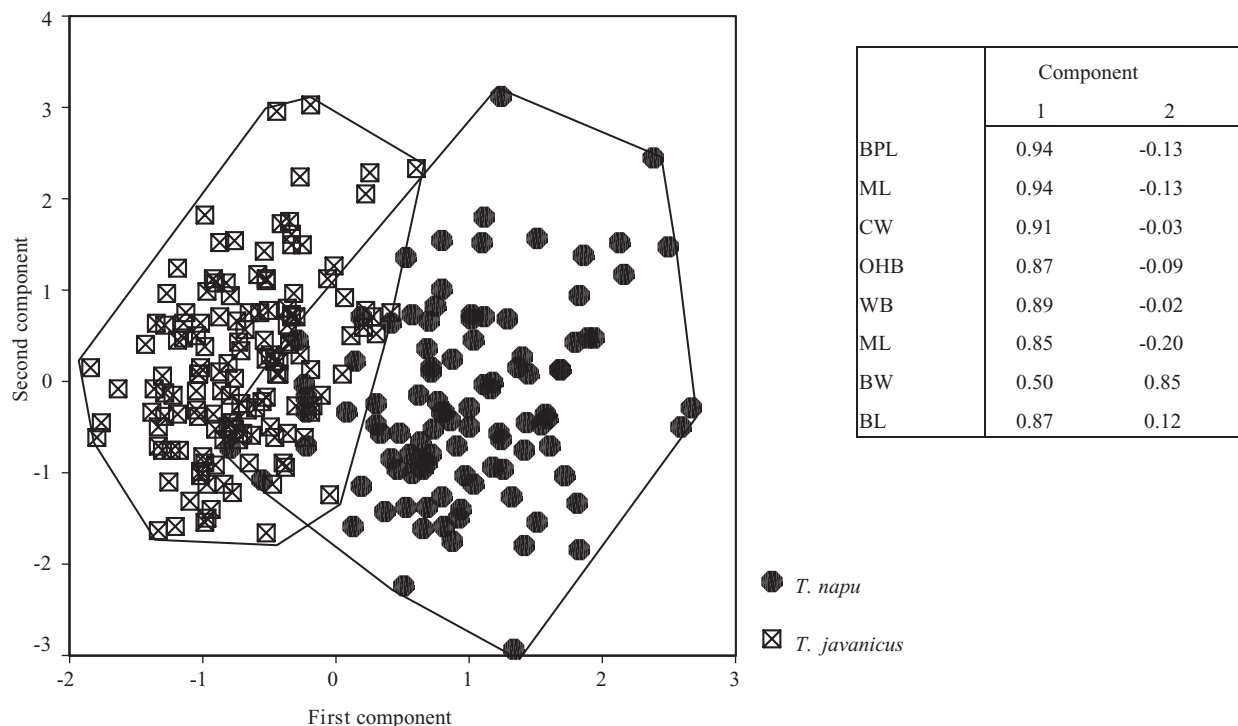
#### DIFFERENCES BETWEEN REPUTED *T. NAPU* AND *T. JAVANICUS/KANCHIL*

An ANOVA revealed that there were no significant differences between the males and females of *T. javanicus/kanchil* and *T. napu*, apart from the canine width and least width across maxilla (which are wider in males because of the larger canine teeth). Also, there were no significant differences between the three age classes of mature mouse-deer, but the juvenile specimens were significantly smaller than the mature specimens. We therefore decided to analyse mature males and females simultaneously and omit the juvenile specimens from the analysis.

A principal component analysis of skull measurements of mature specimens indicated that there were two groups that largely coincided with the conventionally recognized taxa *T. napu* and *T. javanicus/kanchil*, as indeed was indicated on the specimen labels (Fig. 2). Correlations between the variables and the components (see component matrix) showed that the difference between *T. javanicus/kanchil* and *T. napu* was primarily caused by size, as all the correlation coefficients of the first component, which accounted for 73% of the total variance, were very strongly positive, only bullae width having a correlation value of less than 87% (also see Table 1). We had initially left out

the OHO measurement because it was not available for a large number of skulls. When we added it to the analysis the separation between the groups increased (data not shown), but it was unclear whether the increased separation between the groups was real or caused only by the decreased number of specimens in the analysis.

A Categorical Principal Component Analysis of skin coloration patterns did not manage to group specimens within each of the species meaningfully. This may have been because determining colour codes of photographed skin parts was difficult, and it was even harder to compare these data reliably with



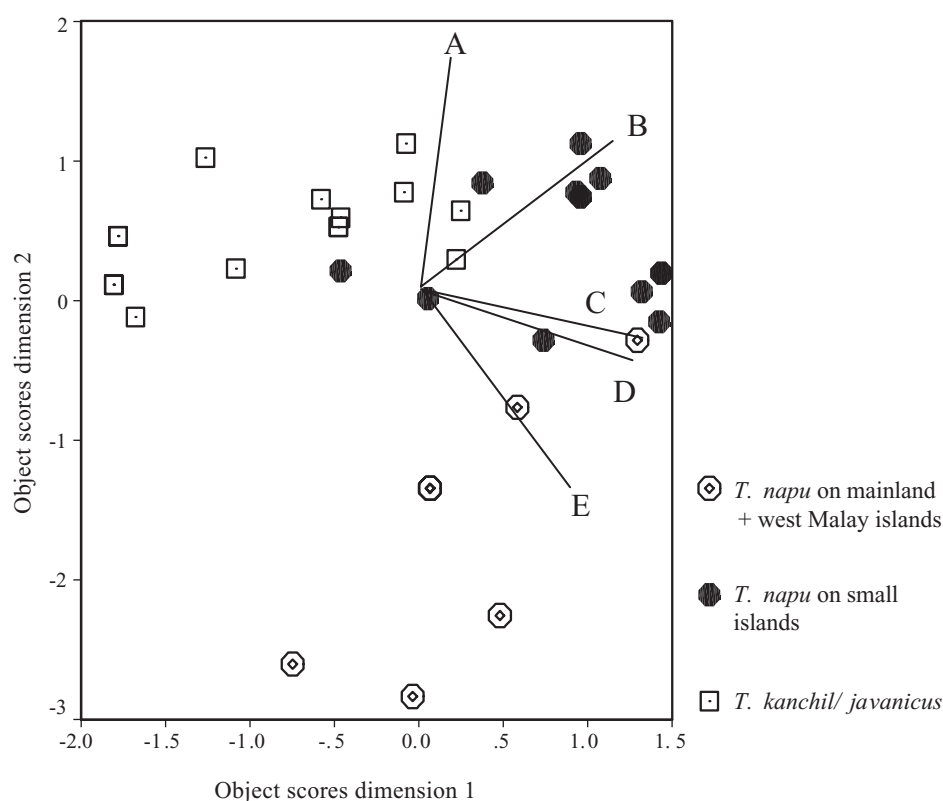
**Figure 2.** Principal component analysis of *T. napu* and *T. javanicus*, and corresponding component matrix.

**Table 1.** Means and standard deviations of *T. javanicus* and *T. napu*. CL = canine length; C-C is the distance between the tips of the canines. For other abbreviations see Methods

	CBL	BPL	ML	ZW	CW	OHB	WB	MH	OHO	BW	BL	IB	CL	C-C
<i>T. javanicus</i>														
Mean	88.5	65.5	73.6	42.1	19.8	26.9	31.3	28.4	19.4	8.8	17.9	5.1	16.0	29.0
N	233	167	165	277	168	171	172	164	91	167	161	161	10	8
SD	4.3	3.1	3.4	1.8	0.9	1.0	1.3	2.1	1.4	0.7	1.1	0.7	4.2	2.5
<i>T. napu</i>														
Mean	102.6	75.0	85.0	48.1	22.4	29.3	34.3	33.2	20.5	9.1	20.2	6.4	23.1	35.2
N	128	121	119	169	115	120	121	114	47	116	115	105	5	4
SD	5.3	4.4	5.1	2.5	1.3	1.5	1.4	2.4	1.9	0.8	1.4	0.8	5.9	2.4

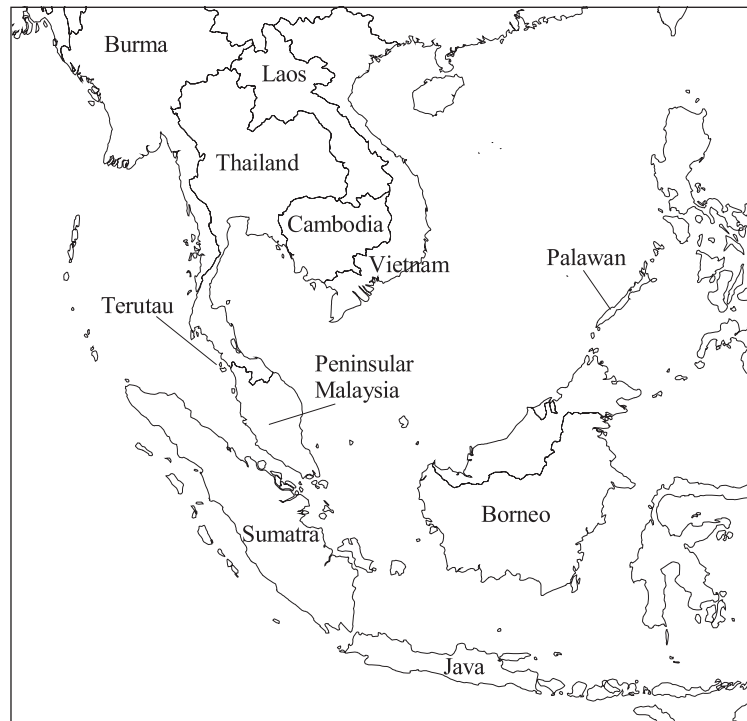
descriptive data from the literature, even though some authors used the same Ridgway colour charts as in this analysis. When we omitted the literature data from the analysis, we found more interesting patterns (see Fig. 3). One group contained all *T. javanicus* (note, however, that no Javan and Sumatran specimens were in the analysis), a second group contained *T. napu* from the small Sundaland islands, and a third group contained *T. napu* from Borneo, the Malay Peninsula, west Malay islands, and Indochina (but no specimens from Sumatra were available for this analysis; for locations see Fig. 4). An analysis of the component loadings of each of the factors showed that *T. javanicus/kanchil* is separated

from *T. napu* primarily by the number of throat stripes, the visibility of the nape line, and the mottling of the upperparts, thereby confirming what has been reported in the literature by many authors. The *T. napu* group was split into two groups primarily on the level of melanism and erythrism. Specimens from the larger islands (Borneo and Sumatra) and the Asian mainland and Malay Peninsula are generally dull, yellowish brown, whereas specimens from the small Sundaland islands show a varying amount of black and/or red in parts of their fur. This melanism was also present in the *T. javanicus/kanchil* group, but the geographical variation of this was less consistent than in *T. napu*.



	Component	
	1	2
mottling of upperparts	0.51	-0.72
level of erythrism	0.63	0.52
level of melanism	0.71	-0.24
number of visible light throat lines	0.74	-0.18
separation of underparts in dark and light patches	0.08	0.82
Eigenvalue	2.25	1.68
Percentage of variance	37.5	28.0

**Figure 3.** Categorical Principal Component Analysis of mouse-deer skin coloration patterns, showing three groups. The lines A–E indicate the component loadings for the variables included in this analysis: A = separation of underparts in dark and light patches; B = level of erythrism; C = number of throat lines; D = level of melanism; and E = mottling of upperparts.



**Figure 4.** Map of the main islands and countries mentioned in the text.

#### DIFFERENCES WITHIN *T. NAPU*

Based on the outcome of a principal component analysis of the *T. napu* skull measurements, we grouped the specimens into four geographical units: (1) Terutau and Langkawi Islands; (2) Borneo, Sumatra, the Malay peninsula, and mainland Asia; (3) islands offshore from the areas in group 2 but excluding those in group 1; and (4) the isolated *T. napu versicolor* population in SE Vietnam (note that *T. napu* does not occur on Java). A discriminant analysis of the adult specimens in these groups resulted in a 90% correct classification of the originally grouped cases. When young adult-adult specimens were added, the classification accuracy dropped to 85.9%, but there was still a clear separation between the four groups (Fig. 5). The SE Vietnam group is distinct from the others as no specimens from this group were embedded in any of the other groups. In addition to this, it was noted that specimens from Balabac, an island south-west of the Philippine island of Palawan, grouped closely together, although they were still embedded in the group of Borneo, Sumatra, and Malaya specimens.

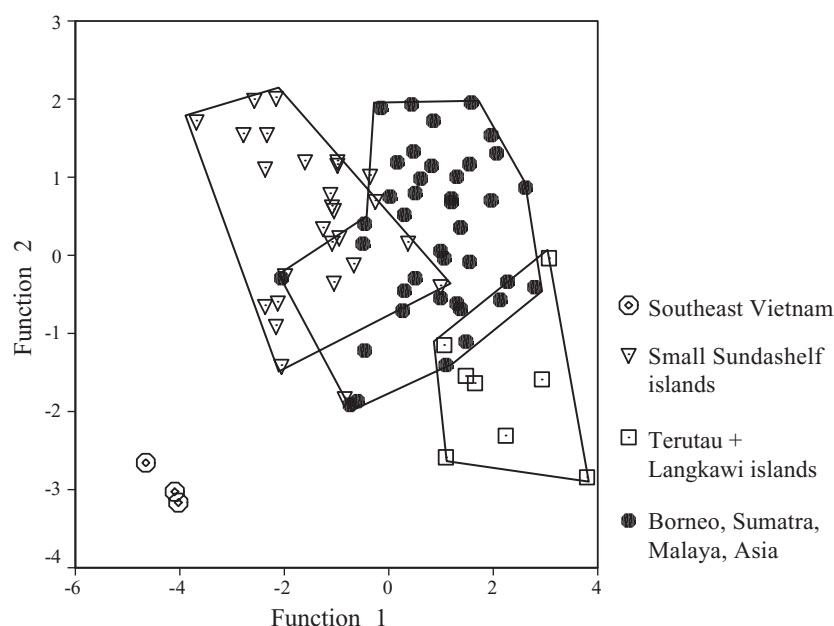
The skulls from Borneo, Sumatra, the Malay peninsula, and mainland Asia have the highest mean values for all the measurements ('Mainland and main islands' in Table 2). The SE Vietnam specimens were primarily distinguished by their overall small size, and a high value for function 3 (not shown here),

which correlated with a relatively wide braincase and condyles. The Terutau and Langkawi specimens were characterized by a low value for function 2, which mostly correlates with relatively long, narrow auditory bullae, a relatively wide skull, i.e. high values for ZW, CW, and WB, and relatively high values for OHO and OHB (see Table 2). The two groups consisting of specimens from Borneo, Sumatra, and Malaya, and small Sundashelf islands specimens partly overlap.

#### *Variation within the Borneo, Sumatra, Malay peninsula, and Asian mainland groups*

A discriminant analysis within the Borneo, Sumatra, Malay peninsula, and Asian mainland geographical groups could not meaningfully distinguish between them. Furthermore, an ANOVA between the nominate form from Sumatra and specimens from Borneo did not result in statistically significant differences between the groups, nor did the same test between Sumatran and Malayan/Thai/Burmese specimens. The means and standard deviations for these groups are provided in Table 3. There was some differentiation between skin patterns from the different regions (we were unable to study any skins from Sumatra), but because the series from each of the regions were too small it remained unclear how the interregional variation related to the observed intraregional variation.





	Function		
	1	2	3
ZW	0.45	0.32	0.29
BL	0.44	0.11	0.07
ML	0.28	0.47	0.27
IB	0.3	0.45	0.2
BW	-0.15	0.35	0.29
OHB	0.32	0.38	0.71
CW	0.24	0.29	0.63
WB	0.31	-0.06	0.55
BP	0.3	0.22	0.42
MH	0.07	0.14	0.4

**Figure 5.** Discriminant analysis of mature specimens of *T. napu* and corresponding component matrix.

One specimen (ZRC 4.4731), a juvenile from Pangkor Island (2 km off the west coast of the Malay peninsula), had skin coloration patterns similar to *T. napu* from the Malay peninsula, with black streaked, yellowish-brown upperparts, dark nape streak, and a normal throat pattern.

