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Morphological and molecular systematics of Southeast Asian spiny rats (genus *Maxomys*) with descriptions of two new species from Indonesia

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Contents

SUMMARY

The spiny rats, species of the genus *Maxomys*, are one of the most common rats in the Southeast Asian region, covering the continent's mainland including the Peninsular Malaysia and islands of Borneo, Sulawesi, Sumatra, Java, and Palawan Island in the Philippines, as well as on several of the smaller islands of Sunda Shelf. Up to now, the knowledge of taxonomy, phylogeny, fur color variation, systematic and biogeography of this genus is very limited. Here, I performed morphological and molecular phylogenetic analyses with specimens of *Maxomys* collected from Indonesia and Malaysia through my field works and those deposited at several museums of Indonesia, United States, Australia, and Canada.

Craniometric measurements and molecular approaches with the mitochondrial cytochrome *b* gene and three nuclear gene sequences on *Maxomys* from Indonesia and Malaysia indicated that the previously known 17 *Maxomys* species, and 15 species are successfully analysed: *M. alticola, M. baeodon, M. bartelsii, M. dollmani, M. hellwaldii, M. hylomyoides, M. inas, M. moi, M. musschenbroekii, M. ochraceiventer, M. pagensis, M. rajah, M. surifer, M. wattsi, M. whiteheadi.* Morphologically, there is one cryptic species and formally considered as a local population of *M. whiteheadi.* Thus, this cryptic species is describe and named as *M. tajuddinii* sp. nov, new species of *Maxomys* from Borneo Island. Otherwise, there is another cryptic population due to molecular data, and describe as new species from Sulawesi Island.

Quantitative measurements of coat color with a spectrophotometer revealed no significant difference in the dorsal pelage showing mostly dark brown (L*= 25-30, a*= 5-7, b*= 10-15). The ventral colorations were variable among the species. I classified five different color types based on the measurements: whitish grey (*M. baeodon, M. whiteheadi, M. musschenbroekii, M. bartelsii,* and *M. dollmani*), orange dark brown (*M. hylomyoides*), chestnut orange (*M. ochraceiventer*), yellowish brown (*M. alticola*) and creamy white (*M. rajah, M. hellwaldii,* and *M. surifer*). These fur color characteristics can be useful in species recognition, together with the craniometric features.

My molecular phylogenetic analyses with both mitochondrial and nuclear gene sequences with the shrew rats (genus *Crunomys*) whose lineage is often considered as a potential outgroup of *Maxomys* showed the monophyly of *Crunomys* but no support for the monophyly of the genus *Maxomys* due to inclusion of *Crunomys* within the cluster of *Maxomys*. The *Maxomys* and *Crunomys* of Sulawesi belonged to four clades sister to extralimital species, suggesting that repeated overwater dispersal between Sundaland – Philippines and Sulawesi have shaped the species diversity in this group.

My morphological and molecular characterizations allow to describe two new species of *Maxomys* from *M. tajuddinii* sp. nov and *M. tompotika* sp. nov from Kalimantan and Sulawesi, respectively. Notably, my analyses further revealed unrecognized diversity in local populations of Sulawesi, suggesting the presence of two or more potentially undescribed species in this island. These descriptions generate new information and to address the taxonomic problems within this genus. It also reflects the uniqueness of both islands. Borneo known as one of biodiversity hotspot in Sunda Shelf supported by high diversity, abundance, and endemism of fauna. Otherwise Sulawesi Island is the largest island in the east of the Wallacea region in which contain a highly diverse, unbalanced fauna, highly endemic fauna, which is primarily derived from Asian lineages.

PREFACE

Southeast Asia is known as one of the region with the megabiodiversity and attracts scientists to study the biodiversity. In the world, 35 “biodiversity hotspots” have been identified as the areas containing high concentrations of endemic species of flora and fauna and Southeast Asia having 50% of the endemic fauna of the world contributes to the worlds biodiversity. The Indo-Malayan Archipelago is one of the richest biodiversity area in the region, mainly because of its dynamic geological history, relatively stable climatic conditions and rapid speciation processes. The zoogeography of this region is complicated, especially the case in Sundaland, the area covering the zoogeographical unit of the Sunda Shelf, unique geological history of Wallacea region and Papua Island.

In order to examine the periodic connections, evolution and geological history, murid rodents can be used as a model to study from fauna. Among the 519 species of the Old World rats and mice, the genus *Maxomys* is one of the most common rodents in the Southeast Asia region. They are distributed from mainland Southeast Asia, throughout much of the Peninsular Malaysia to Borneo, Sulawesi, Sumatra, Java, Palawan Island in the Philippines, as well as on several of the smaller islands of Sunda Shelf until Sulawesi Island.

Members of *Maxomys* are common rats found in lowland and mountain forests until 3000 m above sea level (a.s.l). It is characterised by upperparts brown with very stiff and prominent spines. They have underparts white or buff, and tail short and bicolored, being dark brown or black above and white beneath, separated by a sharp line. Historically, the genus *Maxomys* was first described by Sody on 1936 for *Mus bartelsii*, from the specimen collected from Mount Pangrango, West Java. On 1941, Ellerman placed *Maxomys* as a valid subgenus of *Rattus* by the end of the 1940s until the 1960s. On 1969, Missone removed *Maxomys* from *Rattus* to reinstate it as a genus and suggested that some of the genera were morphologically and phyletically distant from *Rattus,* others were closer; including *Maxomys* was near *Rattus* but not part of it.

The present study documented the use of morphological analysis (craniometric and spectrophotometry measurements), and molecular approaches, employing mitochondrial and nuclear genes to investigate the diversity, variations, the phylogenetic relationships and the biogeography of *Maxomys*. A qualitative analysis on the hair color using a spectrophotometer is a new method that facilitates our understanding the variabilities of the coat color in *Maxomys.*

GENERAL INTRODUCTION

The Indo-Malayan Archipelago is one of the hotspots of biodiversity in the world, mainly because of its dynamic geological history, relatively stable climatic conditions and associated rapid speciation processes (Gathorne-Hardy et al. 2002). The zoogeography of this region is complicated, especially the case in Sundaland, the area covering the zoogeographical unit of the Sunda Shelf, i.e. the Peninsular Malaysia south of the Isthmus of Kra, the larger islands of Sumatra, Borneo, Java, Bali, Palawan, and many smaller islands (Meijaard 2003). The unique geological history, plate tectonics, continental drift and zoogeographic boundaries associated with the Wallace's and the Weber's lines make the Indo-Malayan Archipelago as one of the most interesting area for biogeographical study. The importance of the periodic connections to the evolution of the Sunda Shelf fauna has been studied in detail for some groups. Heaney (1986) suggested that colonisation, extinction, and speciation rates differ among taxonomic groups, with murid rodents being most successful and carnivores least succesfull. He also suggested that related to model of the island biogeography, the speciation must be included as a major variable. Ruedi and Fumagalli (1996) suggested that the separation of the islands may have been perceived as a simultaneous event rather than as a succession of vicariant events due to evidence of a rapid radiation.

The Old World rats and mice, part of the subfamily Murinae in the family Muridae, comprise at least 519 species. This subfamily is larger than all mammal families except the Cricetidae, and also larger than all mammal orders except the bats (Wilson and Reeder 2005). The Indo-Malayan archipelago is the most contributing area to murids diversity in this region.

Indonesia possesses about 55% of 702 mammal species distributed in this country for rats and bats (Suyanto et al. 2002; Maryanto et al. 2007). There are 305 species of terrestrial mammals in the Malaysia archipelago with Murinae constituting 12.1% found in this area (Davison and Zubaid 2007).

Furthermore, the knowledge of murine diversity and relationships in Southeast Asia are severely limited, preventing an integrative understanding of evolutionary and ecological processes in island archipelagos. Species of the genus *Maxomys* are one of the most common rats in the Southeast Asian region. They are distributed widespread throughout Southeast Asia start from mainland Southeast Asia, throughout much of the Peninsular Malaysia to Borneo, Sulawesi, Sumatra, Java, and Palawan Island in the Philippines, as well as on several of the smaller islands of Sunda Shelf. There are 17 species currently being recognised, 14 species from Indonesia, seven species from Malaysia, one species from Vietnam, and one species from Philippines (Corbet and Hill 1992; Musser and Carleton 2005). Now, I added two new species of *Maxomys* collected from Kalimantan and Sulawesi Island.

Previously, many scientists had conducted researches in this region using this family with the main purpose to elucidate the phylogenetics and biogeographical patterns related to geological history in the past event (Heaney 1991a; Watts and Baverstock 1994, 1995; Ruedas and Kirsch 1997; Chaimanee 1998; Verneau et al. 1998; Steppan et al. 2003; Gorog et al. 2004; Jansa et al. 2006), and none of them to investigate the systematical problem within this genus.

Generic classification of *Maxomys* has been very unstable, last detailed summary of the taxonomic history was provided by Musser et al. (1979) together with definition of the genus. However, the definition which only focused on which species belonged to this genus and only a general sketch of the morphological limits of these species was included. There was undescribed species of *Maxomys* from Mindoro Island in the Philippines and two from Central Sulawesi (Corbet and Hill 1992; Musser and Carleton 2005). Ruedas and Kirsch (1997) stated that although they had begun to document phylogenetic trends within *Maxomys*, much work remains to be done on this fascinating genus. Musser (1981) stated that most species of *Maxomys* required careful taxonomic revision and the phylogenetic relationships among them all need to be determined. Gorog et al. (2004) suggested that greater sampling and additional data, including nuclear DNA sequence and morphology, were required to conduct additional tests of regional monophyly, to assess the depth of divergences and to test if the lineages o bserved may represented distinct species.

The present study generated an overview of the morphological and molecular systematics of Southeast Asian spiny rats (genus *Maxomys*). In Chapter I, I documented the information of the taxonomic status of *Maxomys* inferred from morphological traits. Chapter II also generate the morphological analysis emphasizing the quantitative color variation among species of *Maxomys* (Rodentia: Muridae) using spectrophotometry. Thus, I conducted molecular analysis in order to investigate the phylogeny, diversity, and biogeography of Southeast Asian spiny rats (*Maxomys*) in Chapter III. Finally, in Chapter IV I made descriptions of two new species of *Maxomys* from Borneo and Sulawesi islands giving important taxonomic information on *Maxomys*.

CHAPTER I

Taxonomic status of spiny rats (*Maxomys* Jentink, Rodentia) from Indonesia and Malaysia based on morphological study

I.1 Introduction

Recent reappraisal of the mammalian fauna of the Indo-Malayan region has pointed to a dramatically different view of the biogeographic boundaries of the Indo-Malayan and Australian regions from the traditional ones based on Wallace's and Weber's lines (Kitchener et al. 1990; Kitchener and Maryanto 1995). The Indo-Malayan region presents a unique opportunity to study either intra or inter specific morphological variations in relation to geographical barriers. Comprehensive and accurate re-evaluation of morphological characters in certain cases resulted in the discovery of new species. Such re-evalution has been conducted in Indonesia for bats, rodents and primates (Kitchener and Maryanto 1993; Maryanto et al. 1997; Merker and Groves 2006).

Spiny rats, well known as *Maxomys,* are common rats which can be found in lowland and mountain forests up to 3000 m a.s.l., from primary forests, secondary forests, plantations and disturbed areas adjacent to forests (Payne et al. 1985; Corbet and Hill 1992; Francis 2008). The 17 known species of *Maxomys* have widespread distributions starting from the mainland of Southeast Asia, throughout much of the Indochinese region, Peninsular Malaysia to Borneo, Sulawesi, and Palawan, as well as on several smaller islands of the Sunda Shelf (Corbet and Hill 1992; Ruedas and Kirsch 1997; Musser and Carleton 2005).

A number of previous studies have been conducted in order to reveal the taxonomic status of *Maxomys*. However, many scientists have suggested that detailed and accurate re-evalution are still needed before the systematics of this genus is stable. Ruedas and Kirsch (1997) noted that *Maxomys* was a species-rich genus embracing a wide range of morphological, geographic, ecological, and altitudinal variations, and that most species still require rigorous definition.

Musser and Newcomb (1983), Corbet and Hill (1992), Watts and Baverstock (1994), Musser and Carleton (2005) all showed that *Maxomys* was not closely related to *Rattus* as earlier authors (e.g. Ellerman 1941) had placed it. Musser et al. (1979), Corbet and Hill (1992), Musser and Carleton (2005) made detailed definitions of the Sundaic species of *Maxomys*, and offered a working hypothesis about the taxonomy and geographical distribution of *Maxomys.* The genus is divided into 17 species: *M. alticola*, *M. bartelsii*, *M. baeodon*, *M. dollmani*, *M. hellwaldii*, *M. hylomyoides*, *M. inas*, *M. inflatus*, *M. moi*, *M. musschenbroekii*, *M. ochraceiventer*, *M. pagensis*, *M. panglima*, *M. rajah*, *M. surifer*, *M. wattsi,* and *M. whiteheadi.* There was no systematic revision of this genus since then. This re-evaluation of the morphological characters of *Maxomys* was conducted with the main goal to reveal the morphological and geographical variations within this genus. The hypothesis tested here is whether there is significant variation in characters within *Maxomys* species from Indonesia and Malaysia.

I.2 Materials and Methods

A total of 187 skulls from adult specimens consisting of *M. whiteheadi, M. rajah, M. ochraceiventer, M. surifer, M. baeodon, M. pagensis, M. bartelsii, M. inas, M. musschenbroekii, M. hellwaldii, M. wattsi,* and *M. alticola* were studied (Appendix 1). All specimens studied were deposited at Museum Zoologicum Bogoriense (MZB), Museum Zoological UNIMAS (MZU), and Raffles Museum, Singapore. Specimens were judged as adult based on fusion of basisphenoid or basioccipital sutures. Twenty four measurements of craniometric characters were made using digital calipers (Mitutoyo^{TM}) to 0.01 mm. The dimensions and limits are illustrated in Figure 1 and defined in Maryanto (2003). The characters were: GSL (greatest skull length), POW (post orbital width), ZB (zygomatic width), BoZP (breadth of zygomatic plate), IOB (interorbital breadth), NL (nasal length), NW (nasal width), BB (breadth of braincase), BH (braincase height), DL (length of diasthema), PL (palatal length), UMR (upper molar tooth row), IFL (length of incisive foramina), IFB (breadth of incisive foramina), M^1W (upper molar 1 width), M^2W (upper molar 2 width), M^3W (upper molar 3 width), M^1M^1 (distance of right-left upper molar 1), M^2M^2 (distance of right-left upper molar 2), M^3M^3 (distance of right-left upper molar 3), BL (bulla length), MSW (mesopterygoid fossa width), RAP (ramus angular process), MaL (length of mandible).

Two way statistical analyses were used, univariate and multivariate analyses, as described in Maryanto and Sinaga (1998) and Maryanto (2003). Principal Component Analyses (PCA) and Discriminant Function Analyses (DFA) were initially run for all characters for all species as separated groups. Then DFA were run for a subset of five or more characters, based on criteria of minimised wilk's lambda to select the best discriminating variables. The results obtained with a reduced character set were very similar to those based on all characters (Kitchener et al. 1993).

I.3 Results and Discussion

Univariate statistics

Mean, standard deviation, minimum and maximum values and samples size were represented in Table 1. These suggest that *M. hellwaldii* is the largest in size for all skull characters and *M. whiteheadi* (Small size or S) is the smallest species for most characters except for ZP, UMR, IFL, M1W, M^2W, M^3W and BL larger than *M. baeodon* and NW, HB, D, and MSW slightly larger than *M. inas.* The means of *M. whiteheadi* Large size (L) are slightly smaller than *M. ochraceiventer* and clearly larger than *M. whiteheadi* Small size (S) and *M. baeodon.*

Multiple regression

Multiple regression analysis was employed to determine the influence of sex in variation. Sex had no significant effect ($0.05>p>0.01$; $0.01>p>0.001$); and on any individual character ($p>0.001$) (Table 2). Consequently, multivariate analyses were combined for males and females.

Morphological variation within genus Maxomys

PCA analysis of morphology *Maxomys* indicates significant variation between or within *M. whiteheadi* (L), *M. whiteheadi* (S), *M. rajah, M. surifer, M. baeodon, M. ochraceiventer, M. alticola, M. musschenbroekii, M. hellwaldii, M. wattsi, M. pagensis, M. bartelsii,* and *M. inas.* Five principal components (PCs) extracted from 24 measurements accounted for 90.0 % of the total variation (Table 3). The DFA is based on 24 characters, and repeated using a reduced set of five characters in order to avoid over fitting the data (Kitchener and Maryanto 1995). The five characters were selected by minimising Wilk's lambda on the first canonical variate. The DFA plot is based on five characters similar to the complete characters set (Maryanto 2003). The five characters in the DFA are GSL, BB, ZB, NL, PL (Table 4).

This analysis extracted five significant functions, which accounted for 100% of total variations. Discriminant Functions (DF) 1, 2, 3, 4, and 5 accounted for 88.49% ($P<0.001$; df : 60), 4.92% ($P<0.001$; df : 44), 3.23% ($P<0.001$; df : 30), 1.88% ($P<0.001$; df : 18), and 1.49% ($P<0.001$; df : 8) of the variation between populations respectively (Table 5) with 87.7% of the originally grouped cases correctly classified and 12.3% misclassified. Furthermore, the number of functions at group centroids between skull, dental and dentary characters from each species are distinct.

The configurations of PCA and DFA plots suggest that spiny rats in Indonesia and Malaysia comprise thirteen major morphological distinctness (Figures 2, 3, 4, 5, 6, 7, 8, 9). These are: *M. rajah, M. surifer, M. baeodon, M. alticola, M. ochraceiventer, M. whiteheadi*

(S), *M. musschenbroekii, M. hellwaldii, M. wattsi, M. pagensis, M. bartelsii, M. inas,* and the two distinct populations of *M. whiteheadi* (L). Plots of PCA and DFA show that the genus *Maxomys* is divided into three major groups based on body size: group 1 has large body size and contains four species: *M. rajah, M. pagensis, M. wattsi,* and *M. hellwaldii.* Group 2 contains medium body sized species: *M. surifer, M. alticola, M. bartelsii, M. musschenbroekii, M. ochraceiventer,* and *M. whiteheadi* (L). Group 3 has small body size and comprises *M. whiteheadi* (S), *M. baeodon,* and *M. inas.*

Maxomys whiteheadi (L) has distinct morphological characters from the other *Maxomys* shown by good separation from other species and large variation in 24 of the skull, dental and dentary characters measured. This species seems similar in morphological features to *M. whiteheadi* (S) and *M. ochraceiventer,* supported by overlapping measurements in certain individuals of skull characters. Characters examined of this species are strictly distinct from *M. ochraceiventer* collected from entire Borneo Island.

Geographical variation within Maxomys whiteheadi *based on morphological characters*

DFA analysis of geographical variation within *M. whiteheadi* (S) indicates significant variation from three different regions: Sumatra, southern region of Borneo, and northern region of Borneo. Two discriminant functions extracted accounted for a 100% of the total variation (Table 6). The DFA was done on all 24 characters and repeated using a reduced set of seven characters in order to avoid over fitting the data (Kitchener and Maryanto 1995). The seven characters were selected by minimising Wilk’s lambda on the first canonical variate. The DFA plot is based on seven characters similar to the complete characters set (Maryanto 2003). The seven characters in the DFA are BB, IOB, NL, NW, M^1M^1, M^3M^3, and RAP (Table 7). This analysis extracted two significant functions, which accounted for 100% of total variations. Discriminant Functions (DF) 1 and 2 accounted for 94.04% ($P<0.001$; df : 14) and 5.96% ($P<0.05$; df : 6) of the variation between populations respectively (Table 6) with 88.2% originally grouped cases correctly classified and 12.9% misclassified; 82.9% of cross-validated grouped cases were correctly classified. Furthermore, a number of functions at group centroids between skull, dental and dentary characters from each species are also distinct.

The configuration of DFA plots suggests that *M. whiteheadi* (S) is divided into three major geographical populations (Figure 10). The first group comprises populations from (1) Kutai, East Kalimantan and DAS Sebangau, Central Kalimantan; (2) Kayan Mentarang; North-eastern part of Kalimantan; and (3) Mount Palung, Ketapang, West Kalimantan. The second group comprises populations from Sarawak (Northern Borneo; Kubah National Park and UNIMAS peatswamp forest), and the third group comprises populations from the northern part (Deli and South Tapanuli) and the southeastern part (Kalianda, Lampung) of Sumatra. The populations from Sumatra are slightly similar in skull features and some characters overlap for some individuals from Northern or Southern Borneo. However, the populations from Northern Borneo are clearly distinct from Southern Borneo populations. This distinction possibly reflects geographical barriers such as mountains, highlands or large rivers in Borneo.

The DFA plots for *M. whiteheadi* (L) show that there is geographical variation among the populations. Within this populations, there is significant variation between Borneo mainland (represented by specimens from Melak, Kalimantan, Sarawak, and Sabah) and those from both Sumatra and Peninsular Malaysia.

Four discriminant functions were extracted which accounted for 100% of the total variation (Table 8). Discriminant Functions (DF) 1, 2, 3, and 4 accounted for 92.05% ($P<0.001$; df : 32), 6.04% ($P<0.001$; df : 21), 1.44% ($P<0.01$; df : 12), and 0.47% ($P>0.05$; df : 5) of the variation between populations respectively with 100% of the originally grouped cases correctly classified and 90.5% cross-validated grouped cases correctly classified. The eight characters were selected by minimizing Wilk's lambda on the first canonical variate in order to avoid over fitting data. The eight characters in the DFA are BB, ZP, IOB, D, UMR, IFL, MSW, and RAP (Table 9).

The configuration of DFA plots suggest that *M. whiteheadi* (L) is divided into five major geographical populations (Figures 11, 12, 13); these are (1) populations from Melak, Kutai, East Kalimantan, Central Kalimantan (Southern Borneo); (2) populations from Sumatra; (3) a Sarawak group (Northwestern Borneo); (4) a Peninsular Malaysia group; and (5) a Sabah group (Northeastern Borneo). Each of the groups showed good separation between them. Populations from Sumatra seem similar and closely related to the Southern Borneo populations. The Sarawak and Peninsular Malaysia groups are clearly different from the other populations and stand as a single group. These different populations are most likely a reflection of geographical barriers such as mountains, highlands, large rivers and seas in this region which have isolated the populations.

Based on this study, I summarized that *Maxomys* can now be divided into 16 species with *M. whiteheadi* (L) as a distinct new species yet to be described. Based on the features of skins, skulls and body size configuration *M. whiteheadi* (L) seems more similar to *M. whiteheadi* (S) than to *M. ochraceiventer* or *M. baeodon*; both of which is sympatric. Furthermore, skull, dental and dentary characters of *M. musschenbroekii* and *M. wattsi* from Sulawesi show similar features to *Maxomys* populations from Kalimantan, in particular populations of *M. alticola, M. ochraceiventer, M. surifer,* and *M. whiteheadi* (L) an observation supported by overlapping measurements in some cases. *Maxomys wattsi* appears to be closely related to *M. rajah* which is supported by overlaps in measurements. Musser et al. (1979) observed that *M. musschenbroekii* was a small rat, more like *M. alticola, M. inas,* and *M. ochraceiventer* in body size. It was also more similar to those species, and to *M. hylomyoides* and *M. whiteheadi* in features of skin, skull, and teeth than to either *M. hellwaldii* or *M. dollmani*. Ellerman (1941) indicated that *M. musschenbroekii* and *M. whiteheadi* (S) were conspecific but there is no evidence, at least from the study of skins and skulls, to support that view.

The biogeographic boundaries of the species of *Maxomys* in the Southeast Asia region, do not follow the Wallace's Line and show no separation into eastern and western species groups. This is supported by strong evidence about similarity in morphological features from skull characters between eastern and western *Maxomys* species and consistently confirms the observations suggested by Ellerman (1941) and Musser et al. (1979).

CHAPTER II

Quantitative color variation among species of the Southeast Asian spiny rats genus *Maxomys* (Rodentia: Muridae) using spectrophotometry

II.1 Introduction

Mammalian pelage coloration plays important roles in crypsis, intraspecific communication, thermoregulation, predation avoidance and ultraviolet screening (Endler 1990; Caro 2005; Lai et al. 2008). As such, pelage coloration is an important phenotypic character as a result of individual adaptations to the environment and interactions with other animals. Adaptive significance of coloration in animals can be explained by several selective forces (Burtt 1981; Cloudsley-Thompson 1999). The color patterns of animals and their visual backgrounds may be regarded as mosaics of patches which vary in size, shape, brightness and color (Endler 1990). Hypothetically, the different parts of the body in of mammals are subject to multiple, distinct selective pressures, and pelage coloration therefore is of great adaptive importance (Caro 2005).

In mammals, many of the working hypotheses regarding the adaptive value of coat color were proposed more than 100 years ago and progressed little since then (Caro 2005). Recently however, these hypotheses have attracted interest, and are again being explored and tested, especially as my capacity to understand underlying genetic mechanisms has improved (e.g. Ortolani 1999; Stoner et al. 2003a, 2003b; Nachman 2005; Hoekstra 2006; Hoekstra et al. 2006). The three most important adaptive functions of pelage are concealment, communication, and thermoregulation (Cott 1940; Caro 2005; Lai et al. 2008). Previous studies have been conducted related to adaptive functions of pelage coloration in mammals: e.g., changing visual characteristics in order to minimize predator detection (Rowland 2009), inconspicuous or cryptic color patterns against visual background (Endler 1990; Ortolani 1999), and as thermoregulatory properties (Burtt 1981; Walsberg 1983).

Until recently, our ability to determine the validity of mammal pelage coloration as a diagnostic tool for species identification remained a problem. Endler (1990) stated there were five major weaknesses related to color determination on wildlife animal: 1) human subjectivity, 2) the adjacent color patches that can affect the perceived color of a patch, 3) lighting conditions, 4) the variation among normal people, and 5) the differences in vision between humans and the animals in which the color patterns are observed. Aside from matching with the Munsell soil color chart (Lai et al. 2008), there is no quantitative standard color measurements against which one can determine the color patterns.

Rodents, a dominant groups of small mammals represented by more than 2000 species in the world, have various kinds of pelage colorations and play an important role in many ecosystems. Because of their diversity, they provide a good sample to study the variations of pelage color patterns on mammals. Previously, studies of color variations have been conducted in murines based on morphology (Hoekstra 2006; Lai et al. 2008; Rios and Alvarez-Castaneda 2011; Salinas et al. 2015) and evolutionary history or molecular phylogeny (Lovet et al. 1986; Montagutelli 2000; Shimada et al. 2009; Hubbard et al. 2010; Kambe et al. 2011; Kodama et al. 2015).

Within Southeast Asian murine populations, the genus *Maxomys* has a widespread distributions from mainland of SE Asia (Thailand, Vietnam, Malaysia) until Philippines and Indonesia. They also have extensive color variations but this has never been quantified nor placed in the context of a molecular phylogeny. In this preliminary study, I documented the coat color variations within *Maxomys*, mostly from skin specimens deposited at Museum Zoologicum Bogoriense, Indonesia.

II.2 Materials and Methods

I measured 70 skins of *Maxomys* (Appendix 2): *M. hellwaldii, M. musschenbroekii, M. dollmani, M. rajah, M. surifer, M. baeodon, M. ochraceiventer, M. whiteheadi, M. alticola, M. pagensis, M. hylomyoides,* and *M. bartelsii*. All color measurements were made on adults. Singaravelan et al. (2013) noted that the coloration changes during the course of ageing; pups and juveniles were lighter than fully matured adults. I measured the dorsal and ventral pelage colors using a digital colorimeter (Spectrofotometer CM-700D, KONICA MINOLTA).

Each animal was measured at least 5 times shaping a line posteriorly (Figure 14). I used the L*a*b* color space model under standard daylight illumination (Hunter 1948) to quantify different components of the measured color from both SCI (Specular Component Included) and SCE (Specular Component Excluded) techniques. I used SCI and SCE simultaneously from the spectrophotometer and the color measurements were based on specular reflectants (included or excluded). The color space component ‘L*’ represents the level of lightness in color (L* estimates equivalent to ‘brown to black’ eumelanin), a positive value of ‘a*’ is represented in red/magenta, while a negative value of ‘a*’ is represented in green. The positive value of ‘b*’ is represented by the amount of purplish-red (magenta) yellow, while the negative value of ‘b*’ represents blue (a* and b* estimates are equivalent to the ‘yellow to red’ pheomelanin). To further characterize the coat color, principal components analysis (PCA) was used to reduce the L*a*b* color space model into a single component (PC) that represents the largest proportion of variation in coat color and lightness. PCAs were completed in SPSS Inc. (2007). I also use canonical discriminant functions (DFA) to tested the variables that give strong influences to the variance of variables, also in SPSS.

II.3 Results

Descriptive analysis

Mean and standard deviation from the color measurements of *Maxomys* spp. are presented in Table 10. Overall the dorsal coat coloration depicted less variation than ventral coat color among species in the *Maxomys* spp. I examined. Throughout most of their range, dorsal pelage from the specimens are mostly dark brown (ranged from L*= 25-30, a*= 5-7, b*= 10-15 see Table 10), individual hairs are banded, grey in the bases and brown to dark brown until the hair tip (Figure 15a). For ventral color, I detected five different color variations: ranged from whitish grey (ranged from L*= 60 – 70, a*= 1 – 4, b*= 13 – 15; *M. baeodon, M. whiteheadi, M. bartelsii* and *M. dollmani*), orange dark brown (ranged from L*= 40 – 58, a*= 4 – 8, b*= 12 – 25; *M. hylomyoides*), chestnut orange (ranged from L*= 44 –

60, a*= 4 – 11, b*= 14 – 26; *M. ochraceiventer*), yellowish brown (L*= 50 – 65, a*= 5 – 9, b*= 24 – 31; *M. alticola*) and creamy white (L*= 45 – 88, a*= -0.4 – 15, b*= 5 – 35; *M. rajah*, *M. hellwaldii* and *M. surifer*)(Figure 15b and Table 11). As typical for many rodents, individual hairs of this part are mostly uniform in color.