*Borneo and adjacent islands.* An initial analysis of the means of *T. napu* measurements of specimens from Borneo and nearby islands showed that specimens of *T. n. nigricans* ( $N = 7$ ) from the Philippine island of Balabac, north of Borneo, were significantly smaller than any of the other specimens. This raised the possibility that the classification of this subspecies

as *T. napu* was wrong, and that it should have been classified as a member of the *T. javanicus/kanchil* group instead. A discriminant analysis using five skull measurements of young adult, young adult–adult, and adult specimens from Balabac, and of specimens of the *T. javanicus/kanchil* and *T. napu* groups from Borneo, however, showed that the three groups are completely separated (Fig. 6). Balabac specimens were of intermediate length and they were differentiated from the two other groups by low values for WB, CW, OHB, BW, and BL (low BL also translated into a relatively high IB) (see Table 4). Because there were few differences within the Borneo/Sumatra/Malaya group of *T. napu* specimens (see above), and they will probably form

**Table 2.** Means and standard deviations (SD) for mature *T. napu* skulls (mm)

	CBL	BPL	ZW	ML	CW	MH	OHB	WBC	OHO	BL	BW	IB
Mainland and main islands												
Mean	104.3	76.7	48.9	86.5	23.0	33.6	30.1	34.9	21.0	20.5	9.2	6.7
N	95	66	112	66	62	65	66	68	34	62	62	55
SD	5.1	4.3	2.3	5.3	1.1	2.6	1.4	1.3	1.8	1.3	0.8	0.7
Terutau and Langkawi												
Mean	100.7	74.9	47.5	83.6	21.9	32.3	28.3	34.5	17.7	21.2	8.4	6.1
N	10	13	12	11	12	12	12	12	3	13	13	10
SD	3.1	2.8	1.4	3.4	0.6	1.1	1.0	0.6	0.3	0.7	0.3	0.5
Other islands												
Mean	99.9	72.4	46.3	83.2	21.7	32.5	28.4	33.3	19.7	19.4	9.1	6.1
N	34	41	43	40	40	37	41	40	8	40	41	40
SD	5.4	3.7	2.1	4.3	1.2	2.4	1.1	1.2	1.1	1.1	0.8	0.7
SE Vietnam												
Mean	90.5	69.7	42.9	75.7	21.2	32.7	27.2	33.7	18.2	17.9	9.1	4.6
N	2	3	3	3	3	3	3	3	3	3	3	3
SD	0.3	0.8	0.8	1.3	0.3	1.0	0.4	0.2	0.1	0.1	0.0	0.3

**Table 3.** Means and standard deviations (SD) of measurements on mature *T. napu* specimens from Borneo, Malaya, and Sumatra (mm)

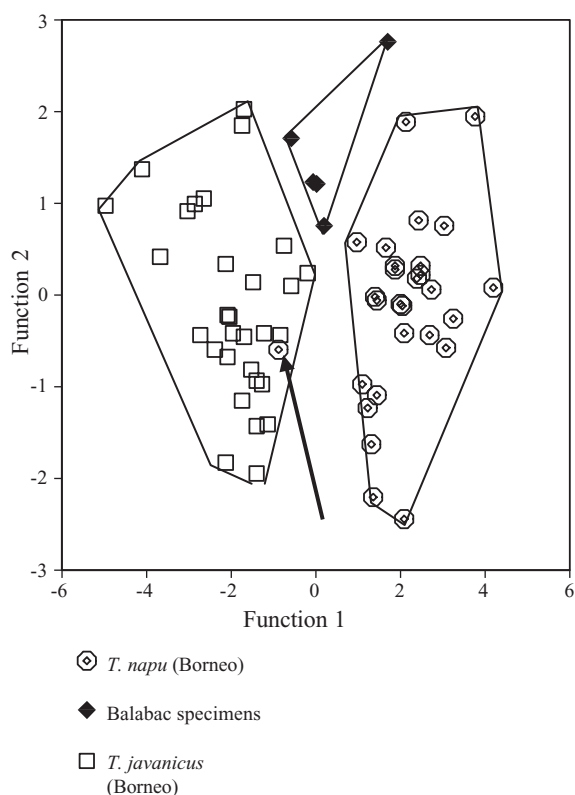
	CBL	BPL	ML	ZW	CW	OHB	WB	MH	OHO	BW	BL	IB
Sumatra												
Mean	107.0	79.1	87.4	49.4	22.8	30.6	34.7	33.7	21.8	9.1	20.5	6.5
N	19	13	14	25	13	13	13	13	9	13	13	12
SD	6.1	4.8	7.5	3.1	1.4	1.7	1.4	3.7	1.9	1.0	1.5	0.8
Malaya, Thailand south of Isthmus of Kra												
Mean	106.7	75.3	85.2	49.4	23.7	30.0	34.8	35.3	20.6	9.6	20.5	7.4
N	3	5	5	5	5	5	5	5	4	5	5	5
SD	0.5	3.7	5.8	2.5	1.0	0.8	1.9	2.4	2.5	0.8	0.5	0.4
Thailand/Burma, north of Isthmus of Kra												
Mean	105.8	78.1	89.0	49.5	23.0	30.7	35.8	33.7		9.8	21.8	6.9
N	5	6	6	6	6	6	6	6		6	6	5
SD	8.7	6.6	7.3	3.2	1.1	1.8	1.6	3.0		0.6	1.2	0.7
Borneo												
Mean	104.1	76.4	86.5	48.8	23.2	30.0	34.9	33.5	21.0	9.2	20.5	6.7
N	52	36	35	60	32	36	38	35	16	32	32	27
SD	3.6	3.1	3.0	1.8	0.7	1.1	1.2	2.0	1.7	0.7	1.1	0.7

one subspecies, we also compared the Balabac specimens to all specimens from this larger group. The two groups were separated in a discriminant analysis with 95% accuracy using the measurements for BPL, ML, ZW, CW, and OHB. An ANOVA showed that the Balabac specimens were significantly smaller ( $P < 0.01$ ) for CBL, BPL, ML, ZW, CW, OHB, and WB. We found similar results for a comparison between the Balabac specimens and the joined groups of Borneo, Sumatra,

and Malaya, and the small Sundashelf islands (minus Bunguran) specimens.

Specimens from Banggi, another island off northern Borneo, also differed from the rest of the Bornean specimens. We only measured two specimens from this island, of which one was juvenile, and we were unable to study any skins. The measurements of the adult specimen suggested that the island taxon is considerably smaller than that from the mainland, but clearly

our sample size was very small. Because Chasen & Kloss (1931) suggested that the Banggi Island specimens were very near to both *T. nigricans* from Balabac and *T. napu borneanus*, we compared the Balabac and Banggi specimens with the nominate subspecies *T. n. napu* to investigate the relationships further. The results were inconclusive, largely because we only measured one Banggi specimen, with additional measurements for two specimens from the literature.



**Figure 6.** Discriminant analysis of *T. javanicus* and *T. napu* specimens from Borneo and specimens from Balabac. The arrow points to a probably misclassified *T. napu banguei* specimen (see text).

When we compared the Banggi specimen with *T. n. nigricans*, *T. napu* from Borneo, and the *T. javanicus/kanchil* group from Borneo, it grouped with the latter (Fig. 6), which suggests that it may initially have been misclassified, and that it should instead be classified as belonging to the *T. javanicus/kanchil* group.

Within Borneo the size of *T. napu* skulls varied considerably. The smallest specimens originated from Sarawak, the largest from Sabah and East Kalimantan, and intermediately sized specimens from West and Central Kalimantan (Table 5). There were no skin descriptions or photographs available to check whether these differences in skull dimension translated into similar groupings of skin patterns.

**Sumatra and west Sumatran islands.** Two subspecies of *T. napu* have been described for mainland Sumatra, the nominate subspecies *T. napu napu* E. Geoffrey & F. Cuvier, 1822, which Sody (1931) restricted to South Sumatra, and *T. n. neubronneri* Sody, 1931, from Aceh, northern Sumatra. Furthermore, several subspecies were described for islands off the west coast of Sumatra, including *amœnus* and *jugularis* (Miller, 1903b) from Mansalar (= Musala) Island, *batuanus* (Miller, 1903c) from Tana Bala Island, and *niasis* (Lyon, 1916) from Nias Island. The subspecies from the islands off the east coast of Sumatra are analysed in the next section.

Within Sumatra, we compared specimens from north ( $N = 7$ ) and south ( $N = 6$ ) of Lake Toba, the main faunal break in Sumatra (Whitten *et al.*, 2000). Similar to what Sody (1931) reported, the northern specimens were larger than those from the south, although none of the differences was significant when tested in an ANOVA. The one specimen from Nias in this research, an adult female, was slightly smaller than the mean values for the northern mainland population, and had a relatively narrow skull (low values for ZW, CW, and WB). Neither a principal component analysis nor a bivariate analysis could significantly

**Table 4.** Means and standard deviations (SD) of measurements for mature mouse-deer from Borneo and Balabac (mm)

	BPL	ML	ZW	CW	OHB	WB	OHO	BW	BL	IB
<b>Balabac</b>										
Mean	69.2	80.2	44.2	19.9	27.5	32.0	20.2	8.4	19.9	6.0
<i>N</i>	6	6	6	6	6	5	5	6	5	6
SD	4.1	3.3	1.4	0.8	0.8	0.7	0.7	0.5	0.8	0.8
<b><i>T. javanicus</i> (Borneo)</b>										
Mean	66.6	74.3	42.4	20.3	27.6	32.6	20.8	9.6	18.7	4.9
<i>N</i>	35	35	65	35	36	36	22	36	33	34
SD	2.9	3.5	1.8	0.9	1.1	1.3	1.2	0.6	0.9	0.6

**Table 5.** Means and standard deviations (SD) of measurements (in mm) for mature specimens of *T. napu* from different parts of Borneo

	CBL	BPL	ML	ZW	CW	OHB	WB	MH	OHO	BW	BL	IB
Sabah and East Kalimantan (north of the Mahakam River)												
Mean	104.6	76.1	85.8	48.9	22.9	29.9	35.0	33.6	20.8	9.0	20.0	6.8
<i>N</i>	33	19	17	34	18	19	19	18	10	17	17	15
SD	4.5	4.0	5.1	2.2	1.0	1.5	1.2	2.5	1.9	0.6	1.5	0.7
Sarawak and NW Kalimantan (north of the Kapuas River)												
Mean	100.5	76.4	86.3	48.7	23.1	30.4	35.7	33.4	20.5	9.1	21.0	6.5
<i>N</i>	6	5	6	8	5	5	6	6	3	4	4	3
SD	3.2	3.7	3.6	1.2	0.6	0.5	0.5	2.2	2.4	1.0	1.0	0.6
West and Central Kalimantan (south of the Kapuas River)												
Mean	103.0	73.5	85.2	48.8	23.4	29.6	35.3	31.2	21.1	8.7	20.3	6.8
<i>N</i>	8	4	4	8	4	4	4	3	3	4	4	3
SD	2.8	4.0	2.4	2.2	0.8	1.1	0.7	2.5	1.0	0.5	0.2	1.1

separate the Nias specimen from the nominate *T. napu* from Sumatra. Miller (1903b) provided measurements for two specimens from Musala (which he assigned to different species); again these were slightly smaller than those from the mainland although larger than the Nias specimen.

#### *Variation within the Terutau/Langkawi group*

To explore the difference between the Terutau specimens and the adjacent group from Borneo, Sumatra, Malay Peninsula, and Asian mainland we compared these without the inclusion of the small Sundaland islands specimens. The two groups were classified with 92.5% accuracy in a discriminant analysis, which means that in that analysis 92.5% of the cases were classified to belong to their original group, the rest having a higher probability of belonging to another group. Furthermore, we conducted three ANOVAs: Terutau/Langkawi vs. the combined Borneo, Sumatra, Malaya, and small Sundaland islands groups (minus Bunguran); Terutau/Langkawi vs. the Borneo, Sumatra, and Malaya group; and Terutau/Langkawi vs. specimens from the adjacent Malay peninsula. All three ANOVAs resulted in significant differences ( $P < 0.01$ ) for CW, OHB, OHO (only the first two tests), BW, and IB (only for the last two tests).

Two subspecies of *T. napu* have been described from these islands, *T. canescens terutus* Thomas & Wroughton, 1909, from Terutau, and *T. canescens umbrinus* Miller, 1900, from Langkawi. The main difference between the two subspecies, according to Thomas & Wroughton (1909), was the dark-coloured nape, considered characteristic of *umbrinus*, which was completely absent in the seven specimens of *terutus* that they investigated. The two *terutus* skins studied in

this research (ZRC 4.4724, 4.4784), however, both had a black stripe in the neck, which connected to a black patch on top of the head. We did not study any skins from Langkawi. We measured one adult skull from Langkawi (BNHM 9.11.1.166) and 12 from Terutau (11 adults, one young adult), and a comparison of skull dimensions showed a major difference. For five of the seven measurements, values for the Langkawi specimen were completely outside the range of the maxima for the Terutau specimens. For instance, CBL for the Langkawi specimen was 108.4 mm, whereas that for the Terutau specimens ( $N = 9$ ) ranged from 97.1 to 102.1. The Terutau specimens were overall considerably smaller than the Langkawi specimen, apart for the relatively high values of ZW, CW, WB, OHO, and OHB, which are exactly those that separated the Terutau/Langkawi group from the Borneo, Sumatra, and Malaya specimens (see above).

#### *Variation among the small Sundaland islands*

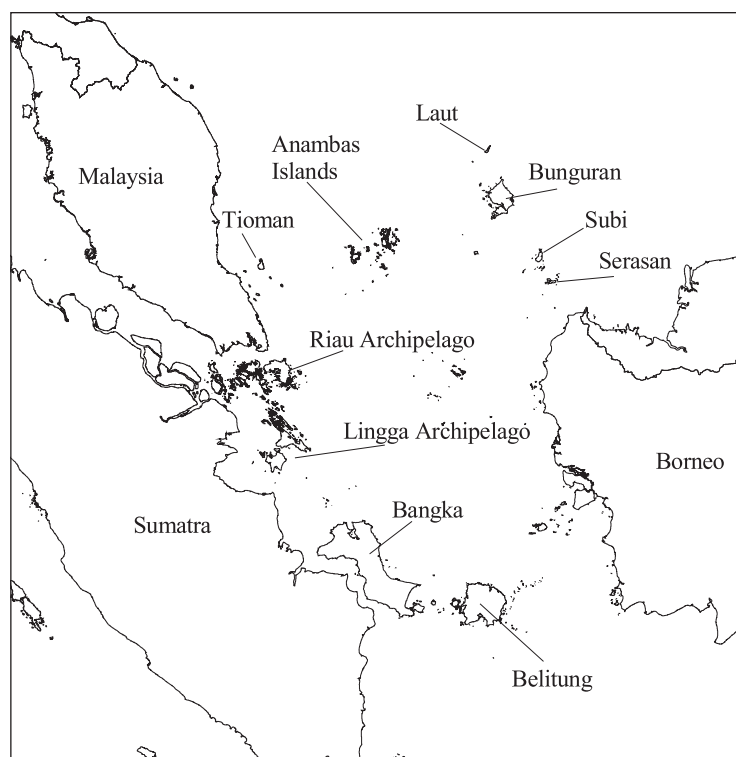
An ANOVA of all skulls of specimens from the Lingga, Riau, and Anambas island groups, and from the islands of Tioman and Bunguran (see Fig. 7) suggested that the specimens from Bunguran were distinct, primarily because they are much larger than the other skulls (Table 6). Measurements for BPL, CBL, WB, CW, ML, and MH differed significantly ( $P < 0.01$ ). Compared with those from Borneo, the Bunguran skulls are larger, but significantly so only for CBL (ANOVA,  $N = 55$ ,  $P < 0.05$ ). The Anambas skulls are smaller than the other Sunda Shelf island specimens, although there is some overlap with the lower end of the Riau, Lingga, Tioman group; in an ANOVA of the two groups only the interbullar distance differed significantly ( $P < 0.01$ ). We further investigated specimens from the small Sundaland islands using bi-



variate analyses. Three combinations, ML vs. MH, ZW vs. WB, and BPL vs. WB, resulted in a distinct differentiation of the three Bunguran specimens from the rest. One of the three Bunguran specimens was a young adult, and when we restricted the analysis to adult specimens the picture was even clearer (see two examples in Fig. 8).

According to Miller (1900) the middle upper premolar (= PM<sup>3</sup>) in the only specimen of *T. rufulus* (from Tioman Island) that he investigated differed from oth-

ers by its nearly equilateral triangular shape, as opposed to the normally square shape of this tooth. All other teeth were similar to those of *T. n. napu*. We found similarly shaped premolars in skulls of both the *T. javanicus/kanchil* and *T. napu* groups, from Laos, Borneo, Peninsular Malaysia, and Vietnam (note that we only noticed this aberration late in our research and may have overlooked further examples of it), which suggests that this dental character has no taxonomic value.



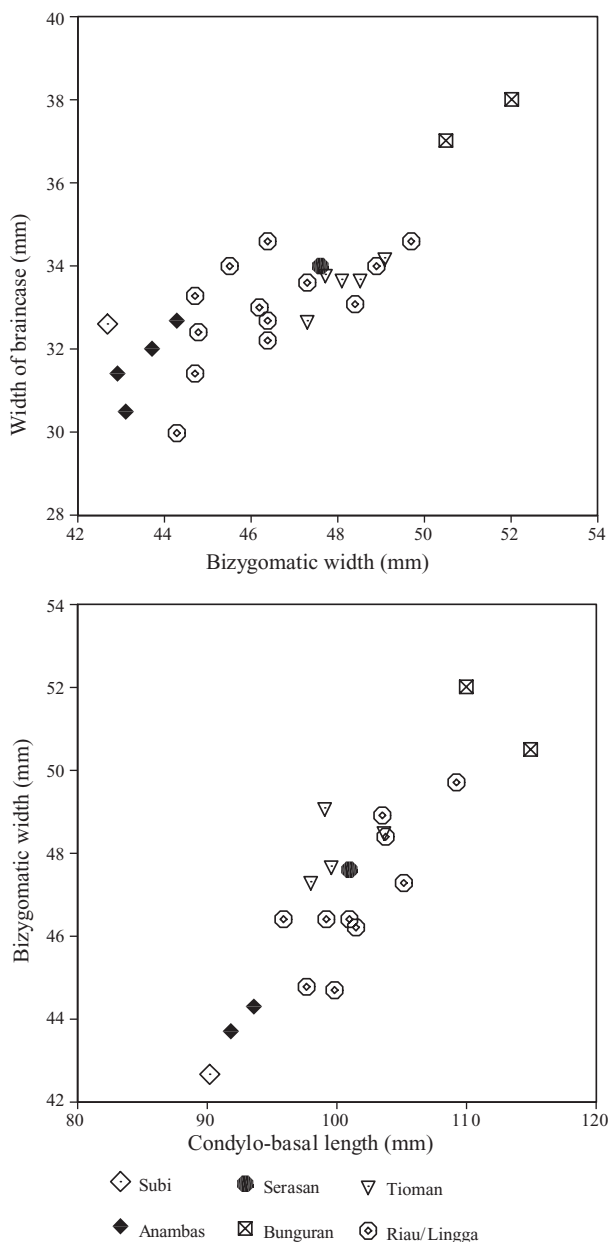
**Figure 7.** Overview of the main islands and island groups of the Sundashelf.