PCA and DFA analyses

I describe color variations using Principal Component Analysis (PCA) from the dependent variables (color variables) and extracted into three components in both dorsal and ventral coloration. I explained a total of 99.28 % (PC1 = 75.38%; PC2 = 23.06%; and PC3 = 0.83%) of the variance in dorsal, and 99.09 % (PC1 = 82.22%; PC2 = 14.83%; and PC3 = 2.04%) of the variance in ventral color ($F<0.05$). I ran the DFA for all variables in dorsal and ventral color, and I detected that in dorsal color variables L* (lightness) and a* if specular components included (SCI) give strong influence to the variations with total of 100% variance extracted from 3 discriminant functions (Function 1 = 71.2 %; Function 2 = 17.5 %; and Function 3 = 11.3 %; $P<0.001$; df = 33). For ventral color, I detected variable L* with specular component included (SCI) and b* with specular component excluded (SCE) as the main variables that give most significant influences with the total variation extracted from two functions (Function 1 = 76.5%; and Function 2 = 23.5%; $P<0.001$; df = 22) (Tables 12 - 15).

Scatter plots of PCA in dorsal color are mostly overlapping among species, and this conclusion is supported by the DFA using the group centroid graph. Consistent with the descriptive analysis, there is less variations on the dorsal color, even though we extracted nearly 100% the variation from the dorsal color. In ventral color, from PCA and DFA scatter plots, we detected five groups that closely each other and consistent to descriptive analysis. First group of *M. hellwaldii*, *M. surifer*, and *M. rajah* clustered close each other, some individuals overlapped, though group centroids are separated. Second group of *M. musschenbroekii*, *M. baeodon*, and *M. whiteheadi* stands closer than the other group, third group of *M. pagensis* and *M. alticola*, fourth group consist of *M. bartelsii* and *M. dollmani*, and fifth group of *M. hylomyoides* and *M. ochraceiventer*. Fifth group seems to be the most distinctive group due to ventral coloration, separated farthest from other groups (Figures 16, 17, 18, 19).

II.4 Discussion

In mammals, especially murines, pelage coloration is one of the key characters to identify the specimen. Therefore, for some species pelage coloration is used as a distinguishing feature of the new species and descriptively determined in the monograph or in the diagnosistic characters. However, these are nearly always based on qualitative observation (Musser 1991, Pimsai et al. 2014). Otherwise quantitative information on color variation is very limited. In murines, few studies have been conducted to determine color variation based on quantitative analysis (Hoekstra and Nachman 2003; Lai et al. 2008; Rios and Alvarez-Castaneda 2011; Salinas et al. 2015). Additionally, some researchers have combined these studies with molecular genetic works (Ounpraseuth et al. 2009; Lamoreux et al. 2010; Kambe et al. 2011; Kodama et al. 2015).

My study aims were to generate preliminary information of quantitative color measurements (Tables 10 - 11 and Figures 16 – 19). As a result, it is clear that for some species, the discrete pelage coloration on ventral side of the body can be used as a distinctive character, however for many species, the similarities of color configuration among species may lead to confusion as to the identity of the species. However, this obstacle can be overcome by also exploring other external characters such as from the skull and dentition.

In this study, I detected that the dorsal coloration of *Maxomys* ranged uniformly from brown to dark brown. This result is consistent with Caro (2005) who mentioned that uniform colorations were found in some mammals (artiodactyls, carnivores, and lagomorphs) in certain habitat, especially closed environments such as tropical forest, dense forest, or swamp forest. The natural habitats of *Maxomys* spp are tropical forests (lowland until montane forest), disturbed forest, and swamp forest. Generally, uniform pelage coloration in rodents provides protective camouflage, which is believed to be driven by the need to avoid detection by predators with the whole pelage matching the background where animals are active (Sumner 1921; Dice 1947; Lawlor 1976; Krupa and Geluso 2000). However, I found more variation in ventral color (five significant lighter color than dorsum) from the specimens, this may be an adaptation to countershade from the sun’s effect (when it shines from above): lightening the dorsum and shading the ventrum (Thayer 1909, Kiltie 1988).

Recent study has demonstrating pelage color measurements using spectrophotometer accurately and precisely quantify color variation among species of *Maxomys* spp., and these data can be useful for further research. Additionally, the observations of coat color variation have played an essential role in the understanding of many fundamental biological processes. Furthermore, molecular study of coat color variation within *Maxomys* spp. is needed to elucidate the mechanisms of phenotypic variation that affect the patterns of divergence, speciation and evolutionary history of *Maxomys.* I failed to obtain sequences of *Mc1r* (melanocortin-1 receptor) gene from *Maxomys*, and it probably will be better to use another gene such as *ASIP* (agouti signaling peptide) gene.

CHAPTER III

Phylogeny, diversity, and biogeography of Southeast Asian spiny rats (*Maxomys*)

III.1 Introduction

Island archipelagos provide important systems for the study of biological diversification and have been the subject of many foundational works in the fields of evolution and ecology (e.g., Darwin 1859; Wallace 1869; MacArthur and Wilson 1963; Grant and Grant 1993). The Indomalayan archipelago, in particular, offers a potential model for island biogeographic study because of its exceptional endemism, its broad transition zone between the Sundaic and Sahulian biotas, and its geographic history, involving sea-level fluctuations and geological changes (Wallace 1869; Myers et al. 2000; Dirzo and Raven 2003; Corlett 2009; Lohman et al. 2011). Although the archipelago is known to contain a mix of Asian and Australian faunal and floral elements, the provenance of many Indonesian lineages remains uncertain, limiting the current value of the region as a model system for understanding ecological and evolutionary processes in a biogeographic context (Lohman et al. 2011).

One of the most diverse mammalian groups in the archipelago is the Old World rats and mice (Murinae), with at least 213 species occurring in the Indomalayan region (Corbet and Hill 1992). Despite the high diversity and abundance of murines in Southeast Asia, few studies have investigated molecular genetic diversity at the phylogeographic level in these animals (but see Steppan et al. [2003] and Gorog et al. [2004]). Among the Murinae, the spiny rats (*Maxomys*) represent a prime subject for biogeographic study because of their abundance, ubiquity, and widespread distribution across the region (Ruedas and Kirsch 1997). Seventeen species are currently recognized, with a generic distribution from mainland Southeast Asia east throughout the Sunda Shelf to some neighboring oceanic islands. Species of *Maxomys* are present on Sumatra, Borneo, the Mentawai Islands, Palawan, many of the smaller islands of the Sunda Shelf, and Sulawesi (Musser and Carleton 2005). Specimens representing an undescribed species from Mindoro Island may extend the range of *Maxomys* to the oceanic Philippines (Musser and Carleton 2005).

The taxonomy of *Maxomys* has been unstable. Sody (1936) proposed the genus for *Rattus bartelsii* (originally named as *Mus bartelsii* [Jentink 1879]) and Musser et al. (1979) later refined this definition by adding 4 species previously associated with *Leopoldamys* (at that time in the genus *Rattus*). New species of *Maxomys* continue to be described (e.g. Chapter IV), and undescribed species have been reported from the Philippines and Sulawesi (Corbet and Hill 1992; Musser and Carleton 2005). In addition, many authors have stated the need for improved information on species limits and phylogenetic relationships (Musser 1969; Musser et al. 1979; Ruedas and Kirsch 1997; Gorog et al. 2004; Musser and Carleton 2005).

The relationships of *Maxomys* to other genera in the Murinae also remain uncertain, and the genus is currently treated as a distinct division (Musser and Carleton 2005). A DNA–DNA hybridization study inferred *Maxomys* to be sister to a clade composed of *Rattus* and *Dacnomys* division members, including the genera *Sundamys, Rattus, Niviventer*, and *Leopoldamys* (Ruedas and Kirsch 1997). Jansa et al. (2006) inferred a sister relationship between *Maxomys* and *Crunomys* (*Crunomys* division), but included only one species of *Maxomys* in their analyses. Buzan et al. (2011) found *Crunomys* was nested within *Maxomys*, but they included only one species of *Crunomys*. Within *Maxomys*, Ruedas and Kirsch (1997) inferred a sister relationship between *M. surifer* and *M. bartelsii*, whereas the phylogenetic positions of *M. ochraceiventer*, *M. rajah*, and *M. whiteheadi* varied among analyses. Otherwise, relationships among species of *Maxomys* have not been examined in an explicit phylogenetic context. Gorog et al. (2004) investigated phylogeographic patterns within *M. whiteheadi* and *M. surifer* and found relatively ancient divergences among populations that were connected by dry land during Pleistocene sea-level lowstands; they therefore rejected the hypothesis of widespread migration of these lineages across the exposed Sunda Shelf during the late Pleistocene.

With the basic goal of improving knowledge of the diversity and biogeography of *Maxomys*, I investigated relationships in a broad sample of species and populations using new and published sequences of 1 mitochondrial and 2 nuclear loci. Specifically, I attempted to answer the following questions: (1) Where does *Maxomys* fit phylogenetically among Indomalayan murines?, (2) Is *Maxomys* closely related to species of the *Rattus*, *Dacnomys*, or *Crunomys* divisions?, (3) Is *Maxomys* monophyletic?, (4) Are the *Maxomys* of Sulawesi the product of an in situ radiation or the result of repeated colonization?, (5) Do distinct phylogenetic units exist within species of *Maxomys* that may represent cryptic species?. To address these questions I performed phylogenetic analyses of 13 of the 17 known species of

Maxomys, plus a broad sample of outgroup species, including members of the *Chrotomys, Crunomys, Dacnomys, Dasymys, Phloeomys, Pseudomys,* and *Rattus* divisions.

III.2 Materials And Methods

Taxon sampling.—There are 17 currently recognized species of *Maxomys*, many of which have broad distributions in Southeast Asia and occur on multiple islands (Musser et al. 1979; Musser and Carleton 2005). *Maxomys rajah, M. surifer,* and *M. whiteheadi* are known from the Peninsular Malaysia, Sumatra, Borneo, and Java; *M. alticola, M. baeodon,* and *M. ochraceiventer* are endemic to Borneo; *M. hylomyoides* and *M. inflatus* are endemic to Sumatra; *M. bartelsii* is endemic to Java; *M. pagensis* is endemic to the Mentawai Islands; *M. dollmani, M. hellwaldii* (sometimes referred to as *M. hellwaldi* [e.g., Musser 1969]), *M. wattsi*, and *M. musschenbroekii* are endemic to Sulawesi; *M. panglima* is endemic to the Palawan group of islands in the Philippines; *M. inas* is endemic to the Peninsular Malaysia; and *M. moi* is found in Thailand, Laos, Vietnam, and China. I sequenced the mitochondrial cytochrome-b (*Cytb*) gene in 130 specimens of *Maxomys* and 2 unlinked coding nuclear genes (interphotoreceptor retinoid-binding protein [IRBP] and growth hormone receptor [GHR]) in a subset of this diversity (24 IRBP and 23 GHR samples). The subset of specimens for which I obtained nuclear DNA sequences was chosen to represent divergent lineages on a preliminary estimate of the mitochondrial gene tree. Sequenced specimens cover the geographic range of the genus, with samples taken from sites in Vietnam, the Peninsular Malaysia, Borneo, Sumatra, Java, Sulawesi, Palawan, and the Mentawai Islands (Figure 20).

My sampling represents 12 currently recognised species, including *M. bartelsii, M. dollmani, M. hellwaldii, M. hylomyoides, M. moi, M. musschenbroekii, M. ochraceiventer, M. pagensis, M. panglima, M. rajah, M. surifer, M. whiteheadi,* one new species from Borneo (*M. tajuddini* sp. nov), and 2 potentially undescribed species from Sulawesi (one population described as *M. tompotika* sp. nov). To these data, I added 26 previously published *Cyt-b* sequences from additional localities for *M. ochraceiventer, M. rajah, M. surifer, and M. whiteheadi* (Figure 20). I failed to obtain samples of *M. alticola, M. baeodon, M. inas, M. inflatus*, and *M. wattsi*. For use as outgroups, I sequenced and downloaded sequences from several other genera of murines. All new sequences were deposited in GenBank (KC878024–KC878203, KC878206–KC878208, and KC878210 – KC878238. However, I have not examined many of the specimens associated with published GenBank sequences. I therefore retain the taxonomic names published on GenBank in my figures and in Appendix 3, even when they conflict with our identifications of closely related specimens. I have not examined Museum of Texas Tech University (TK) 152985 from Borneo and I therefore label it as *Maxomys* sp., despite its close relationship to *Maxomys tajuddinii* sp. nov in mitochondrial DNA (mtDNA; see below). I also refer to 2 potentially undescribed species from Sulawesi as *Maxomys* sp. because I have not examined the specimens (Museum Zoologicum Bogoriense [MZB] 23104, 23105) and as *M. cf. hellwaldii* (*M. tompotika* sp. nov) because the external morphology of this series (Field Museum of Natural History [FMNH] 213370–213372, 213451, 213452) qualitatively resembles that of *M. hellwaldii*.

Molecular genetics.—Genomic DNA was isolated from muscle or liver tissue using either the cetyltrimethylammonium bromide (Ducroz et al. 1998; Lecompte et al. 2005) or guanidine thyocyanate (Esselstyn et al. 2008) protocol. I amplified and sequenced *Cytb* using the standard conserved mammalian primers MVZ05 and MVZ16 following Smith and Patton (1993), with annealing temperatures of 52^0 – 54^0C. I also amplified and sequenced fragments of 2 nuclear exons, GHR and IRBP, using primers GHREXON10, GHREND, 119A2, and 878F (Jansa and Voss 2000; Adkins et al. 2001). I used annealing temperatures of 47^0 – 50^0C for these loci. Thermal cycling profiles for polymerase chain reaction and cycle sequencing followed Jansa and Weksler (2004), Steppan et al. (2005), and Rowe et al. (2008).

Phylogenetic analyses.—I estimated bayesian and likelihood topologies, branch lengths, and nodal support independently for each gene and for a concatenated alignment. DNA sequences were edited using Geneious Pro 5.5.6 (Drummond et al. 2011). I aligned sequences using the native algorithm of the same software. Initial alignments were examined by eye and found to be unambiguous. I then removed identical haplotypes to minimize the computational burden during phylogenetic analyses. The concatenated alignment included all mitochondrial haplotypes, with individuals preferentially chosen as those with nuclear gene sequences. This matrix was thus mostly complete at *Cyt-b*, but sparsely sampled for the 2 nuclear genes (see Appendix 3). I estimated an appropriate model of sequence evolution for each gene (GTR + C + I for Cytb and IRBP; HKY + C + I for GHR) using the Bayesian information criterion in MrModeltest 2.3 (Nylander 2004). I used the preferred model in all Bayesian and likelihood phylogenetic analyses, with the concatenated analysis partitioned by gene. This partitioning strategy was determined a priori. Phylogenies were rooted with *Phloeomys,* but also included species of *Anisomys, Apomys, Batomys, Berylmys, Bunomys, Chiromyscus, Conilurus, Crunomys, Dacnomys, Dasymys, Leopoldamys, Mastomys, Mus, Niviventer, Paruromys, Rattus, Rhynchomys*, and *Srilankamys* to test the monophyly of *Maxomys*. My Bayesian analyses used MrBayes 3.2 (Ronquist et al. 2012). Markov chain Monte Carlo searches of tree space included 4 runs with 4 chains each. Each run consisted of 5×10^6 generations with parameters sampled every 1,000 generations. Initial analysis had very low swap rates among cold and hot chains, thus I lowered the temperature setting to 0.1. After examining the trends and distributions of parameters, including the likelihood, in Tracer version 1.4 (Rambaut and Drummond 2007), I discarded the first 501 samples of each run as burnin, and pooled the 4 runs to give 1.8×10^4 trees in the posterior distribution. Effective sample sizes of all parameters were > 2000. In addition to my Bayesian analysis, I used the Webbased RAxML Black Box software (Stamatakis 2006) to estimate maximum-likelihood topologies and provide maximum-likelihood bootstrap support values. Bootstrap support values were derived from 100 replicates.

III.3 Results

My initial *Cyt-b* alignment contained sequences from 188 individuals, including outgroups; after eliminating duplicate haplotypes, the data set was 72% complete (28% of characters missing); it contained 1,140 nucleotide positions and 153 unique haplotypes. No insertions, deletions, or premature stop codons were observed. Mean, uncorrected, interspecific (*Crunomys* and *Maxomys*) sequence divergences in *Cytb* were 0.04–0.15, whereas maximum intraspecific divergences for species sampled from multiple localities were 0.01–0.08 (Table 16). The GHR alignment contained 50 taxa, 822 nucleotide positions, 3 insertions–deletions (indels), and 4% missing data. The IRBP alignment contained 52 taxa, 747 nucleotide positions, 1 indel, and 5% missing data.

Maxomys was not monophyletic in any of our analyses because *Crunomys* was nested within it. However, the monophyly of *Crunomys* + *Maxomys* to the exclusion of other sampled murines was well supported (posterior probability [PP] ≥ 0.95, bootstrap support [BS] ≥ 70) in analyses of all data sets except IRBP, where PP = 0.91 and BS = 84 (Figures 21 - 24). Our phylogenetic estimates provided strong support for many recent relationships, but several deep nodes within the clade (*Maxomys* + *Crunomys*), especially those surrounded by short internal branches, received little support (Figures 21 - 24). Although *Crunomys* is nested within *Maxomys*, species of *Crunomys* formed a monophyletic group in all trees except the GHR gene tree, in which the 2 sampled species were recovered as paraphyletic with respect to *M. dollmani* and *M. hellwaldii* (Figures 21 and 22). *Maxomys* + *Crunomys* was recovered as a well supported sister to a clade of *Dacnomys* and *Rattus* division members, in which the latter division was monophyletic, but the former was not (Figures 21 - 24). As reported previously, the paraphyly of the *Dacnomys* division was caused by the position of *Srilankamys* as sister to the *Rattus* division (Buzan et al. 2011; Figures 21 - 24). Within *Crunomys* + *Maxomys* relationships among species of *Maxomys* were not well supported in any of our analyses, with a few notable exceptions. All 3 analyses (Figures 21 - 24) recovered a clade uniting *M. panglima*, *M. pagensis*, and *M. rajah*. One *Cytb* sequence from GenBank (JF436990) was reported as *M. rajah* in an earlier study, but clusters with specimens I identified as *M. surifer*. I have not examined this specimen, but it appears to be misidentified. Setting this specimen aside, all of our samples of *M. rajah* form a clade. The combined data analysis also recovered a well-supported clade that groups an unrecongised species of *Maxomys* from Sulawesi with a clade comprising the Sulawesian species *M. dollmani* and *M. hellwaldii* (Figure 21). The latter 2 species also were recovered as a clade in independent analyses of the 2 nuclear genes (Figures 23 and 24). Finally, a clade comprising *M. hylomyoides*, *M. whiteheadi*, and *M. musschenbroekii* is recovered in all 3 analyses, although IRBP lends little support to this clade (Figures 22 - 24). A clade comprising 1 or 2 additional species from Borneo (*M. tajuddinii* sp. nov and an unidentified *Maxomys*) also join this clade in the combined-data analysis (Figures 21 and 22). I found 4 independent clades of species from Sulawesi, including *M. dollmani* + *M. hellwaldii* + *Maxomys* sp., *M. musschenbroekii*, *M.* cf. *hellwaldii*, and *Crunomys celebensis*. If each of these lineages represents a separate invasion of Sulawesi, then the island has been colonised at least 4 times by this group of rats. However, back-colonisations of Sundaland or the

Philippines, or both, from Sulawesi provide alternative explanations that cannot be tested without comprehensive taxon sampling and well-supported species-level relationships. Only 1 of the clades from Sulawesi contains multiple currently recognised species, but substantial geographic variation is present in mtDNA of *M. musschenbroekii*. Several currently recognised species contain divergent lineages worthy of closer taxonomic research. *M. whiteheadi*, one of the widespread species, contains divergent lineages from Sumatra, the Malay Peninsula, Thailand, and Borneo. Within *M. surifer*, a species with a similar distribution, I found 5 distinct clades represented by populations from Vietnam, Borneo, Sumatra, Thailand, and Peninsular Malaysia. Several GenBank sequences identified by others as either *Maxomys* sp. or *M. rajah* are closely related to specimens we identified as *M. surifer* (Figure 21). Setting aside the specimens I have not examined, all remaining *M. surifer* formed a clade. Two populations of *M. hylomyoides*, a Sumatran endemic, were not recovered as a clade, because *M. tajuddinii* sp. nov and an unidentified specimen from Borneo (TK 152985) cluster with the Mt. Singgalang (site 10; Figure 22) population of *M. hylomyoides* (although with poor support). Among the samples of *M. musschenbroekii*, a Sulawesi endemic, I recovered 3 distinct and geographically structured haplogroups, which correspond to previous designations of Areas of Endemism (Evans et al. 2003b). The distinct haplogroups of *M. musschenbroekii* include samples from Malili (SE Area of Endemism, site 24; Figure 20); Mt. Tompotika at the terminus of the east peninsula (E Area of Endemism, site 25); and Mts. Balease (site 22), Gandangdewata (site 20), Rorekatimbo (site 21), and Latimojong (site 23), all in Sulawesi's Central Area of Endemism.

III.4 Discussion

My phylogenetic analyses of 13 recognised and two potentially undescribed species (*M.* cf. *hellwaldii* and *Maxomys* sp., both from Sulawesi) of *Maxomys* revealed several interesting findings that bear on the taxonomy and biogeography of *Maxomys*. First, regarding taxonomy, most currently named species that I sampled and two putative new species (both from Sulawesi) appear to be genetically distinct from one another and form monophyletic groups (Figure 21). Potential exceptions include *M. pagensis*, which is closely related to *M. rajah*, and *M. tajuddinii* sp. nov and TK 152985, which are nested within *M. hylomyoides* (Figure 22). Previous authors have noted the probable existence of undescribed species of *Maxomys* on Sulawesi, but have yet to formally describe these putative species (e.g., Musser 1969; Corbet and Hill 1992); the putative undescribed species I sampled here (*M.* cf. *hellwaldii* and *Maxomys* sp.) may correspond to those mentioned in earlier reports. One specimen that identified as *M. dollmani* (Museum of Vertebrate Zoology [MVZ] 225725) has mtDNA most closely related to specimens of *M. hellwaldii* (Figure 21), suggesting that mitochondrial introgression or other forms of gene flow may occur between these morphologically distinguishable sister species. Additional genetic and population sampling will be necessary to understand the extent of interaction between these species.

Second, I identified several species with geographically structured genetic diversity that require closer taxonomic investigations, such as the populations of *M. surifer* and *M. whiteheadi* from the Sunda Shelf (Gorog et al. 2004) and *M. hylomyoides* from Sumatra (Table 16). Similar observations have been made in other Sunda Shelf taxa (Esselstyn et al.

2010; Oliveros and Moyle 2010; Wilting et al. 2012), which, given the very recent dry land connections between Java, Sumatra, Borneo, and Peninsular Malaysia, begs explanation. Plausible isolating mechanisms include climatic and habitat barriers (Heaney 1991a; Bird et al. 2005) and idiosyncratic extinctions (Wilting et al. 2012). *M. musschenbroekii*, an endemic of Sulawesi, also contains substantial geographic variation in its mtDNA (Figure 22; Table 16). Distinct haplogroups of this species correspond to previous delimitations of Areas of Endemism (Evans et al. 2003b). Areas of Endemism on Sulawesi have been defined based on genetic diversity of primates and amphibians, but may provide a consistent geographic framework for distinct lineages of many plants and animals on Sulawesi (Evans et al. 2003b). If boundaries of Areas of Endemism are indeed consistent among many lineages, these may have been caused by the island's history as an archipelago (Hall 2002), with current borders between Areas of Endemism corresponding to geological sutures between paleoislands. However, testing this hypothesis and plausible alternatives is difficult because of the lack of literature on paleoclimatic or paleohabitat differences that might have generated similar patterns.

Third, I find that *Crunomys* (with 3 of the 4 named species sampled) is monophyletic, but nested within *Maxomys* (Figures 21 - 24). In nomenclature, *Crunomys* (Thomas, 1898) has priority over *Maxomys* (Sody, 1936). However, I refrain from synonymising these 2 genera because of the lack of resolution in the deeper nodes of our phylogenetic estimates. Moreover, the type species of *Crunomys, C. fallax*, has yet to be included in phylogenetic analyses. Assuming *C. fallax* is closely related to the other species of *Crunomys*, some taxonomic changes will be necessary. However, lacking greater phylogenetic resolution, I cannot say whether all species of *Maxomys*, or a subset of them, should be placed in *Crunomys*.

Previously, both *Crunomys* and *Maxomys* have been difficult to place in a phylogenetic context. Species of *Maxomys* were often treated as members of *Rattus* until Misonne's (1969) revision. Musser et al. (1979) confirmed the distinction of *Maxomys*, but changed the composition of the genus substantially by uniting several members of *Rattus* under *Maxomys*. Several previous studies using various approaches such as electrophoretic data (Chan et al. 1979), albumin immunology (Watts and Baverstock 1994), karyotypes (Gadi and Sharma 1983), and DNA–DNA hybridisation (Ruedas and Kirsch 1997) have supported the distinction of *Maxomys*. Thomas (1898) initially placed *Crunomys* in the Hydromyinae, but later expressed doubt regarding this arrangement (Thomas 1907). Ellerman (1941) and Misonne (1969) put *Crunomys* in Murinae, and Musser (1982) suggested it as a possible member of an endemic Philippine radiation of murines including shrewrats (e.g., *Archboldomys* and *Chrotomys*) and terrestrial and arboreal rats (e.g., *Batomys*, *Carpomys*, and *Crateromys*). Musser and Heaney (1992) refined this hypothesis, suggesting a close relationship between *Archboldomys* and *Crunomys*, but Rickart et al. (1998) and Rickart and Heaney (2002) refuted this idea. More recently, Jansa et al. (2006) found a sister relationship between *Crunomys* and *M. whiteheadi*, the only *Maxomys* included in their phylogeny, and Buzan et al. (2011) inferred *Crunomys* to be nested in a clade of 3 species of *Maxomys.* My results support the definition by Musser et al. (1979) of *Maxomys*, with the exceptions that *Crunomys* should be a member and *Crunomys* is the appropriate name for some or all of this clade. In addition, the results show *Maxomys* + *Crunomys* is sister to a clade of *Dacnomys* and *Rattus* division members, as previously inferred by Buzan et al. (2011) and Balakirev et al. (2012). The results regarding membership in the *Rattus* and *Dacnomys* divisions are consistent with those of Buzan et al. (2011) and I therefore recommend *Srilankamys* be transferred to the *Rattus* division.

Biogeographically the relationships among species of *Maxomys* provide insights on the diversification of *Maxomys* across Wallace's Line, on both the Sunda Shelf and Sulawesi. Sulawesi is neither Asian nor Australian, but rather contains an exceptional number of endemic species derived from a mixture of Sundaic and Sahulian lineages (Whitten et al. 2002; Lohman et al. 2011). These species have assembled through a combination of colonisation and in situ diversification (Stelbrink et al. 2012), but the role of each process remains obscure in many lineages. From inferred phylogenetic topology, with 4 independent clades of *Maxomys* + *Crunomys* on Sulawesi, suggests that these rats have crossed between Sulawesi and the Sunda Shelf multiple times. Although the exact number and direction of colonisations remains ambiguous, it is clear from the polyphyly of the *Maxomys* of Sulawesi that multiple colonisation events (in one direction or the other) took place. This indicates that for these rats, the deepwater barriers surrounding Sulawesi have been relatively permeable. In addition to the important role of interisland colonisation in generating diversity, the presence of multiple species in 1 Sulawesi clade (*M. dollmani* + *M. hellwaldii* + *Maxomys* sp. [Figures 22 - 24]) suggests *in situ* processes also have been important generators of diversity. Shrews, fanged frogs, and various lineages of arthropods also have colonised Sulawesi multiple times and experienced *in situ* diversification (Ruedi et al. 1998; Evans et al. 2003a; Esselstyn et al. 2009; Stelbrink et al. 2012). In the case of *Maxomys*, only the lineage containing *M. dollmani*, *M. hellwaldii*, and *Maxomys* sp. appears to have produced species *in situ*. However, denser sampling and finerscale taxonomic research of species such as *M. musschenbroekii* or inclusion of currently unsampled species (*M. wattsi*), or both, may bring forth additional cases of *in situ* diversification.

In summary, I find evidence suggesting that *Crunomys* of the Philippines and Sulawesi form a monophyletic group nested within *Maxomys*; taxonomic revision is necessary to move all or some *Maxomys* to *Crunomys* so that genera represent natural groupings; potentially undescribed species of *Maxomys* are present on Sulawesi; multiple interisland colonisation events are necessary to explain the current species distributions and relationships of *Maxomys*; and several species (*M. hylomyoides*, *M. musschenbroekii*, *M. surifer*, and *M. whiteheadi*) contain substantial geographic structure in their mtDNA.

CHAPTER IV

Descriptions of two new species of the genus *Maxomys* from East Kalimantan, Borneo Island and Mount Tompotika, Sulawesi Island

IV.1 Introduction

The mammalian fauna of Southeast Asia represents an excellent subject for investigating the interrelationships of diversity, species richness, species endemism, island area, and isolation. Many of the islands that lie south of Indochina, in western Indonesia, are merely highpoints on an immense shallow continental shelf known as the Sunda Shelf (Heaney 1986). These islands were repeatedly connected by dry land in times of low sea level during and prior to the Pleistocene (Voris 2000). Thus, the islands of the Sunda Shelf potentially offer numerous opportunities for testing hypotheses of community assembly and diversification. Unfortunately, the region's potential as a model system for understanding evolutionary and ecological processes is limited by a lack of basic information on species limits and phylogenetic relationships in many groups of organisms.

As the largest island on the Sunda Shelf, Borneo has more endemic mammal species than any other islands on the region. However, despite long-term interest among biologists in Borneo's mammalian diversity, a general lack of information on species distributions and relationships suggests a need for further biodiversity inventories and systematic examinations of putative clades and species. All previous systematic reviews (e.g., Corbet and Hill 1992, Musser and Carleton 2005), indicate large gaps in our knowledge of Borneo's mammalian biodiversity. Only the distributions of some primates (e.g., *Pongo pygmaeus* Linnaeus, 1760) are reasonably well documented (Rijksen and Meijaard 1999).

Among Borneo's native mammals, murid rodents are especially diverse yet very poorly known. Twenty six species are currently recognised from the island, including 9 Bornean endemics (Payne et al. 1985; Corbet and Hill 1992; Suyanto et al. 2002). For the genus *Maxomys* Sody, 1936, Borneo represents a center of both diversity and endemism with six of 14 species occurring on the island, three of them endemics. The Bornean *Maxomys* are relatively easy to identify using external characters of size and colour. For instance, the large species *M. rajah* Thomas, 1894 and *M. surifer* Miller, 1900 can be distinguished by their pelage colours, as can the medium species *M. alticola* Thomas, 1888 and *M. ochraceiventer* Thomas, 1894, and the small species *M. whiteheadi* Thomas, 1894 and *M. baeodon* Thomas, 1894. During an expedition to East Kalimantan in May 2006, eight individuals of *Maxomys* spp. were collected with body proportion and color were not quite right with *M. whiteheadi* Thomas, 1894 and suspected as distinct species.

Despite the high diversity, abundance and endemism of Borneo Island in Sunda Shelf, Sulawesi island, the largest island in the Wallacea biodiversity hotspot, is known to contain a highly diverse, unbalanced fauna, typical of large, oceanic islands (Musser 1987; Steelbrink et al. 2012). Among mammals, the island holds a unique and largely endemic fauna, which is primarily derived from Asian lineages (Musser 1987). Of the 129 described mammal species, 68 (54%) are endemic to the island (Musser and Durden 2002; Esselstyn et al. 2012; Mortelliti et al. 2012). Most of the endemic species are terrestrial species of rodents and shrews (53 described species). These include 17 genera, of which 13 genera are endemic to the island (Rowe et al. 2014). The murid rodent fauna contains a remarkable diversity of forms, including the giant *Paruromys*, the tiny arboreal mouse *Haeromys*, the short-legged diurnal shrew-rat *Melasmothrix*, the lowland spiny shrew-rat *Echiothrix*, the tufted-rumped *Eropeplus*, and the molarless shrew-rat *Paucidentomys vermidax*.

Maxomys, one of the most common murines in Southeast Asia, is represented by four endemic species on Sulawesi, namely *M. hellwaldii*, *M. dollmani*, *M. musschenbroekii*, and *M. wattsi* (Musser 1969; Musser 1991). The taxonomic status of *Maxomys* is in flux, since Musser (1991) describing *M. wattsi*, stated that there are two unknown species *Maxomys* remaining to be described. In chapter 3, I estimated phylogenetic relationships in a broad sample of *Maxomys*, including many individuals from Sulawesi. Their inferences showed that a series of specimens from Mt. Tompotika, Sulawesi, which were initially identified as *M.*cf. *hellwaldii* are not closely related to true *M. hellwaldii*. This distinct population was most closely related to *M. ochraceiventer* from Borneo, albeit with limited node support.

In the present study, I make morphological comparisons between these new specimens from Borneo and Mt. Tompotika and all extant species of *Maxomys* from Borneo and Sulawesi islands. The results suggest the new specimens warrant recognition as a new species, and I formally describe them as such.

Here, I re-examine the East Kalimantan and Mt. Tompotika specimens and describe them as representing new species of *Maxomys*.

IV.2 Materials And Methods

Study area and fieldwork

Surveys were conducted in Melak district, East Kalimantan from 14 to 31 May 2006. Field surveys in Sarawak, Sabah and Peninsular Malaysia were conducted from February to November 2008 (Table 17, Figure 25). I also surveyed small mammals on Mount Tompotika, Luwuk Banggai, Central Sulawesi Province for 8 days during April 2011. Specimens were collected using snap traps baited with roasted coconut and peanut. Traps were set in wandering lines with inter-trap spacing of 3–5 m and individual traps were placed in positions of likely capture (e.g., near burrows and along fallen logs).

Fifty to 100 cage traps and pitfall traps (40 buckets with drift fence) were deployed on each site for three to five nights. The traps were placed in a grid along forest trails with an inter-trap distance of 5 to 10 m. I used peanut butter, banana, oil palm fruits and salted fish as bait. Traps were checked twice daily, at about 6.30 am and 5 pm. Identification of specimens followed Corbet and Hill (1992), Payne et al. (1985) and Francis (2008).

All captured mammals, except for voucher museum specimens were tagged prior to release. Nearly all of the comparative materials consist of standard museum preparations: a stuffed skin and accompanying cranium and mandible. A few samples were preserved in formalin and are currently stored in a 70% ethanol. The whole samples of the new rat were preserved in 5% formalin for 4 to 5 days and subsequently transferred to a 70% ethanol solution for permanent storage.

Specimens were mostly preserved in formalin and later transferred to 70% ethanol, with skulls removed from some individuals and later cleaned by dermestid beetles. Other specimens were preserved as dried skins and cleaned skeletons. I compared specimens of *Maxomys* from Mt. Tompotika to all other known species of *Maxomys* from Sulawesi. These include specimens from a variety of localities, but in general, I attempted to compare the Tompotika series to specimens from nearby localities (Figure 26). I examined specimens (Appendix 4) deposited at the Museum Zoologicum Bogoriense, Bogor (MZB), Field Museum of Natural History, Chicago (FMNH), American Museum of Natural History, New York (AMNH), and Louisiana State University Museum of Zoology, Baton Rouge (LSUMZ).

Morphological data and analyses

I collected standard external measurements (total length, tail length, hind foot length [including the claw], ear length, and mass) from specimens in the field using metric rulers and Pesola spring scales (accuracy to 1 g) (Figure 1, following Musser (1991), Musser and Newcomb (1983) and Musser et al. (2005)). I gathered these same measurements from the specimen tags and field notes of collectors, or from published papers (from Musser 1991 for *M. wattsi*) for specimens from other localities. I took cranial measurements using digital calipers (precise to 0.01 mm) from the skulls and dentaries of all species of Borneo, Malaysia, and Sulawesi *Maxomys* following Chapter I (Figure 1). Measurements were taken from only adult specimens with fully fused cranial sutures.

I calculated standard descriptive statistics (mean, standard deviation and range) for each measurement. Anatomical terminology follows Musser (1991), Musser and Newcomb (1983) and Musser et al. (2005). I employed multivariate statistical analyses to understand the nature and distribution of morphometric variation. These included for principal component analysis (PCA) using untransformed cranial variables and the correlation matrix. I also ran a discriminant function analysis (DFA) using IBM SPSS Statistics 13 in SPSS Inc. (2007) using stepwise methods.

IV.3 Results

On the basis of the distribution of morphological variation detected in specimens of Bornean *Maxomys*, I compare the definition of *M. whiteheadi* and describe as the first new species. Otherwise, specimens from Mt. Tompotika, Sulawesi island are compare to all known *Maxomys* from this island and describe as the second new species in this study. The following systematics section describes the differences between the geographic groups of *M. tajuddinii* sp. nov. and *M. tompotika* sp. nov to facilitate the identification and classification of its distinctness.

IV.3.1 Description of new species of *M. tajuddinii* sp. nov from East Kalimantan

Maxomys whiteheadi Thomas, 1894

Holotype. ~ British Museum of Natural History, no number, 18 March 1888.

Type Locality. ~ Mount Kinabalu, North Borneo, 3000 ft.

Diagnosis. ~ Thomas (1894) described *M. whiteheadi* as small size spiny rat, with hindfoot length approximately 27 mm, length of tail similar to head and body length, nearly naked and bicolor, fur spiny, rufous above, with tips of spines wholly brown, black, or ochraceous, with bases slaty, but not sharply defined, hands and feet white, soles slate, mammae formula 2 + 2 = 8, bullae small, and palatal foramina short.

Distribution. ~ Borneo Island and adjacent, small islands, namely Serasan Island, Natuna and Sumatra. Also present on Peninsular Malaysia, possibly extending N of the Isthmus of Kra into Thailand (Corbet and Hill 1992, van Strien 2006).

Maxomys tajuddinii sp. nov

Holotype. ~ Museum Zoologicum Bogoriense (MZB) 29080 (MW field number 307); an adult male, weight 66 g.; ethanol preserved (70%) whole body, with skull and dentary removed and cleaned. The specimen was originally fixed in 5 % formalin and preserved in 70 % ethanol, collected by A. S. Achmadi and I. Maryanto on 22 May 2006 from peat swamp forest area, in logged, mixed dipterocarp forest on waterlogged, periodically inundated sandy clay.

Type Locality. ~ One kilometer west of Empakuq village, ca. 10 km toward Melak town, Kutai district (1° 19' 8.11" S, 120° 6' 8" E), East Kalimantan, Indonesia.

Paratypes. ~ Six adult females and three adult males, as follows:

Six adult females: MZB 29058, 29062, 29066 collected on 26 May 2006 with weight respectively 57 g, 62 g, 50 g.; MZB 29068, 29070 collected on 28 May 2006 with weight respectively 70 g, and 62 g.; MZB 29086 collected on 24 May 2006 with weight 65 g; and one adult male: MZB 29077 collected on 22 May 2006 with weight 52 g. All of these specimens were collected from the same locality with the holotype, by A. S. Achmadi and I. Maryanto. I also collected two adult males from Fraser Hill Forest Reserve (TK153703 and TK153717) on 10 July 2008 with weight 70 and 85 g, Sumatra (MZB28960 – 28968) represented by seven adult males and two adult females with weights 73, 74, 67, NA, 57, 87, 84, 121, and 85 gs. collected by Maharadatunkamsi between 2 – 11 January 2007 (see

Appendix 4.). Both spesimens from Balambangan Island (male, no. 471) and Jambusan cave (female, no.1618) external date and measurements were not recorded (no field labels and catalog). All skulls and dentaries were separated, carcasses fixed in 5 % formalin and preserved in 70 % ethanol.

Etymology. ~ The new species is named after Professor Dr. Mohd. Tajuddin Abdullah, who is commonly known as Mr. T or Taj. Dr. Tajuddin has dedicated most of his life to the study of mammalian ecology, biogeography, phylogenetics, phylogeography, and conservation using classical and molecular genetic approaches in the Sunda region. As a biology lecturer, he has inspired many students to enter research careers. The authors are extremely pleased to honor him by attaching his name to this new species.

Diagnosis. ~ *M. tajuddinii* sp. nov. distinguished from any other species in *Maxomys* Sody, 1936 by the following combination of traits: (1) sharp demarcation between dorsal and ventral surface on the flanks; (2) tail slightly similar to longer than head and body length, tapered and bicoloured, brownish black in dorsal surface and creamy white colour in ventral surface; (3) fur covering head and body long and thick, spinous, and dense; (4) brownish orange buff upperparts, creamy white underparts, long and dense guard hair, spinous with black on the tips; (5) rostrum long and narrow relative to its length; (6) incisive foramina narrow relative to its length, its posterior margins located slightly in front of first molar or not quite reaching to the level of front side of first molars; (7) first upper molar with three roots; (8) cusp t^4 complete on first and second molars; (9) scales of tail among 10 – 12 scales per cm.

Descriptions. ~ Details of external, cranial, dental traits and pelage are described below. *M. tajuddinii* sp. nov. is a moderately medium size of spiny rats, it has average body size, weight ranges from 50 – 70 g. The dense fur covering the upperparts of the head and body is brownish orange buff until in front of rump and dark brown for the rest comprising three types of hairs. The underfurs are thin, soft and gray for their entire length. The overfur layer is formed by wide, flexible and spinous, basal half of each is gray and the half of its length is orange to brownish orange and buff on the tip. Guard hairs are scattered throughout the coat, beyond the overhairs, the basal half of each is grey and half of distal black or brown and spiny. Banding patterns of the different hairs combine in the dorsal coat to produce an overall brownish orange buff extending from nose to in front of rump, covering thighs and shoulders, and dark brown for the rest.

The ventral coat is shorter than fur covering the upperparts and formed by two kinds of hairs. The underfur hairs are gray for most of their lengths and have silvery or white tips. Hairs comprising the overfur are gray for most of their length and solid creamy white along the distal. Banding patterns of combination in the ventral coat as an overall whitish gray extends from chin to base of tail and undersides of limbs. Most important traits of *M. tajuddinii* sp. nov. regarding to coat is sharp demarcation in tone between dorsal and ventral fur extends from chin to base of tail (Figure 27).

Eyes are relative small compare to head area, narrow, circular, with dark brown ring around. Eyelids are dark brown. Mystacial, submental, superciliary, genal, and interramal vibrissae as armory of sensory hairs also present in this species. The mystacial vibrissae are either dark brown or brownish black, fine, and very long. The longest in each pair of superciliary vibrissae barely extend past the pinnae. The submental and interramal vibrissae are short and unpigmented. The few short genal vibrissae are dark brown for most of their lengths. The pinnae (external ears) are small, and relatively disproportionate to body size. Each is dark brown, oval in outline, and rubbery in texture. Short and soft brown hairs (visible under magnification) are sparsely over both outer and inner surfaces.

The slim, tapered tail is either similar or slightly longer than length of head and the body, and round in cross-section. The dorsal and lateral surfaces are brownish black (produced by either brown or black pigment in scales and the bristles emerging from them); the ventral surface is creamy white or unpigmented from base to tip. There are 10 to 12 overlapping rings per centimeter on each adult tail and three hairs arise from the base of each epidermal tail scale. The mammae of female identified has four pairs (2 + 2) of mammae; one pectoral, on postaxillary, and two inguinal.

Skull. ~ *Maxomys tajuddinii* sp. nov. has an elongate, gracile skull, wide rostrum, and wide and rounded braincase. The outlines of rostrum is moderately long and wide, its sides gradually tapering towards the anterior end. Anterior margin of the nasal is sharply convex, and posteriorly the adjacent premaxillaries project appreciably beyond the nasal-frontal suture and give the distal portion of the rostrum a pointed configuration. Dorsal portion of each lacrimal bone is small, rectangular, and fused with dorsal maxillary zygomatic root and no shared suture with the frontal. Thin capsular walls of the nasolacrimal foramina bulge slightly on sides of the rostrum anterior to the zygomatic plates. Posterior to each capsule is the shallow outline of a zygomatic notch, which reflects a short anterior spine. Dorsolateral margins of the interorbital are defined by wide and high ridges that sweep back along dorsolateral postorbital margins of the frontals and onto the parietals (as temporal ridges) where they diminish in prominence only near the exoccipital-parietal suture (Figure 28).

The outline of the sturdy rostrum is broken only by slightly swollen nasolacrimal capsules and infraorbital fissure. The diastemal region is breached by long and narrow incisive foramina. The posterior margins of these openings are either slightly to the anterior of front faces of the first molar or even front faces of them. The outline of incisive foramina is long and narrow relative to its length, their posterior margins located slightly in front of first molar or not quite reaching to the level of front side of first molars. The bony palate is wide, partly a reflection of the toothrows that diverge posteriorly. The palate is perforated by a pair of posterior palatine foramina opposite the union of second and third molars. A broad mesopterygoid fossa is situated posterior to the bony palate; its dorsoventral walls are breached by sphenopalatine vacuities. The postpalatal region (from the posterior margin of the bony palate to the ventral lip of the foramen magnum) is short relative to palatal length. Sides of the braincase are nearly vertical from the temporal beading to squamosal roots of the zygomatic arches. The zygomata are sturdy and project slightly laterally to connect braincase and rostrum in two parallel bony strands. The bullar capsules are small relative to braincase breadth and cranial expanse and can be appreciated in the lateral view of the cranium.

Each dentary of *M. tajuddinii* sp. nov. appears sturdy, and composed by small and delicate coronoid process as in other species of *Maxomys* Sody, 1936 (Musser 1981, Musser et al. 1979). The incisors appears sturdy, enamel faces of upper and lower molars are smooth, without grooves, dark orange on uppers and pale orange on lowers incisors. The uppers are moderately short and curve caudad after emerging from the rostrum (opisthodont conformation). The lowers are moderately long and curved, their cutting tips slightly curved. The pattern of molar roots in the sample of *M. tajuddinii* sp. nov. is simple and primitive for murids (Musser and Newcomb 1983). The molars of this species are robust, wide, and low-crowned (brachyodont). Within the upper rows, the first tooth inclines slightly against the anterior margin of the second, and it leans against the third. Within the lower row, the third molar leans slightly against the second, and that tooth rests on the first. The cusps of all the molars are situated closely adjacent to one another.

The occlusal surfaces of the brachyodont (low-crowned) molars are simple in topography. Coronal patterns of the molars are primarily consisting of laminae and cusps. The first upper molar consists of two anterior rows of cusps, each in the form of a broad and large chevron, somewhat diamond-shaped posterior surface. The anterior chevron of first uppermolar is comprised of cusps t^1, t^2, and t^3, coalesced one to each other, so that their limits are obliterated, especially for adults. A large cusp of t^1, single chevron, and coalesced with posterior mass of cusps t^8 and t^9 at each second and third upper molar. The small third upper molar consists of a large oblong cusp t^1 and chunky posterior surface, which is consists primarily of cusp t^8 merged cusp t^9 to form distorted diamond-shaped chewing surface. The occlusal pattern of third molar is basically compacted form of that characterising the second molar; a conspicuous cusp t1, no cusp t3, and small posterior oblong chunk (Figure 29). A cusp of t^7 is difficult to detect in all uppermolar, and its possibilities not present in this species.

The lower molars are long relative to length of mandibulary skull; sturdy and exhibit uncomplicated patterns. The occlusal surfaces of the first lower molars consist of an oblong anteroconid comprised by the fusion of anterolabial and anterolingual cusps, and behind two chevron-shaped laminae represent fusions of protoconid-metaconid and hypoconid-entoconid respectively, and rounded or oval posterior cingulum plastered against the back margin of the second lamina. Except for lacking a complete anteroconid, occlusal cusp patterns of the second lower molar resemble patterns as seen in the first. An anterior lamina and either round or oblong, large posterior cusp are the simple elements of the third lower molar. A front chevron formed by union of protoconid and metaconid, behind that a large round to oblong structure representing the complete fusion of hypoconid and entoconid. There are difficulties on determining the frequency of accessory cusps and cusplets within lower molars in this species.

Distribution and habitat. ~ Since the first expedition conducted in Melak, Kutai, East

Kalimantan and collected the interesting specimens, other surveys followed afterward to reveal range of *M. tajuddinii* sp. nov. distributions. The surveys showed that *M. tajuddinii* sp. nov. occurs not only in Kalimantan, but also appears in several places such as Sarawak (Kubah National Park) and Peninsular Malaysia (Fraser's Hill Forest Reserve). From the Museum samples either Museum Zoologicum Bogoriense and Museum Zoological UNIMAS, we also found the specimens of *M. tajuddinii* sp. nov. collected from Sumatra, Jambusan Cave (Sarawak) and Balambangan Island (Sabah). The measurements and traits were taken and characterised; then included to analyses.

Provisionally *M. tajuddinii* sp. nov. has wide range of distributions start from Kalimantan, Sarawak, Sabah, Peninsular Malaysia and Sumatra Island which provide different type of habitats. The holotype and some of the paratypes were collected and sympatric to *M. whiteheadi* Thomas, 1894 at logged mixed dipterocarp forest on waterlogged, periodically inundated sandy clay soil and on medium brown clay forest and swamp forest. The habitats at Kubah National Park and Fraser's Hill Forest Reserve are mostly mixed dipterocarp forests with lower kerangas, which are highlands and quite different from Melak (lowland forest).

Differential diagnosis. ~ *M. tajuddinii* sp. nov. is readily diagnosed by the following characters and combinations which will distinguish this species with samples from any other species of *Maxomys.* In body conformation, limb and tail proportions and general morphology of skull and dentition, this species most closely resembles species of *M.*

whiteheadi Thomas, 1894. Certain diagnostic traits are especially distinctive. *M. tajuddinii* sp. nov. has a larger body than *M. whiteheadi* Thomas, 1894 and its fur color is also quite different especially for ventral coat and sharp demarcation between dorsal and ventral surfaces on the flanks. Compared directly to the measurements of *M. whiteheadi* Thomas, 1894 from Museum Zoologicum Bogoriense and the original description by Thomas (1894), it appears clearly different. The comparisons with descriptions by Corbet and Hill (1992) appears slightly different because they characterised, provided a provisional diagnosis and contents of *Maxomys* complex, but their exposition was intended to be a working hypothesis, not a systematic revision in detail (Table 18).

The following traits and measurements are the comparisons between *M. tajuddinii* sp. nov. and *M. whiteheadi* Thomas, 1894: head and body lengths respectively are 106.84 mm (95.36-121.5 mm) and 101.18 mm (91.2-111.08 mm); tail length 113.89 mm (106.9-122.3 mm) and 101.71 (94.77-107.17 mm); hind foot length 28.64 mm (27.62-30.04 mm) and 24.76 (23.49-25.92 mm); greatest scale length 36.38 mm (34.19-39.71 mm) and 32.4 mm (29.08-35.13 mm); zygomatic breadth 16.35 mm (15.31-18.21 mm) and 14.75 mm (13.31-15.92 mm); zygomatic plate length 3.22 mm (2.79-3.72 mm); upper molar row 5.89 mm (5.23-6.44 mm); incisive foramina length 5.18 mm (4.52-5.94 mm); diastema 9.36 mm (8.17-10.93 mm); and nasal length 12.29 mm (11.20-13.83 mm) and 10.86 mm (9.12-12.36 mm). There is sharp demarcation between dorsal and ventral coat which does not appear in *M. whiteheadi* Thomas, 1894; and also the distinctive creamy white color on ventral fur. A shorter tail percentage (90 – 100%) seen distinct from *M. whiteheadi* Thomas, 1894 (105 – 120%).

The skull of *M. tajuddinii* sp. nov. is larger in size than *M. whiteheadi* Thomas, 1894 due to greatest scale length. Other skull characters also exhibit that this species larger in range either breadth or length on each trait as show in Table 19. The molar size of *M. tajuddinii* sp. nov. is slightly larger than the other one.

Crania and dentaries of the two species are contrasted as seen in Figures 30 – 32. Absolute size is an obvious distinguishing trait but other differences exist. The significant differences and seen apparently in the illustrations are rostrum longer and wider than *M. whiteheadi* Thomas, 1894 relative to its length; wide and high ridges bordering the postorbital region that sweep back along dorsolateral postorbital margins of the frontals and onto the parietals (as temporal ridges) where they diminish in prominence only near the exoccipital-parietal suture; and longer and wider bony palate than *M. whiteheadi* Thomas, 1894. Molar occlusal patterns of the two species are closely similar.

Multivariate analyses. ~ Discriminant Function Analysis or DFA carried out to distinguish and strengthen the descriptive analysis as mentioned earlier that the morphology of *M. tajuddinii* sp. nov. and *M. whiteheadi* Thomas, 1894 are clearly distinct. Cranial, dentary and dental measurements are analysed, and in addition the skull measurements of *M. ochraceiventer* Thomas, 1894 and *M. baeodon* Thomas, 1894 also analysed compared directly to *M. tajuddinii* sp. nov. as supporting data.

The number of data sets are too large, and to avoid over fitting the data, which is inherent on analysing of large characters data sets in DFA, the data sets of skull characters are reduced to subsets of three characters. These selected skull characters are braincase breadth (BB), palatal length (PL) and ramus angular process (RAP) (Table 20). These characters are selected to minimise the value of Wilks' lambda. All selected skull characters are important in the discriminant function and their coefficient values load heavily (> 0.5) on Function 1. The test functions of the skull, dentary, and dental characters have significant influence (P<0.001, df : 3), with cumulative canonical correlation between the two species of 100 %. Furthermore, the number of functions at group centroids between skull, dental and dentary characters of *M. tajuddinii* sp. nov. and *M. whiteheadi* Thomas, 1894 are 3.184 and -0.672. The plots of function 1 and the frequency indicate that the three skull, dental, dentary characters resulting 100% distinctness between the two species (Figures 33 – 35 and Tables 21 and 22).

Discriminant function analyses of full characters data sets either between *M. tajuddinii* sp. nov. and *M. baeodon* Thomas, 1894 or *M. tajuddinii* sp. nov. and *M. ochraceiventer* Thomas, 1894 resulting significant influence with cumulative canonical correlation between the two species of 100% (P<0.001, df : 1 with *M. baeodon* Thomas, 1894 and P<0.001, df : 1 with *M. ochraceiventer* Thomas, 1894). The number of functions at group centroids between skull, dental and dentary characters of *M. tajuddinii* sp. nov. and *M. baeodon* Thomas, 1894 are 1.015 and -3.551; and number of functions at group centroids between skull, dental and dentary characters of *M. tajuddinii* sp. nov. and *M. ochraceiventer* Thomas, 1894 are 2.273 and -0.325. The plots of function 1 and the frequency indicated that the skull, dental, dentary characters 100% separated between the two species of *M. tajuddinii* sp. nov. with either *M. baeodon* Thomas, 1894 or *M. ochraceiventer* Thomas, 1894 (Figures 33 – 35 and Table 22).

Scatter plots of skull characters show that the palatal length of *M. tajuddinii* sp. nov. is generally larger relative to molar 1 to molar 1, width of molar 1, ramus angular process and post orbital width of *M. whiteheadi* (Figure 36). Similar evidence occurs for character of ramus angular process which larger relative to molar 1 to molar 1, width of molar 1 and post orbital width of *M. whiteheadi* (Figure 37).

IV.3.2 A new species of *Maxomys* from Mount Tompotika, Central Sulawesi Province, Indonesia

My morphological examinations of specimens of Sulawesian *Maxomys*, which were prompted by the molecular phylogenetic results in Chapter III clearly show that the Tompotika series initially referred to *M. hellwaldii* is morphologically distinct from all known species of *Maxomys* and we therefore name it as a new species.

Maxomys tompotika sp. nov.

Holotype. ~ FMNH 213454 / MZB 36997; an adult female, collected 11 April 2011 in lowland forest, prepared as a stuffed skin, with the skull (Figure 38) and skeleton cleaned by dermestid beetles. A liver sample was preserved in RNALater in the field and subsequently frozen. The type specimen will be transferred to the MZB.

Type Locality. ~ Mount Tompotika, Dusun Trans Tanah Merah, Sampaka Village, Bualemo District, Luwukbanggai Regency, Central Sulawesi Province (0.65008^0S 123.12868^0E, 350 m asl).

Referred Specimens. ~ I refer 28 additional specimens, 15 (FMNH 213370–213378, 213383, 213384, 213451–213453, and 213455) are from the type locality. Six (FMNH 213379–213382, 213385, and 213386) are from a nearby site at 600 m elevation (0.66287^0S

123.13175^{0}E) and six (FMNH 213388–213393) from farther up the mountain at 760 m (0.66834^{0}S 123.13276^{0}E). All paratypes were preserved as fluid specimens, with some of the skulls removed and cleaned.

Etymology. ~ *tompotika* is named after its geographical provenance of Mt. Tompotika, a mountain in eastern Sulawesi.

Distribution and habitat. ~ Known only from Mt. Tompotika in secondary lowland tropical forest.

Diagnosis. ~ *Maxomys tompotika* sp. nov has: 1) moderately large body size (weights of 7 adults range from 150–186 g; 170 - 189 mm head and body length [HB]), 2) long and slender body; 3) large pinnae; 4) soft and dense fur with short, black guard hairs; 5) long vibrissae (ca. 36% of HB); 6) light brown colour on upperparts with yellowish cream underparts separated by a sharp demarcation; 7) long hindfeet (25% of HB); 8) short tail (94% HB); 9) dorso-ventrally bicolored tail with dark brown to black colour on dorsum and paler (creamy white to white) on venter; 10) tail with short and dense black hairs; 11) moderately sized skull with long, narrow rostrum; 12) short, wide incisive foramina and 13) small auditory bullae.

Descriptions and comparisons. ~ *Maxomys tompotika* sp. nov is characterised by a longer, more slender body (weights of 7 adults range from 150–186 g) than the other *Maxomys* from Sulawesi (give similar measurements for other species). It has longer ears (Ears/HB = 16%) than other Sulawesian *Maxomys* (*M. hellwaldii*: ~13%, *M. dollmani*: 14%, *M. musschenbroekii*: 15%, *M. wattsi*: 13.9%). The short (<15 mm), thin, soft individually and dense fur covering upperparts of head and body and is shorter and brighter than in *M. dollmani*, *M. musschenbroekii*, or *M. hellwaldii,* and much coarser and slightly shorter than in *M. wattsi*. The pelage colour is light brown on upperparts and yellowish cream on underparts with a sharp demarcation between ventral and dorsal flanks. The guard hairs are scattered throughout the dorsal coat but are nearly undetectable because they are about the same diameter and length as the over-hairs; all are gray for about two-thirds of their length, and tipped with dark brown or black. Both over hairs and guard hairs are thin and pliable; none are wide, flattened, or rigid. Generally, species of *Maxomys* have short and spiny furs, with tapered guard hairs that extend beyond the over hairs. Among all 17 described *Maxomys* species, there are five species characterised by short, soft, and dense hairs namely *M. bartelsii, M. moi, M. hylomyoides, M. wattsi,* and *M. dollmani* (Musser 1969; Musser et al. 1979; Musser 1991). The pelage is soft, short and dense in most specimens of *M. hellwaldii* and *M. musschenbroekii*, but spiny in some individuals, especially at low elevations, and short and spiny in the other 11 known *Maxomys* species (Musser *et al.* 1979). The mystacial vibrissae are dense and stiff, the longest approaching 50 mm and extending beyond the ears. The base of each vibrissa is black with silvery tips or the distal quarter entirely unpigmented.

The tail is slightly shorter than length of head and body (ca. 95%), with bicolored tail (proximal half dorsally dark brown and ventrally white, distal half white) covering by short, dense and soft hairs). The slim, tapered tail from the base to the tip as typical of other murine rodents. Musser et al. (1979) stated that tail length of *Maxomys* is generally shorter to slightly longer than head and body, but *M. dollmani* has much longer tail length relative to head and body length. There are 12 - 15 overlapping scale rows per centimeter on each adult tail and two to three hairs arise from the base of each epidermal tail scale. Females possess three pairs (1 + 2) of mammae; one is axillary and two are inguinal, similar to the pattern in *M. dollmani*, *M. bartelsii,* and *M. inflatus* (Sunda Shelf) (Musser 1969; Musser et al. 1979).

The forefeet of *M. tompotika* sp. nov are unpigmented on both dorsal and ventral palmar surfaces with short typical murine claws (sharp and ivory-colored). Tops of the metacarpal region and digits are densely furred with silver hairs. The palmar surface is formed by three large interdigital pads, along with the thenar and hypothenar pads. The hindfeet are long relative to length of head and body (ratio of HF/HB = 25%) and whitish on dorsal surface and black on ventral of plantar surface. Six pads are usual on each plantar surface with four interdigital mounds, one small hypothenar and large elongated thenar. Long brown hairs mixed with silver strands overlay the top of the feet coming out from the base of each digit, curl over and extend beyond each claw. Claws are ivory in tone, long, sharp, and larger than those on the frontfeet.