**Table 6.** Means and standard deviation (SD) of measurements for mature specimens of *T. napu* from the small Sundaland islands (mm)

	CBL	BPL	ML	ZW	CW	OHB	WB	BW	BL	IB
<b>Anambas islands</b>										
Mean	96.9	72.7	81.1	45.9	21.2	27.4	32.9	8.9	19.5	5.1
N	4	3	3	4	3	3	3	3	3	3
SD	4.9	2.0	4.2	2.2	1.0	0.8	1.0	0.5	1.0	1.2
<b>Bunguran Island</b>										
Mean	108.5	80.8	91.0	49.1	24.2	29.0	36.3	9.8	20.9	6.3
N	4	2	2	4	2	2	2	2	2	2
SD	7.8	4.9	6.9	2.0	1.8	2.7	1.1	1.6	1.1	0.8
<b>Lingga, Riau, and Tioman islands</b>										
Mean	100.0	72.9	84.2	46.7	22.1	28.7	33.3	9.4	19.4	6.2
N	18	23	22	22	22	23	23	23	23	22
SD	3.2	2.4	3.1	1.7	0.8	1.0	0.8	0.8	1.1	0.6

DIFFERENCES WITHIN THE  
*T. JAVANICUS/KANCHIL* GROUP

Experimentation with different geographical samples of the *T. javanicus/kanchil* group in a discriminant analysis revealed that there were considerable differences between skulls of adult specimens from Borneo, Java, the islands west of the Malay Peninsula (Langkawi, Butang, Rawi, and Pipidon, see Fig. 9), and a combined group of specimens from Sumatra, the Malay peninsula, mainland Asia, and all islands on the Sunda Shelf (Fig. 10). In particular, the west



**Figure 8.** Bivariate plots for reputed *T. napu* specimens from the small Sundaland islands.

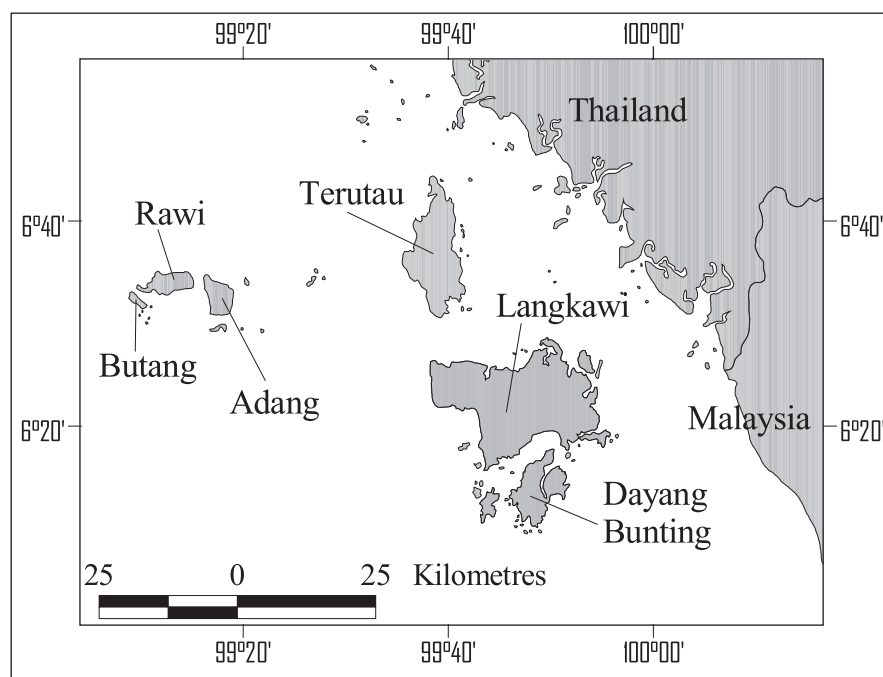
Malay islands specimens were well separated from the others. They were primarily distinguished from the other skulls by their narrow auditory bullae, and narrow, short skulls (low value for ZW, CW, and BPL in function 2, see correlation matrix and Fig. 10). The Javan skulls were also distinguished by their narrow auditory bullae and narrow braincase, and they also have longer and higher mandibles, a character they shared to some extent with the Langkawi, Rawi, and Adang skulls. Bornean skulls had wider auditory bullae, a wider braincase and smaller mandibles, especially those from Sabah. The specimens from Sumatra, the Malay peninsula, mainland Asia, and the small Sundaland islands were intermediate in these characters (see Table 7 for an overview of the mean values).

Interestingly, when we added the measurements for OHO to the analysis, and treated the Sabah specimens as a distinct group, the separation between the remaining groups increased significantly to a 94% accurate classification ( $N = 50$ ), and in particular the group of specimens from Java stood out for their lack of overlap with other groups (Fig. 11). This character was only available for one of the Terutau/Langkawi specimens, and therefore it could not be used to investigate the relation of *T. javanicus/kanchil* from these islands to others. Regardless, OHO and to a lesser extent OHB were important characters that differentiated between Bornean and Javan *T. javanicus/kanchil* (Fig. 11, and corresponding correlation matrix). In Figure 11, we also show that three specimens (RML 3774, 4600, 4601) from Padang, Sumatra, consistently grouped with the Sabah specimens. When all young adult and young adult-adult specimens were added to this analysis, the three groups were still separated with an accuracy of 87.7% ( $N = 73$ ).

The full implications of these results will be addressed in more detail in the Discussion section, but it is appropriate to note at this point that it would be difficult to continue to associate the Java and Sumatra/Borneo/Malay peninsula smaller mouse-deer in a single species. For the latter group, the name *T. kanchil* has priority.

*Variation within Java*

Dobroruka (1967) reported the existence of two distinct subspecies of mouse-deer on Java, which he called *T. j. pelandoc* (from the north coast of West Java Province) and *T. j. focalinus* (from the western part of Java and to the southern coast). A principal component analysis of the Javan skulls revealed some grouping of specimens from the two same geographical areas, especially those from central West Java and to a lesser extent those from the south coast (Fig. 12). The three specimens from the north coast, including the type locality of *T. j. pelandoc* as fixed by Dobroruka (1967), appeared to group with



**Figure 9.** Map of the Terutau and Langkawi island groups west of the Malay and Thai peninsula.

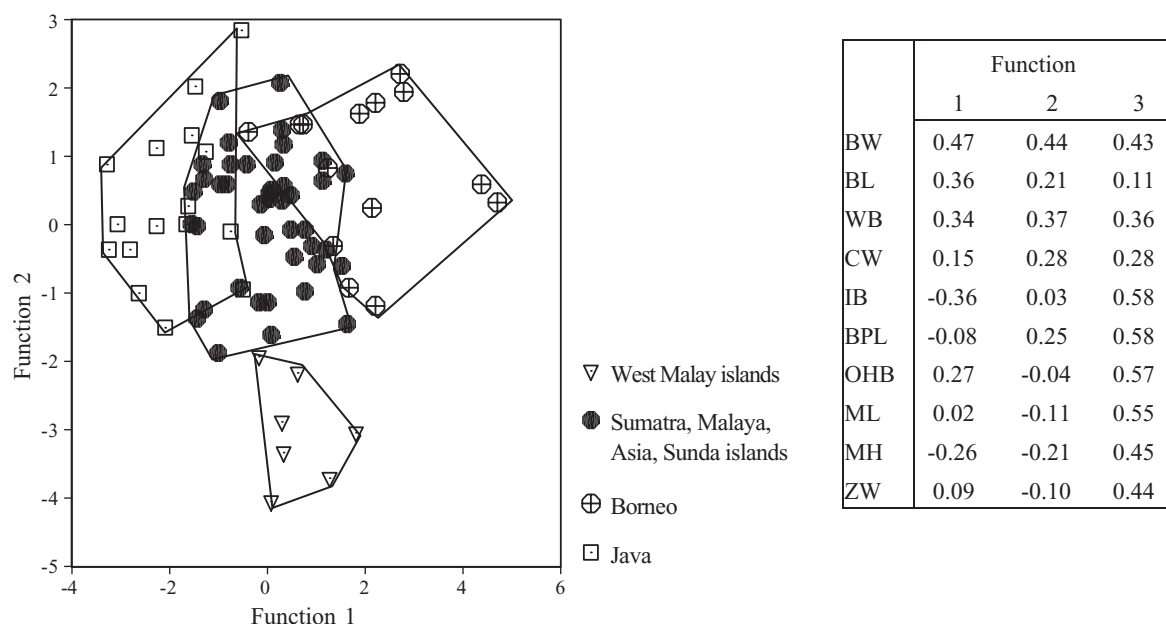
**Table 7.** Means and standard deviations (SD) for skull measurements on adult *T. javanicus* and *T. kanchil* specimens (mm)

	BP	ML	ZW	CW	OHB	WB	MH	OHO	BW	BL	IB
<b>Borneo</b>											
Mean	67.2	75.1	42.6	20.3	27.6	32.6	28.3	20.7	9.7	19.0	4.9
N	20	20	22	21	21	21	20	14	21	19	20
SD	2.5	2.7	1.7	0.9	1.1	1.3	1.8	1.0	0.6	0.8	0.7
<b>Sumatra, Malaya, mainland, Sunda islands</b>											
Mean	65.2	73.5	42.3	19.6	26.5	31.1	28.4	19.2	8.7	18.1	4.9
N	55	54	116	55	56	56	52	29	54	54	51
SD	2.8	3.1	1.8	0.7	0.9	0.9	1.6	1.2	0.6	1.0	0.5
<b>Langkawi, Adang and Rawi</b>											
Mean	64.6	76.4	42.8	19.1	27.3	30.6	30.1	20.0	8.4	17.8	4.9
N	8	8	9	8	8	9	9	1	8	8	8
SD	1.1	1.4	0.7	0.7	0.4	1.0	1.3	0.	0.4	1.0	0.5
<b>Java</b>											
Mean	68.1	75.8	42.3	19.9	27.2	31.2	30.0	18.8	8.6	17.5	5.7
N	21	21	21	21	21	21	19	18	19	17	19
SD	3.0	3.0	1.9	0.8	1.0	1.4	2.0	1.0	0.6	1.1	0.6

those from the south coast, where *T. j. focalinus* should occur. Because we had only photographed three of the 26 corresponding skins it was impossible to determine whether these two groups coincided with the subspecific characteristics of the taxa described by Dobruruka.

*Variation within the Borneo, Sumatra, Malaya, Asian mainland and small Sundaland islands group*

*Borneo and adjacent islands.* There were clear size differences between skulls of *T. kanchil* from different regions of Borneo, with larger specimens occurring in



**Figure 10.** Discriminant analysis of adult *T. javanicus*-like specimens, with corresponding correlation matrix.

Sabah and smaller specimens in West Kalimantan and Sarawak (Table 8). In particular, the relatively wide skulls and large bullae of the Sabah specimens differentiated them from Sarawak and West Kalimantan specimens.

In a principal component analysis, these Sabah and Sarawak/West Kalimantan groups completely separated (Fig. 13). We used this analysis to allocate three specimens from East Kalimantan to the two different groups: one specimen (ZMA 22.824) from the area between the Sebuksu and Sembakung Rivers, just south of the Sabah–East Kalimantan border, clearly grouped with the Sabah specimens, whereas two specimens (ZMC 08198; 08200) from the Bengen River in central East Kalimantan (0°31'N, 115°53'E) grouped with the Sarawak/West Kalimantan group. In the earlier mentioned discriminant analysis of all Javan *T. javanicus* specimens, *T. kanchil* from Sabah, and all other *T. kanchil* specimens, the Sabah group almost completely separated from a group combining all other *T. kanchil* specimens, except for three specimens from Padang, West Sumatra (RML 3774, 4600, 4601), that consistently grouped with the Sabah specimens.

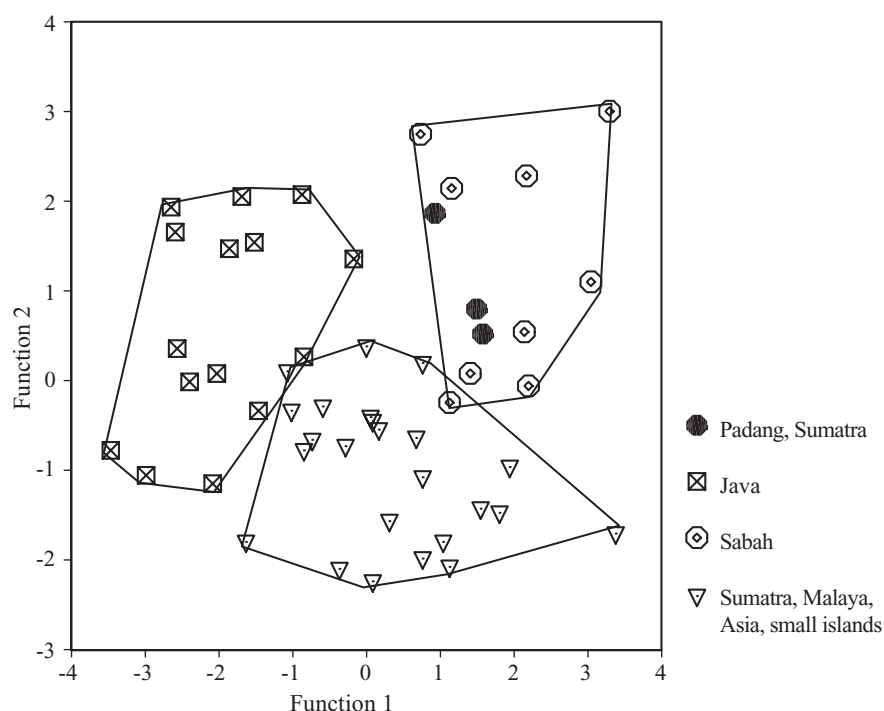
One specimen (FMNH 85912) was omitted from the analysis because it was very unusual. This specimen from Kalabakan, Tawau, Sabah, was labelled as a male, and its age determined as young adult; but it had very small (2–3 mm) canines that looked more robust than normal female canines, and its body weight was only 1500 g, as indicated on the label. Possibly this was a sick animal. We were unable to study the skin and it is unclear whether this is an aberrant

specimen or something taxonomically different from the normal Sabah form.

*Sumatra, Asian mainland and the Malay/Thai peninsula.* Above we have shown that *T. versicolor* is distinct from all *T. napu* taxa. When we compared all *T. kanchil* subspecies of Indochina and the Malay Peninsula with *T. versicolor*, it became clear that *T. versicolor* was also distinct from them (Fig. 14). *T. versicolor* was primarily distinguished from the others by the high value for BPL and ZW (see correlation matrix in Fig. 14).

Within *T. javanicus* of the Malay Peninsula and Asian mainland there was little variation in skull dimensions (Table 9). Only the type specimen of *T. k. williamsoni*, from northern Thailand, stood out by its large size. This specimen was larger than the means of all other mouse-deer from the Asian mainland and Malaya (except *T. napu*), whereas for most of the individual measurements it was also larger than the maximum values for the Malayan and mainland Asia *T. kanchil* subspecies. Neither a principal component analysis nor a discriminant analysis could meaningfully separate the other specimens from mainland Asia and the Malay/Thai peninsula into geographical groups. There was some differentiation between skulls assigned to *T. k. fulviventer* and *T. k. ravus*, from the south and centre of the Malay peninsula, respectively, but the two groups did not separate well in a principal component analysis. In a discriminant analysis that included specimens of *T. k. fulviventer*, *T. k. ravus*/*T. k. angustiae* (grouped together because of geograph-





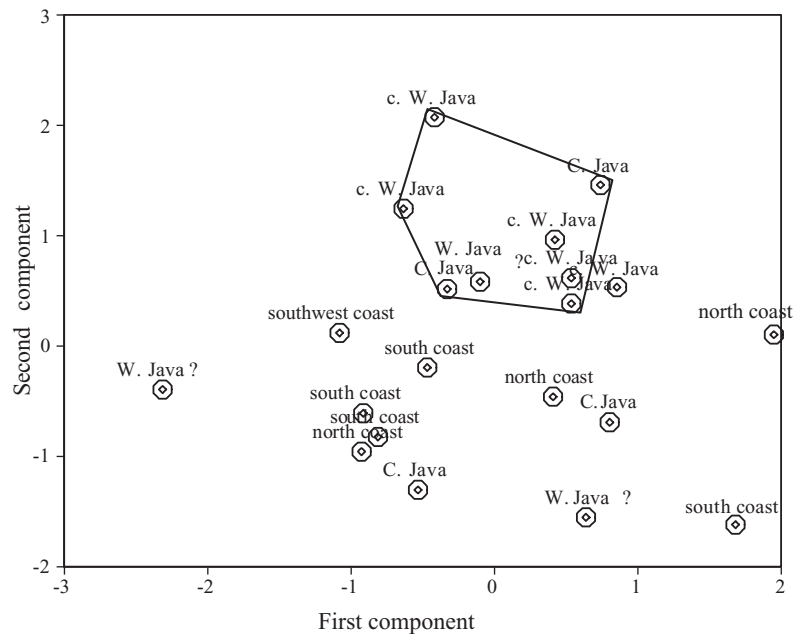
	Function	
	1	2
OHO	0.58	0.50
BL	0.39	0.13
MH	-0.27	0.26
BPL	-0.21	0.70
OHB	0.23	0.65
WB	0.39	0.52
IB	-0.33	0.42
BW	0.31	0.36

**Figure 11.** Discriminant analysis of *T. javanicus*-like specimens, which includes the measurements for the occipital height from opisthion.

ical proximity and low number of specimens for more northerly *T. k. angustiae*), *T. k. affinis* from Indochina, and specimens from the west Malay islands (Langkawi and Rawi), the *T. k. ravus* specimens grouped closely with those from the west Malay islands (Fig. 15). Also, the *T. k. fulviventer* and *T. k. affinis* specimens grouped closely together. Classification accuracy was 79%. When we added the Sumatra specimens to this analysis they largely overlapped with *T. k. fulviventer* and *T. k. ravus*/*T. k. angustiae*.

The skins of the Malayan and mainland Asian subspecies differed to some extent. In the northern Malay/Thai peninsula and on the Asian mainland, the upper parts were generally duller (less reddish) and less suffused with black than those from the southern Malay

Peninsula, which tended to be more reddish brown. Most mainland Asia specimens had vague nape streaks (or lacked them completely as in the *T. k. williamsoni* specimen), whereas they were clear in most specimens from the Malay Peninsula. The most northern specimens of the darker form originated from Bang Nora, Siam (ZRC 4.4850 and 4.4851) at 6°25'60"N, but we could not identify the locality of a dark specimen from Lam Ra Trang, northern Malay peninsula (ZRC 4.4881). The most southern specimen of the lighter form probably originated from the Krabi area, assuming that this is what the label localities 'Grahi' and 'Grabi' refer to. None of the means of all measurements of the northern and southern form are significantly different.



**Figure 12.** Principal component analysis of young adult–adult and adult skulls from Java. The polygon indicates all specimens from central West Java.