The skull of *tompotika* is sturdy, the rostrum is long and wide, its sides gradually tapering towards the anterior end. The braincase shape is wide. The zygomatic arch is delicate and thin with small and narrow infraorbital foramen. The incisive foramen is long and broad relative to its length, and their posterior margins located slightly in front of the first molar or not quite reaching to the anterior side of first molar. The dorsolateral margins of the interorbital are defined by prominent temporal ridges that sweep back along dorsolateral postorbital margins of the frontals and onto half distal of parietals (Figures 3 and 4). The bullar capsules are small relative to cranial expanse (BL/GSL = 12%) for a murine and smaller than in any other Sulawesian *Maxomys* (*M. hellwaldii*~13%, *M. dollmani*~14%, *M. wattsi*~13%, and *musschenbroekii*~13%) (Musser et al. 1979; Musser 1991).

Generally, Musser et al. (1979) characterised *Maxomys* with the following traits: long and wide rostrum, tapers anteriorly, and extends in front of the incisors, the nasals are long and oblanceolate in dorsal view and the anterior margins are triangular, wide interorbital, broad and inflated braincase outlined by prominent ridges. Additionally, the incisive foramina are short, wide, and posterior margins are far in front of the anterior margins of the first molar (Corbet and Hill 1992).

The dentary of *M. tompotika* sp. nov is sturdy, typical of murine rodents. The dental formula of *tompotika* sp. nov is 1/1 0/0 0/0 3/3. The incisors appear sturdy, enamel faces of upper and lower molars are smooth, without grooves, dark orange on uppers and pale orange on lowers incisors. The upper incisors are moderately short and curve caudad after emerging from the rostrum (opisthodont conformation) and the lower incisors are longer that typical of murine rodents (Musser 1981; Musser et al. 1979). The pattern of molar roots in the specimen of *M. tompotika* sp. nov is simple and primitive, which is typical for murids (Musser and

Newcomb 1983). The molars of this species are robust, small and wide relative to the bony palate breadth, and low-crowned (brachyodont). The cusps of all the molars are situated adjacent to one another. The mandibular angular process is wide and elongate but otherwise the dentary is typical of murine rodents. No specific or distinctive characters were noted from the dentition including formula, cusps patterns on molars or molar shape itself, and seems similar to other *Maxomys* species from Sulawesi or Sunda Shelf (see Misonne 1969; Musser 1969; Musser et al. 1979; Musser 1991; Musser and Newcomb 1983).

*Statistical and molecular evidence***.** ~ Morphological and molecular evidences clearly support the distinction of *Maxomys tompotika* sp. nov from all known Sulawesian *Maxomys* species. Obviously, there are six distinct characters distinguished *tompotika* sp. nov from other Sulawesian *Maxomys* such as TTL, Ear, GSL, NL, WB and IFL depicted from univariate descriptive analysis (Tables 23 and 24). Principal component analysis was carried out for full data sets of cranial and dental characters and also computed for six selected characters as the most obvious distinctive characters showed previously. Both analyses found substantial multivariate differences separating *tompotika* sp. nov from other Sulawesian *Maxomys* by 68.16% (Component 1) and 22.14 % (Component 2) for skull and dental traits, 57.90% (Component 1) and 21.82 % (Component 2) for six selected characters. The bivariate plots of specimen scores projected on the 1st and 2nd principal components summarise the quantitative affinities of *tompotika* sp. nov that clusters near to *M. hellwaldii* and placed far from *dollmani*, *musschenbroekii*, or *wattsi*. These are indicating that morphologically *tompotika* sp. nov is most similar to *M. hellwaldii*, but distinguished by some characters as mention previously (Figures 39 – 42, Tables 25, 26).

Consistent with, and strengthening to the hypothesis tested from molecular inferrences presented on Chapter III, this study clarifies the existence of distinct populations from Sulawesi based on morphological approaches (descriptive and statistical) by using the same specimens identified as *M.* cf. *hellwaldii*. The descriptions clearly confirm the distinction between *tompotika* sp. nov and the other known Sulawesian *Maxomys* and clustered separately as mentioned previously that *M.* cf. *hellwaldii* form a different clade with other *Maxomys* from Sulawesi (separately from the clades of *M. dollmani* + *M. hellwaldii* + *M*. sp. and *M. musschenbroekii*) (Figure 21). This distinct population also supported by highly interspecific sequence divergence (> 0.10) between *tompotika* sp. nov (*M.* cf. *hellwaldii*) from described *Maxomys* species from Southeast Asia in chapter three.

IV.4 Discussion

M. tajuddinii sp. nov inhabits lowland forest in the Sunda Shelf region and is sympatric with *M. whiteheadi.* As currently understood, *M. whiteheadi* is one of the species that has a very widespread distribution, spanning Peninsular Malaysia, Sumatra and Borneo Island. Corbet and Hill (1992) stated that there were no fixed differences among populations of *M. whiteheadi* from those islands. *M. tajuddinii* sp. nov is not only distinctive from its morphology, but also phylogenetically (Figure 22). Given available data, it seems *M. tajuddinii* sp. nov is nested within *M. hylomyoides*, the endemic species from Sumatra Island

and thus far found in montane forest in Mount Tujuh, Mount Kerinci and Mount Singgalang.

Otherwise, *M. tompotika* sp. nov is one of Sulawesian *Maxomys* that inhabits lowland forest and has never been sampled at higher elevations (lower montane and upper montane forest). Musser (1991) defined the distribution of Sulawesian *Maxomys* such as *M. musschenbroekii* as occurring throughout Sulawesi at elevations ranging from near sea level to summits of mountains, *M. dollmani* occurs in both lowland evergreen forest and lower montane formations (higher elevation trapping needed at moss forest), and *M. wattsi* was known and restricted only to lower and upper montane forest. Otherwise, *M. hellwaldii* is recorded from throughout Sulawesi at lower elevation (<1000 m) of lowland forest, but excluding eastern tip peninsula, where *M. tompotika* is found (Corbet and Hill 1992; Musser et al. 2010). The specimens of *tompotika* sp. nov found sympatry with some other Sulawesian native murines such as *M. musschenbroekii*, *Rattus hoffmanni*, and *Paruromys dominator*. Previously, there was no record of small mammals inventory including murines diversity from the far limits of the eastern peninsula, and the closest area to Mt. Tompotika that have been sampled for small mammals was Mt. Tambusisi, located at the base of eastern peninsula, and Musser (2010) defined as east-central block of Central Sulawesi.

As I know, Sulawesi harbours a suite endemic species — Musser (2014) recorded at least 53 species of murines, and these were recently supplemented by new discoveries (Esselstyn et al. 2012; 2015; Mortelliti et al. 2012; Rowe et al. 2014, 2016) of species / genera endemic to Sulawesi. I assume the species of *tompotika* sp. nov is nocturnal and also endemic to Sulawesi island, specifically from eastern part of this island. The description here, of *M.*

tompotika sp. nov, brings the number of endemic murine rodent species to 56. Several previous studies tested the hypothesis of the distinction (intraspecific or interspecific divergence) catalysed by habitat fragmentation (Area of Endemism) and I assume that *M. tompotika* sp. nov is one of the species that resulted from this condition. They suggest that eastern part of Sulawesi represent a different area of endemism from central region or others (Setiadi et al. 2011, Shekelle et al. 2010, Merker et al. 2009, Campbell et al. 2007, Evans et al. 2008, Evans et al. 2003a, Evans et al. 2003b, Evans et al. 2003c, and McGuire et al. 2007). They posited that habitat fragmentation in Sulawesi resulted in shared patterns of endemism by using tarsiers, bats, toads, monkeys, fanged frogs, and flying lizards. In Chapter III, I mention that there is species complex comprising *M. musschenbroekii* that shows similar diversity patterns of endemism and further study is needed to investigate this cryptic species.

Taxonomic notes

Musser et al. (1979) revised *Maxomys* and classified the genus into 16 species in total from Southeast Asia. Three additional species have been made namely *M. wattsi* (Musser 1991) from Sulawesi and two more new species: *M. tajuddinii* sp. nov from Sunda Shelf and *M. tompotika* sp. nov from Sulawesi island. These descriptions bring the number of *Maxomys* species to 19 and highlight the possibility of further discoveries of new species. Some previous publications reference undescribed *Maxomys* species and additional species descriptions are expected (e.g. Musser 1991 and this study). In addition, some publications suggested that future works and revision needed to resolve the *Maxomys* complexity

(Balakirev et al. 2013; Fabre et al. 2013).

Conservation

Maxomys tompotika sp. nov was caught in Mt. Tompotika, a small mountain in eastern tip of Sulawesi that retains a comparatively large portion of the east peninsula's lowland forest. Mostly forest have been logged during the 1990s and are yet unrecovered. Otherwise, the minings (gold and nikel), oil palm plantation and agricultural also caused deforestation, habitat loss that threaten the populations of some endemic species. Considering the rate of forest disturbance, conservation activities represent an important tool to highlight the importance of remaining natural forest. The good condition is in part due to the presence of AlTo (*Alliance for Tompotika Conservation*), an NGO that started to conserve endangered species and natural areas in eastern peninsula.

GENERAL DISCUSSION

Wallace (1863) divided South East Asia into the Indochinese (Indo-China), Sundaic, Philippines and Wallacean zoogeographic subregions. The Indonesian archipelago, in particular, has fascinated biogeographers since Alfred Russell Wallace's pioneering studies in documented extremely high levels of diversity in the region and the sharp biogeographical divide between the Sunda islands (the western part of the archipelago) and Sulawesi (Wallace 1863). The island of Borneo itself, along with Sulawesi is playing important role for biogeography of this region because of bordering Wallace's faunal divide as western boundary of Wallacea, a transitional area between Asiatic and Australian biotas, where organisms show a high degree of endemism (Whitten et al. 2002; Moss and Wilson 1998; Woodruff 2010).

The diversity of *Maxomys*, as mention in previous chapters (2 and 4) are distributed from Indochina until Sulawesi island. Here, I documented the *Maxomys* diversity and the distributions divided by the regions following Wallace (1863):

Indochinese region

Musser et al. (1979) mentioned that *Maxomys* was a Sundaic genus, mostly found in the Malay Peninsula south of the Isthmus of Kra until Sunda Shelf; only two species were found *(M. surifer* and *M. moi*) were found in Indochinese: *surifer* in Thailand and *moi* was endemic to Laos and Vietnam. Pimsai et al. (2014) also found *M. surifer* from Myanmar, Thailand, Peninsular Malaysia and Singapore. Here I documented the external and craniometric measurements of *M. moi* from 16 specimens collected from Vietnam (Appendix 6, Tables 27, 28): total length (TTL) = 345,73 ± 23,60 mm; tail length (TL) = 176,07 ± 13,03 mm; hindfoot (HF) = 38,27 ± 1,58 mm; ear (E) = 24,73 ± 1,49 mm.

Sundaic region

Sundaic regions, also called Sundaland, it includes Malay peninsula (south of Isthmus Kra), Sumatra, Java and Borneo Islands. Previously Musser et al. (1979) stated there were 11 species recorded from Sundaland. Four species recorded from Peninsular Malaysia (*M. inas, M. surifer, M. rajah* and *M. whiteheadi*), six species inhabiting Borneo Island (*M. alticola, M. baeodon, M. ochraceiventer, M. rajah, M. surifer* and *M. whiteheadi*), six species found in Sumatra and small adjacent islands (*M. hylomyoides, M. inflatus, M. rajah, M. surifer, M. whiteheadi* and one endemic species to Mentawai island namely *M. pagensis*). Three species were found in Java island namely *M. bartelsii, M. surifer* and *M. whiteheadi*. This study added one new species from the region namely *M. tajuddinii* sp. nov and all the measurements presented on Tables 23 and 24.

Wallacea region

Sulawesi island is the largest area in the region which separated from the Asian continental shelf (Sunda) on the West by Wallace’s Line and from the Australian continent (Sahul) on the East by Weber’s Line. Sulawesi holds a composite of Asian and Australian biodiversity (Wallace 1876). The island itself was formed by a complex geological history, involving the coalescence of landmasses of Asian, Australian, and oceanic origin (Hall 2002). This geological history has produced a diverse and highly partitioned fauna, in which each biogeographic region, or area of endemism, holds a unique set of species (Evans et al. 2003a). The central core and the north, east, southeast, and southwest peninsulas of the island respectively comprise five primary areas of local endemism on Sulawesi.

Musser (1991) reported there are three described species of *Maxomys* from this island (*M. musschenbroekii, M. hellwaldii* and *M. dollmani*). Thus, he described new species of *M. wattsi* from the specimens collected from Mount Tambusisi, Central Sulawesi and noted there are two distinct populations from different locality. Moreover, the present study generated new descriptions of *M. tompotika* sp. nov from east peninsula (see Chapter IV). Total of five species of *Maxomys* has been recorded from this island.

Understanding the distributional patterns of Maxomys *in Southeast Asia and its biogeographical diversification*

There are some biogeographic patterns in the distributions of Muridae in Southeast Asia, particularly in Peninsular Malaysia and Indonesian archipelago. The genus *Maxomys,* which is one of the most important genera that a key role in Sundo-Wallacean zoogeographic studies (Ruedas and Kirsch 1997); generally colonise into Borneo from Peninsular Malaysia; whether related to the Pleistocene land bridge biogeography in the Sunda Shelf (Heaney 1991a and b) or need a deeper history of preglacial vicariance in Southeast Asia for this genus

(Gorog et al. 2004). The current study seems follows the suggestion by Gorog et al. (2004). They proposed that *M. surifer, L. sabanus* and *M. whiteheadi* dispersed throughout their current ranges in the early Pliocene before the long-standing connections between Indochina, Java, Sumatra, Borneo and the Peninsular Malaysia were severed. At this time, a relatively stable perhumid climate had characterised the region for several million years and tropical rain forest was widespread, presumably on the exposed regions of the shelf as well as on the islands, peninsula and mainland. Fossil evidence supported the early presence of *Maxomys* and *Leopoldamys* in the region: the putative sister taxon of *Maxomys*, the extinct *Ratchaburamys ruchae,* was known from the late Pliocene to early Pleistocene northern Peninsular Malaysia (Chaimanee 1998). This is supported by the current results neither from phylogenetic relationships or morphological traits. For an example, the specimens of *M. musschenbroekii* which were endemic to Sulawesi (east of Wallace's Line) form a clade and displayed closest affinity to *M. whiteheadi* (Figures 22 – 24), the other *Maxomys* species that present on Sunda Shelf (west of Wallace's Line). These findings are very important to revealed the long biogeographical history related to geologic and tectonic movements of Borneo and Sulawesi islands.

Based on the present findings, some speculations related to *Maxomys* diversification: (1) firstly, the existence of multiple interisland colonisations events (Borneo – Sulawesi Island or vice versa). Previous studies had conducted about the connections between these two islands. Inger and Voris (2001) stated that based on geological evidence indicates that there were two intervals when fauna1 exchange of frogs (genus *Megophrys*) between Borneo and Southwestern Sulawesi could have occurred: during the Eocene by overland movements. As the fragments of Sulawesi began to assemble during the Miocene (10 – 20 Mya), the eastern Philippines were drifting from the Southeast Asia and passed close to the northern arm of Sulawesi at the same time that a string of volcanoes ran northeastward from Sulawesi towards the Philippines (Hall 1998). Moss and Wilson (1998) supported that land migration of terrestrial organisms between Borneo, mainland of Southeast Asia and some of Sunda islands, would have been possible throughout much of Tertiary (mainly Eocene to Oligocene epoch), since at least a transitory land connection was inferred to have existed between these areas until the Plio/Pleistocene epoch. They also concluded that Western Sulawesi had been accreted to eastern Borneo by the late Cretaceous, and by the early Eocene there were continuous land areas in the Schwaner Mountains, Northwest Kalimantan, the Mangkahilat peninsular and parts of Western Sulawesi. The dispersal of certain flora and fauna between Borneo and Sulawesi could have occurred at this glacial period. The speculation from this evidence is this land bridge would be a probable pathway for *Maxomys* to colonise Sulawesi and *in situ* diversification happened. Otherwise, this also indicates that for these rats, the deepwater barriers surrounding Sulawesi have been relatively permeable. Inger and Voris (2001) also postulated that faunal exchange of frogs (genus *Megophrys*) could have occurred at Pleistocene epoch when sweepstakes migration across a narrowed Makassar Strait would have been required. Its reasonably when Bornean lineages have close relationships to Sulawesi lineages as occurred in this study between *M. whiteheadi* and *M. musschenbroekii*.

Secondly, the evidence of genetic diversity among *M. musschenbroekii* is corresponding to the previous delimitations of the Area of Endemism in Sulawesi island (Evans et al. 2003b). Previously, the Area of Endemism (AoE) was hypothesised based on macaque work which divided Sulawesi into seven areas of endemism. Thus, the follow-up studies have shown that genetic and/or morphological structuring in other taxa may deviate slightly from this pattern (e.g., *Bufo celebensis*, Evans et al. 2003b; *Draco* lizards, McGuire et al. 2007), or even deviate dramatically (*Lamprolepis* skinks, Linkem et al. 2013). Some of the inferred biogeographical boundaries between AoEs reflect the merged paleo-islands or tied to the tectonic history of the island (Shekelle et al. 2010). Broader sampling in this area and deeper taxonomic investigations are needed in order to generate data and tested the hypothesis of AoE.

Rodent fauna of Sulawesi Island : diversity, new discoveries, and distributions

Among terrestrial small mammals, the rodent fauna of Sulawesi is entirely endemic and contains a wide range of morphological and apparently ecological diversity. Wallace (1869) reported 21 species of mammal from Sulawesi, but that number had increased to 127 species by the time Musser and Carleton (2005) synthesised the literature. Within the last three years, six species and four genera have been added to this list (Esselstyn et al. 2012, 2015; Mortelliti et al. 2012; Musser 2014; Rowe et al., 2014, 2016). The fauna includes at least 21 genera of terrestrial small mammals, of which 17 are endemic, and includes morphological oddities such as giant woolly rats with tufted rumps (*Eropeplus*), short-legged diurnal vermivores (*Melasmothrix*), and terrestrial insectivorous squirrels (*Hyosciurus*). Prior to the initiation of surveys since 2010, 51 species from 18 genera of rodents were known, many from only one or two localities, includes the discoveries of new species and genera (a molarless rat~*Paucidentomys vermidax*, the Sulawesi water rat~*Waiomys mamasae,* hog-nosed shrew rat~*Hyorhinomys stuempkei*, Sulawesi's root rat~*Gracilimus radix*, *Bunomys torajae*, and *Margaretamys christinae*) which proved that rodent fauna in Sulawesi is dramatically undersampled. This study added one new species of *Maxomys tompotika* sp. nov which endemic to this island.

Finally, further research is needed to study Indonesian small mammals diversity, especially murines in certain areas such as Borneo or Sulawesi islands. Bickford et al. (2007) stated that the understanding of the species morphological limits, geographic ranges, elevational distributions, and habitat use is very limited, all of which have stymied assessments of conservation threats to Indonesian biodiversity and also limited understanding of the biogeographic history of Southeast Asian mammals.

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APPENDICES

Appendix 1. List of samples used in analysis of Chapter I.

Maxomys whiteheadi (Small body size)

MZB 29090 Female, MZB 29092 Female, MZB 29073 Male, MZB 29093 Male, MZB 29094 Male, MZB 29098 Male, MZB 29099 Male, MZB 29100 Male, MZB 29102 Male, MZB 29103 Female, MZB 29104 Female, MZB 23645 Female, MZB 23642 Female, MZB 23641 Male, MZB 29059 Female, MZB 29061 NR, MZB 29064 Female, MZB 29071 Female, MZB 29081 Female, MZB 23607 Female, MZB 23601 Male, MZB 23651 Male, MZB 23647 Male, MZB 23638 Male, MZB 15384 Male, MZB 26247 Male, MZB 22220 Female, MZB 22212 NR, MZB 22215 Female, MZB 26251 Male, MZB 22217 Female, MZB 22222 Male, MZB 26253 Male, MZB 26234 Male, MZB 26246 Male, MZB 22210 Male, MZB 11647 Female, MZB 13338 Female, MZB 18347 Male, MZB 18370 Male, MZB 18371 Male, MZB 24986 Female, MZB 5661 Male, MZB 15383 Male, MZB 15569 Female, MZB 15571 Female, MZB 20560 Male, MZB 20569 Female, MZB 20580 Female, MZB 20567 Male, MZB 20582 Male, MZB 20559 Male, MZB 20574 Female, MZB 20571 Male, MZB 20562 Female, MZB 20568 Male, MZB 24944 Female, MZB 24957 Female, MZB 2071 Female, MZB 24931 Female, MZB 15385 Female, MZU TK152846 Female, MZU 819 Male, MZU TK156129 NR, MZU 1844 Male, MZU TK152353 NR, MZU 326 Male, MZU 1052 Female, MZU TK152362 NR, MZB NA014 NR, MZB 5679 Male, MZB 5673 Male, MZB 5663 Male, MZB 24893 Male, MZB 24963 Male, MZB 24898 Male, MZB 13031 Female, MZB 15382 Male, MZB 23648 Male, MZB 29065 Female, MZB 29067 Female, MZB 29069 Female, MZB 22233 Female, MZB 29074 Male, MZB 29078 Male, MZB 29082 Female, MZB 29083 Female, MZB 29084 Male, MZU TK152862 NR, MZB 29076 Female.

Maxomys whiteheadi (Large body size)

MZB 29058 Female, MZB 29062 Female, MZB 29066 Female, MZB 29068 Female, MZB 29070 Female, MZB 29077 Male, MZB 29080 Male, MZB 18482 NR, MZB 29086 Female, MZB 28961 Male, MZB 28962 Female, MZB 28960 Female, MZB 28963 Male, MZB 28967 Male, MZB 28968 Male, MZU TK153703 Male, MZU TK153717 Male, MZU TK152349 NR, MZU TK152861 NR, MZU 471 Male, MZU 1618 Female.

Maxomys wattsi

MZB 12159 Male, MZB 12160 Male, MZB 12161 Male, MZB 12163 NR

Maxomys surifer

MZB 4961 Male, MZB 4962 Female, MZB 4969 Female, MZB 4971 Female, MZB 4974 Male, MZB 4976 NR, MZB 4977 Female, MZB 4978 Male, MZB 4979 Male, MZB 4983 Female, MZB 4984 Male, MZB 4985 Male, MZB 4987 Female.

Maxomys rajah

MZU TK152850 Male, MZU TK152852 Male, MZB 14756 Female, MZB 14774 NR, MZB 14779 Male, MZB 14752 Male, MZB 22496 Male, MZB 22621 Female, MZB 23661 Male, MZB 23662 Male, MZB 23663 Female, MZB 27436 Not recorded.

Maxomys pagensis

MZB 22355 Female, MZB 2885 Female, MZB 17565 Male.

Maxomys ochraceiventer

MZB 23606 Male, MZB 23971 Male, MZB 23970 Female.

Maxomys musschenbroekii

MZB 26935 Female, MZB 26942 Female, MZB 26943 Male, MZB 26945 Male, MZB 26946 Male, MZB 26950 Female, MZB 26951 Male, MZB 26953 Male, MZB 26955 Male, MZB 26956 Male, MZB 26960 Female.

Maxomys hellwaldii

MZB 26964 Male, MZB 26971 Female, MZB 26982 Male, MZB 26988 Male, MZB 26991 Male, MZB 27163 Female.

Maxomys bartelsii

MZB 2188 Male, MZB 9537 Male, MZB10135 Male, MZB 10872 Male, MZB 10875 Female, MZB 10876 Female, MZB 10877 Male, MZB 12430 Female, MZB 12462 NR, MZB 12919 Male, MZB 22525 Male.

Maxomys baeodon

MZU TK152835 Male, Raffles Museum 3312 Male, Raffles Museum 3533 Male, Raffles Museum 3543 Female, Raffles Museum 3571 Female, Raffles Museum 3224 Female.

Maxomys alticola

Raffles Museum 4213 Male, Raffles Museum 4203 Male, Raffles Museum 4214 Male, Raffles Museum 4013 Male, Raffles Museum 4223 Female, Raffles Museum 4215 Male.

Maxomys inas

MZB 13432 Female.

Appendix 2. List of specimens used in Chapter II

Maxomys hellwaldii

MZB27294, MZB27285, MZB27292

Maxomys musschenbroekii

MZB36137, MZB36139, MZB36144, MZB26962

Maxomys pagensis

MZB2883, MZB2884, MZB28335, MZB28338, MZB28336, MZB2885, MZB17565

Maxomys hylomyoides

MZB5705, MZB5710, MZB3159

Maxomys bartelsii

MZB22525, MZB9547, MZB10875, MZB32889, MZB12429, MZB12449, MZB10137

Maxomys dollmani

NMVC37233/KCR1956

Maxomys alticola

MZB5631, MZB5632

Maxomys ochraceiventer

MZB23606, MZB23598

Maxomys baeodon

MZB14773, MZB14781, MZB14748, MZB14746, MZB14745, MZB14747

Maxomys rajah

MZB36881, MZB14754, MZB16138, MZB13028, MZB22496, MZB26824, MZB36105

Maxomys surifer

MZB4980, MZB34369, MZB4982, MZB13335, MZB30328

Maxomys whiteheadi

MZB24438, MZB22603, MZB22602, MZB22606, MZB24485, MZB24479, MZB22233, MZB22243, MZB24524, MZB24527, MZB28967, MZB22686, MZB22609, MZB22608, MZB30717, MZB34145, MZB28961, MZB28962, MZB28963, MZB5667, MZB13129, MZB13327, MZB34139

Appendix 3. List of specimens, localities, and GenBank accession numbers of samples used in Chapter III.

Species Name	**Catalog Number**	**Locality**	**Fig. 20 Locality**	**CytB**	**IRBP**	**GHR**
Anisomys imitator	ABTC 45107			EU349732	EU349833	DQ019052
Apomys datae	FMNH 167243				EU349836	KC878169
Apomys datae	FMNH 188298			HM371072		
Bandicota bengalensis	T0656				AM910945	
Batomys granti	USNM 458943			EU349738	EU349838	AY294917
Berylmys bowersi	MVZ 186482			KC878024	KC878201	DQ019056
Bunomys chrysocomus	ABTC 65755			KC878025	EU349839	EU349795
Bunomys chrysocomus	MZB 23066			KC878026		KC878170
Bunomys penitus	FMNH 213103			KC878027	KC878202	KC878171
Chiromyscus chiropus	ABTC 69097			EU349739	EU349840	EU349796
Conilurus penicillatus	ABTC 7411			EU349743	EU349844	DQ019057
Crunomys celebensis	NMV C37047	Mt. Gandangdewata, Sulawesi	20	KC878028	KC878203	KC878172
Crunomys melanius	FMNH 147105	Mt. Kitanglad, Philippines	28	DQ191477	DQ191506	GQ405379
Crunomys suncoides	FMNH 147942	Mt. Kitanglad, Philippines	28	DQ191478	DQ191507	
Dacnomys millardi	MVZ 186519			KC878029	KC878206	
Dasymys incomtus	ABTC 65735			EU349744	KC878207	EU349798
Leopoldamys sabanus	TK 152988			JF437016		
Leopoldamys sabanus	CMNH 102138			KC878030	KC878208	DQ019063
Mastomys erythroleucus	ABTC 65697			EU349718	KC878210	AM910959
Maxomys bartelsii	ABTC 48063	Mt. Gede, Java	13	EU349762	EU349857	DQ019066
Maxomys bartelsii	FMNH 212799	Mt. Gede, Java	13	KC878031		
Maxomys bartelsii	MZB 30331	Mt. Ciremai, West Java	14	KC878032	KC878211	KC878173
Maxomys cf. hellwaldii	FMNH 213370	Mt. Tompotika, Sulawesi	25	KC878037		
Maxomys cf. hellwaldii	FMNH 213371	Mt. Tompotika, Sulawesi	25	KC878038		
Maxomys cf. hellwaldii	FMNH 213372	Mt. Tompotika, Sulawesi	25	KC878039	KC878212	KC878174
Maxomys cf. hellwaldii	FMNH 213451	Mt. Tompotika, Sulawesi	25	KC878040		

Maxomys cf. hellwaldii	FMNH 213452	Mt. Tompotika, Sulawesi	25	KC878041		
Maxomys dollmani	MVZ 225723	Mt. Balease, Sulawesi	22	KC878033		
Maxomys dollmani	MVZ 225724	Mt. Balease, Sulawesi	22	KC878034		
Maxomys dollmani	MVZ 225725	Mt. Balease, Sulawesi	22	KC878035	KC878213	KC878175
Maxomys dollmani	MZB 34949	Mt. Gandangdewata, Sulawesi	20	KC878036		
Maxomys hellwaldii	MVZ 225744	Malili, Sulawesi	24	KC878042		
Maxomys hellwaldii	MVZ 225762	Malili, Sulawesi	24	KC878043		
Maxomys hellwaldii	MVZ 225768	Mt. Balease, Sulawesi	22	KC878044	KC878214	KC878176
Maxomys hellwaldii	MVZ 225773	Malili, Sulawesi	24	KC878045		
Maxomys hylomyoides	FMNH 212900	Mt. Tujuh, Sumatra	11	KC878046	KC878216	KC878177
Maxomys hylomyoides	FMNH 212901	Mt. Tujuh, Sumatra	11	KC878047	KC878217	KC878178
Maxomys hylomyoides	FMNH 212902	Mt. Tujuh, Sumatra	11	KC878048		
Maxomys hylomyoides	FMNH 212903	Mt. Tujuh, Sumatra	11	KC878049		
Maxomys hylomyoides	FMNH 212980	Mt. Singgalang, Sumatra	10	KC878050	KC878218	KC878179
Maxomys hylomyoides	FMNH 212981	Mt. Singgalang, Sumatra	10	KC878051		
Maxomys hylomyoides	FMNH 212982	Mt. Singgalang, Sumatra	10	KC878052		
Maxomys hylomyoides	FMNH 212983	Mt. Singgalang, Sumatra	10	KC878053		
Maxomys hylomyoides	FMNH 212984	Mt. Singgalang, Sumatra	10	KC878054		
Maxomys hylomyoides	FMNH 213419	Mt. Tujuh, Sumatra	11	KC878055		
Maxomys moi	ROM 111318	Quang Nam, Vietnam	4	KC878056	KC878219	KC878180
Maxomys moi	ROM 111328	Quang Nam, Vietnam	4	KC878057	KC878220	KC878181
Maxomys moi	ROM 111367	Quang Nam, Vietnam	4	KC878058		
Maxomys musschenbroekii	FMNH 213076	Mt. Latimojong, Sulawesi	23	KC878059		
Maxomys musschenbroekii	FMNH 213077	Mt. Latimojong, Sulawesi	23	KC878060		
Maxomys musschenbroekii	FMNH 213078	Mt. Latimojong, Sulawesi	23	KC878061		
Maxomys musschenbroekii	FMNH 213079	Mt. Latimojong, Sulawesi	23	KC878062		
Maxomys musschenbroekii	FMNH 213080	Mt. Latimojong, Sulawesi	23	KC878063		
Maxomys musschenbroekii	FMNH 213084	Mt. Latimojong, Sulawesi	23	KC878064		
Maxomys musschenbroekii	FMNH 213280	Mt. Latimojong, Sulawesi	23	KC878065		