**Table 8.** Means and standard deviations (SD) for mature specimens of the Bornean *T. kanchil* subspecies

	CBL	BPL	ML	ZW	CW	OHB	WB	MH	OHO	BW	BL	IB
Sarawak, West Kalimantan												
Mean	85.7	64.9	72.1	40.3	20.3	26.9	31.7	26.7	20.6	9.7	18.7	4.5
N	6	7	7	7	7	7	7	7	1	7	7	6
SD	3.4	3.0	3.4	1.8	0.9	1.1	1.2	0.8	0.	0.9	1.1	1.0
Sabah												
Mean	91.4	67.8	76.2	43.3	20.6	28.0	33.1	29.5	20.9	9.5	18.7	5.2
N	27	24	23	30	23	24	24	22	18	24	21	23
SD	3.4	2.6	2.9	1.5	1.0	1.0	1.2	2.8	1.3	0.6	0.8	0.8

A principal component analysis of the Sumatran specimens did not reveal much geographical structure in the data, but this may have been because there was only one specimen from South Sumatra in the analysis, whereas the majority were from north Sumatra, and three specimens from west Sumatra. The one south Sumatran specimen stood out because of its wide auditory bullae and related small interbullae distance, but it is unclear whether this result is of any significance.

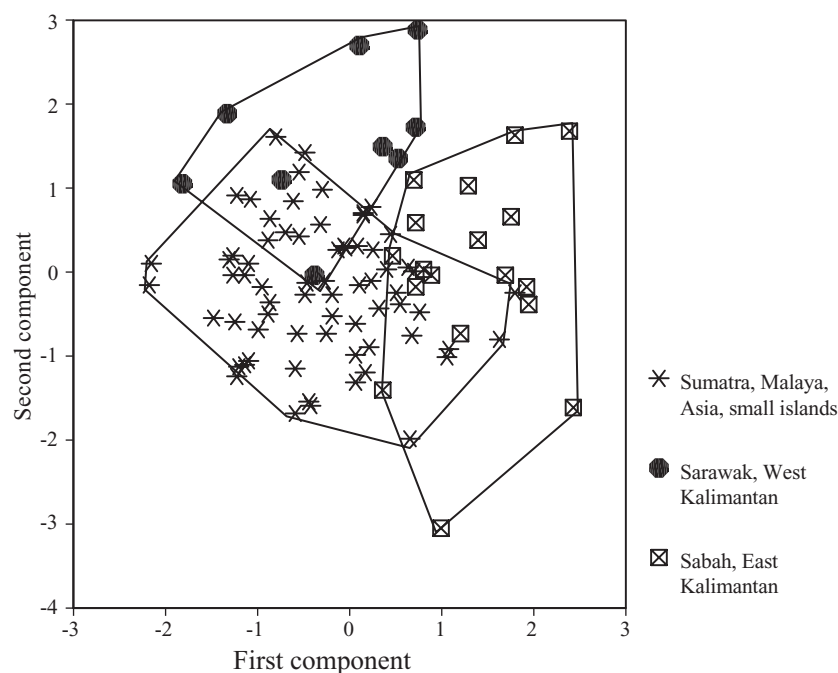
# DISCUSSION

## PATTERNS OF MORPHOLOGICAL VARIATION IN MOUSE-DEER

### *Colour variation in mouse-deer*

The subspecies of *T. napu* on small islands are commonly subject to melanism. The dark lines on the

throat become darker and also broader, often leaving only small white spots. Also in the *T. javanicus/kanchil* group there is some degree of melanism in specimens on small islands, leading to the development of extra dark, transverse lines, which make the throat pattern hard to distinguish from that of *T. napu*. Melanism is not restricted to the throat, but the head, neck and back may also be mixed with additional black hairs. The whole neck may be black, so that a nape-stripe cannot be seen (van Dort, 1986). Often this increased blackness appears to be the result of changed banding patterns on individual hairs. Whereas in the mainland type the black hair segment is located in the middle, it is located at the hair tip in some of the blacker island taxa. Also, an increased density of all-black hairs leads to greater overall blackness of the coat (see also Miller, 1903a).



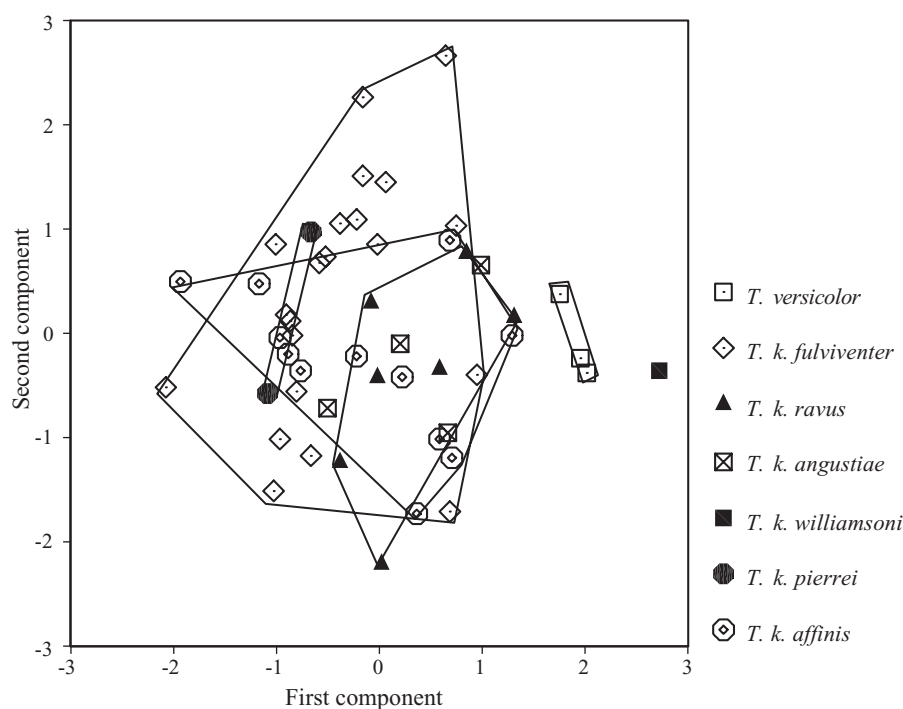
	Component	
	1	2
BPL	0.87	-0.16
ML	0.85	-0.22
ZW	0.84	-0.23
OHB	0.75	-0.12
CW	0.70	0.09
WB	0.72	0.21
MH	0.58	-0.44
BW	0.52	0.73
BL	0.67	0.40

**Figure 13.** Principal component analysis of mature *T. kanchil* specimens from Sabah and East Kalimantan, Sarawak and west Kalimantan, and all other mature *T. kanchil* specimens.

On several islands, *T. napu* typically has a red colour (erythrism). Even the nape-stripe is red, somewhat darker than the orange-red neck. The lines from the eye to nose are deep black, and the red back is mixed with black (van Dort, 1986). From studies of hair and skins and from information in the literature it appears that increased redness is the combined results of fewer all-black and black-tipped hairs in the coat, and possibly also an actual increased redness in the hair pigment.

Miller (1910) summarized these colour changes as follows. The primitive type of *T. napu* on the mainland has: (1) a mixed brown and black neck, the black concentrating along the nape to form an evident nape stripe; (2) a normal throat pattern with a

median white longitudinal stripe, on each side of which is a similar stripe, the three meeting in a broad white mass; the space between median and lateral stripes is brown as in the side of the neck or somewhat darker; a brown transverse band or collar separates the stripes from the white of the chest. The two lines of variation are (1) toward predominance of yellowish brown and (2) toward predominance of black. As mentioned above, the colour variations in *T. javanicus* are less striking. Hershkovitz (1967) provided a hypothetical explanation for these changes from the banded hair pattern to all black or all red in his theory of metachromism, and mouse-deer seem to provide a very suitable group to test this model.



	Component	
	1	2
BPL	0.88	0.06
ML	0.79	0.04
ZW	0.84	-0.21
CW	0.73	-0.26
OHB	0.58	-0.50
WB	0.73	-0.08
BW	0.47	0.74
BL	0.70	0.40

**Figure 14.** Principal component analysis of *T. kanchil* subspecies from Malaya and the Asian mainland and *T. versicolor*, and corresponding correlation matrix.

#### *Colour variation in relation to taxonomy*

The melanistic and erythristic island forms have in the past been assigned to many species and some to subspecies, as it was maintained that the characteristic coloration was often consistent within specimens from one island. The following example indicates that colour morphs should be used with reservation in mouse-deer taxonomy. Miller (1903b) described two species on Musala, a 65-km<sup>2</sup> island, some 15 km off the west Sumatran coast, *T. amœnus* and *T. jugularis*. These differed mainly in their colours. *T. amœnus*, of which Miller saw two specimens, was yellowish, with a dark neck, closely resembling *T. nigricollis* from Singkep Island on the east coast of Sumatra, but with

normal throat markings, including clear white stripes. Miller (1903b) described *T. jugularis* as being the same size and same colours as *T. amœnus*, except for some differences in the underparts. *T. jugularis* lacked the white stripes on the throat, and there were some differences in the amount of speckling in the neck and on the cheeks. Miller especially regarded the lack of white on the throat, which he found in 17 specimens, as evidence for a distinct species. Chasen (1940) suggested that these two taxa represent two phases of one subspecies and assigned them both to *T. j. amœnus*. We agree with his conclusion, but add to this that it should be noted that many island taxa have been assigned to species level based on variation in colours



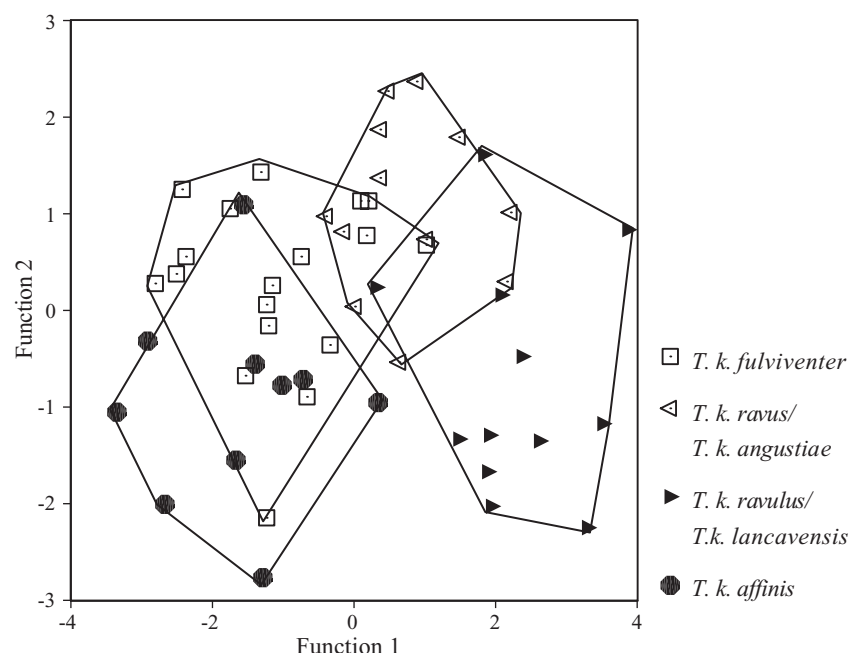
**Table 9.** Mean skull measurements for mature specimens of *T. kanchil* and *T. versicolor* from the Asian mainland and Malay Peninsula

	CBL	BPL	ML	ZW	CW	NL	OHB	WB	MH	OHO	BW	BL	IB
<i>T. williamsoni</i>													
Mean	94.5	69.7	77.4	45.2	20.9	29.3	28.7	33.3		21.9	9.1	19.8	5.7
N	1	1	1	1	1	1	1	1		1	1	1	1
SD	—	—	—	—	—	—	—	—		—	—	—	—
<i>T. versicolor</i>													
Mean	90.5	69.7	75.7	42.9	21.2	34.3	27.2	33.7	32.7	18.2	9.1	17.9	4.6
N	2	3	3	3	3	1	3	3	3	3	3	3	3
SD	0.3	0.8	1.3	0.8	0.3	0.	0.4	0.2	1.0	0.1	0.0	0.1	0.3
<i>T. k. ravus</i>													
Mean	87.9	65.4	73.3	41.3	19.7	27.7	27.3	31.1	28.1	18.9	8.5	17.6	5.3
N	5	7	7	7	7	6	7	7	7	2	7	7	6
SD	1.4	1.6	1.2	0.6	0.4	2.1	1.0	0.9	1.6	0.6	0.5	1.2	0.6
<i>T. k. fulviventer</i>													
Mean	85.3	63.0	70.8	40.2	19.5	25.2	26.6	31.0	26.7	20.5	8.7	17.5	4.8
N	10	23	22	23	24	18	24	24	25	4	24	24	24
SD	2.4	2.4	2.5	1.2	0.7	1.8	0.8	1.0	1.3	0.7	0.5	1.0	0.5
<i>T. k. angustiae</i>													
Mean	86.1	65.9	73.0	41.3	19.6	27.0	27.1	31.1	27.7	19.7	8.3	18.4	5.0
N	3	4	4	4	4	4	4	4	4	3	4	4	4
SD	1.6	2.4	2.1	0.8	0.9	1.7	0.6	0.6	1.0	0.6	0.4	1.2	0.2
<i>T. k. affinis</i>													
Mean	86.0	62.4	70.5	40.7	20.1	26.5	26.3	31.0	27.7	18.2	8.4	17.1	5.2
N	9	14	15	14	13	14	14	14	12	6	14	14	13
SD	3.8	3.1	3.5	1.1	0.8	2.7	1.2	1.2	1.8	1.0	0.4	1.1	0.6
<i>T. k. pierrei</i>													
Mean	83.6	61.8	71.1	40.2	19.4	25.8	25.6	30.2	28.2	18.0	8.5	16.5	4.7
N	2	2	2	2	2	2	2	2	2	2	2	2	2
SD	2.2	2.1	0.8	0.7	0.4	2.5	0.1	0.6	0.7	1.1	0.6	0.0	0.1

of the same type and magnitude as in the above colour morphs.

The above example raises the suggestion that colour variation in mouse-deer is regulated by relatively simple genetic changes. These could express themselves in small populations that, as a result of inbreeding and genetic drift, have low levels of heterozygosity so that homozygous genotypes coding for the red/yellow and black could increase in frequency. We hypothesize that as island mouse-deer populations became isolated in the period following the last of the Pleistocene glacials, they experienced genetic bottlenecks. This effect would have been exacerbated by the further sea-level rises to 5 m above present day sea-levels in the mid-Holocene (e.g. Tjia, 1976; Geyh, Kudrass & Streif, 1979; Thomas, Thorp & McAlister, 1999), which would especially have affected the low-lying islands by decreasing the habitable area.

An analysis of colour patterns in relation to island size supports the above hypothesis. The subspecies described from the largest islands (besides Sumatra, Java and Borneo) are those from Bangka (11 413 km<sup>2</sup>), Belitung (4788 km<sup>2</sup>) and Nias (4048 km<sup>2</sup>). Lyon (1906) described the two Bangka species *T. bancanus* and *T. luteicollis* as very closely related to large and small Sumatran mouse-deer, but brighter in the former and generally duller coloured in the latter; the *T. kanchil*-like *T. billitonius* from Belitung (see Fig. 7 for locations) is quite a dark and dull coloured taxon. The colour of *T. napu niasis* shows no differences from that of the nominate form (Lyon, 1916). The most extreme melanistic and erythristic forms were found on islands between 100 and 400 km<sup>2</sup>, with the larger Bintang Island (1173 km<sup>2</sup>) an exception. Interestingly, many of the very small islands (<100 km<sup>2</sup>) had relatively low levels of increased melanism/erythrism. The reason



	Function	
	1	2
ML	0.59	-0.18
ZW	0.28	-0.19
OHB	0.22	0.11
MH	0.30	-0.53
BL	0.05	0.22
BW	-0.19	0.07
WB	-0.16	0.26
IB	0.10	-0.01
BPL	0.31	0.24
CW	-0.20	-0.12

**Figure 15.** Discriminant analysis of non-juvenile specimens of *T. kanchil* from the Malay peninsula, the Asian mainland and the islands west of the Malay peninsula, with corresponding correlation matrix.

for this is unclear, but it is possible that these islands have only recently been colonized or that mouse-deer have been introduced by people. Also, the very small sizes of these islands would increase extinction probability and make it more likely that the islands had been recently colonized.

*The relationship between body size and island area*

During the research we became aware that body size of both *T. javanicus* and *T. napu* varied considerably

between islands. Different body sizes have often been used to assign island taxa to new species or subspecies and it is therefore important to investigate whether body size is determined by genetic characters or whether it is the result of phenotypic plasticity. To do this we charted the mean total length (as reported in the literature) of various species and subspecies (including both males and females) against the size of the island on which they occurred (Fig. 16). In *T. napu* the variation in body size is explained for 66.5% by the

size of the island on which a taxon occurs (Fig. 16). In *T. javanicus*, however, there is hardly any correlation between the two factors. We do not have enough knowledge regarding the ecological differences between the two species to hypothesize on the cause of this size phenomenon. An anonymous reviewer has suggested the following intriguing explanation: 'It could be that mainland *napu* is the larger of a pair of species and holds *javanicus* in check. When *napu* becomes confined on islands its size diminishes, but *javanicus* is already smaller, so the island effect has less scope to show itself'.

#### TAXONOMIC DISTINCTIONS BASED ON THE CRANIOMETRICAL RESULTS

The results of craniometrical analyses suggest that the Asian Tragulidae can be separated into three species groups: (1) *T. napu*-group; (2) *T. javanicus/kanchil*-group; and (3) *T. versicolor*. Within the *T. napu*-group there appear to be two distinct species: *T. napu* s.s. and *T. nigricans*. Within the *T. javanicus*-group there appear to be three distinct species: *T. javanicus*, *T. kanchil*, and *T. williamsoni*. Below we suggest a new taxonomy of Asian mouse-deer at species level based on the results of the metrical skull analysis.

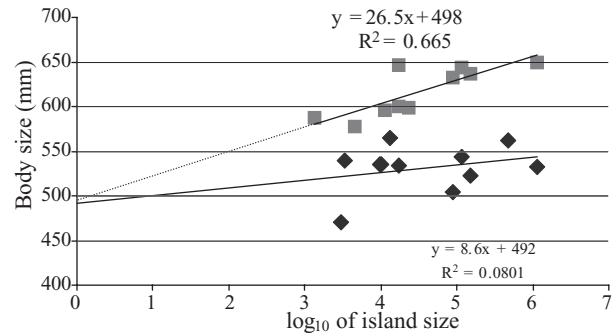
##### *T. napu*

This species was readily differentiated from members of the *T. javanicus/kanchil* group by its larger size, relatively small auditory bullae (possibly, as suggested to us by an anonymous reviewer, an effect of negative allometry) and, in most specimens, the distinct coat coloration. Within this species, three geographical groups emerged, none of which was distinct enough to be assigned to species level.

The analysis of skull measurements suggested that *T. napu*-like mouse-deer from the small Sundaland islands cannot be completely separated from the nominate form from Sumatra, Malaya, and Borneo. The analysis of skin patterns and colours separated these island specimens from the mainland specimens based on increased levels of erythrism and melanism, a character, however, that they share with other island taxa and with some specimens from the mainland. We therefore suggest assigning all Sunda Shelf island taxa to subspecies of *T. napu*, apart from those that deviate significantly from the common characteristics. Below we will discuss the descriptions of the individual taxa.

##### *T. versicolor*

The craniometrical results clearly show that this species from southern Vietnam is distinct from both *T. javanicus* and *T. napu*, and so far from being a



**Figure 16.** The relationship between log<sub>10</sub> island area and body size in *T. javanicus* (lower regression line) and *T. napu* (upper regression line).

subspecies of *T. napu* as conventionally regarded, it cannot even be convincingly allocated to either of the two widespread species-groups. In addition, skin coloration pattern and roughness of neck hair are unlike any other mouse-deer that we have seen.

##### *T. nigricans*

The results of the statistical comparison between the Balabac specimens and the nominate form *T. napu* confirm that this taxon is diagnosably distinct. It also differs significantly from *T. javanicus*. We therefore recommend that this taxon should be reassigned to a separate species, *Tragulus nigricans* Thomas, 1892.

##### *T. javanicus*

Statistical analysis of skull form suggests that the *javanicus*-like mouse-deer of Borneo, Sumatra, Java, Malaya, and the Asian mainland can be separated into three distinct groups, of which the Javan group did not overlap at all with the others. Together with its unique coloration (see below for detailed discussion), this sets aside the Javan taxon as a distinct species. In the Introduction we argued that *T. javanicus* Gmelin, 1788 is the appropriate name for the Javan taxon.

##### *T. kanchil*

Having separated *T. javanicus* as a species peculiar to Java, the next available name for the remaining mouse-deer, including those from Sumatra, is *T. kanchil* Raffles, 1822.

Within *T. kanchil*, the Borneo group was reasonably well separated from the group containing Sumatran, small Sundaland islands, Malayan, and mainland Asian specimens, but not completely. The Bornean

specimens as a whole were similarly coloured to those from Sumatran but, as we note below, there is a striking division to be made within Borneo.

#### *T. williamsoni*

Although this species is based on one specimen only, we provisionally assign it to species level because of its very large size.

### DISCUSSION OF GEOGRAPHICAL VARIATION WITHIN SPECIES

#### *T. napu*

*Geographical variation in present sample.* Within the group of greater mouse-deer specimens from Borneo, Sumatra, Malaya, and mainland Asia, which were identified in this research, three subspecies have been proposed: *T. n. napu* from Sumatra, *T. n. borneanus* from Borneo, and *T. n. canescens* from the Malay/Thai peninsula (Chasen, 1940). Although, in the original description, Miller (1902b) claimed that *T. borneanus* could easily be separated from the Sumatran *T. napu*, Lyon (1911) reported that, in a comparison of a large number of specimens from various localities in Borneo and Sumatra, the two subspecies were almost identical in size, colour, and cranial characters. We also found that skin coloration between Sumatran and Bornean *T. napu* varied only slightly. Furthermore, Chasen & Kloss (1931) remarked that it would be difficult, if not impossible, to identify individual specimens of *T. napu* from Borneo and the Malay peninsula on colour. Again, we largely agree, although most skins from the Malay peninsula were slightly darker than those from Sumatra and Borneo. We recommend dropping the subspecific name for the Bornean race and assigning it to the nominate form from Sumatra, *T. napu napu*. Following Lyon's (1911) recommendation, the population on Laut Island, south-east of Borneo, should then also be assigned to the same subspecies as it is almost indistinguishable from the mainland form.

*T. canescens* Miller, 1901, with type locality Trang on the southern Thai peninsula, became *T. napu canescens* after Bonhote's (1903) revision. Miller (1901b) claimed that *T. canescens* was larger than *T. napu* from Sumatra in skull length and in length and width of the auditory bullae, but the data in Table 3 suggest the opposite. Miller investigated only three specimens and these may have been exceptionally large; the 11 specimens used in this research suggest that in size the Malay population is not significantly different from the nominate Sumatran population. Lydekker (1915) also suggested that *T. n. canescens* differed very slightly, if at all, from the Sumatran *T. n. napu*. Chasen (1940) listed *T. canescens* as a synonym of

*T. napu napu* and we follow him in this. The population from Pangkor Island, off the west coast of the Malay peninsula, probably also belongs to this subspecies as the skin of one specimen was indistinguishable from other Malay peninsula skins.

Sody (1931) separated the north Sumatran form of *T. napu*, which he named *T. j. neubronneri*, from the southern form largely on differences in the lengths of the mandibular tooththrows. This character was not measured in the present research, but according to Sody the mean values varied between  $47.5 \pm 0.79$  mm ( $N = 6$ ) for the northern specimens and  $42.3 \pm 0.58$  mm ( $N = 7$ ) for the southern specimens; this difference seems significant. The only two specimens from North Sumatra (RML cat.ost.e and ZRC 4.4932, both from the Medan area) measured in this research were distinguished from the nominate form additionally by the high values for OHB (mean 32.1 mm,  $N = 2$ ) and for one specimen the high value for OHO (25.0 mm). This is considerably above the mean for the nominate form and also the other subspecies of *T. napu*. Chasen (1940) synonymized *T. j. neubronneri* with *T. n. napu*, but we provisionally maintain it as a distinct subspecies, unless new data become available that suggest that the differences in populations of the large mouse-deer along the length of Sumatra are clinal.

Based on skull characters, we could not significantly separate the Nias taxon from the nominate form. Lyon (1916) distinguished *T. n. niasis* from Nias Island from the nominate form by its smaller size, lighter weight, and distinctly shorter hind foot; there were no differences in colour between *T. n. niasis* and the nominate form. The hind foot of adult specimens varied from 135 to 142 mm ( $N = 8$ ) in the Nias form and, according to Lyon, from 145 to 152 mm in Sumatran specimens. This appears to be a significant difference, but it is limited to only one character and we recommend maintaining this taxon as a provisional subspecies *T. n. niasis*.

Thomas & Wroughton (1909) described *T. canescens terutus* and mentioned that it closely resembled typical *T. canescens* in coloration. Our analysis showed that most of the specimens from Terutau, but not all, were differentiated from the nominate form by relatively long, narrow auditory bullae, a relatively wide skull, i.e. high values for ZW, CW, and WB, and relatively high values for OHO and OHB. We therefore recommend retaining the subspecies *T. napu terutus* for this taxon. It appears that the Langkawi mouse-deer, by contrast, is similar to the mainland taxon (but note that this is based on only one specimen from Langkawi). Kloss (1918) suggested assigning the Langkawi mouse-deer to *T. napu napu* and we agree.

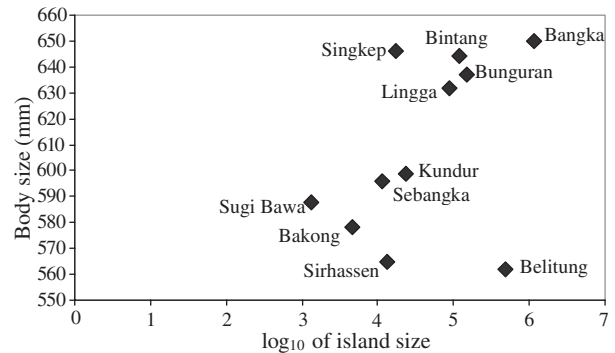
The results of the statistical analysis of Sunda Shelf island mouse-deer clearly showed that



*T. bunguranensis* Miller, 1901 from Bunguran Island was distinct from all other island taxa of *T. napu*. *T. bunguranensis* was primarily differentiated from other small Sundaland island mouse-deer by its size. If we take into account that this taxon occurs on a rather large island, the large size difference is no longer surprising; there appears to be a positive correlation between body size and island size (Fig. 17). Regardless, the body lengths of *T. bunguranensis* used in Figure 17 were available for only three specimens, one of which was very small and possibly subadult. If actual skull dimensions are analysed using only specimens that are clearly adult the size difference is much greater. With a mean CBL of 108.7 mm ( $N = 3$ ,  $SD = 6.8$ ), *T. bunguranensis* is slightly larger than the mainland forms of Sumatra and the Malay Peninsula and much larger than the Bornean form of *T. napu* (compare Tables 3 and 6), although it does not completely separate the Bunguran taxon from Sumatran, Bornean, and Malayan *T. napu*. Based on this, we recommend maintaining this taxon as *T. n. bunguranensis*, but we note the considerable differences between this island form and other island forms, which may warrant future reassignment to full species status.

The mouse-deer from Tioman Island, just off the east coast of the Malay Peninsula, was described by Miller (1900) as *T. rufulus*. We found that externally this taxon is similar to specimens from Batam (described below), with which it shares the bright reddish-brown upperparts. All but one of the Tioman specimens that we studied lacked a nape stripe and one specimen had a vague nape stripe. Miller (1900) distinguished this taxon from others by the shape of the middle upper premolar, but in the results we have already documented that this character is of no taxonomic value, especially because Miller had only one specimen. Our results indicate that based on pelage coloration this population can be retained as a subspecies, *T. n. rufulus*.

We investigated eight specimens from Batam Island, but an ANOVA revealed no significant differences in skull form and dimensions from *T. n. rufulus* from Tioman, to which it looks similar. The proper taxonomy of this taxon is unclear. Gray (1836) described *Moschus stanleyanus* as being clearly different from all other species by the brightness of its colouring and by the absence of a nuchal streak; it was based on living animals of unknown provenance, and various suggestions have been made as to their origins – the Sunda islands by Milne-Edwards (1864) and the Malay Peninsula by several other authors, but Kloss (1918) argued that Gray's description could only refer to a Batam specimen because of the brightness of its colouring, the absence of the nuchal streak, and the white on the under surface of the body. Miller (1906b)



**Figure 17.** Relationship between  $\log_{10}$  island area and body length in *T. napu*. Note that the aberrant Belitung specimen may be *T. kanchil* rather than *T. napu*.

had already named the Batam taxon *T. perflavus*, because he considered Gray's description to be too unspecific to determine the origin of *stanleyanus*. The measurements of the type specimen of *T. stanleyanus* suggest that it cannot in fact be reliably ascribed to Batam. The type specimen, an old female, is very large, with a CBL of 117 mm. Only one of the 149 *T. napu* specimens that we measured exceeded this measurement, an adult male from Sumatra; the mean CBL for Batam specimens was 99.8 mm ( $N = 7$ ) and the maximum value was 103.7 mm. Kloss (1918) acknowledged that the type was a large individual, but claimed that Batam animals attain these dimensions. We do not agree, recommend keeping *T. stanleyanus incertae sedis* and suggest using the next available name for this subspecies; as pointed out above, the Batam taxon is externally similar to *T. n. rufulus* from Tioman Island. We therefore suggest assigning these to the same taxon, for which the name *T. n. rufulus* has priority. This taxon then occurs on the central islands of the Riau Archipelago, i.e. Batam, Galang, Setoko (= Sekikir) and Bulan, and on Tioman.

Miller (1903a) described *T. formosus* from Bintang Island as similar in general appearance to *T. pretiosus* from Lingga Island, but with dark nape stripe less defined, fulvous of neck and throat more red, underparts usually more washed and yellowish, and premolars larger. Furthermore, Kloss (1918) remarked that some individuals from Bintang closely approach Batam animals. We studied skins of these subspecies and found that the colour differences as described above are indeed not consistent. The dark nape stripe is well defined in several Bintang specimens and there is no consistent difference in either the fulvous of the neck and throat or the yellow wash on the underparts. Miller (1903a) claimed that the size of the maxillary premolars of the type of *T. formosus* was 19 mm as opposed to 18 mm in the type of *T. pretiosus* from

Lingga, whereas the measurements of the mandibular premolars were, respectively, 19 and 18.4 mm [confusingly, Miller (1906b) provided a mandibular premolar length of 19 mm for the type of *T. pretiosus*, making either of the two claims incorrect]. These differences are very small and we doubt whether they would be statistically significant. Furthermore, Miller (1902a) mentioned that the teeth and skull of *T. pretiosus* were similar to those of *T. napu* and that the peculiarities of the first specimen obtained by Dr Abbott, the collector, presumably the type mentioned above, were the result of 'senile changes'. The data therefore indicate that *T. formosus* and *T. n. pretiosus* do not differ and that both can be assigned to the same subspecies, and that this can in turn cannot be distinguished from *T. rufulus* for Batam and Tioman.

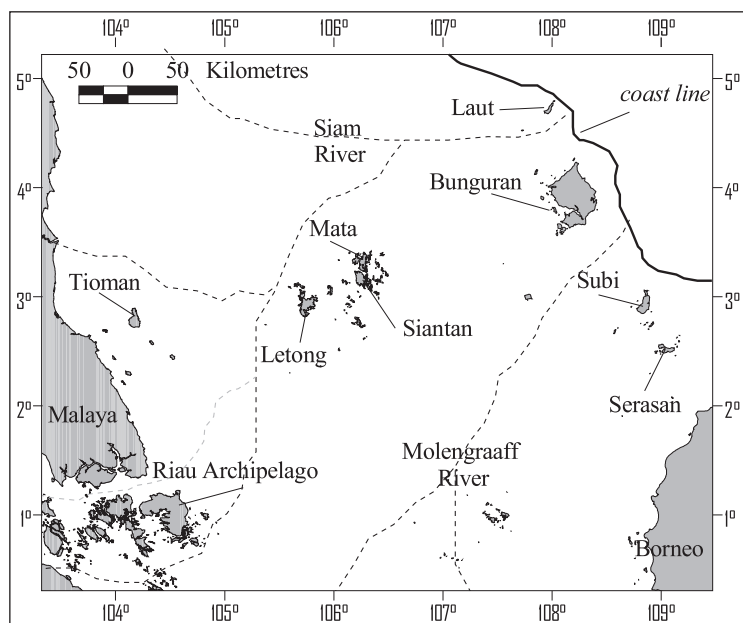
We measured the type specimen, an adult male, of *T. javanicus* (recte *napu*) *abjectus* from Sirhassen (= Serasan) (see Fig. 7). This specimen was slightly smaller than the average *T. napu* specimen from nearby Borneo, with relatively inflated auditory bullae (CBL = 100.9 mm, ML = 86.0 mm, ZW = 47.6 mm, WB = 34.0 mm, BW = 9.3 mm, and BL = 20.5) (compare with Table 3). According to Chasen (1935a), *T. javanicus abjectus* is inseparable in colour from the paler examples of Malayan *T. napu* and in size slightly smaller than *T. napu* from the Malay States and Borneo. As pointed out above, isolation on a small island leads to dwarfing in *T. napu*. Chasen (1935a) only provided the total length measurement for one specimen (565 mm), which, however, fits well in the island area – body size relationship depicted in Figure 17. We therefore recommend assigning the Serasan mouse-deer to *T. n. napu*.

We measured the type specimen, an adult male, of *T. kanchil abruptus* from Subi, also in the South Natuna island group. Chasen (1940) assigned this taxon, after initially having assigned it to the smaller *T. kanchil*, to the larger species, called by him *T. javanicus* (in Chasen, 1935a); he did so because this taxon has the large feet of what is today called *T. napu*. Van Dort (1986) argued that foot length may be a local ecological adaptation; we therefore doubt whether it could be a reliable reason for reclassifying it. The CBL for the adult male specimen from Subi is 90.5 mm, whereas the mean CBL for adult *T. kanchil* specimens from nearby Borneo is 88.9 mm ( $N = 30$ ,  $SD = 7.5$ ) and that for Bornean *T. napu* specimens is 104.1 mm ( $N = 18$ ,  $SD = 3.6$ ). Based on skull length (and we found similar results for skull width) it is therefore more likely that the Subi taxon is indeed related to *T. kanchil* rather than to *T. napu*. The bivariate plots in Figure 8 also support that conclusion, because the Subi specimen is located outside the lower limits of *T. napu* specimens from other small Sunda Shelf islands. Chasen's (1935a) original

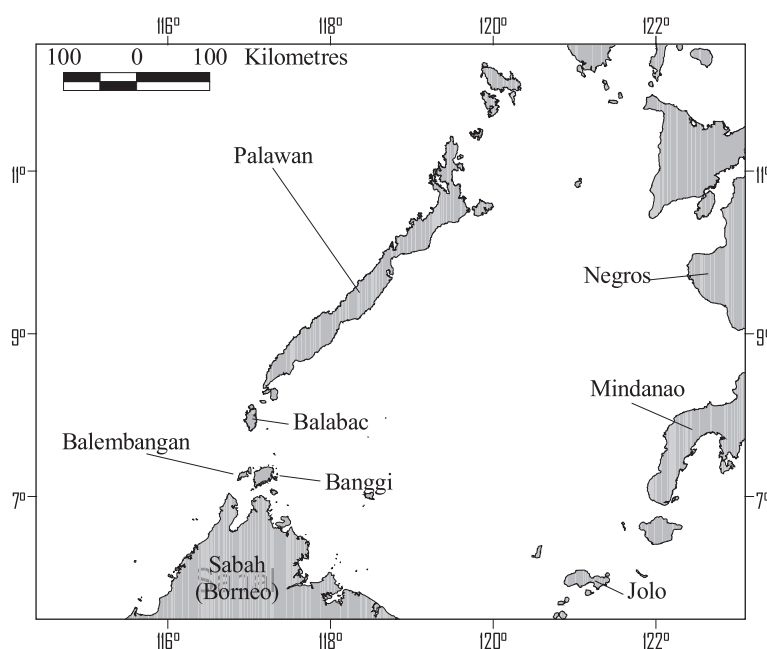
description further supports our conclusion, noting that it is nearest in colour to *T. k. klossi* from northern Borneo. We therefore suggest re-assigning this taxon to *T. kanchil* and, while using the name *T. k. abruptus*, we anticipate that it may well prove a synonym of *T. k. hosei* from north-west, west, east, and south Borneo (see below).