Maxomys musschenbroekii	FMNH 213281	Mt. Latimojong, Sulawesi	23	KC878066		
Maxomys musschenbroekii	FMNH 213394	Mt. Tompotika, Sulawesi	25	KC878067	KC878221	KC878182
Maxomys musschenbroekii	FMNH 213395	Mt. Tompotika, Sulawesi	25	KC878068	KC878222	KC878183
Maxomys musschenbroekii	FMNH 213396	Mt. Tompotika, Sulawesi	25	KC878069		
Maxomys musschenbroekii	FMNH 213397	Mt. Tompotika, Sulawesi	25	KC878070		
Maxomys musschenbroekii	FMNH 213398	Mt. Tompotika, Sulawesi	25	KC878071		
Maxomys musschenbroekii	FMNH 213446	Mt. Rorekatimbo, Sulawesi	21	KC878072		
Maxomys musschenbroekii	MVZ 225727	Mt. Balease, Sulawesi	22	KC878073		
Maxomys musschenbroekii	MVZ 225728	Mt. Balease, Sulawesi	22	KC878074		
Maxomys musschenbroekii	MVZ 225729	Malili, Sulawesi	24	KC878075		
Maxomys musschenbroekii	MVZ 225730	Malili, Sulawesi	24	KC878076		
Maxomys musschenbroekii	MVZ 225731	Malili, Sulawesi	24	KC878077		
Maxomys musschenbroekii	MVZ 225732	Malili, Sulawesi	24	KC878078		
Maxomys musschenbroekii	MVZ 225733	Mt. Balease, Sulawesi	22	KC878079		
Maxomys musschenbroekii	MVZ 225734	Mt. Balease, Sulawesi	22	KC878080		
Maxomys musschenbroekii	MVZ 225735	Mt. Balease, Sulawesi	22	KC878081		
Maxomys musschenbroekii	MVZ 225737	Mt. Balease, Sulawesi	22	KC878082		
Maxomys musschenbroekii	MVZ 225738	Mt. Balease, Sulawesi	22	KC878083		
Maxomys musschenbroekii	MVZ 225739	Mt. Balease, Sulawesi	22	KC878084		
Maxomys musschenbroekii	MVZ 225740	Mt. Balease, Sulawesi	22	KC878085		
Maxomys musschenbroekii	MVZ 225741	Mt. Balease, Sulawesi	22	KC878086		
Maxomys musschenbroekii	MVZ 225742	Mt. Balease, Sulawesi	22	KC878087		
Maxomys musschenbroekii	MVZ 225743	Malili, Sulawesi	24	KC878088		
Maxomys musschenbroekii	MVZ 225745	Malili, Sulawesi	24	KC878089	KC878224	KC878184
Maxomys musschenbroekii	MVZ 225746	Malili, Sulawesi	24	KC878090		
Maxomys musschenbroekii	MVZ 225747	Malili, Sulawesi	24	KC878091		
Maxomys musschenbroekii	MVZ 225748	Malili, Sulawesi	24	KC878092		
Maxomys musschenbroekii	MVZ 225749	Malili, Sulawesi	24	KC878093		
Maxomys musschenbroekii	MVZ 225750	Malili, Sulawesi	24	KC878094		

Maxomys musschenbroekii	MVZ 225751	Malili, Sulawesi	24	KC878095		
Maxomys musschenbroekii	MVZ 225752	Malili, Sulawesi	24	KC878096		
Maxomys musschenbroekii	MVZ 225753	Malili, Sulawesi	24	KC878097		
Maxomys musschenbroekii	MVZ 225754	Malili, Sulawesi	24	KC878098		
Maxomys musschenbroekii	MVZ 225755	Malili, Sulawesi	24	KC878099		
Maxomys musschenbroekii	MVZ 225756	Malili, Sulawesi	24	KC878100		
Maxomys musschenbroekii	MVZ 225757	Malili, Sulawesi	24	KC878101		
Maxomys musschenbroekii	MVZ 225758	Malili, Sulawesi	24	KC878102		
Maxomys musschenbroekii	MVZ 225759	Malili, Sulawesi	24	KC878103		
Maxomys musschenbroekii	MVZ 225760	Malili, Sulawesi	24	KC878104		
Maxomys musschenbroekii	MVZ 225761	Malili, Sulawesi	24	KC878105		
Maxomys musschenbroekii	MVZ 225763	Malili, Sulawesi	24	KC878106		
Maxomys musschenbroekii	MVZ 225764	Malili, Sulawesi	24	KC878107		
Maxomys musschenbroekii	MVZ 225765	Malili, Sulawesi	24	KC878108		
Maxomys musschenbroekii	MVZ 225766	Malili, Sulawesi	24	KC878109		
Maxomys musschenbroekii	MVZ 225767	Mt. Balease, Sulawesi	22	KC878110		
Maxomys musschenbroekii	MVZ 225769	Mt. Balease, Sulawesi	22	KC878111		
Maxomys musschenbroekii	MVZ 225770	Mt. Balease, Sulawesi	22	KC878112		
Maxomys musschenbroekii	MVZ 225771	Malili, Sulawesi	24	KC878113		
Maxomys musschenbroekii	MVZ 225772	Malili, Sulawesi	24	KC878114		
Maxomys musschenbroekii	MVZ 225774	Malili, Sulawesi	24	KC878115		
Maxomys musschenbroekii	MVZ 225775	Malili, Sulawesi	24	KC878116		
Maxomys musschenbroekii	MVZ 225776	Malili, Sulawesi	24	KC878117		
Maxomys musschenbroekii	MVZ 225777	Malili, Sulawesi	24	KC878118		
Maxomys musschenbroekii	MVZ 225778	Malili, Sulawesi	24	KC878119		
Maxomys musschenbroekii	MZB 34728	Mt. Gandangdewata, Sulawesi	20	KC878124	KC878223	KC878185
Maxomys musschenbroekii	MZB 34894	Mt. Gandangdewata, Sulawesi	20	KC878120		
Maxomys musschenbroekii	MZB 34895	Mt. Gandangdewata, Sulawesi	20	KC878121		
Maxomys musschenbroekii	MZB 34898	Mt. Gandangdewata, Sulawesi	20	KC878122		

Maxomys musschenbroekii	MZB 34899	Mt. Gandangdewata, Sulawesi	20	KC878123		
Maxomys musschenbroekii	NMV C37061	Mt. Gandangdewata, Sulawesi	20	KC878125		
Maxomys musschenbroekii	NMV C37062	Mt. Gandangdewata, Sulawesi	20	KC878126		
Maxomys musschenbroekii	NMV C37063	Mt. Gandangdewata, Sulawesi	20	KC878127		
Maxomys ochraceiventer	KNP027	Kubah National Park, Sarawak	15	JF436978		
Maxomys ochraceiventer	RG072	Sarawak, Malaysia	15	JF436982		
Maxomys ochraceiventer	RG086	Sarawak, Malaysia	15	JF436983		
Maxomys ochraceiventer	RG092	Sarawak, Malaysia	15	JF436984		
Maxomys ochraceiventer	TK 152861	Kubah National Park, Sarawak	15	JF437017		
Maxomys pagensis	MZB 28335	Mentawai Island, Sumatra	9	KC878128	KC878225	KC878186
Maxomys panglima	KU 165356	Puerto Princesa, Palawan, Philippines	27	KC878129	KC878226	KC878187
Maxomys panglima	KU 165357	Puerto Princesa, Palawan, Philippines	27	KC878130		
Maxomys panglima	KU 165358	Puerto Princesa, Palawan, Philippines	27	KC878131		
Maxomys panglima	KU 165455	Mt. Mantalingajan, Palawan, Philippines	26	KC878132		
Maxomys panglima	KU 165456	Mt. Mantalingajan, Palawan, Philippines	26	KC878133		
Maxomys panglima	KU 165457	Mt. Mantalingajan, Palawan, Philippines	26	KC878134		
Maxomys rajah	BTA020	Batang Ai National Park, Sarawak	16	JF437003		
Maxomys rajah	EKS026	Johor, Malay Peninsula	8	JF436976		
Maxomys rajah	FH049	Johor, Malay Peninsula	8	JF436997		
Maxomys rajah	LB066	Pahang, Malay Peninsula	7	JF436999		
Maxomys rajah	LB067	Pahang, Malay Peninsula	7	JF436996		
Maxomys rajah	LB068	Pahang, Malay Peninsula	7	JF437000		
Maxomys rajah	MVZ 192207	Bukit Lawang, Sumatra	12	KC878136		
Maxomys rajah	MVZ 192210	Bukit Lawang, Sumatra	12	KC878137	KC878227	
Maxomys rajah	ROM 113124	Endau Rompin National Park, Malay Peninsula	8	KC878135	KC878228	KC878195
Maxomys sp.	MZB 23104	Lore Lindu NP, Central Sulawesi	21	KC878138	KC878215	
Maxomys sp.	MZB 23105	Lore Lindu NP, Central Sulawesi	21	KC878139		
Maxomys sp.	TK 152985	Niah National Park, Sarawak	17	KC878140		
Maxomys rajah [surifer]	EKS011	Johor, Malay Peninsula	8	JF436990		

Maxomys surifer	FMNH 212914	Mt. Tujuh, Sumatra	11	KC878141	KC878229	KC878188
Maxomys surifer	FMNH 212915	Mt. Tujuh, Sumatra	11	KC878142	KC878230	KC878189
Maxomys surifer	FMNH 212916	Mt. Tujuh, Sumatra	11	KC878143		KC878190
Maxomys surifer	FMNH 213421	Mt. Tujuh, Sumatra	11	KC878144		
Maxomys surifer	FMNH 213422	Mt. Tujuh, Sumatra	11	KC878145		
Maxomys surifer	MM06	Sarawak, Malaysia	15	JF437004		
Maxomys sp. *[surifer]*	R3116	Kanchanaburi, Thailand	1	HM217405		
Maxomys sp. *[surifer]*	R3118	Kanchanaburi, Thailand	1	HM217406		
Maxomys surifer	R3464	Loei, Thailand	3	HM217420		
Maxomys surifer	R4223	Loei, Thailand	3	HM217445		
Maxomys surifer	ROM 107723	Mt. Yok Don, Vietnam	5	KC878146	KC878231	KC878191
Maxomys surifer	ROM 107778	Mt. Yok Don, Vietnam	5	KC878147		
Maxomys surifer	ROM 110900	Cat Tien National Park, Vietnam	6	KC878148		
Maxomys surifer	ROM 113024	Endau Rompin National Park, Malay Peninsula	8	KC878149	KC878232	KC878192
Maxomys surifer	ROM 113025	Endau Rompin National Park, Malay Peninsula	8	KC878150	KC878233	
Maxomys rajah [surifer]	TB011	Pahang, Malay Peninsula	7	JF437011		
Maxomys tajuddinii sp. nov	MZB 29066	Melak, Kutai Barat, East Kalimantan	19	KC878151		
Maxomys whiteheadi	TK152836	Kubah National Park, Sarawak	15	JF437019		
Maxomys whiteheadi	TK152846	Kubah National Park, Sarawak	15	JF437018		
Maxomys whiteheadi	MNHN 1999-514	Thailand, specific locality unknown		EU292150		
Maxomys whiteheadi	MZB 23645	Melak, Kutai Barat, East Kalimantan	19	KC878152		
Maxomys whiteheadi	MZB 23651	Melak, Kutai Barat, East Kalimantan	19	KC878153		
Maxomys whiteheadi	MZB 29092	Melak, Kutai Barat, East Kalimantan	19	KC878154		
Maxomys whiteheadi	MZB 29093	Melak, Kutai Barat, East Kalimantan	19	KC878155		
Maxomys whiteheadi	MZB 29099	Melak, Kutai Barat, East Kalimantan	19	KC878156		
Maxomys whiteheadi	Pueh006	Mount Pueh, Sarawak, Malaysia	15	JF437002		
Maxomys whiteheadi	RG081	Sarawak, Malaysia	15	JF436985		
Maxomys whiteheadi	ROM 113074	Endau Rompin National Park, Malay Peninsula	8	KC878157	KC878234	KC878193
Maxomys whiteheadi	ROM 113100	Endau Rompin National Park, Malay Peninsula	8	KC878158		KC878194

Maxomys whiteheadi	TK 156110	Kubah National Park, Sarawak	15	JF436995		
Maxomys whiteheadi	UMMZ 174492	Bukit Baka National Park, West Kalimantan	18	DQ191481		
Maxomys whiteheadi	MVZ 192215	Bukit Lawang, Sumatra	12	KC878159		
Maxomys whiteheadi	MVZ 192217	Bukit Lawang, Sumatra	12	KC878160		
Mus musculus	LAB STRAIN			AF520621	EU349863	M33324
Niviventer bukit	FMNH 212795			KC878161		
Niviventer bukit	FMNH 212796			KC878162	KC878235	KC878196
Niviventer bukit	FMNH 212797			KC878163		
Niviventer bukit	WAM38541			KC878164		KC878197
Niviventer fulvescens	ABTC 115924			KC878165		KC878198
Niviventer fulvescens	R3459				HM217657	
Paruromys dominator	NMV C37024			KC878166	KC878236	KC878199
Phloemys pallidus	WCS 931040			EU349775	KC878237	DQ019070
Rattus hoffmanni	MVZ 225736			KC878167		
Rattus hoffmanni	MVZ 225813			KC878168	KC878238	KC878200
Rattus norvegicus	Rnor_5.0			Rnor_5.0	Rnor_5.0	Rnor_5.0
Rattus rattus	MVZ 221220			JQ814282		
Rattus rattus	T-660					AM910976
Rattus rattus	T820				HM217606	
Rattus villosisimus	ABTC 00549			EU349783		EU349826
Rattus villosisimus	ABTC 08439				HQ334576	
Rhynchomys isarogensis	USNM 573905			EU349784	AY326108	DQ019075
Srilankamys ohiensis	ZMFK 2008.375			JN009856	JN009857	JN009860

Appendix 4. List of specimens used in Chapter IV ~ *Maxomys tajuddinii* sp. nov

NO	SPESIES	Museum No.	SEX	LOCALITY	Depository	Notes
1	*M. whiteheadi*	29090	Female	Melak, Kutai Barat, Kalimantan Timur	MZB	
2	*M. whiteheadi*	29092	Female	Melak, Kutai Barat, Kalimantan Timur	MZB	
3	*M. whiteheadi*	29073	Male	Melak, Maruwai, Kalimantan Timur	MZB	
4	*M. whiteheadi*	29093	Male	Melak, Kutai Barat, Kalimantan Timur	MZB	
5	*M. whiteheadi*	29094	Male	Melak, Kutai Barat, Kalimantan Timur	MZB	
6	*M. whiteheadi*	29098	Male	Melak, Kutai Barat, Kalimantan Timur	MZB	
7	*M. whiteheadi*	29099	Male	Melak, Kutai Barat, Kalimantan Timur	MZB	
8	*M. whiteheadi*	29100	Male	Melak, Kutai Barat, Kalimantan Timur	MZB	
9	*M. whiteheadi*	29102	Male	Melak, Kutai Barat, Kalimantan Timur	MZB	
10	*M. whiteheadi*	29103	Female	Melak, Kutai Barat, Kalimantan Timur	MZB	
11	*M. whiteheadi*	29104	Female	Melak, Kutai Barat, Kalimantan Timur	MZB	
12	*M. whiteheadi*	23645	Female	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
13	*M. whiteheadi*	23642	Female	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
14	*M. whiteheadi*	23641	Male	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
15	*M. whiteheadi*	29059	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	
16	*M. whiteheadi*	29061	NR	Intulingau, Maruwai, Kalimantan Timur	MZB	
17	*M. whiteheadi*	29064	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	
18	*M. whiteheadi*	29071	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	
19	*M. whiteheadi*	29081	Female	Melak, Maruwai, Kalimantan Timur	MZB	
20	*M. whiteheadi*	23607	Female	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
21	*M. whiteheadi*	23601	Male	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
22	*M. whiteheadi*	23651	Male	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
23	*M. whiteheadi*	23647	Male	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
24	*M. whiteheadi*	23638	Male	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
25	*M. whiteheadi*	15384	Male	Top of Gunung Bungkuk, Bengkulu	MZB	
26	*M. whiteheadi*	26247	Male	DAS Sebangau, Kalimantan Tengah	MZB	
27	*M. whiteheadi*	22220	Female	DAS Sebangau, Kalimantan Tengah	MZB	
28	*M. whiteheadi*	22212	NR	DAS Sebangau, Kalimantan Tengah	MZB	
29	*M. whiteheadi*	22215	Female	DAS Sebangau, Kalimantan Tengah	MZB	
30	*M. whiteheadi*	26251	Male	DAS Sebangau, Kalimantan Tengah	MZB	
31	*M. whiteheadi*	22217	Female	DAS Sebangau, Kalimantan Tengah	MZB	
32	*M. whiteheadi*	22222	Male	DAS Sebangau, Kalimantan Tengah	MZB	
33	*M. whiteheadi*	26253	Male	DAS Sebangau, Kalimantan Tengah	MZB	
34	*M. whiteheadi*	26234	Male	DAS Sebangau, Kalimantan Tengah	MZB	
35	*M. whiteheadi*	26246	Male	DAS Sebangau, Kalimantan Tengah	MZB	
36	*M. whiteheadi*	22210	Male	DAS Sebangau, Kalimantan Tengah	MZB	
37	*M. whiteheadi*	11647	Female	Labuhan Ratu, Kec.Jabung, Lampung Tengah	MZB	
38	*M. whiteheadi*	13338	Female	Mulyorejo, Way Abung III, Lampung, Sumatra	MZB	
39	*M. whiteheadi*	18347	Male	Pasir mayang, Jambi	MZB	
40	*M. whiteheadi*	18370	Male	Kebun Karet, Kec.Teboulu,Kab.Bungotebo, Jambi	MZB	
41	*M. whiteheadi*	18371	Male	Kebun Karet, Kec.Teboulu,Kab.Bungotebo, Jambi	MZB	
42	*M. whiteheadi*	24986	Female	Tapanuli Selatan, Sumatra Utara	MZB	

NO	SPESIES	Museum No.	SEX	LOCALITY	Depository	Notes
43	*M. whiteheadi*	5661	Male	Muara Dua, Palembang	MZB	
44	*M. whiteheadi*	15383	Male	Top of Gunung Bungkuk, Bengkulu	MZB	
45	*M. whiteheadi*	15569	Female	Camp S Santan, Dirgahayu, Ketaun, Bengkulu	MZB	
46	*M. whiteheadi*	15571	Female	Camp S Santan, Dirgahayu, Ketaun, Bengkulu	MZB	
47	*M. whiteheadi*	20560	Male	Gunung Palung, Ketapang, West Kalimantan	MZB	
48	*M. whiteheadi*	20569	Female	Gunung Palung, Ketapang, West Kalimantan	MZB	
49	*M. whiteheadi*	20580	Female	Bukit Baka, Bukit Raya, Sintang, West kalimantan	MZB	
50	*M. whiteheadi*	20567	Male	Gunung Palung, Ketapang, West Kalimantan	MZB	
51	*M. whiteheadi*	20582	Male	Bukit Baka, Bukit Raya, Sintang, West kalimantan	MZB	
52	*M. whiteheadi*	20559	Male	Gunung Palung, Ketapang, West Kalimantan	MZB	
53	*M. whiteheadi*	20574	Female	Gunung Palung, Ketapang, West Kalimantan	MZB	
54	*M. whiteheadi*	20571	Male	Gunung Palung, Ketapang, West Kalimantan	MZB	
55	*M. whiteheadi*	20562	Female	Gunung Palung, Ketapang, West Kalimantan	MZB	
56	*M. whiteheadi*	20568	Male	Gunung Palung, Ketapang, West Kalimantan	MZB	
57	*M. whiteheadi*	24944	Female	Tapanuli Selatan, Sumatra	MZB	
58	*M. whiteheadi*	24957	Female	Tapanuli Selatan, Sumatra	MZB	
59	*M. whiteheadi*	2071	Female	Deli, Sumatra Utara	MZB	
60	*M. whiteheadi*	24931	Female	Tapanuli Selatan, Sumatra	MZB	
61	*M. whiteheadi*	15385	Female	Top of Gunung Bungkuk, Bengkulu	MZB	
62	*M. whiteheadi*	TK152846	Female	Kubah National Park, Sarawak	UNIMAS	
63	*M. whiteheadi*	819	Male	Unimas Peatswamp	UNIMAS	
64	*M. whiteheadi*	TK156129	NR	Not recorded	UNIMAS	
65	*M. whiteheadi*	1844	Male	Kubah National Park, Sarawak	UNIMAS	
66	*M. whiteheadi*	TK152353	NR	Kubah National Park, Sarawak	UNIMAS	
67	*M. whiteheadi*	326	Male	Unimas Peatswamp	UNIMAS	
68	*M. whiteheadi*	1052	Female	Unimas Peatswamp	UNIMAS	
69	*M. whiteheadi*	TK152362	NR	Kubah National Park, Sarawak	UNIMAS	
70	*M. whiteheadi*	NA014	NR	Not recorded	MZB	
71	*M. whiteheadi*	5679	Male	Pendeng, 550 m, Lampung	MZB	
72	*M. whiteheadi*	5673	Male	Lesten, 700 m, Lampung	MZB	
73	*M. whiteheadi*	5663	Male	Kalianda, Lampung	MZB	
74	*M. whiteheadi*	24893	Male	Kawasan Tesso Nilo, Riau	MZB	
75	*M. whiteheadi*	24963	Male	Tapanuli Selatan, Sumatra Utara	MZB	
76	*M. whiteheadi*	24898	Male	Kawasan Tesso Nilo, Riau	MZB	
77	*M. whiteheadi*	13,031	Female	Bukit Bawang, Kec. Bohorak, Sumatra Utara	MZB	
78	*M. whiteheadi*	15,382	Male	Top of Gunung Bungkuk, Bengkulu	MZB	
79	*M. whiteheadi*	23,648	Male	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
80	*M. whiteheadi*	29,065	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	
81	*M. whiteheadi*	29,067	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	
82	*M. whiteheadi*	29,069	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	
83	*M. whiteheadi*	22,233	Female	DAS Sebangau, Kalimantan Tengah	MZB	
84	*M. whiteheadi*	29,074	Male	Melak, Maruwai, Kalimantan Timur	MZB	
85	*M. whiteheadi*	29,078	Male	Melak, Maruwai, Kalimantan Timur	MZB	
86	*M. whiteheadi*	29,082	Female	Melak, Maruwai, Kalimantan Timur	MZB	

NO	**SPESIES**	**Museum No.**	**SEX**	**LOCALITY**	**Depository**	**Notes**
87	*M. whiteheadi*	29,083	Female	Melak, Maruwai, Kalimantan Timur	MZB	
88	*M. whiteheadi*	29,084	Male	Melak, Maruwai, Kalimantan Timur	MZB	
89	*M. whiteheadi*	TK152862	NR	Kubah National Park, Sarawak	UNIMAS	
90	*M. whiteheadi*	29,076	Female	Melak, Maruwai, Kalimantan Timur	MZB	
91	*M. tajuddinii* sp. nov	29,058	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
92	*M. tajuddinii* sp. nov	29,062	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
93	*M. tajuddinii* sp. nov	29,066	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
94	*M. tajuddinii* sp. nov	29,068	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
95	*M. tajuddinii* sp. nov	29,070	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
96	*M. tajuddinii* sp. nov	29,077	Male	Melak, Maruwai, Kalimantan Timur	MZB	Paratype
97	*M. tajuddinii* sp. nov	29,080	Male	Melak, Maruwai, Kalimantan Timur	MZB	Holotype
98	*M. tajuddinii* sp. nov	18,482	NR	Gn.Kerinci, Sungai Penuh, Jambi	MZB	
99	*M. tajuddinii* sp. nov	29,086	Female	Melak, Maruwai, Kalimantan Timur	MZB	Paratype
100	*M. tajuddinii* sp. nov	28,961	Male	Hutan gambut awang, Kec.Sungai Rawa, Inderapura, Riau	MZB	Paratype
101	*M. tajuddinii* sp. nov	28,962	Female	Hutan gambut awang, Kec.Sungai Rawa, Inderapura, Riau	MZB	Paratype
102	*M. tajuddinii* sp. nov	28,960	Female	Hutan gambut awang, Kec.Sungai Rawa, Inderapura, Riau	MZB	Paratype
103	*M. tajuddinii* sp. nov	28,963	Male	Hutan gambut awang, Kec.Sungai Rawa, Inderapura, Riau	MZB	Paratype
104	*M. tajuddinii* sp. nov	28,967	Male	BKM KM 70 Pangkalan Kerinci,Kab.Palalawan, Riau	MZB	Paratype
105	*M. tajuddinii* sp. nov	28,968	Male	BKM KM 70 Pangkalan Kerinci,Kab.Palalawan, Riau	MZB	Paratype
106	*M. tajuddinii* sp. nov	TK153703	Male	Fraser's Hill, Malay Peninsula	UNIMAS	Paratype
107	*M. tajuddinii* sp. nov	TK153717	Male	Fraser's Hill, Malay Peninsula	UNIMAS	Paratype
108	*M. tajuddinii* sp. nov	TK152349	NR	Kubah National Park, Sarawak	UNIMAS	Paratype
109	*M. tajuddinii* sp. nov	TK152861	NR	Kubah National Park, Sarawak	UNIMAS	Paratype
110	*M. tajuddinii* sp. nov	471	Male	P. Balambangan, Sabah	UNIMAS	
111	*M. tajuddinii* sp. nov	1618	Female	Jambusan Cave, Bau, Sarawak	UNIMAS	
112	*M. ochraceiventer*	23,606	Male	Desa Pa'Raye, Long Bawon, Nunukan, Kayan Mentarang	MZB	
113	*M. ochraceiventer*	23,971	Male	Lampunut, Maruwai, Kalimantan Timur	MZB	
114	*M. ochraceiventer*	23,970	Female	Lampunut, Maruwai, Kalimantan Timur	MZB	
115	*M. baeodon*	TK152835	Male	Kubah National Park, Sarawak	UNIMAS	
116	*M. baeodon*	3312	Male	Bettotan, Sandakan, Sabah	Raffles Museum	
117	*M. baeodon*	3533	Male	Raeyoh, Sabah	Raffles Museum	
118	*M. baeodon*	3543	Female	Raeyoh, Sabah	Raffles Museum	
119	*M. baeodon*	3571	Female	Raeyoh, Sabah	Raffles Museum	
120	*M. baeodon*	3224	Female	Bettotan, Sandakan, Sabah	Raffles Museum	

Appendix 5. List of specimens used in Chapter IV ~ *Maxomys tompotika* sp. nov

Maxomys hellwaldii

MVZ225744, MZB26964, MZB26971, MZB26982, MZB26988, MZB26991, MZB27163, FMNH218893, FMNH218894, FMNH219016.

Maxomys tompotika sp. nov

FMNH213370, FMNH213371, FMNH213451, FMNH213454, FMNH213452, FMNH213453

Maxomys dollmani

MVZ225723, AMNH101087, AMNH101094, AMNH224863

Maxomys musschenbroekii

MVZ225737, MVZ225764, MVZ225758, MVZ225757, MVZ225752, MVZ225740, MVZ225738

Maxomys wattsi

AMNH265079, AMNH265081

Appendix 6. List of additional specimens of *Maxomys* from museums collection.

M. moi

ROM111367, ROM111328, ROM111295, ROM111294, ROM111290, ROM111289, ROM111318, NMNH357774, NMNH358025, NMNH358026, NMNH358027, NMNH321354, NMNH321355, NMNH321356, NMNH321357, NMNH321358, NMNH321359

M. inas

NMNH171980, NMNH283549, NMNH283553, NMNH311444, NMNH311443, NMNH307601, NMNH307600, NMNH307599, NMNH489043, NMNH489044, NMNH489276

M. inflatus

AMNH106380, AMNH106387, AMNH106390, AMNH106388, AMNH106389

FIGURES AND TABLES

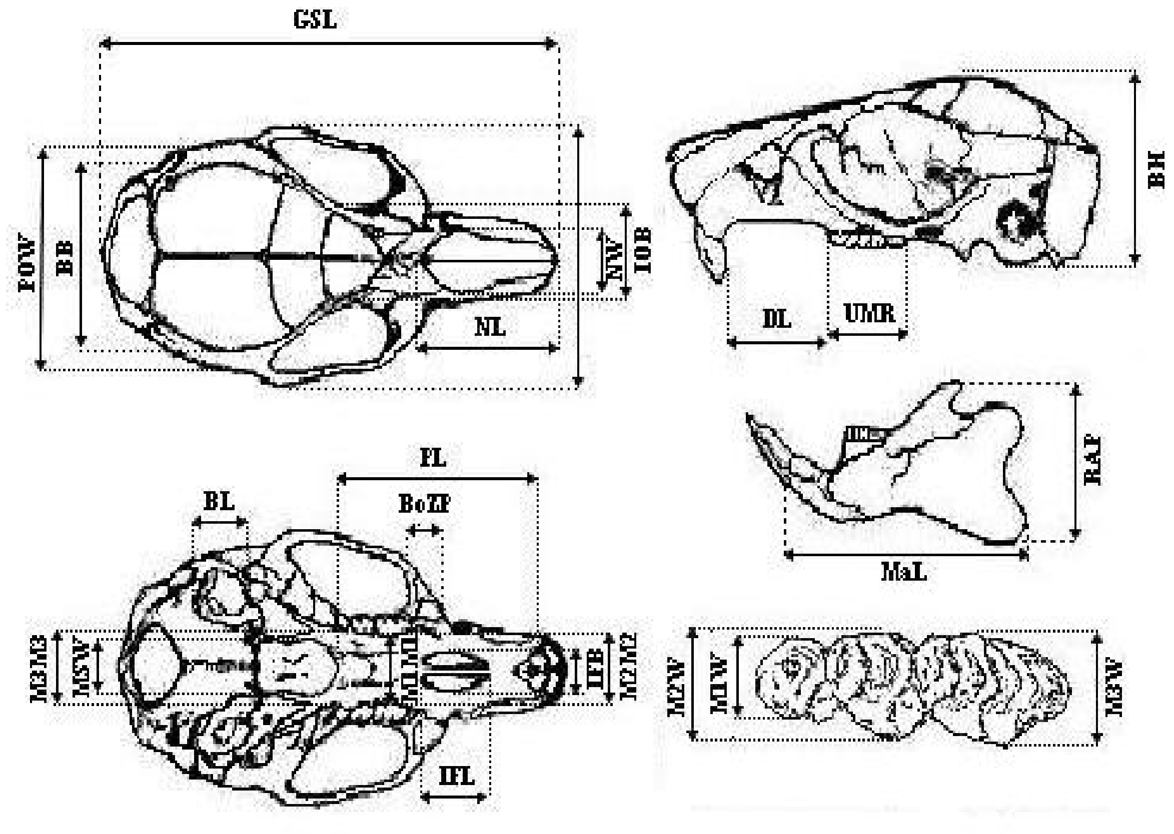

Fig. 1. Views of cranium and molars of *Maxomys*, showing limits of cranial and dental measurements. See text for abbreviations and additional information.