Three subspecies have been described within the Anamba islands group, which includes the islands of Siantan, Mata, and Jimaja (= Letong) (see Fig. 18). E.M. measured five specimens from Siantan and one from Mata (none from Letong). Initially, Chasen & Kloss (1928b) described the taxa from Siantan and Mata as subspecies of *T. kanchil*, i.e. *T. k. siantanicus* and *T. k. anambensis*, but later Chasen (1940) assigned them to *T. napu*, without justifying his decision. In 1928, Chasen and Kloss stated that *T. k. siantanicus* bore a close superficial resemblance to *T. n. stanleyanus* from the Riau islands, but did not have the large robust skull of the 'napu' group; and they reported that the series was so variable that the description of any one animal would be of little use. Overall, the upperparts were orange-ochraceous, without any black mottling; the absence of mottling would suggest that it was not related to *T. napu*. CBL of the type specimen, an adult male, was 78 mm and ZW was 45.5 mm. Such small sizes do not occur in any other adult specimens of *T. napu*. A discriminant analysis of all *T. napu*, all *T. kanchil*, and four Siantan specimens also revealed that *T. k. siantanicus* was more similar to *T. kanchil* than to *T. napu*. The type specimen of *T. k. anambensis*, an adult female, has a slightly larger skull (CBL = 80 mm, ZW = 42.5), but this is still well outside the range of *T. napu*. *T. k. anambensis* differs from *T. k. siantanicus* in being less rufous and more yellow above, but for both forms Chasen & Kloss (1928b) remarked on their considerable variability and the two taxa appear to be weak subspecies. Because we were unable to compare the skins of these two taxa, we recommend provisionally recognizing them as distinct subspecies, *T. k. anambensis* and *T. k. siantanicus*, but anticipate that ultimately both forms will be reassigned to one subspecies.

Chasen (1940) also described a third subspecies in the Anambas Islands group, *T. javanicus hendersoni* from Jimaja (= Letong) Island. According to him, *T. j. hendersoni* differed from the other two by the complete absence of the bright orange-buff areas on the underparts, which was so marked in the other two taxa; but among the four skins of *T. k. siantanicus* that we studied, only two had the large orange-buff areas on the underparts, one had whitish underparts, and another had a narrower white central patch with a broad reddish median band. There is therefore no justification for differentiating the one *T. k. hendersoni*



**Figure 18.** Sundashelf islands in the South China Sea. Thick solid line indicates the coastline during the last glacial maximum. Dotted lines indicate the main Sundashelf river systems during the last glacial maximum (after Voris, 2000).



**Figure 19.** Map of the islands between northern Borneo and Palawan.

specimen from *T. k. siantanicus* based on coat coloration. Based on the skull measurements it is impossible to judge whether *T. n. hendersoni* is more closely related to *T. napu* or to *T. javanicus*, because the only specimen is an immature female with CBL = 74.9 mm. The total length of 600 mm ( $N = 1$ ) of this specimen,

as provided by Chasen (1940), is larger than that of the types of *T. k. anambensis* and *T. k. siantanicus* (535 mm), but again it is unclear whether these differ significantly (note that a total length of 600 mm or more in mouse-deer was only found in specimens with CBL > 87.8 mm and that therefore Chasen's skull or

body measurements may have been erroneous). Overall, it appears that the three forms have similar coat colorations and that there is probably considerable variation within each of the islands; there are also some differences in size. We think that it is most likely that the three taxa on these remote islands are subspecies of the same species, *T. kanchil*; van Dort (1986) also suggested a single species, but referred the taxa to *T. napu*. Because we have no further evidence, we suggest following Chasen's taxonomy and leaving the Letong subspecies as *T. n. hendersoni*, but re-examination is in order in future.

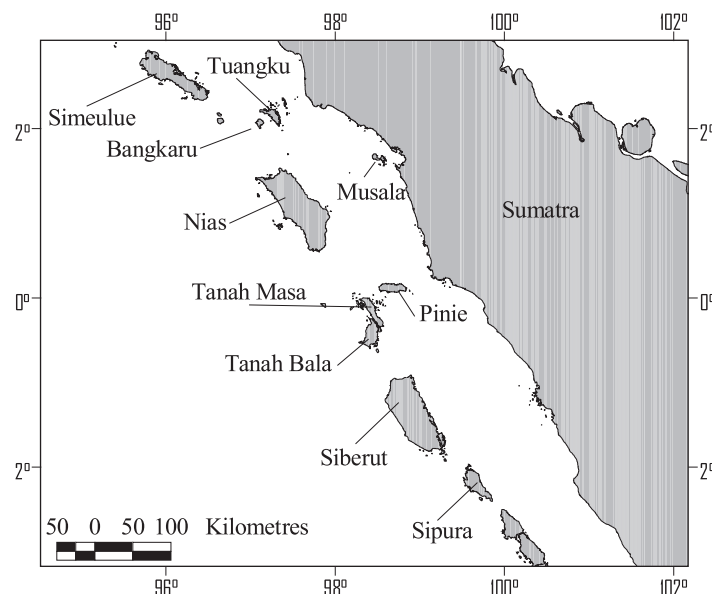
Chasen & Kloss (1931) described *T. javanicus banguei* as a subspecies on Banggi Island, north of Sabah, northern Borneo. The few measurements analysed in this research confirm its distinctiveness, and the smaller size of the specimens and different throat patterns described by Chasen & Kloss (1931) warrant its retention as a distinct subspecies. Our craniometrical analysis suggested that the Banggi specimen is more closely related to *T. kanchil* than to either *T. napu* or *T. nigricans*, but Chasen & Kloss's (1931) description, especially the throat patterns and coloration of the upper parts, appears to refer to a *napu*-related taxon. We here follow Chasen (1940) and recognize this subspecies as *T. n. banguei*.

A single specimen (FMNH 141133) collected on Balambangan Island, offshore north Borneo (see Fig. 19), and labelled '*T. napu banguei*', may represent *T. kanchil*. This young-adult female specimen is considerably smaller than *T. napu banguei* in all skull measurements, which fall within the range of

*T. kanchil* from the mainland. Another possibility would be that the Balambangan specimen is *T. nigricans*, because its skull dimensions are also similar to that form, but the distance between Balabac and Balambangan is c. 55 km and the two islands are separated by a deep strait, whereas from Balambangan to Banggi it is only 5 km and to the mainland c. 20 km. This issue cannot be resolved at present.

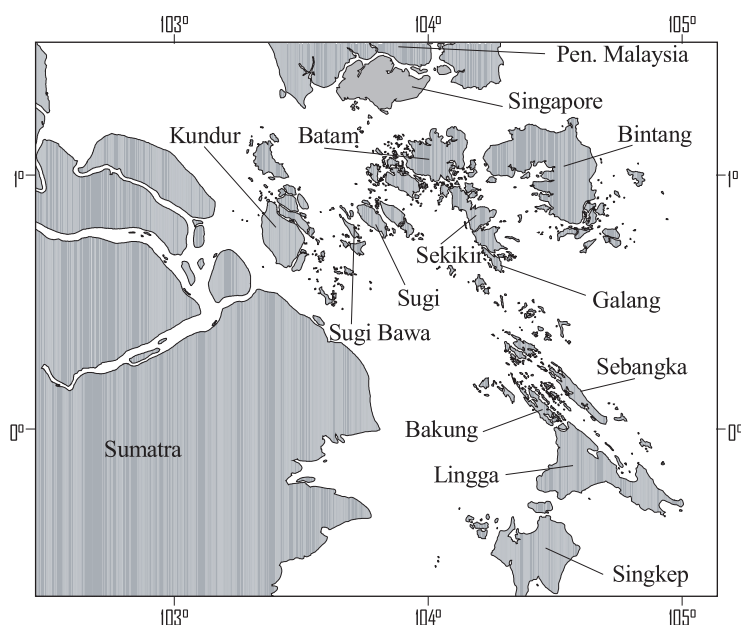
*Comments on other selected subspecies.* *T. n. amoenus* and *T. n. jugularis* Miller, 1903 from Musala Island (off west Sumatra, see Fig. 20). As discussed above in the section on melanism and erythrism, we consider the two described subspecies from Musala Island to be colour morphs of the same taxon and follow Chasen's (1940) suggestion to assign them to *T. javanicus* (recte *napu*) *amoenus*. We did not have any data on the other island taxa west of Sumatra (see Fig. 20), i.e. *T. brevipes* from Bangkaru Island; *T. russulus* and *T. n. batuanus* from Tana Bala and Tana Masa; and *T. pinus* from Pinie, and we will address these in future research.

*T. billitonus* Lyon, 1906 from Belitung. Interestingly, *T. billitonus* seems to be a relatively small taxon in relation to the large size of Belitung Island (see Fig. 17). A mean value for CBL of 95.3 ( $N = 9$ ) is in the range of values for *T. javanicus* rather than *T. napu* (see Table 1). Until more data become available we recommend following Lyon's taxonomic recommendation and provisionally leaving the taxon in *T. napu*, but we note that it may have to be reassigned to *T. kanchil*.



**Figure 20.** Map of the islands west of Sumatra.





**Figure 21.** Map of the Riau and Lingga Archipelagos.

*T. nigrocinctus* Miller, 1906 from Kundur and Great Karimon (= Karimun Besar) (see Fig. 21) is quite different from the other taxa in the Riau and Lingga Archipelagos because of its clear black neck and the colour of the lower side of the tail, which is yellowish-brown, both character states unique among the species in the archipelago (Miller, 1911). Chasen (1940) called this taxon *T. javanicus* (recte *napu*) *nigrocinctus*, but because of its unique colour patterns *T. nigrocinctus* could probably be retained as a distinct species.

*T. bancanus* Lyon, 1906 from Bangka. According to Lyon this taxon is very closely related to *T. napu* of Sumatra, but brighter in colour and with slightly smaller skull. He reported measurements of five adult specimens from Bangka with the following means: CBL = 103.8 mm, ZW = 48.6 mm. When compared with the values for *T. napu napu* (s.s.), these means are similar to those for the Bornean specimens (see Table 3). The only remaining differentiating character is the brighter colour, which Lyon described as tawny-ochraceous, as opposed to ochraceous in *T. napu*, although everywhere this is largely obscured by the conspicuous black tips of the hairs (Lyon, 1906). The large island of Bangka is in the middle of a late Pleistocene landbridge and watershed between Borneo and Sumatra and gene flow would have probably occurred between these areas until this island was isolated after the last glacial maximum. This implies a close relationship between the Bangka taxon and *T. n. napu* from Sumatra and Borneo.

Lyon's (1906) statement that this is indeed the case and the lack of consistent differentiation from the mainland form in coat colour probably favour inclusion in *T. n. napu*.

#### *T. versicolor*

Figure 5 showed that *T. versicolor* is distinct from all other *T. napu* specimens. The skulls are significantly smaller than all others, but relatively wide, with wide bullae (possibly an allometric effect, smaller species having larger bullae, as again suggested to us by an anonymous reviewer) and very long nasals (the latter measured only in one specimen). Thomas (1910) classified these unusual mouse-deer from Annam as belonging to the *T. napu*-group based on their coarse hair, which he considered characteristic, their relatively long canines, and the fact that a population of very different looking *T. kanchil* had already been described for the area.

Thomas also, however, noted some major differences between *T. versicolor* and *T. napu*. Firstly, the Annam specimens were very small compared with the geographically nearest *T. napu* specimens, those of Thailand and Burma. The large auditory bullae were much more rounded and inflated than in either of the other forms (i.e. *T. k. affinis* and *T. napu*). Finally, the skin coloration set it apart from any of the known forms; he described the marked contrast between the anterior half of the specimens, which was ochraceous-buff, whereas the posterior half, starting behind the shoulders, was clear grey (described as 'brown-grey (silver)')



by van Dort, 1986). Thomas also indicated that there was no dark median line on the white underparts, which again would set it apart from all other mouse-deer. van Dort (1986) added to this that there are no dark lines from the eye to the nose; additionally, she stated that some specimens have a throat pattern with three white and two coloured stripes, which are characters of *T. javanicus*, whereas there are others with the *napu*-like five white and four dark stripes. Another differentiating character, which E.M. observed in the type of *T. versicolor*, is the absence of the dark collar that is present in all *T. javanicus*, *T. kanchil*, and *T. napu* specimens, apart from a few specimens of *T. k. ravus* (also see Kloss, 1918). The reddish throat lines converge at the posterior end but do not touch, so that the central, white throat line is directly connected to the white on the underparts. None of the other *Tragulus* specimens that we have seen had throat hair as coarse as *T. versicolor* and we cannot agree with Thomas' conclusion that this character suggests a close relation between *T. napu* and *T. versicolor*. The evidence supports the conclusion that *T. versicolor* is a species distinct from both the *T. javanicus* and the *T. napu* species groups.

#### *T. nigricans*

Thomas (1892) described *T. nigricans* as a new species of mouse-deer from Balabac, the Philippines. He thought it to be allied to *T. napu* because of their similarities in size and arrangement in colours. Miller (1901a) stated that colour patterns in *T. nigricans* were essentially the same as in *T. napu bunguranensis* from Bunguran Island, but the skins that E.M. studied were rather different. The upperparts of *T. nigricans* are broadly washed with black, whereas *T. bunguranensis* is uniformly ochraceous. The neck of *T. nigricans* is mixed black and fulvous, whereas the neck in *T. bunguranensis* is completely black.

Our recommendation to designate the Balabac taxon as a distinct species follows Sanborn (1952) and Rabor (1977), who similarly assigned full specific status to it. Rabor (1977) reported that the species was introduced to Palawan and to 'a small island north of Palawan', but that it had not successfully established a breeding population; the present status of the species on those two islands is unknown.

#### *T. javanicus*

Two different taxa of mouse-deer have been described from Java, a grey-necked form and a red-necked form. Miller (1903a) named the former *T. focalinus*, because he assumed that the name *T. javanicus* referred to the large mouse-deer, which is now thought not to occur on Java. *T. focalinus* was distinguished from all other

*T. javanicus*-like mouse-deer by the great width and distinctness of the tawny superciliary stripes and by the grizzled grey neck, which is strikingly contrasted with the tawny body and head; in addition, according to Miller, the nape stripe is absent, although the dark crown sometimes slightly extends onto the nape, and compared with *T. kanchil* from Sumatra, the rostrum is shorter and the auditory bullae are narrower. Miller noted that the specific name *pelandoc* Hamilton Smith, 1827 had been twice applied to a grey-necked *Tragulus*, by Blyth (1858) and by Stone & Rehn (1902); but this name was based on Raffles' 'Pelandok', which referred to an animal from Sumatra, not Java. Miller therefore introduced the name *focalinus* for the Javan species.

Dobroruka (1967) suggested that a second mouse-deer taxon existed on Java, distinct from the grey-necked form described by Miller. This was based on five specimens in the Zoological Museum of the Humboldt University in Berlin. Miller had studied three of these in 1904 and wrote on the label: 'If actually from Java, probably sp. nov.'; one of the others was known to be from Cheribon (= Cirebon), on the north coast of West Java Province. The ground colour of these specimens is orange-brown, slightly grizzled with black and all specimens had a clear, almost black nape stripe. The cheeks and the sides of the neck are orange-buff, as opposed to the grey in *T. focalinus*. Dobroruka noted the general external similarity of these specimens to *T. j. luteicollis* from Bangka Island and also *T. j. kanchil* from Sumatra and *T. j. hosei* from Borneo. Bonhote (1903: 292) had also remarked that one specimen that he studied resembled the typical *kanchil* on the nape (presumably by having a clear nape stripe and reddish neck). Based on this evidence Dobroruka therefore recognized a distinct subspecies, which he called *T. javanicus pelandoc*, restricting the type locality to Cirebon. He suggested that the grey-necked form *Tragulus j. javanicus* (Osbeck, 1765 = *focalinus* Miller, 1903a) was restricted to the western part of Java and to the southern coast. van Dort (1986), who studied skins of Javan mouse-deer, found all kinds of forms that were intermediate between the two supposed Javan subspecies and there were also forms that closely resembled *T. k. kanchil* from Sumatra, but which did not come from Cirebon. She concluded that there was probably only one taxon on Java.

Our craniometrical data indicate that there may indeed be two distinct mouse-deer taxa on Java (Fig. 12). The data are, however, inconclusive and, for instance, the only specimen from Cirebon grouped with those from the south coast; further research, particularly on skin patterns of Javan mouse-deer, is required. None of the specimens studied by Dobroruka (1967) was included in the present research, and

future work regarding the specific status of Javan mouse-deer should address these.

Finally, there are three *T. napu* specimens said to be from Java, two of which were from the Mt Wilis area (RML 4938, 4939, 4941), collected by the archaeologist E. Dubois, presumably for reference purposes for Pleistocene material. A discriminant analysis in which these three specimens were entered as unknowns, together with *T. javanicus* specimens (from Java) and *T. napu* specimens from Sumatra and Borneo, grouped them with the *T. napu* sample. It may be that Dubois collected these specimens during his earlier fieldwork in Sumatra, after which they were mislabelled; but why there should be such a specific reference to a location ('Mt Wilis', a volcano in East Java) remains unclear.

### *T. kanchil*

*Geographical variation in the present sample.* Four subspecies of *T. javanicus* have been described for Borneo: *T. kanchil hosei* (Bonhote, 1903), from the Baram River, Sarawak; *T. virgicollis* (Miller, 1903a), from Mt Dulit, Sarawak, but said by the describer to extend to the Kinabatangan River and the Sandakan area in Sabah; *T. kanchil klossi* (Chasen, 1935b) from Bettotan, Sandakan, east Sabah; and *T. kanchil longipes* (Lyon, 1908b), described from Sumatra and said by him to extend not only through central east Sumatra but throughout west, south-west, and south-east Borneo. The range that Miller provided in his description of *T. virgicollis* covers those of *T. j. hosei* and *T. j. klossi*. Chasen (1940) included *T. j. virgicollis* in *T. j. hosei* without commenting on it.

Chasen (1935b), in his description of *T. k. klossi*, stated that the nine examples on which his new subspecies was based were still referred to *T. k. longipes* in Chasen & Kloss (1931), but that he now (Chasen, 1935b) rejected this and considered *T. k. klossi* distinct from both *T. k. hosei* and *T. k. longipes*. The Sabah subspecies was said to differ from the Sarawak subspecies (*T. k. hosei*) in its generally duller and paler coloration, lacking the rich fulvous element in the pelage, this being replaced by a yellower, buffy colour and with coarsely grizzled upperparts (Chasen & Kloss, 1931). Our data suggest that *T. k. klossi* is larger than the other samples from Borneo and also from the rest of the range of *T. kanchil*, but it could not be separated completely from them; we would have been able to separate the Sabah specimens completely if three West Sumatran specimens had not consistently grouped with those from Sabah. The skins of these West Sumatran specimens were normal Sumatra skins, and unlike *T. k. klossi* (E. Colijn, pers. comm., 13 October 2002). Future research will further investigate these widely separated populations of

*T. kanchil*, and we anticipate that *T. k. klossi* would be upgraded to full species level; we note that it has a unique coat coloration not found in any other subspecies of *T. kanchil*, the upper parts being mottled as in *T. napu* (van Dort, 1986). For now, we recommend maintaining it as a distinct subspecies, whose range includes the northern area of East Kalimantan Province, north of the Sembakung River and east and central Sabah. We did not study any skulls from western Sabah and we are unsure whether that area belongs to the range of *T. k. klossi* or *T. k. hosei*. The nearest locality of the latter subspecies is the Baram River in northern Sarawak.

In his description of the subspecies from Sarawak, Bonhote (1903) mentioned that *T. k. hosei* was larger than the mainland form *T. k. affinis*, the most noticeable point of difference being in the bullae, which were very much swollen and rounded and nearly twice as large. We noted the same difference in our research, although there was still some overlap between *T. k. hosei* specimens and specimens from Sumatra, Malaya, mainland Asia, and the small Sundaland islands. Bonhote (1903) also commented on the anterior margin of the premaxillae, which bend abruptly downwards from the anterior end of the nasals, whereas in the Malaya and mainland Asia forms it goes down in a more gradual slope. We did not notice this character in our research. Because *T. k. hosei* differs in skin coloration from *T. k. klossi*, and because there are also differences in skull morphology, we suggest provisionally maintaining *T. k. hosei* as a valid subspecies, whose range would then include Sarawak and probably most of Kalimantan, although we had no specimens from South Kalimantan Province.

We investigated the affinities of four specimens from the tiny, 0.36-km<sup>2</sup>, island of Berhala, between Singkep and the Sumatran mainland. A discriminant analysis grouped these specimens with those from Sumatra and Malaya, suggesting that it should be assigned to *T. k. kanchil*, as was also suggested by Chasen & Kloss (1928a). van der Meer-Mohr, (1930) reported that this population may have been introduced in the late 19th century, when a local king went on pilgrimage to the island and on that occasion took with him a number of live mouse-deer.

Our craniometrical analysis revealed that the *T. kanchil* skulls from the Malay/Thai peninsula and mainland Asia could be grouped into four more or less distinct groups (excluding *T. williamsoni* from north Thailand to which we assign full species status): *T. k. affinis* (synonym *T. k. pierreii*) from Vietnam, Laos, Cambodia, and eastern Thailand; a combined group of *T. k. ravus* and *T. k. angustiae* from south-west Thailand and the central and northern Malay peninsula; *T. k. fulviventer* from the southern Malay peninsula; and specimens from the Langkawi, Rawi

and Butang Islands. Analysis of coat coloration largely confirms these patterns, indicating a transition from a darker form in the southern Malay peninsula to a lighter form in the northern peninsula and on the Asian mainland. The separation between these two main colour forms appears to be around the Thailand–Malaysia border. Our southern form approximately coincides with the subspecies *T. k. fulviventer*, which Kloss (1918) restricted in the north to between latitudes 6° and 7°N. Gray (1836) assigned the name *T. fulviventer* to specimens with pale fulvous underparts from the Malay islands and peninsula, and Kloss (1918) maintained the subspecies with a restricted range of Singapore (= type locality) and the southern Malay Peninsula, while admitting that the characters described by Gray characterize only a minority of specimens. We apply the name *T. k. fulviventer* to the taxon from the southern Malay peninsula, south of 7°N.

Miller (1902b) described *T. ravus* with type locality Trang in southern Thailand (7°32'N, 99°35'E), stating that this species resembled *T. pallidus* from Laut Island (see description below), but was larger, the general colour less pallid, legs more red, and dark nape stripe ill defined. Kloss (1918) gave the range of this subspecies as from Perlis (northern Malaysia) and Pattani (c. 7°N) to as far north as Bandon (c. 14°N). Apart from the paler upperparts, this taxon is distinguished from *fulviventer* by a less distinct nape stripe (Kloss, 1918). As it coincides with the northern form that we found in our own results, we use the name *T. k. ravus* for the subspecies from the northern Malay peninsula. Chasen (1940) added the mouse-deer population from Lontar Island (= Lantar = Ko Lanta Noi) to *T. k. ravus*.

We investigated skins and skulls of five specimens from the range of *T. kanchil angustiae*, which Kloss (1918) described from South Tenasserim in Burma. He stated that the colour was as in *T. k. ravus*, but the nape stripe was well defined and wider than in *T. k. fulviventer*, and the white of the breast was separated from that of the abdomen by a Y-shaped extension from the sides. We found this latter character in specimens from other localities, including Malaysia, Borneo, and Bunguran, so it is not diagnostic for *T. k. angustiae*. The range of this subspecies, according to Kloss (1918), included the type locality Bankachon (10°09'N, 98°35'E) in Burma and Maprit in southern Thailand (10°42'N, 99°19'E), Yé (c. 15°20'N) in northern Tenasserim and Hat Sanuk (c. 11°45'N) in southern Thailand. The Haungtharaw Valley, a locality even further north than Yé (16°30'N, 98°13'E) (in Yin, 1967) may also contain this subspecies. We also found the alleged well-defined nape stripe of *T. k. angustiae* in two specimens from Koh Lala (near Rajburi, south-west Siam). The range of

*T. k. angustiae* appears to be bordered in the south by the Isthmus of Kra, an important zoogeographical boundary between the Sundaic and Indochinese Subregions (Corbet & Hill, 1992); in the east and north, the Chao Phraya River may be the boundary, although insufficient material from that region is available to say this with any degree of certainty. The type specimen is not different in shape or size from the other *kanchil*-like specimens from Malaya and the Asian mainland. The well-defined nape stripe character seems to distinguish *T. k. angustiae* from its northern and eastern neighbour *T. k. affinis* and its southern neighbour *T. k. ravus*.

As mentioned in the results, our craniometrical analyses could not meaningfully distinguish the 20 *T. kanchil* specimens from Indochina and Thailand from those on the Thai/Malay peninsula. Gray (1861) described the Indochinese population as *T. affinis*, a pale mouse-deer similar to *T. javanicus* (from Java), with the side of the neck similar in colour to the side of the body. There was no blackening in the neck. Gray described this new species based on five (or possibly six) specimens that Dr Mouhot collected in Cambodia. As these specimens were similar to one that had been in the museum for many years and to which Gray had given the name *T. affinis* (as a *nomen nudum*) in 1843, he collectively named the new specimens after the earlier one; the earlier specimen had come from Singapore but Gray assumed that this was only the port of transit. Kloss (1916a) reasoned that because the original name *T. affinis* had been a *nomen nudum*, until rendered available for use by Gray's description of the Cambodian animals, *T. affinis* should be confined to Indo-China and he confirmed the above description of a pale mouse-deer taxon lacking a neck stripe. Further localities for this subspecies given by Kloss (1918) are Dong Phya Fai in Thailand, South Annam (= central Vietnam), south-east and east Thailand, and the range of mountains between Ayuthia and Khorat.

Bonhote (1903) described *T. k. pierrei* based on a type specimen from Bien Hoa, lower Cochin China (= southern Vietnam). Four years later, however, he synonymized it with *T. k. affinis*, because '*T. affinis* was chiefly based on specimens from Cochin China' (Bonhote, 1907). This is incorrect, because Gray's specimens of *T. affinis* originated from Cambodia and not Cochin China, but Bonhote's original description of *T. k. pierrei* does confirm that it is similar to *T. k. affinis*, both being pale and lacking the blackening of the neck. Osgood (1932) suggested that the mouse-deer from Indo-China are somewhat duller in colour than '*ravus* and *affinis*', with the heads, especially, being more greyish or brownish and more contrasted with the body and that the dark nuchal area was rather well marked; he hypothesized that



*T. k. affinis* would be intermediate between *T. k. ravus* and the Indochinese specimens (which Bonhote initially assigned to *T. k. pierrei*). An ANOVA of the measurements from east and west of the Mekong River – which we expected to be the main biogeographical division between these possible subspecies (see Meijaard & Groves, in press) – showed that only the width of the auditory bullae differed, but not significantly ( $P = 0.099$ ,  $N = 15$ ). Interestingly, Bonhote (1903) similarly noted that the bullae of *T. k. pierrei* were relatively broad. Until further data become available we recommend following Bonhote's (1907) decision to synonymize *T. k. pierrei* with *T. k. affinis*. This then extends the range of *T. k. affinis* to the whole of Vietnam, probably as far north as the Red River.

In our craniometrical analysis, adult mouse-deer specimens from Langkawi, Rawi, and Butang formed a somewhat distinct group from all other *kanchil*-like mouse-deer (Fig. 10), primarily because of their short, narrow auditory bullae and narrow braincase. Two subspecies have been described from these islands, *T. lancavensis* from Langkawi Miller, 1903 and *T. ravulus* Miller, 1903 from Adang and Rawi Island, in the Butang Islands group. According to Miller, *T. lancavensis* was similar to *T. ravus* from the opposite mainland, but general colour slightly more yellow and underparts extensively washed with orange-buff. The latter character, which led to a separation of the white groin from the white chest, was not constant, but Miller, uncharacteristically, considered it sufficiently prevalent to assign the Langkawi taxon to a separate species. In the ten skins of this taxon that we studied, this character was not always present and the amount of orange-buff varied considerably. Kloss (1918) remarked that he found himself unable to separate Langkawi examples, which were much more brightly coloured than *T. k. ravus*, from the more southern form of *T. k. fulviventer*, yet its craniometrical similarities are with *T. k. ravus*. For the time being we cannot determine to which subspecies the Langkawi form is more closely related, and its subspecific status should be retained until further data become available.

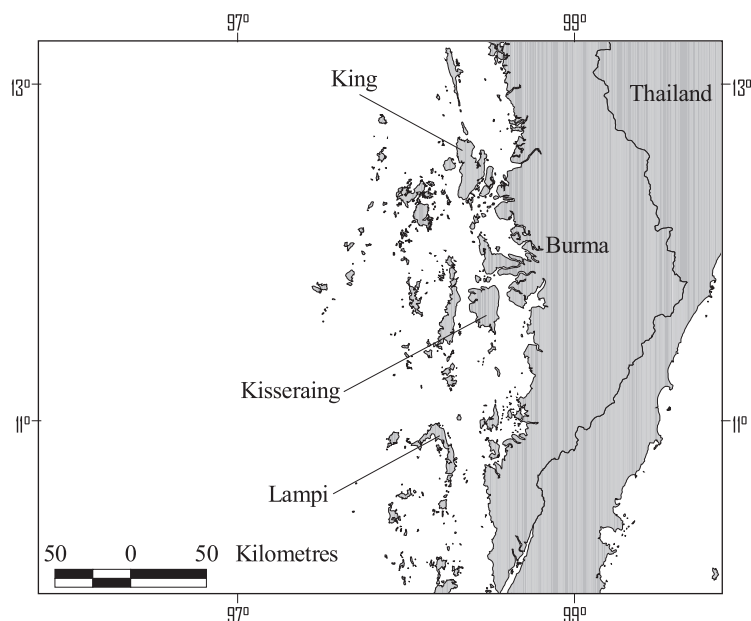
The colour of *T. ravulus* from Adang and Rawi closely resembled that of *T. k. ravus*, but it is paler and has a less defined nape stripe. Miller thought it to be different from the mainland form, because of the smaller upper premolars of *T. k. ravulus*; the material at hand was, however, not enough to prove that that character was constant (Miller, 1903a). Our craniometrical analysis shows that *T. k. ravulus* is further distinguished from all other *T. kanchil* taxa by its short, narrow auditory bullae, short nasals, short mandibles, and narrow braincase, but these features are insufficiently distinct to separate this taxon as a

distinct species. We therefore recommend maintaining it as a subspecies, *T. k. ravulus*.

Chasen (1940) described two subspecies of *T. kanchil* from islands off the west coast of peninsular Thailand: *T. k. insularis* from Junk Seylon (= Phuket), Sireh (= Ko Sire) and Panjang (= Ko Yao Yai), and *T. k. pidonis* from Koh Pipidon. *T. k. insularis* is in general colour intermediate between *T. k. ravus* from the opposite mainland and *T. k. fulviventer*, but with the nape stripe obsolete and less conspicuous than in either of the two races. Compared with *ravus*, *insularis* has the upper parts and throat stripes rather darker and the under parts more richly coloured. *T. k. pidonis* is a pale form, very close to *T. k. ravulus* (see above), but the limbs even paler than in that form. Chasen remarked that *T. k. pidonis* was not a well-marked subspecies, with at least one specimen (out of three) from Koh Pipidon being intermediate in appearance between *T. k. ravulus* and the type specimen of *T. k. pidonis*. We were unable to study any specimens of *T. k. insularis* and we have no option but to maintain this subspecies in the meantime. Among the skulls that we studied were two specimens from Koh Pipidon (ZRC 4.4917 and 4.4918, both adult specimens), which stood out from the other *T. kanchil* specimens because of the high values for ML (mean = 77.1, SD = 1.2) and MH (mean = 30.1, SD = 0.9), but not enough to separate them completely from the others. Nasal length in this taxon significantly differentiated the specimens from Koh Pipidon from all other *T. kanchil* taxa ( $P < 0.01$ ). The mean value of NL for *T. k. pidonis* was 32.1 mm (SD = 1.7,  $N = 2$ ), which was much higher than the mean values of NL for the other *T. kanchil* taxa, which ranged from 24.2 mm (SD = 1.2,  $N = 2$ ) in *T. k. ravulus* to 27.1 mm (SD = 3.0,  $N = 10$ ) in *T. k. lancavensis*; in the methodology we explained the difficulty in reliably measuring NL and the data need to be rechecked before we can use this character to differentiate *T. k. pidonis* from other taxa.

Miller (1903a) described *T. lampensis* from Lampee (= Lampi = Lanbi Kyun) Island in the Mergui Archipelago (see Fig. 22) as similar to *T. lancavensis* (*lapus calami*) but yellower throughout, particularly on the underparts. According to Miller, skull and teeth of this taxon did not differ from those of *T. lancavensis* and *T. j. ravus*, which our measurements on the only specimen from this island (BNHM 23.1.6.72) confirmed. We recommend provisionally retaining the subspecies *T. k. lampensis*.

*T. luteicollis* from Bangka Island (see Fig. 7) was described by Lyon (1906) based on 18 specimens. He thought it to be very closely related to *T. kanchil* of Sumatra, from which it differed in a generally duller colour, especially on the side of the neck and head and with less black upperparts. Dobroruka (1967) sug-



**Figure 22.** Mergui Archipelago.

gested that the red-necked form from Java (which he named *T. j. pelandoc*, see section on *T. javanicus* for description) was very similar to *T. j. luteicollis*, which could suggest that animals from the Bangka region migrated into Java, possibly during the last glacial maximum when these land areas were physically connected. We were unable to study skins of this taxon, but measured two skulls (ZMA 22.863, 22.864). Apart from the relatively long mandibles (ML = 77.4 mm) and long nasal bones (NL = 29.4 mm) in one of the two specimens, these skulls did not differ much from Sumatran or Bornean specimens. We suggest maintaining *T. k. luteicollis* as a provisional subspecies.

Miller (1903a) described *T. kanchil subrufus* from Singkep Island (see Fig. 21). Chasen (1940) further mentions the islands of Lingga and Penuba (near Lingga) as part of this taxon's range. According to Miller (1903a) the skull and teeth do not differ from those of *T. kanchil* from Sumatra, but its slightly more yellow upperparts allow differentiation from the Sumatran form. We measured the paratypes of this taxon from Lingga (FMNH 43336 and 43337) and these did not differ significantly from the Sumatran specimens. This seems to be a weak subspecies closely allied to *T. k. kanchil*.

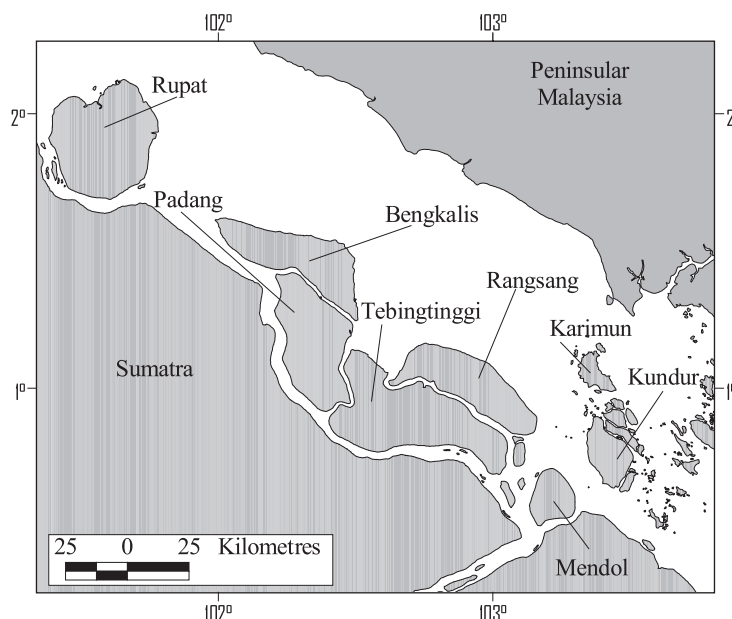
Miller (1903a) described *T. rubeus* from Bintang (see Fig. 21) as being similar to *T. subrufus* from Singkep and Lingga, but with slightly larger skull and teeth and brighter colours. It is distinguished from all other members of the *T. kanchil* group in its dark, rich colour and broad but inconspicuous nape stripe. The latter character seems invalid, because we saw one specimen

(ZRC 4.4884) that had a distinct nape stripe. Our craniometrical analysis of three specimens did not reveal any significant differences between skulls from Bintang and from Sumatra, but when compared to the two specimens from Lingga there was a significant difference in bullae length ( $P < 0.01$ ). Mean BL for *T. rubeus* is 18.7 mm (SD = 0.21,  $N = 3$ ) and for *T. k. subrufus* it is 17.6 mm (SD = 0.07,  $N = 2$ ). Based on this distinction we maintain the Bintang taxon as *T. k. rubeus*.