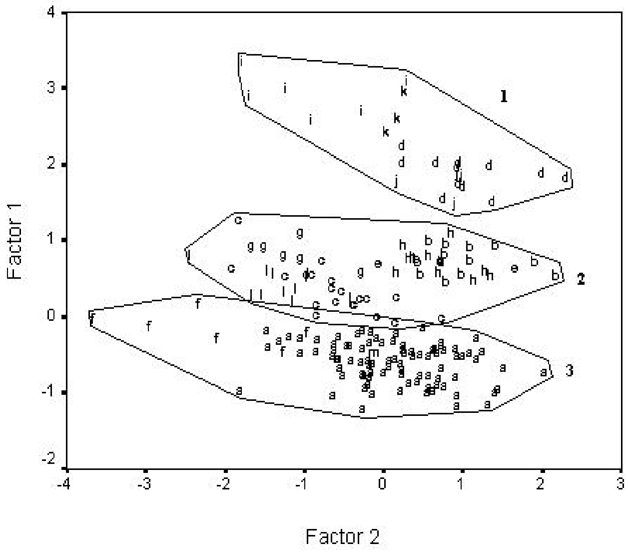

Fig. 2. Plot of scores on factor axes 2 and 1 from principal component analysis (PCA) of 24 skull measurements of *Maxomys.* Groups classification: a, *M. whiteheadi* (S); b, *M. surifer;* c, *M. whiteheadi* (L); d, *M. rajah;* e, *M. ochraceiventer;* f, *M. baeodon;* g, *M. alticola;* h, *M. musschenbroekii;* i, *M. hellwaldii;* j, *M. wattsi;* k, *M. pagensis;* l, *M. bartelsii;* m, *M. inas;* (1), large body size; (2), medium body size; and (3), small body size.

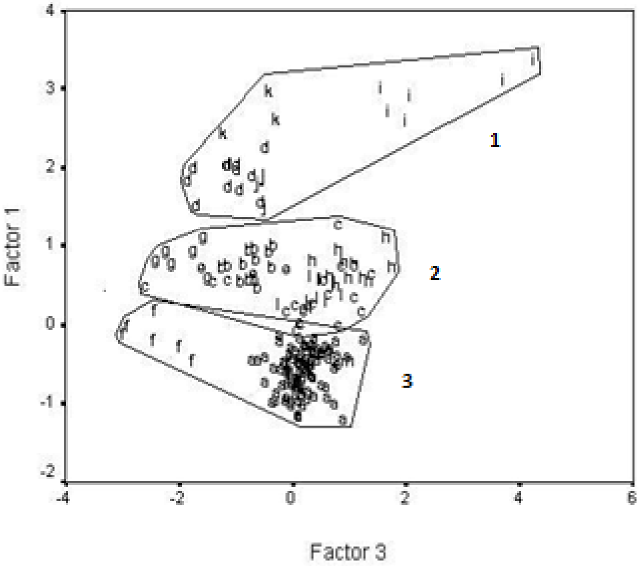

Fig. 3. Plot of scores on factor axes 3 and 1 from principal component analysis (PCA) of 24 skull measurements of *Maxomys.* Groups classification: a, *M. whiteheadi* (S); b, *M. surifer;* c, *M. whiteheadi* (L); d, *M. rajah;* e, *M. ochraceiventer;* f, *M. baeodon;* g, *M. alticola;* h, *M. musschenbroekii;* i, *M. hellwaldii;* j, *M. wattsi;* k, *M. pagensis;* l, *M. bartelsii;* m, *M. inas;* (1), large body size; (2), medium body size; and (3), small body size.

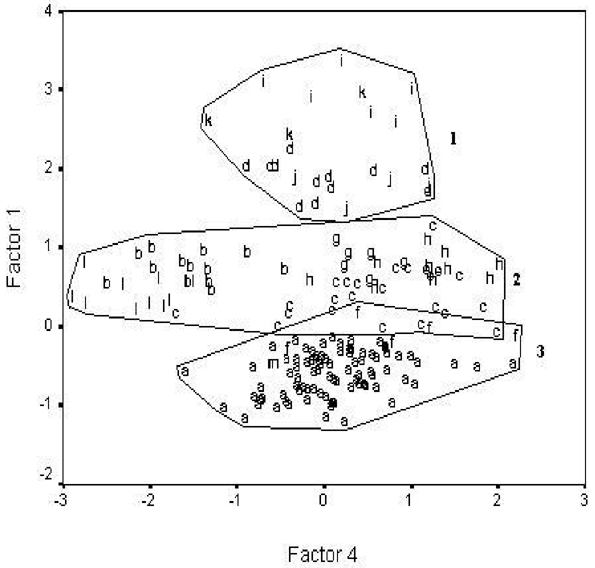

Fig. 4. Plot of scores on factor axes 4 and 1 from principal component analysis (PCA) of 24 skull measurements of *Maxomys.* Groups classification: a, *M. whiteheadi* (S); b, *M. surifer;* c, *M. whiteheadi* (L); d, *M. rajah;* e, *M. ochraceiventer;* f, *M. baeodon;* g, *M. alticola;* h, *M. musschenbroekii;* i, *M. hellwaldii;* j, *M. wattsi;* k, *M. pagensis;* l, *M. bartelsii;* m, *M. inas;* (1), large body size; (2), medium body size; and (3), small body size.

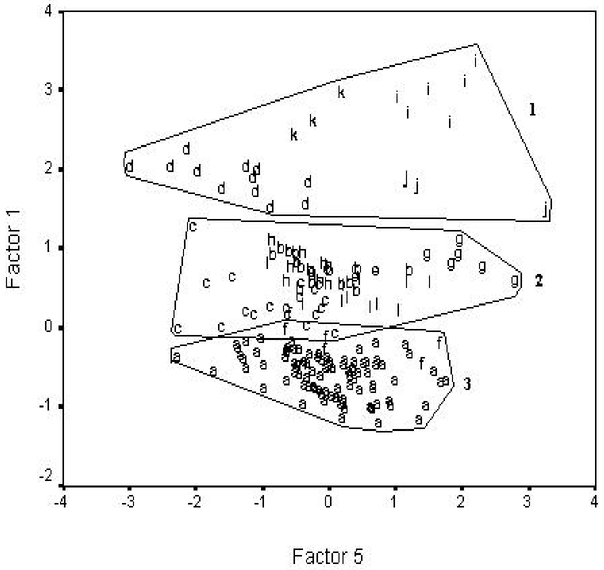

Fig. 5. Plot of scores on factor axes 5 and 1 from principal component analysis (PCA) of 24 skull measurements of *Maxomys.* Groups classification: a, *M. whiteheadi* (S); b, *M. surifer;* c, *M. whiteheadi* (L); d, *M. rajah;* e, *M. ochraceiventer;* f, *M. baeodon;* g, *M. alticola;* h, *M. musschenbroekii;* i, *M. hellwaldii;* j, *M. wattsi;* k, *M. pagensis;* l, *M. bartelsii;* m, *M. inas;* (1), large body size; (2), medium body size; and (3), small body size.

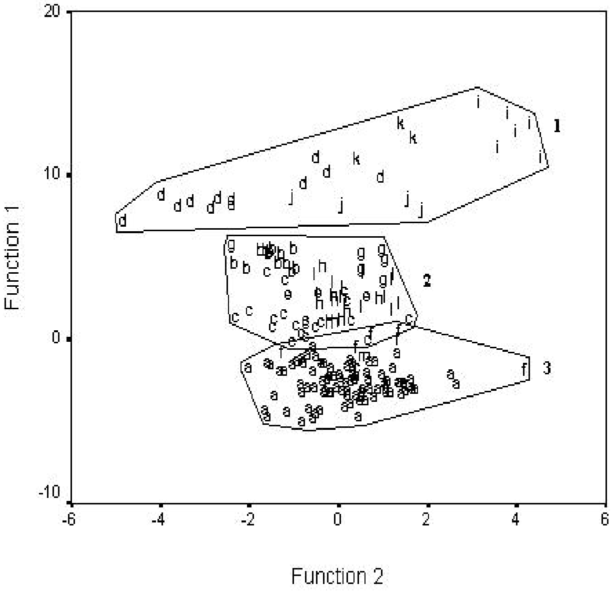

Fig. 6. Plot of scores on function axes 2 and 1 from discriminant function of five dominant variables skull measurements of *Maxomys.* Groups classification: a, *M. whiteheadi* (S); b, *M. surifer;* c, *M. whiteheadi* (L); d, *M. rajah;* e, *M. ochraceiventer;* f, *M. baeodon;* g, *M. alticola;* h, *M. musschenbroekii;* i, *M. hellwaldii;* j, *M. wattsi;* k, *M. pagensis;* l, *M. bartelsii;* m, *M. inas;* (1), large body size; (2), medium body size; and (3), small body size.

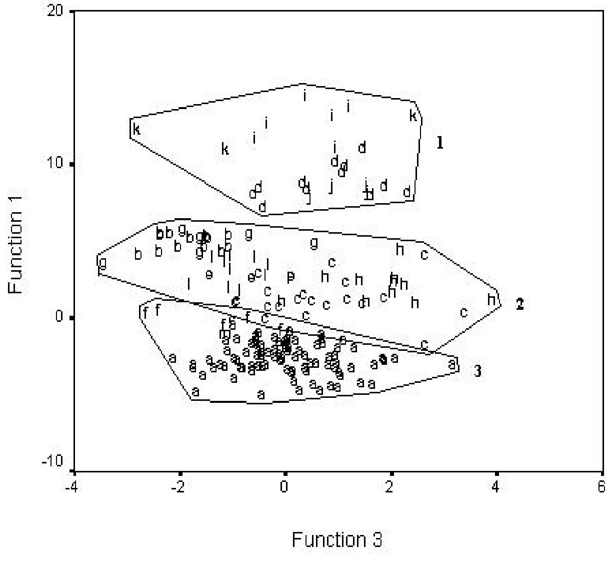

Fig. 7. Plot of scores on function axes 3 and 1 from discriminant function of five dominant variables skull measurements of *Maxomys.* Groups classification: a, *M. whiteheadi* (S); b, *M. surifer;* c, *M. whiteheadi* (L); d, *M. rajah;* e, *M. ochraceiventer;* f, *M. baeodon;* g, *M. alticola;* h, *M. musschenbroekii;* i, *M. hellwaldii;* j, *M. wattsi;* k, *M. pagensis;* l, *M. bartelsii;* m, *M. inas;* (1), large body size; (2), medium body size; and (3), small body size.

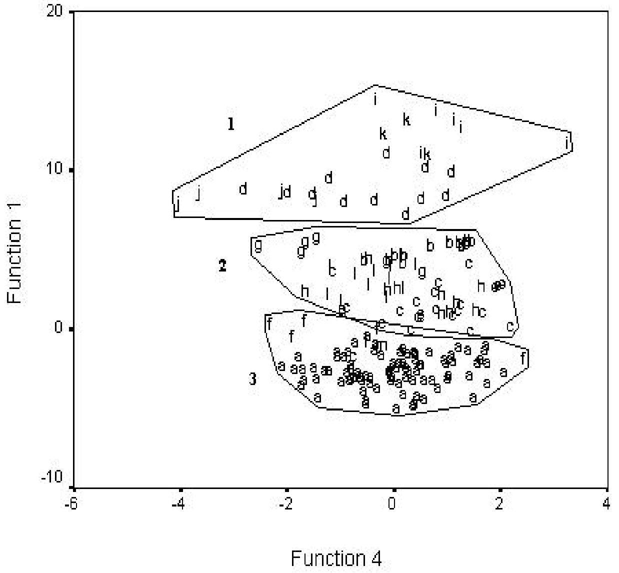

Fig. 8. Plot of scores on function axes 4 and 1 from discriminant function of five dominant variables skull measurements of *Maxomys.* Groups classification: a, *M. whiteheadi* (S); b, *M. surifer;* c, *M. whiteheadi* (L); d, *M. rajah;* e, *M. ochraceiventer;* f, *M. baeodon;* g, *M. alticola;* h, *M. musschenbroekii;* i, *M. hellwaldii;* j, *M. wattsi;* k, *M. pagensis;* l, *M. bartelsii;* m, *M. inas;* (1), large body size; (2), medium body size; and (3), small body size.

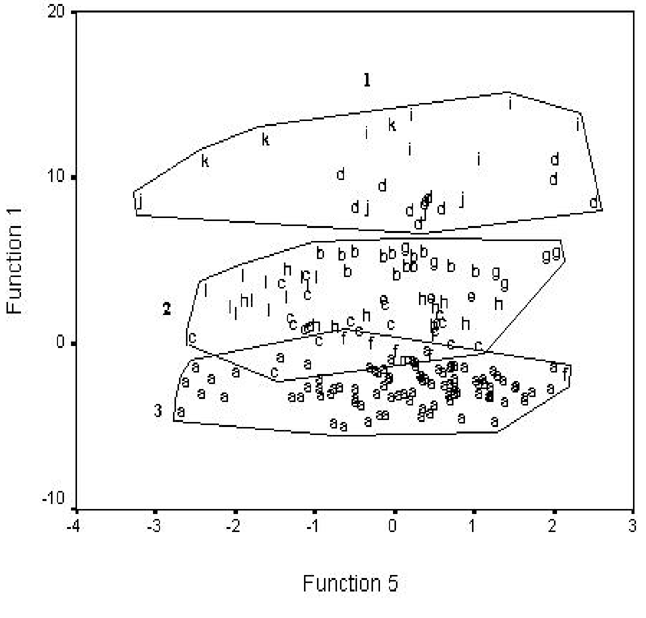

Fig. 9. Plot of scores on function axes 5 and 1 from discriminant function of five dominant variables skull measurements of *Maxomys.* Groups classification: a, *M. whiteheadi* (S); b, *M. surifer;* c, *M. whiteheadi* (L); d, *M. rajah;* e, *M. ochraceiventer;* f, *M. baeodon;* g, *M. alticola;* h, *M. musschenbroekii;* i, *M. hellwaldii;* j, *M. wattsi;* k, *M. pagensis;* l, *M. bartelsii;* m, *M. inas;* (1), large body size; (2), medium body size; and (3), small body size.

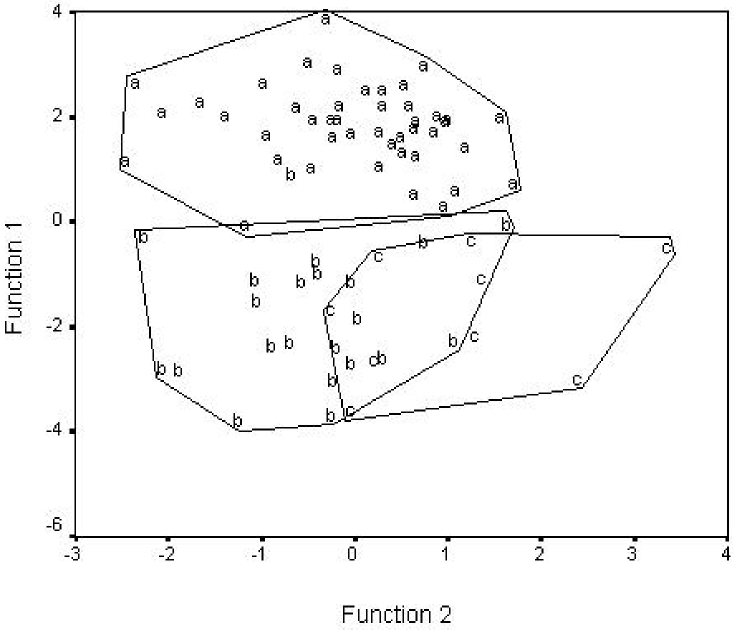

Fig. 10. Plot of scores on function axes 2 and 1 from discriminant function of seven dominant variables skull measurements from *M. whiteheadi* (S). Group classifications: a, Southern Borneo; b, Sumatra; and c, Northern Borneo.

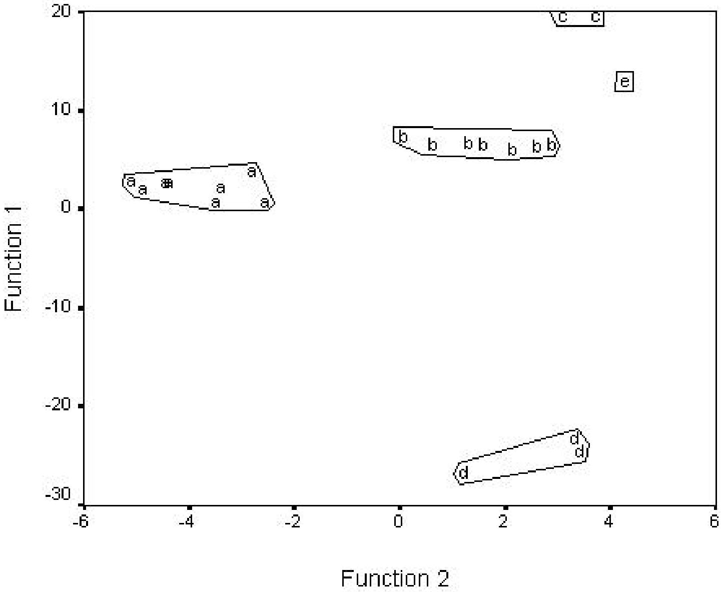

Fig. 11. Plot of scores on function axes 2 and 1 from discriminant function of eight dominant variables skull measurements from *M. whiteheadi* (L). Group classifications: a, Southern Borneo; b, Sumatra Island; c, Malaya Peninsular; d, Northwestern Borneo; and e, Northeastern Borneo.

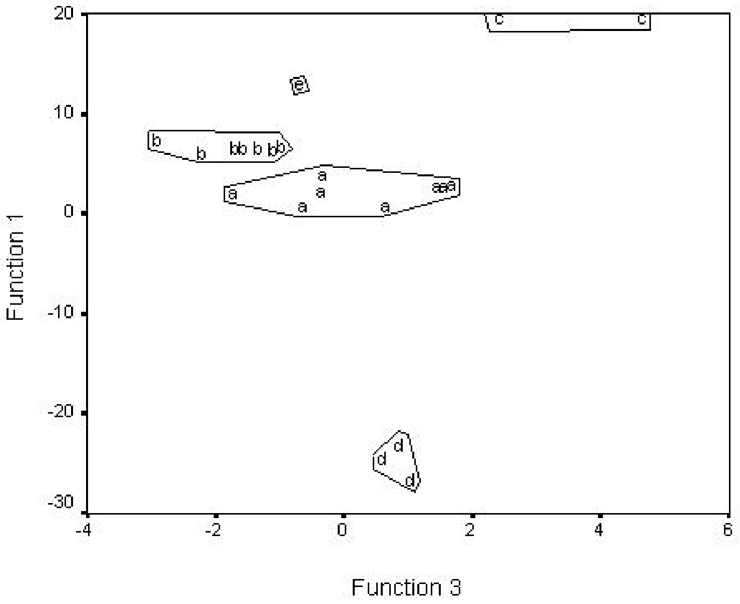

Fig. 12. Plot of scores on function axes 3 and 1 from discriminant function of eight dominant variables skull measurements from *M. whiteheadi* (L). Group classifications: a, Southern Borneo; b, Sumatra Island; c, Malaya Peninsular; d, Northwestern Borneo; and e, Northeastern Borneo.

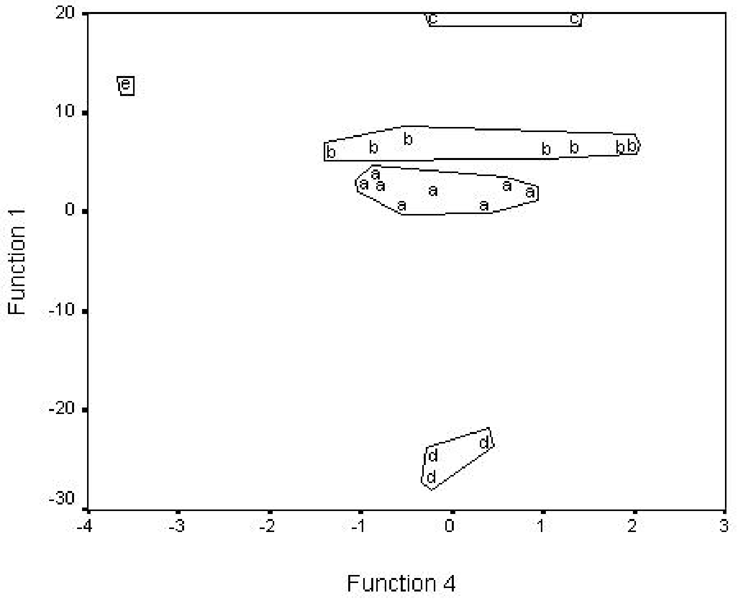

Fig. 13. Plot of scores on function axes 4 and 1 from discriminant function of eight dominant variables skull measurements from *M. whiteheadi* (L). Group classifications: a, Southern Borneo; b, Sumatra Island; c, Malaya Peninsular; d, Northwestern Borneo; and e, Northeastern Borneo.

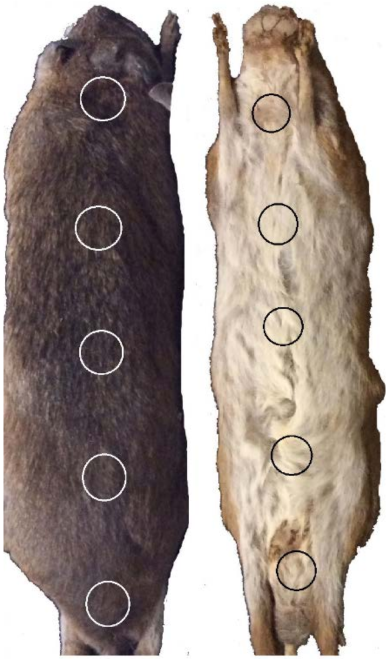

Fig 14. Photograph of a specimen of *Maxomys* sp. showing the five points over the dorsal and ventral body region, namely the neck, upper back, middle back, lower back, and rump, where we measured the pelage color.

Fig. 15. Representative variation in coat color (*a. dorsal pelage and b. ventral pelage*) among species of *Maxomys* spp.

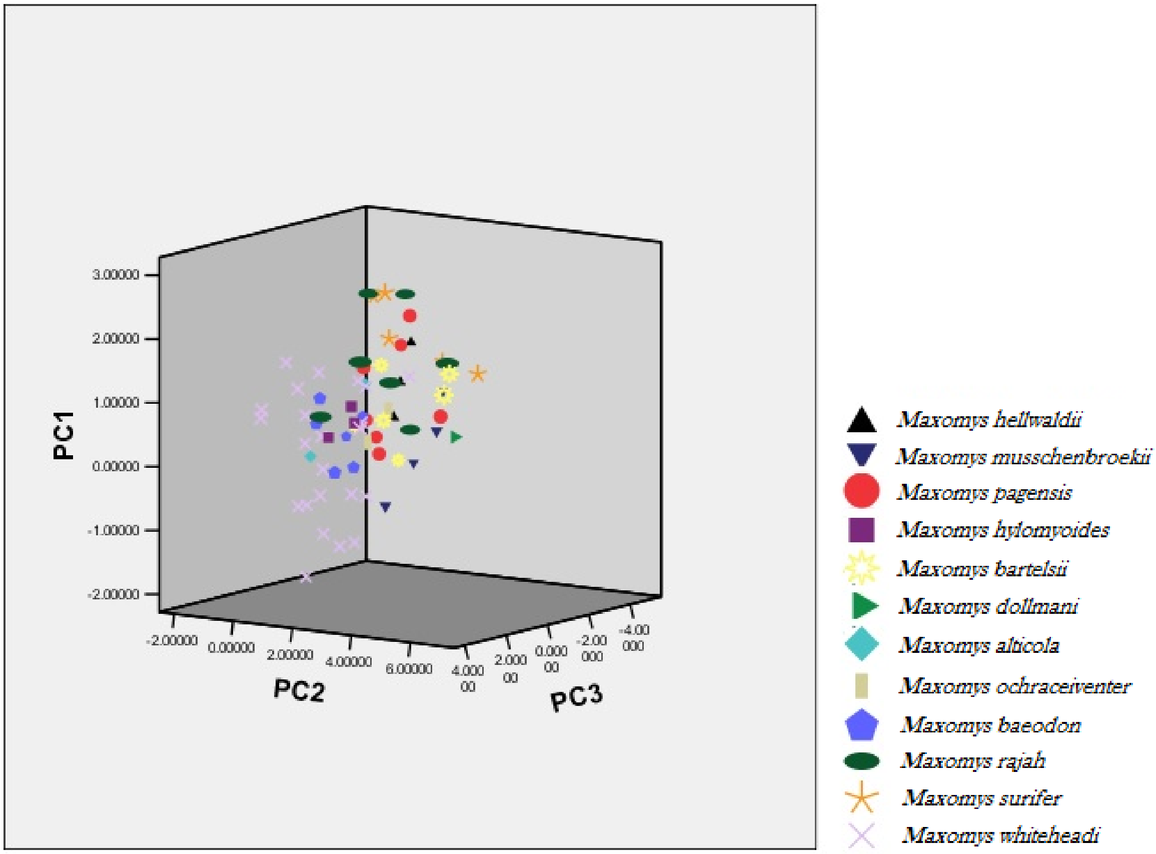

Fig. 16. Three dimensional scatter plot from three components (PC1, PC2, and PC3) of PCA extracted from dorsal fur color variations among species of *Maxomys* spp.

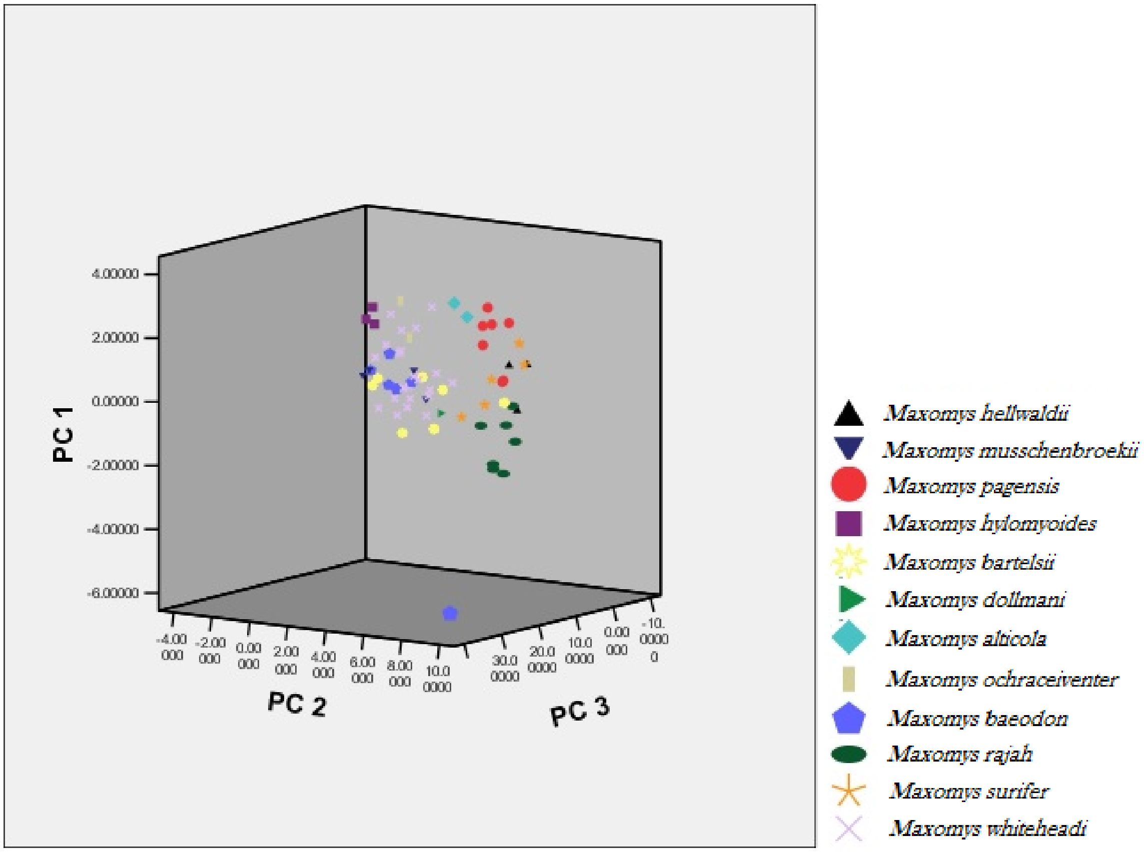

Fig. 17. Three dimensional scatter plot from three components (PC1, PC2, and PC3) of PCA analysis that extracted from ventral fur color variations among species of *Maxomys* spp.