Our craniometrical analysis could not separate the five specimens of *T. kanchil everetti* Bonhote, 1903, from Bunguran in the Natuna islands group, from other *T. kanchil* specimens. It was described as similar to *T. k. hosei* from Borneo, except that the red on the flanks was much deeper and that it had larger teeth and smaller bullae compared with the Bornean subspecies. In the same year, Miller (1903a) independently described this taxon from Bunguran, but named it *T. natunae*. Both Miller's and Bonhote's descriptions were published in March and the priority of names is unclear; because we consider it a valid subspecies, we follow Chasen (1940), the first reviser, and use the name *T. k. everetti*.

*Comments on other selected subspecies.* *T. j. pumilus* Chasen, 1940 from the Great Redang Island, off Trengganu, on the east coast of the Malay peninsula. According to Chasen, *T. j. pumilus* was like *T. k. fulviventer* from the opposite mainland, but smaller. Total length of the specimen, which had complete adult dentition, was 470 mm. This is at the lower end of the size range of *T. k. fulviventer*, but not out-





**Figure 23.** Malacca Strait islands between Sumatra and the Malay peninsula.

side it. Total size for non-juvenile *T. k. fulvivent* specimens, as indicated on our specimen labels, varied from 470 to 513 mm. It seems likely that *T. j. pumilus* should be synonymized with *T. k. fulvivent*.

Lyon (1908a) described *T. fulvicollis* from Bengkalis and added the islands of Padang, Rupat, Tebingtinggi, and Rangsang (= Rangsang) (see Fig. 23) to its range. These low-lying islands (maximum altitude is about 15 m) are situated only a few kilometres off the east coast of Sumatra and can be considered an extension of the swamps of eastern Sumatra. According to Lyon, *T. fulvicollis* was somewhat like *T. rarus* from the Malay peninsula, but much larger and more richly coloured, especially about the neck and forelegs, whereas it differed from the Sumatran *T. kanchil* in its larger size and lighter colour. The coloration characters were, however, not consistent, because Lyon stated that certain specimens from Sumatra showed *T. fulvicollis* characters. An ANOVA of the measurements given in Lyon (1908a) showed that the 33 specimens of *T. fulvicollis* were significantly larger than *T. kanchil* ( $P < 0.001$ ) for ZW (mean = 43.7 mm, SD = 1.4, for *T. kanchil* measurements see Table 7) and for basal length of skull, but bi-variate plots could not completely separate *T. fulvicollis* from *T. kanchil* specimens. We were unable to study skulls or skins of this taxon and recommend following Chasen's (1940) recognition of *T. k. fulvicollis*.

*T. pallidus* was described by Miller (1901a) based on one specimen from the small island of Laut, north of Bunguran, Natuna islands group. It was smaller than the *T. javanicus* (= *kanchil*) from Borneo and Bunguran and very pale in colour. Miller (1902b) noted the

similarities between *T. pallidus* and *T. rarus*, which could suggest that *T. pallidus* is more closely related to the forms from the northern Malay peninsula and the Asian mainland than to the southern *T. kanchil* forms. Figure 18 provides a possible explanation. If the mouth of the Siam River entered the South China Sea during the last glacial maximum to the south of the Laut Island area, land-based migration directly from Indochina would have been possible. Because we were unable to study skins or skulls of this taxon, we recommend following Chasen's (1940) taxonomy and assign the taxon to *T. k. pallidus*.

Miller (1906a) described *T. carimatae* from Karimata, an island off the west coast of Borneo. The colours of *T. carimatae* very closely resembled those of the Sumatran *T. kanchil* and also the skull dimensions of these taxa were very similar. The main distinguishing character of *T. carimatae* was the larger teeth. Miller found absolute differences between the lengths of both the maxillary and the mandibular tooththrows in *T. carimatae* and *T. kanchil* from Tapanuli Bay, west Sumatra. As the latter location seemed to us an unusual choice for comparison (Karimata is well to the east of Sumatra), we also checked these teeth dimensions in specimens from the geographically closer areas of western Borneo (Lyon, 1911), eastern Sumatra (Lyon, 1908a), and Bangka (Lyon, 1906). Tooththrows in *T. carimatae* are absolutely larger than those from eastern Sumatra and western Borneo, but they are similar to those in Bangka specimens; the population differs from the Bangka taxon in being slightly larger and having a less yellow neck (Lyon, 1906). van Dort (1986), who measured one specimen

from Karimata, reported a CBL of 95.6 mm, which would be longer than any other *T. kanchil* skulls (including the very large *T. williamsoni*), although she suggested that this was an individual exception. Until we can actually study the skins of *T. k. luteicollis* and *T. carinatae* it is impossible to judge whether the yellowish colour of the neck in these taxa differs significantly.

#### *T. williamsoni*

Kloss (1916b) stated that in size the very large subspecies *T. kanchil williamsoni*, from northern Thailand, most closely agreed with *T. versicolor*, but because in colour it was similar to *T. affinis*, he regarded it as unquestionably belonging to *T. kanchil*. Table 9 and Figure 14 show indeed that the single available skull of *T. k. williamsoni* is much larger than any other *T. kanchil* taxa from the Asian mainland and Malay Peninsula. The type specimen (BNHM 47.1510) originated from Meh Lem, Muang Pre, Song forest, North Siam (18°25'N, 100°23'E), which is in the far north of Thailand. The range of this species seems to be restricted in the east by the Mekong River, because specimens from northern Laos, east of the Mekong River, clearly grouped with *T. k. affinis*. The southern boundary of the species is unclear, but the species may be restricted to the higher altitude areas of northern Thailand, whereas *T. k. affinis* occurs in the lower southern and eastern parts. It would be interesting to see whether the populations reported by villagers from north Laos, west of the Mekong, in Xaignabouli Province (Duckworth, 1994; Duckworth *et al.*, 1999: 269), group with *T. williamsoni* or with *T. k. affinis*. It is unclear on which side of the Mekong River the mouse-deer from Yunnan Province, China, occur because the mouse-deer distribution maps in Ohtaishi & Gao (1990) and Sheng & Ohtaishi (1993) do not show sufficient detail.

#### TAXONOMIC PROPOSALS

The results of this research suggest that, based on cranial morphometrics, there are six species within the genus *Tragulus*, within which we found sufficient evidence to recognize 24 subspecies. It should, however, be noted that we were unable to study specimens of all described subspecies, and more subspecies could be recognized in future research.

#### THE NAPU GROUP

*Tragulus napu*, with the following subspecies:

- Tragulus napu napu* – Borneo, Laut (SE Borneo), Serasan, Bangka, Sumatra, Malay and Thai Peninsula, Burma, Langkawi and Pangkor
- Tragulus napu bunguranensis* – Bunguran

*Tragulus napu rufulus* – Batam, Galang, Setoko (= Sekikir), Bulan, Tioman, Bintang, Lingga, Bakong, Sebangka

*Tragulus napu banguai* – Banggi, Balembangan

*Tragulus napu neubronneri* – North Sumatra

*Tragulus napu niasis* – Nias

*Tragulus napu terutus* – Terutau

*Tragulus nigricans* – Balabac

#### TRAGULUS VERSICOLOR

*Tragulus versicolor* – south-east Vietnam

#### TRAGULUS JAVANICUS GROUP

*Tragulus javanicus* – Java

*Tragulus kanchil*, with the following subspecies

*Tragulus kanchil kanchil* – Sumatra, Mendol, Berhala

*Tragulus kanchil abruptus* – Subi

*Tragulus kanchil siantanicus* – Siantan

*Tragulus kanchil anambensis* – Mata

*Tragulus kanchil klossi* – Sabah

*Tragulus kanchil hosei* – Sarawak, West Kalimantan, Central Kalimantan

*Tragulus kanchil fulviventer* – southern Malay peninsula

*Tragulus kanchil ravus* – northern Malay peninsula, southern Thailand, Langkawi

*Tragulus kanchil angustiae* – Burma, south-western part of the Thai mainland, probably limited to the west of the Chao Phraya River

*Tragulus kanchil affinis* – Vietnam, Cambodia, Laos, south-east and east Thailand

*Tragulus kanchil ravulus* – Adang, Rawi

*Tragulus kanchil pidonis* – Koh Pipidon

*Tragulus kanchil luteicollis* – Bangka

*Tragulus kanchil subrufus* – Singkep

*Tragulus kanchil rubeus* – Bintang

*Tragulus kanchil everetti* – Bunguran

*Tragulus williamsoni* – northern Thailand and possibly Yunnan Province, China

#### ACKNOWLEDGEMENTS

We would like to thank the curators of the collections in which specimens were studied: Dr P. J. H. van Bree and Mr A. Rol (Amsterdam), Dr C. Smeenk (Leiden), Ms P. Jenkins and Mr R. Harbord (London), Mrs Yang Chang Man (Singapore), Dr Suyanto (Cibinong), Dr C. Leh (Kuching), and Dr L. Heaney and W. Stanley (Chicago). Special thanks are due to Ed Colijn who investigated some skins for us in the Leiden Museum. We also thank Will Duckworth, Joe Walston and Tony Lynam for sharing their field data with us. We thank the Sarawak Biodiversity Council for allowing E.M. to visit the Sarawak Museum collection. We are extremely grateful to the Field Museum in Chicago for providing E.M. with a travel grant to visit the collec-

tion. Finally, we would like to acknowledge the contributions of two unusually perspicacious anonymous reviewers of the first draft of this paper, and we thank P. Grubb for reading the manuscript and providing some very useful comments.

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- Anambas Islands ( $N = 4$ ): ZRC 4.4920; 4.4921; 4.4922; 4.4924
- Balabac (*T. nigricans*) ( $N = 7$ ): BNHM 94.2.4.16; 94.6.8.4; FMNH 11308; 21326; 62821; 62823; 62824
- Bangi ( $N = 1$ ): BNHM 47.1513
- Bangka ( $N = 2$ ): ZMA 22.863; 22.864
- Batam ( $N = 3$ ): ZRC 4.4761; 4.4762; 4.4763
- ?Batam ( $N = 5$ ): ZRC 4.4765; 4.4766; 4.4767; 4.4772; 4.4779
- Berhala ( $N = 4$ ): ZMA 22.865; 22.866; 22.867; 22.868
- Bintang (*T. kanchil*) ( $N = 3$ ): ZRC 4.4884; 4.4933; 4.4934
- Bintang (*T. napu*) ( $N = 3$ ): ZRC 4.4743; 4.4886; 4.4929
- ?Bintang (*T. napu*) ( $N = 2$ ): ZRC 4.4744; 4.4745
- Borneo (*T. kanchil*) ( $N = 41$ ): BNHM 55.1011; 55.1012; ZMC, 08197; 08198; 08200; 11658; 14193; FMNH 15570; 18558; 32694; 33513; 33514; 33515; 33517; 33518; 33521; 33528; 68766; 68767; 68768; 68775; 68776; 68777; 68778; 85123; 85124; 85128; 85129; 85132; 85912; 85913; SM (two unnumbered specimens); SM 62.2.31; 68.210; 68.225; 68.229; 68.232; 8/5/62; ZMA 22.824; 22.825; ZRC 4.4830
- Borneo (*T. napu*) ( $N = 46$ ): BNHM 10.4.5.129; 10.5.5.125; ZMC, 11661; 11662; 11663; 18053; (one unnumbered specimen); FMNH 141017; 141133; 18559; 33530; 68769; 68770; 85914; 85915; 85954; 88778; RML cat.ost.d; cat.ost.f; cat.ost.h.; SM (four unnumbered specimens); SM 1; 111.89; 19.8.51; 198/7; 2; 68.1.8; 68.19; B2; ZMA 22.889; 22.890; 22.901; 22.919; 25.152; 25.153; ZRC 4.4735; 4.4737; 4.4738; 4.4740; 4.4741; 4.4742; ZMA 22.870
- Bulang ( $N = 2$ ): ZRC 4.4777; 4.4781
- Bunguran (*T. kanchil*) ( $N = 3$ ): ZRC 4.4805; 4.4807; 4.4810
- Bunguran ( $N = 5$ ): ZMA 22.869; 4.4806; 4.4809; 4.4811; 4.4926
- Galang ( $N = 1$ ): ZRC 4.4930
- Java ( $N = 34$ ): BNHM 1938.11.30; 52b; 9.1.5.837; 9.1.5.841; 9.1.5.843; 9.1.5.850; 9.1.5.852; 9.1.5.853; ZMC 07910; 10150; FMNH 34189; 34190; 48935; RML (one unnumbered specimen); RML 14520; 14523; 172; 33767; 4932; 4933; 4935; 4936; ZMA 22.844; 22.845; 22.846; 22.848; 22.854; 22.855; 22.856; 22.857; 22.858; 22.859; 22.861; ZRC 4.4755
- Karimun ( $N = 1$ ): ZRC 4.4758
- Lampi ( $N = 1$ ): BNHM 23.1.6.72
- Langkawi (*T. kanchil*) ( $N = 11$ ): ZRC 4.4793; 4.4832; 4.4833; 4.4835; 4.4836; 4.4837; 4.4838; 4.4839; 4.4840; 4.4841; 4.4842
- Langkawi (*T. napu*) ( $N = 1$ ): BNHM 9.11.1.166
- Lingga (*T. kanchil*) ( $N = 2$ ): FMNH 43336; 43337
- ?Lingga (*T. napu*) ( $N = 4$ ): ZRC 4.4895; 4.4900; 4.4901; 4.4902
- Lontar ( $N = 1$ ): ZRC 4.4875
- mainland Asia (*T. kanchil*) ( $N = 30$ ): BNHM 14.12.8.237; 28.7.1.150; 33.4.1.498; 33.4.1.499;

## APPENDIX 1

### TEXT AND TRANSLATION FROM GMELIN (1788)

'Magnitudine vix cuniculum aequavit, nec pedes multo crassiores, quam *Tragulus pygmaeus*, habuit. Auriculae nudaе, ut & nasus; sinus inguinales & ante oculos nulli, scopae genuum quoque defunt. Cauda longiuscula, villosa, ferruginea, subtus & apice alba. Ungulae spurize exiguae. Color fere Caviae Acuti, ferrugineus, fuscis pilis mixtus, subtus longitudinaliter albus. Cervix gryseo canescente, fuscisque pilis mixta; collum subtus album, maculis binis, subconnexis, cervicis colore; Pili duo longi sub gula, divergentes. Caput ferrugineum, vertice longitudinaliter nigricante'.

[In size hardly equals a rabbit, nor are its feet much thicker compared to *Tragulus pygmaeus*. Ears naked, as also the nose; no inguinal or preocular cavities, knee-brushes also absent. Tail rather long, hairy, ferrugineous, white below and at tip. Nape grey, with light and dark hairs mixed; neck below white, with a pair of spots, barely touching, of the colour of the nape; two long streaks under the throat, divergent. Head ferrugineous, with vertex longitudinally blackish.]

## APPENDIX 2

### LIST OF SPECIMENS STUDIED

Adang ( $N = 1$ ): ZRC 4.4845



- 47.1510; 55.3225; 6.11.6.40; 61.4.12.20; 61.4.12.7;  
78.6.17.18; FMNH 36725; 38012; 38022; 39144;  
39145; ZRC 4.4795; 4.4796; 4.4797; 4.4798; 4.4799;  
4.4800; 4.4801; 4.4803; 4.4850; 4.4851; 4.4914;  
4.4955; 4.4959; 4.4961; 4.4964
- Malay/Thai peninsula (*T. kanchil*) ( $N = 23$ ): FMNH  
90446; 98652; 98653; RML cat.ost.c; ZRC 4.4804;  
4.4813; 4.4814; 4.4828; 4.4853; 4.4855; 4.4861;  
4.4862; 4.4863; 4.4865; 4.4866; 4.4869; 4.4876;  
4.4879; 4.4880; 4.4881; 4.4883; 4.4915; 4.4946
- Malay/Thai peninsula (*T. napu*) ( $N = 14$ ): BNHM  
66.4012; 66.4015; 55.3214; FMNH 83107; 83108;  
ZRC 4.4729; 4.4730; 4.4733; 4.4753; 4.4757; 4.4889;  
4.4891; 4.4892; 4.4893
- Me Song (Thailand) *T. williamsoni* ( $N = 1$ ): BNHM  
47.1510
- Nhatrang (Vietnam) *T. versicolor* ( $N = 3$ ): BNHM  
6.11.6.33; 6.11.6.38; 6.11.6.39
- Pangkor ( $N = 1$ ): ZRC 4.4731
- Pipidon ( $N = 2$ ): ZRC 4.4917; 4.4918
- Rawi ( $N = 2$ ): ZRC 4.4847; 4.4848
- Serasan ( $N = 1$ ): BNHM 47.1514
- Singkep ( $N = 1$ ): ZMA 22.870
- Subi ( $N = 1$ ): BNHM 47.1507
- Sumatra (*T. kanchil*) ( $N = 10$ ): FMNH 43338; 43339;  
RML 11811; 33769; 33770; 3774; 4600; 4601;  
cat.ost.j; ZMA 23.340
- Sumatra (*T. napu*) ( $N = 16$ ): BNHM 51b; RML 33777;  
4940; cat.ost.e; cat.ost.g; ZMA 22.876; 22.877;  
22.878; 22.884; ZMC 08349; 11271; 12591; 15098;  
15099; ZRC 4.4932; 4.4941
- Terutau ( $N = 12$ ): BNHM 55.3222; 9.11.1.164; ZRC  
4.4723; 4.4724; 4.4725; 4.4782; 4.4784; 4.4788;  
4.4789; 4.4791; 4.4792; 4.5666
- Tioman ( $N = 13$ ): ZRC 4.4711; 4.4712; 4.4713; 4.4715;  
4.4716; 4.4717; 4.4718; 4.4719; 4.4720; 4.4722;  
4.4903; 4.4904; 4.4905