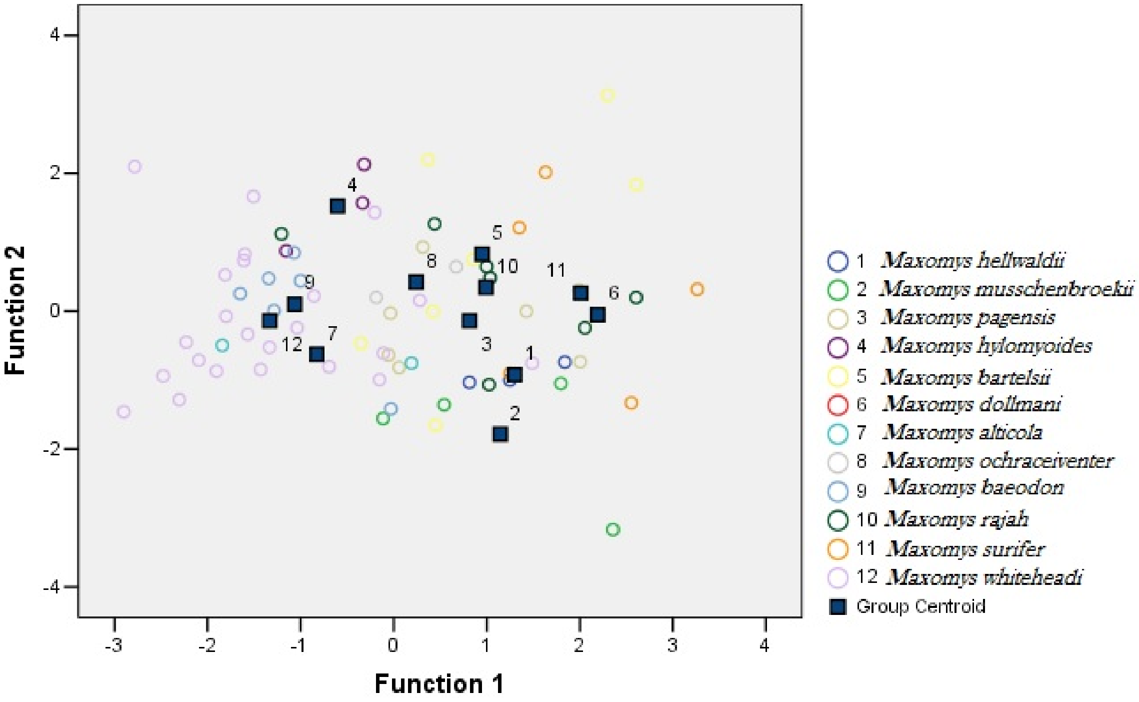

Fig. 18. Plot of group centroid from DFA analysis (Function 1 and 2) among species of *Maxomys* based on dorsal coloration.

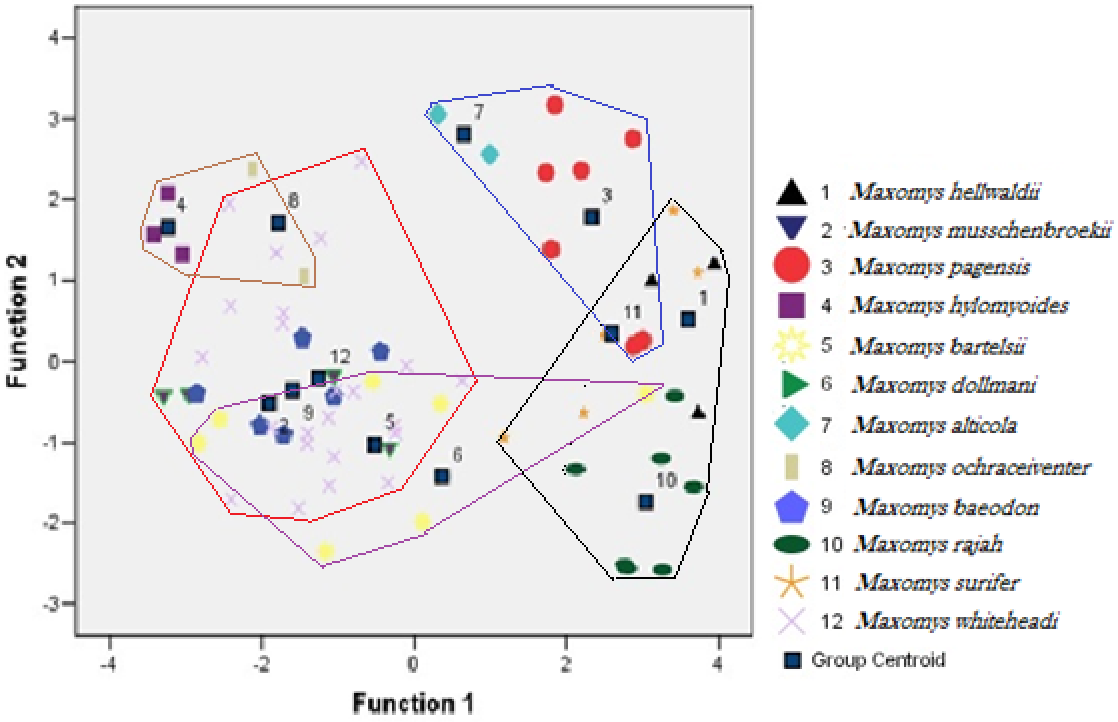

Fig. 19. Plot of group centroid from DFA analysis (Function 1 and 2) among species of *Maxomys* based on ventral coloration.

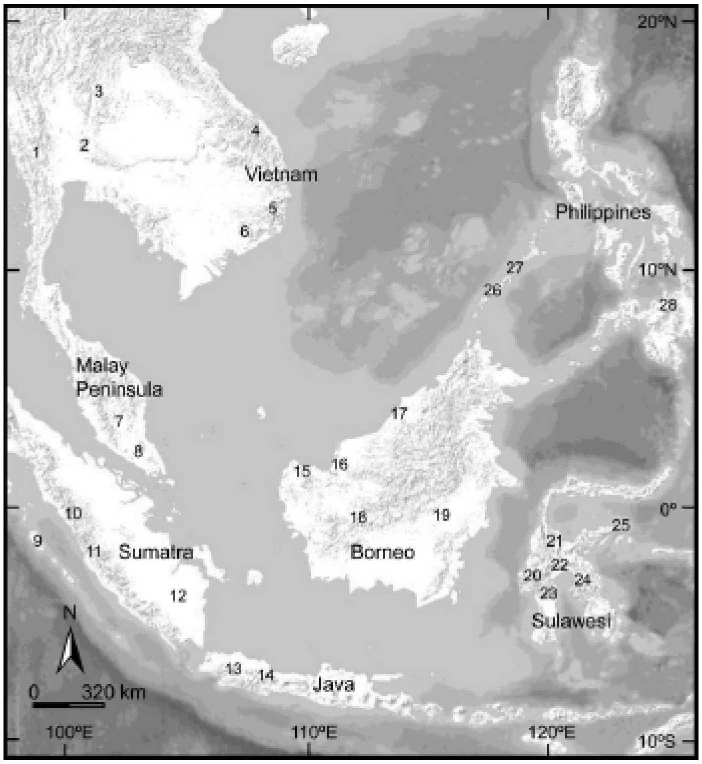

Fig. 20. Map of Southeast Asia, showing localities of *Maxomys* specimens used in this study. Locality numbers are referenced in the phylogeny of Figures 21 and 22.

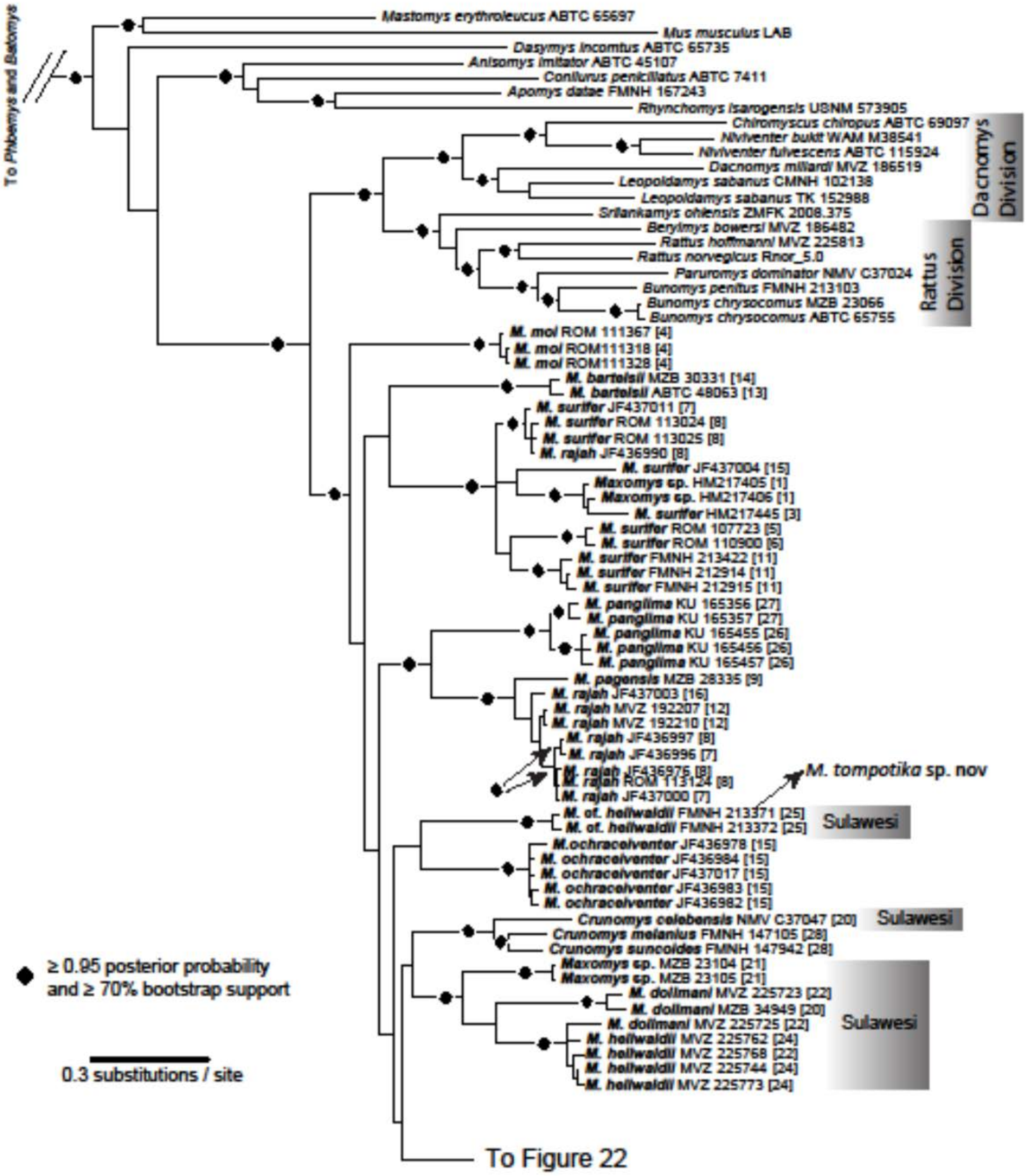

Fig. 21. Bayesian estimate of phylogeny of Southeast Asian *Maxomys* derived from analysis of concatenated DNA sequences. Nodes that received strong support in both Bayesian and likelihood analyses are marked with a black diamond. Terminals are labeled with species names and either a museum voucher number or a GenBank accession number. The bracketed number on ingroup terminals refers to localities in Fig. 20.

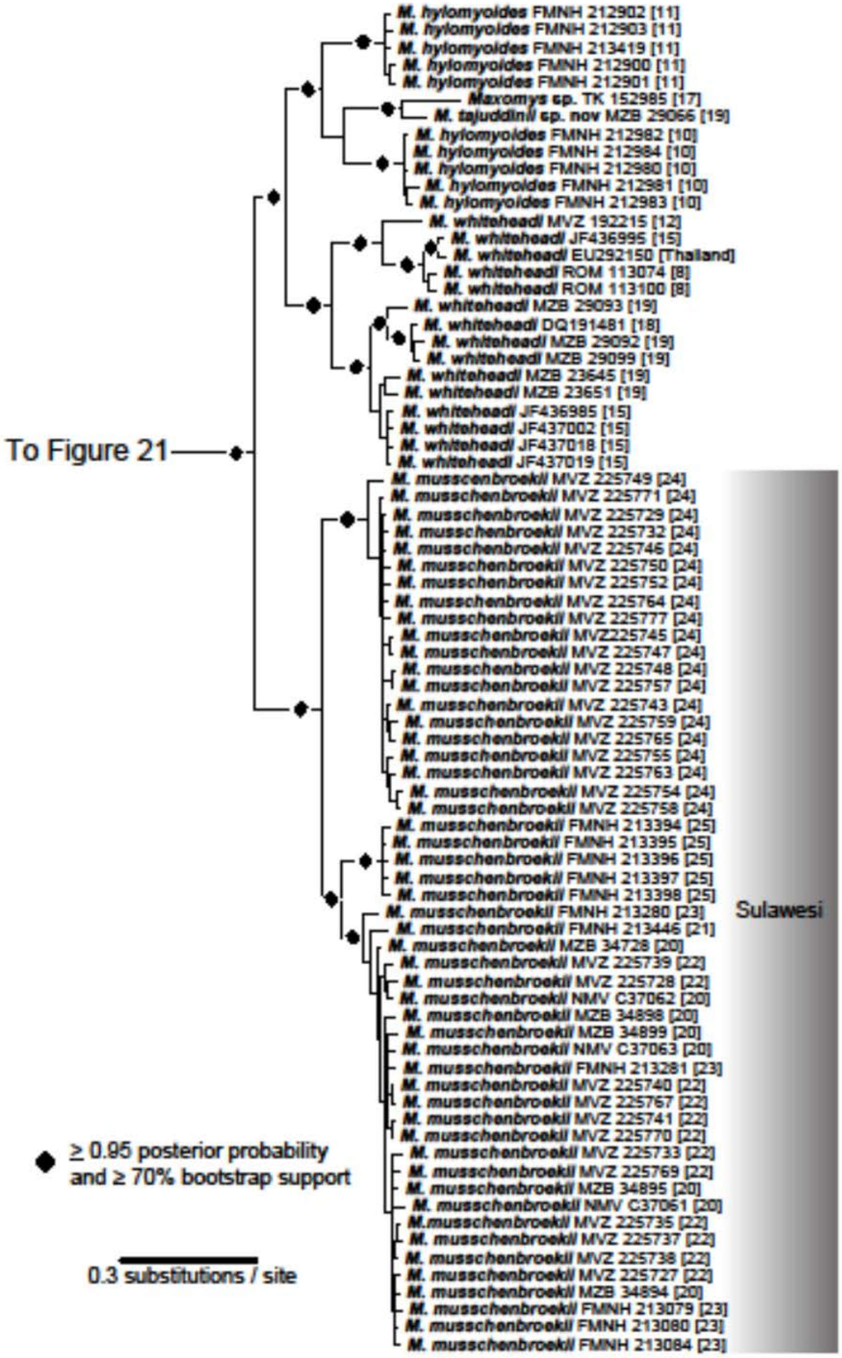

Fig. 22. Bayesian estimate of phylogeny of Southeast Asian *Maxomys* derived from analysis of concatenated DNA sequences. Nodes that received strong support in both Bayesian and likelihood analyses are marked with a black triangle. Terminals are labeled with species names and either a museum voucher number or a GenBank accession number. The bracketed number on ingroup terminals refers to localities in Fig. 20.

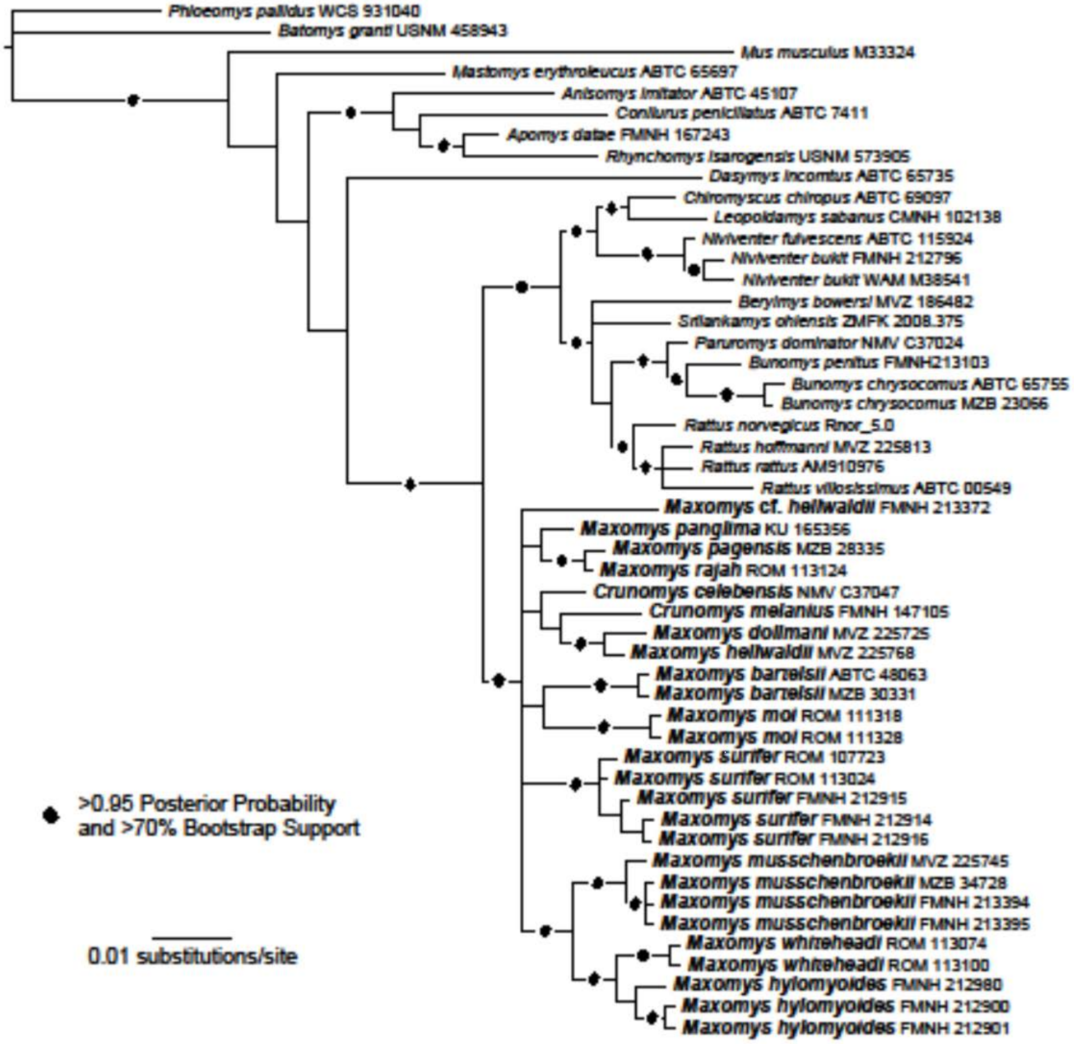

Fig. 23. Bayesian estimate of phylogeny of Southeast Asian *Maxomys* derived from analysis of Growth Hormone Receptor sequences. Nodes that received strong support in both Bayesian and likelihood analyses are marked with a black triangle. Terminals are labeled with species names and either a museum voucher number or a GenBank accession number.

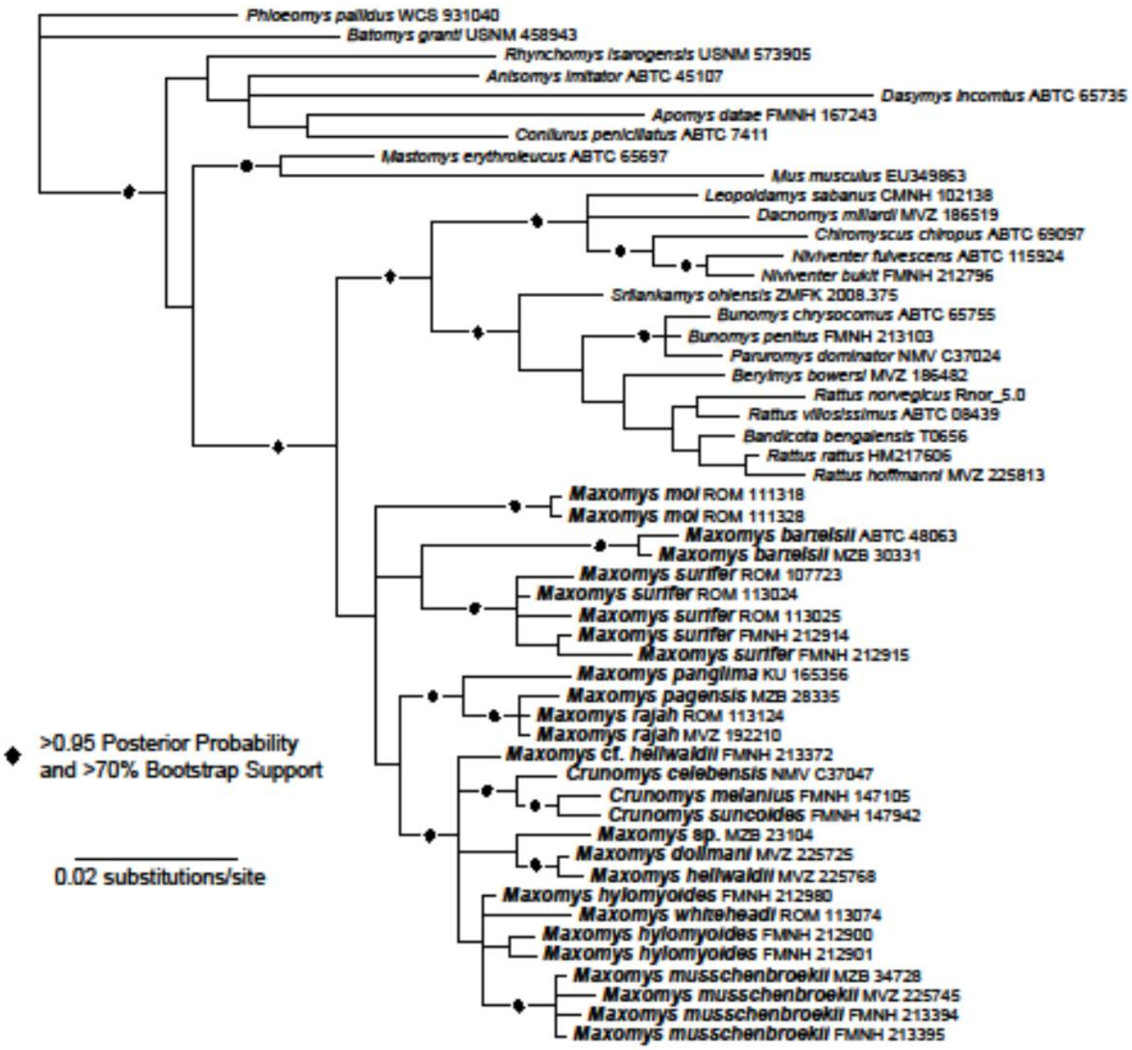

Fig. 24. Bayesian estimate of phylogeny of Southeast Asian *Maxomys* derived from analysis of Interphotoreceptor Retinoid Binding Protein sequences. Nodes that received strong support in both Bayesian and likelihood analyses are marked with a black triangle. Terminals are labeled with species names and either a museum voucher number or a GenBank accession number.

Fig. 25. Selected sites sampling in this study. 1. Kinabalu Park, Sabah; 2. Fraser's Hill forest reserve; 3. LEWS, Sarawak; 4. Niah National Park, Sarawak; 5. Melak district, East Kalimantan (adapted from Google Earth.com)

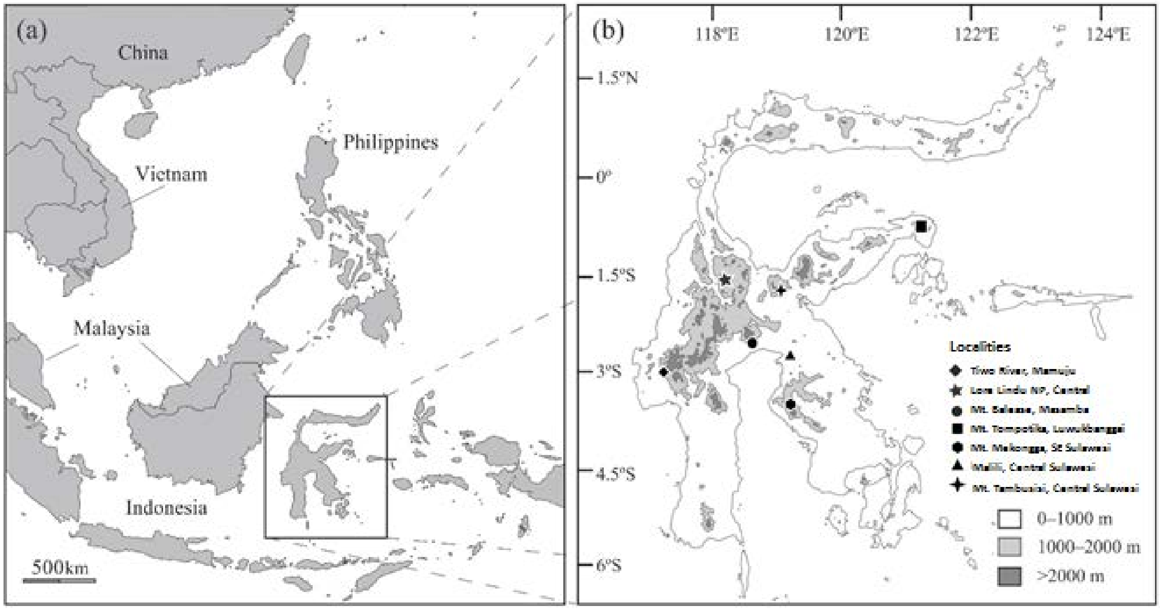

Fig. 26.. Maps of (a) Southeast Asia, showing the position of Sulawesi Island and (b) Sulawesi, showing the localities of *Maxomys* specimens used in this study.

Fig. 27. Sharp demarcation between dorsal and ventral coat of *M. tajuddinii* sp. nov. showed by arrows in the flanks; A. Live sample (TK153717) B. Dead and dried specimen (Holotype)

Fig. 28. Views (x 1) of cranium and dentary of the holotype *M. tajuddinii* sp. nov. (MZB29080) from East Kalimantan

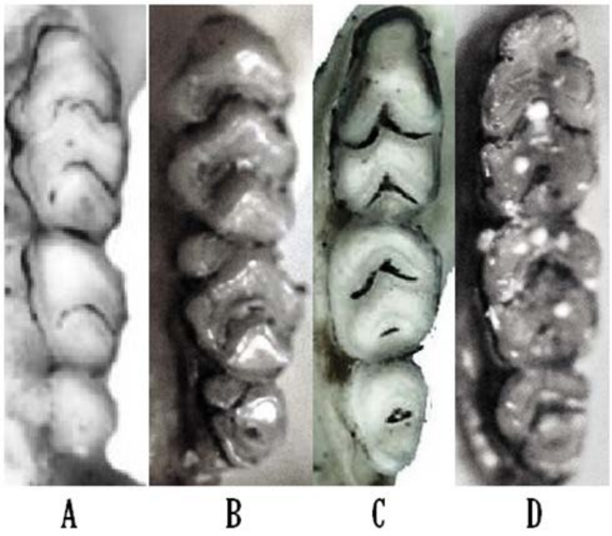

Fig. 29. Occlusal views (approximately x 10) of adult upper and lower molars in species of *M. tajuddinii* sp. nov. From left to right; A. Uppermolars of MZB29080 (Holotype); B. Uppermolars of TK153717 (Malay peninsular); C. Lower molars of MZB29080 (Holotype); Lowermolars of TK153717 (Malay peninsular).

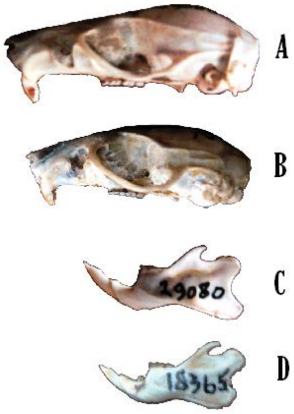

Fig. 30. Lateral Views (x 1) of head skulls appears differences between *M. tajuddinii* sp. nov. (A and C; Holotype; MZB29080) and *M. whiteheadi* Thomas, 1894 (B and D; MZB18365)

Fig. 31. Dorsal views (x 2) comparing adult crania of species *Maxomys*. From left to right; A. *M. tajuddinii* sp. nov (TK153703); B. *M. tajuddinii* sp. nov (MZB29080, Holotype); C. *M. whiteheadi* Thomas, 1894 (MZB14749); D. *M. whiteheadi* Thomas, 1894 (MZB18365)

Fig. 32. Ventral views (x 2) comparing adult crania of species *Maxomys*. From left to right; A. *M. tajuddinii* sp. nov (TK153703); B. *M. tajuddinii* sp. nov (MZB29080, Holotype); C. *M. whiteheadi* Thomas, 1894 (MZB14749); D. *M. whiteheadi* Thomas, 1894 (MZB18365)

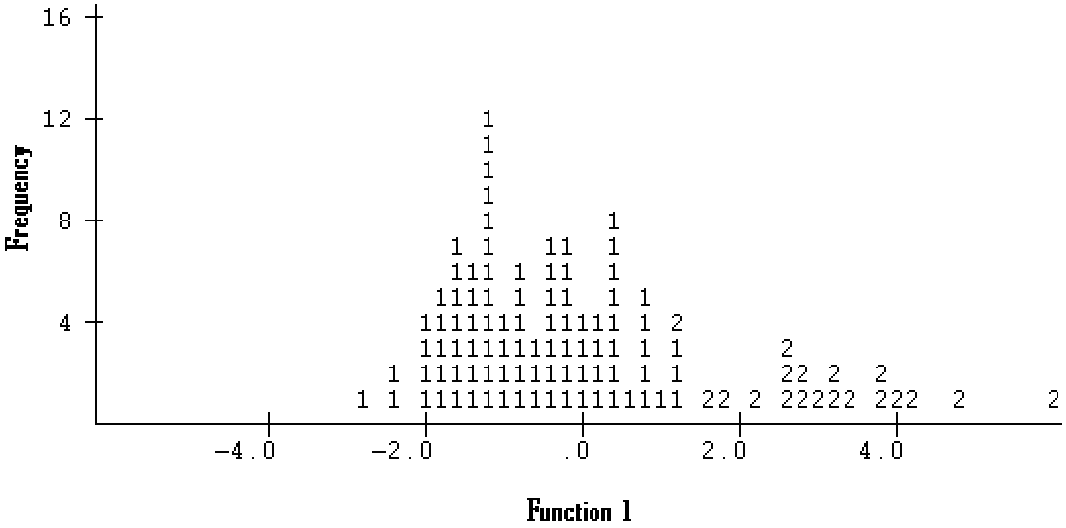

Fig. 33. Plot of a number of function 1 and frequency of variables skull measurements from (1) *M.whiteheadi* Thomas, 1894 and (2) *M. tajuddinii* sp. nov.

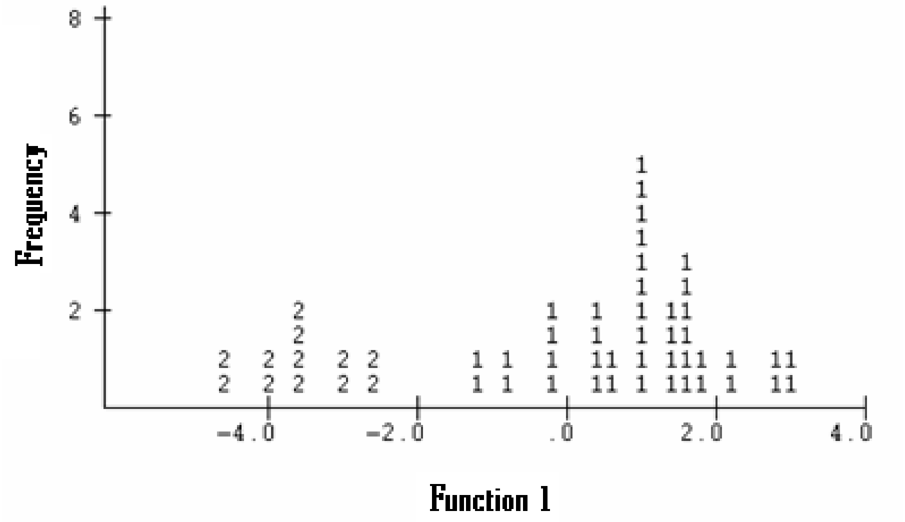

Fig. 34. . Plot of a number of function 1 and frequency of variables skull measurements from (1) *M. tajuddinii* sp. nov. and (2) *M. baeodon*

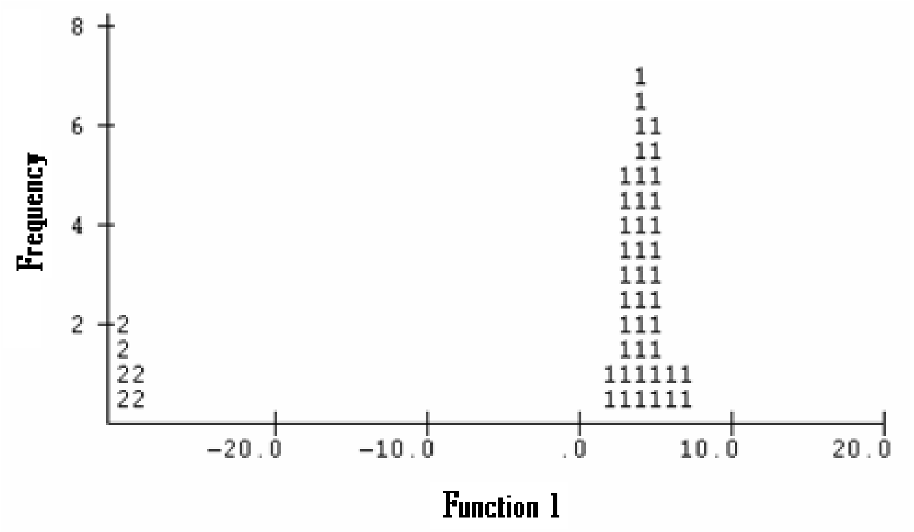

Fig. 35. Plot of a number of function 1 and frequency of variables skull measurements from (1) *M. tajuddinii* sp. nov. and (2) *M. ochraceiventer* Thomas, 1894

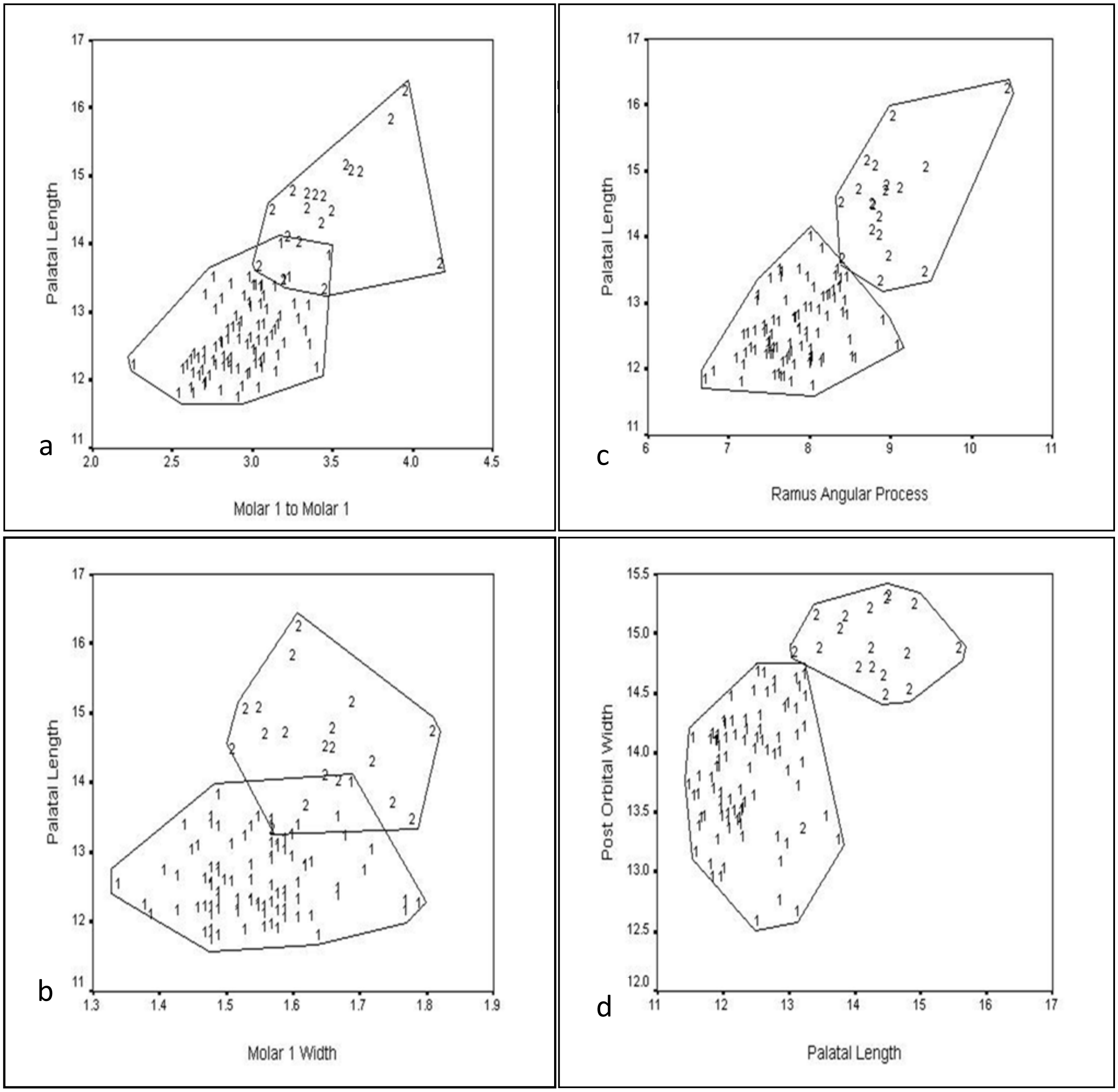

Fig. 36. Bivariate plots of : a. palatal length against molar 1 to molar 1; b. palatal length against molar 1 width; c. palatal length against ramus angular process and d. palatal length against post orbital width. (1) *M. whiteheadi*; (2). *M. tajuddinii* sp. nov.

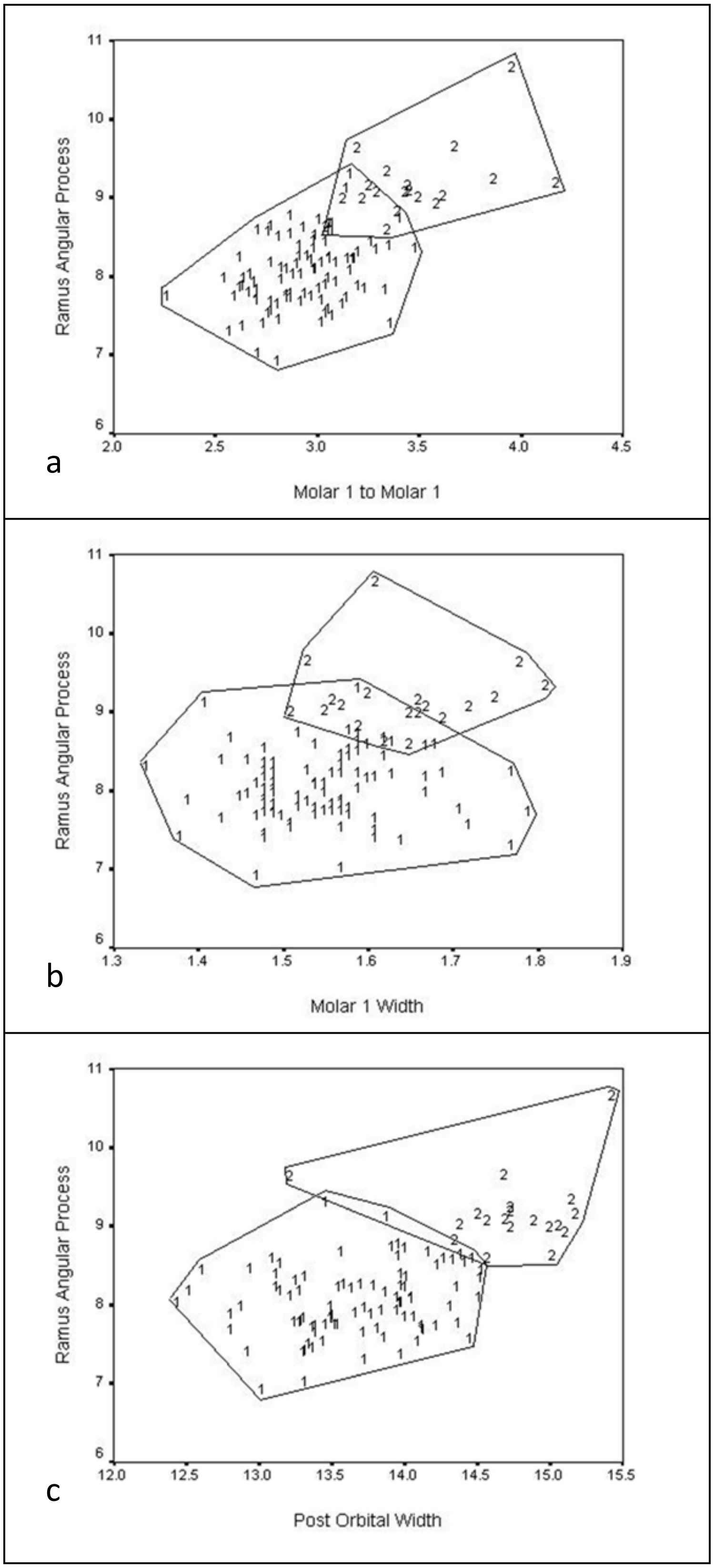

Fig. 37. Bivariate plots of : a. ramus angular process against molar 1 to molar 1; b. ramus angular process against molar 1 width and c. ramus angular process against post orbital width. (1) *M. whiteheadi*; (2). *M. tajuddinii* sp. nov.

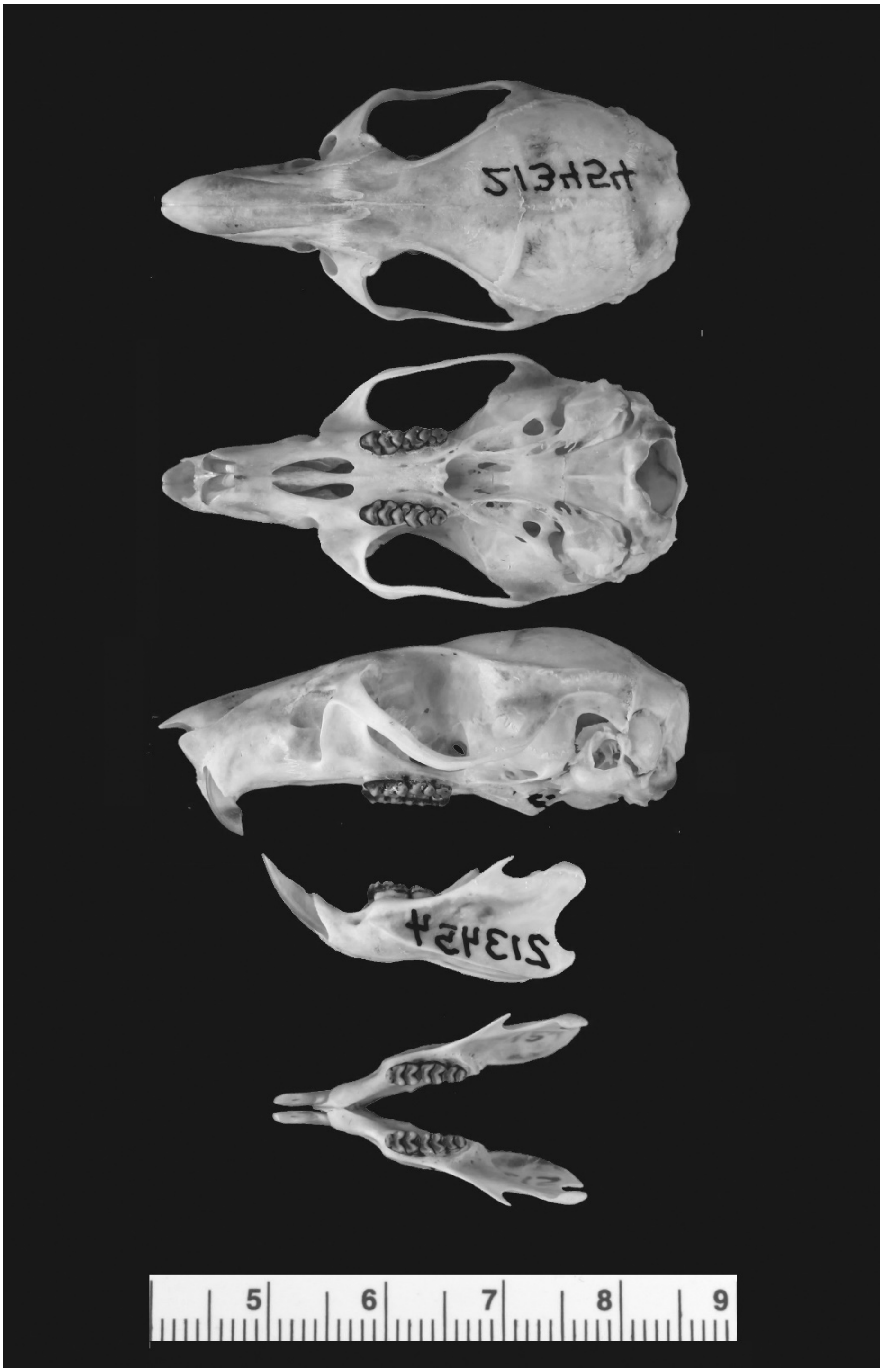

Fig. 38. Views (x 1) of cranium and dentary of the holotype *M. tompotika* sp. nov. (MZB36997/FMNH213454) from Mt. Tompotika, Sulawesi.

Fig. 39. Dorsal views comparing adult cranial of species *Maxomys*. From left to right; A. *M. hellwaldii* (JAE4586); B. *M. dollmani* (FMNH218893); C. *M. tompotika* sp. nov (MZB MZB36997/FMNH213454, Holotype); D. *M. wattsi* (MZB12164/AMNH265079); and E. *M. musschenbroekii* (JAE4650).

Fig. 40. Ventral views comparing adult cranial of species Maxomys. From left to right; A. *M. hellwaldii* (JAE4586); B. *M. dollmani* (FMNH218893); C. *M. tompotika* sp. nov (MZB MZB36997/FMNH213454, Holotype); D. M. wattsi (MZB12164 / AMNH265079); and E. *M. musschenbroekii* (JAE4650).

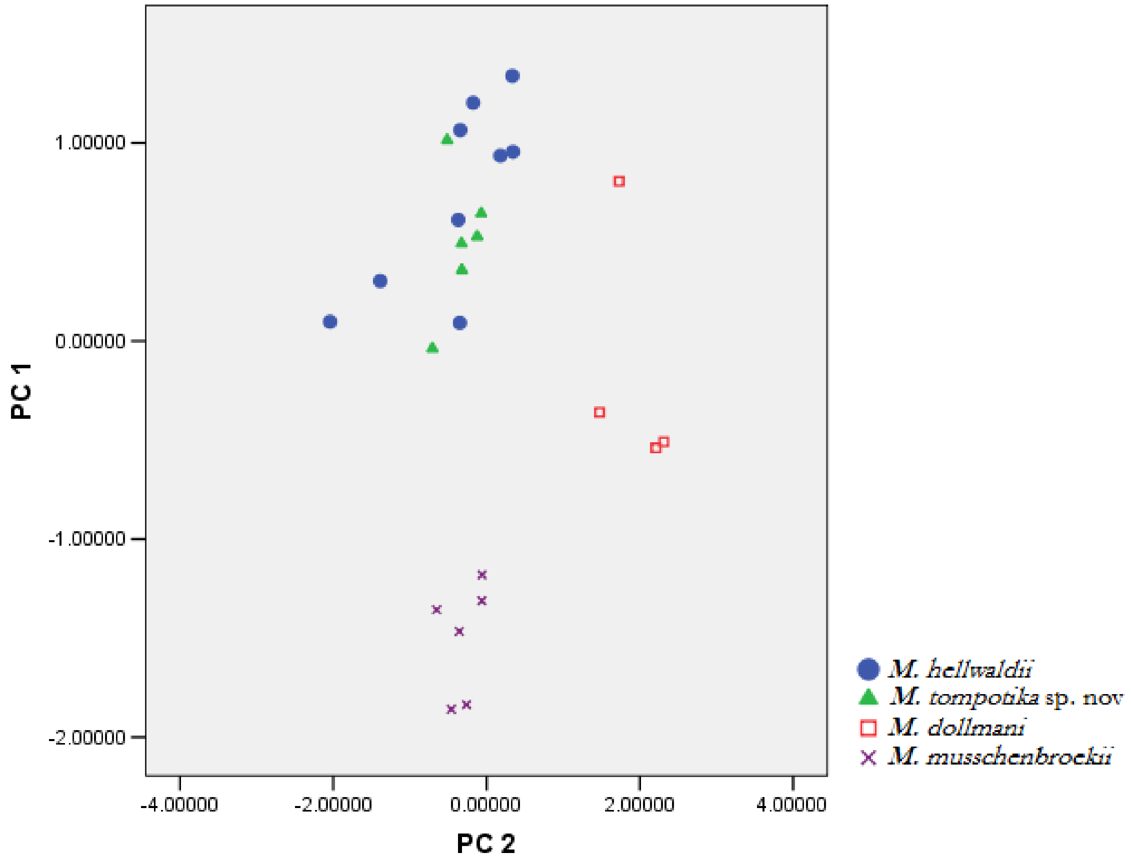

Fig. 41. Bivariate plot of the 1st and 2nd principal component derived from analysis of external characters taken from all known species of *Maxomys* from Sulawesi.

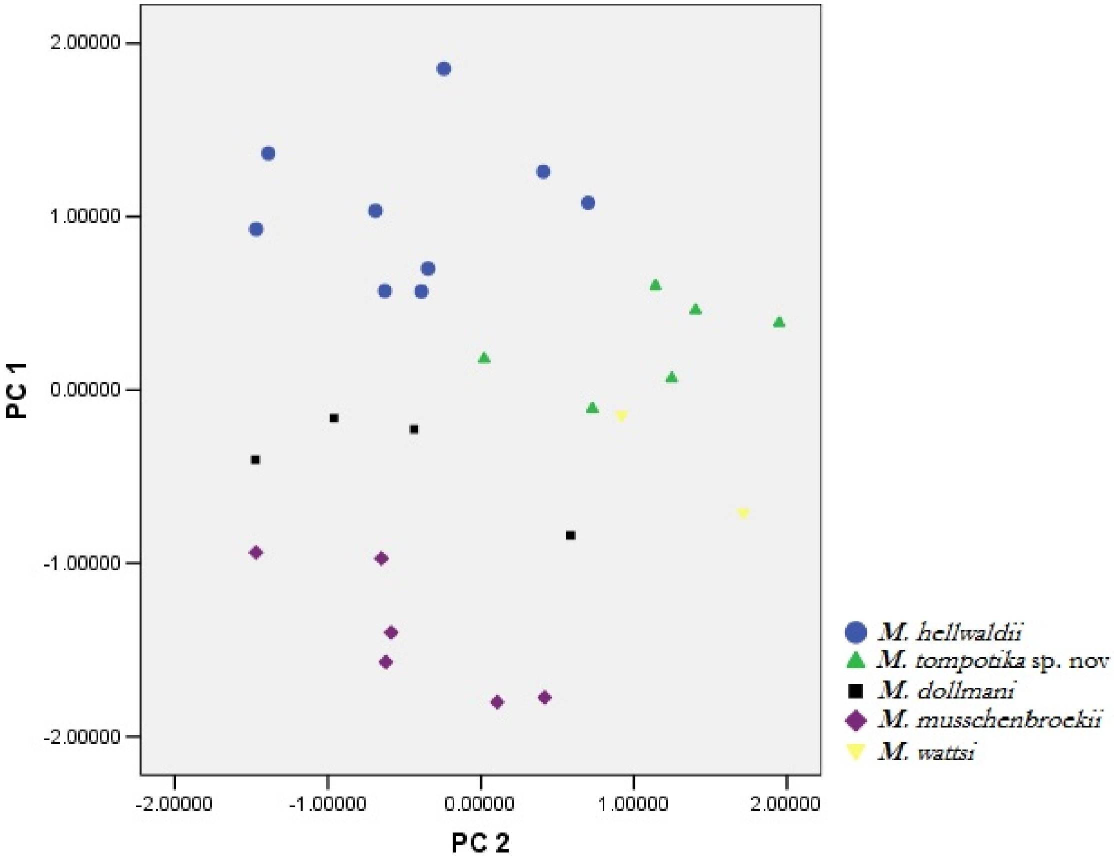

Fig. 42. Bivariate plot of the 1st and 2nd principal component derived from analysis of 24 cranial dimensions taken from all known species of Sulawesian *Maxomys*.

Table 1. Univariate analysis : mean, number of individuals, standard deviation, maximum and minimum values of skull and external characters.

Species	GSL	BB	ZB	ZP	IOB	NL	NW	POW	HB	D	PL	UMR
Maxomys whiteheadi (S)												
N	90	90	90	90	90	90	90	90	90	90	90	90
Mean	32.40	13.69	14.75	2.87	5.62	10.86	3.71	13.44	9.26	8.10	12.38	5.36
S D	1.32	0.49	0.53	0.22	0.29	0.62	0.25	0.47	0.36	0.46	0.52	0.26
Minimum	29.08	12.45	13.31	2.40	4.94	9.12	3.09	11.99	8.39	7.27	11.51	4.84
Maximum	35.13	14.54	15.92	3.52	6.25	12.36	4.17	14.27	9.97	9.35	13.78	6.14
Maxomys whiteheadi (L)												
N	21	21	21	21	21	21	21	21	21	21	21	21
Mean	36.38	14.67	16.35	3.22	6.21	12.29	3.98	14.44	9.93	9.36	14.34	5.89
S. D	1.39	0.52	0.64	0.29	0.48	0.66	0.26	0.44	0.46	0.65	0.72	0.31
Minimum	34.19	13.22	15.31	2.79	5.35	11.20	3.37	13.39	9.04	8.17	13.11	5.23
Maximum	39.71	15.43	18.21	3.72	6.99	13.83	4.38	15.15	11.07	10.93	16.02	6.44
Maxomys musschenbroekii												
N	11	11	11	11	11	11	11	11	11	11	11	11
Mean	37.15	14.98	17.17	3.46	6.24	12.80	3.89	14.71	10.34	9.33	14.46	6.31
S. D	1.27	0.35	0.53	0.25	0.19	0.69	0.33	0.14	0.26	0.33	0.55	0.19
Minimum	35.17	14.5	16.15	3.17	5.89	11.86	3.33	14.47	9.95	8.85	13.87	5.86
Maximum	39.66	15.57	18.02	4.06	6.52	14.20	4.34	14.91	10.75	9.85	15.82	6.61
Maxomys ochraceiventer												
N	3	3	3	3	3	3	3	3	3	3	3	3
Mean	37.69	15.74	16.59	3.01	6.60	12.60	4.33	14.61	10.63	9.26	14.57	6.12
S. D	0.58	0.21	0.27	0.13	0.39	0.29	0.04	0.22	0.38	0.07	0.21	0.15
Minimum	37.26	15.54	16.29	2.86	6.23	12.34	4.30	14.40	10.37	9.19	14.45	5.94
Maximum	38.35	15.96	16.81	3.10	7.01	12.91	4.37	14.83	11.06	9.33	14.81	6.22
Maxomys baeodon												
N	6	6	6	6	6	6	6	6	6	6	6	6
Mean	34.09	14.31	15.05	2.38	6.50	12.38	4.05	13.92	10.23	9.24	12.86	4.56
S. D	0.75	0.41	0.45	0.34	0.24	0.83	0.21	0.62	0.50	0.26	0.81	0.22
Minimum	33.10	13.92	14.49	1.95	6.15	11.35	3.87	13.12	9.73	8.92	11.23	4.25
Maximum	35.20	15.04	15.66	2.77	6.83	13.26	4.41	14.80	11.10	9.53	13.36	4.86
Maxomys wattsi												
N	4	4	4	4	4	4	4	4	4	4	4	4
Mean	41.70	16.03	18.73	3.17	7.42	16.95	4.70	15.80	11.52	10.74	16.77	6.63
S. D	1.39	0.67	0.34	0.25	0.12	0.79	0.20	0.33	0.21	0.47	0.57	0.20
Minimum	40.43	15.13	18.25	2.81	7.29	16.27	4.52	15.47	11.24	10.21	15.95	6.38
Maximum	43.56	16.70	18.98	3.39	7.54	17.85	4.98	16.25	11.75	11.36	17.25	6.80

Table 1. continued

Species	**IFL**	**IFB**	**M1W**	**M^2W**	**M^3W**	**M^1M^1**	**M^2M^2**	**M^3M^3**	**BL**	**MSW**	**RAP**	**DL**
Maxomys whiteheadi (S)												
N	90	90	90	90	90	90	90	90	90	90	90	90
Mean	4.58	2.40	1.55	1.46	1.14	2.95	3.35	3.81	4.51	2.49	7.85	15.66
S. D	0.30	0.18	0.09	0.09	0.09	0.22	0.26	0.27	0.24	0.17	0.44	1.19
Minimum	3.95	2.07	1.34	1.24	0.83	2.27	2.76	3.12	4.00	2.03	6.73	5.94
Maximum	5.30	2.85	1.79	1.68	1.36	3.49	4.01	4.48	5.40	3.09	9.11	17.50
Maxomys whiteheadi (L)												
N	21	21	21	21	21	21	21	21	21	21	21	21
Mean	5.18	2.80	1.64	1.56	1.18	3.53	3.85	4.30	4.76	2.78	8.97	17.41
S. D	0.42	0.27	0.10	0.09	0.09	0.32	0.23	0.23	0.46	0.30	0.44	0.91
Minimum	4.52	2.20	1.45	1.40	1.04	3.05	3.50	4.03	3.77	2.16	8.40	16.24
Maximum	5.94	3.16	1.81	1.73	1.34	4.18	4.52	5.04	5.49	3.21	10.46	19.80
Maxomys musschenbroekii												
N	11	11	11	11	11	11	11	11	11	11	11	11
Mean	5.37	2.59	1.88	1.79	1.25	3.25	3.77	4.41	5.25	2.97	9.63	19.13
S. D	0.26	0.19	0.08	0.05	0.06	0.12	0.14	0.18	0.20	0.20	0.33	0.90
Minimum	5.08	2.32	1.75	1.72	1.15	3.09	3.51	4.11	5.04	2.63	9.19	18.31
Maximum	5.89	2.86	2.02	1.91	1.35	3.47	3.94	4.72	5.76	3.36	10.16	21.55
Maxomys ochraceiventer												
N	3	3	3	3	3	3	3	3	3	3	3	3
Mean	4.60	2.78	1.87	1.76	1.43	3.47	3.85	4.27	4.79	2.86	9.10	17.93
S. D	0.22	0.29	0.04	0.10	0.17	0.29	0.16	0.17	0.15	0.03	0.14	0.32
Minimum	4.43	2.49	1.83	1.65	1.24	3.18	3.70	4.10	4.62	2.83	8.97	17.57
Maximum	4.84	3.06	1.90	1.82	1.57	3.76	4.01	4.43	4.88	2.89	9.25	18.16
Maxomys baeodon												
N	6	6	6	6	6	6	6	6	6	6	6	6
Mean	4.44	2.67	1.53	1.45	1.04	3.99	4.00	4.23	3.66	2.64	7.91	16.83
S. D	0.24	0.19	0.03	0.09	0.10	0.39	0.36	0.36	0.41	0.22	0.45	0.87
Minimum	4.07	2.42	1.49	1.27	0.94	3.52	3.48	3.70	3.22	2.40	7.31	15.69
Maximum	4.74	2.87	1.58	1.52	1.23	4.53	4.43	4.61	4.18	3.00	8.65	18.25
Maxomys wattsi												
N	4	4	4	4	4	4	4	4	4	4	4	4
Mean	5.91	3.42	2.10	1.98	1.46	3.50	4.03	4.42	5.34	3.06	9.55	21.36
S. D	0.46	0.08	0.02	0.04	0.13	0.19	0.32	0.19	0.19	0.09	0.45	0.84
Minimum	5.36	3.36	2.07	1.94	1.32	3.22	3.63	4.23	5.12	2.95	9.11	20.32
Maximum	6.36	3.53	2.12	2.03	1.57	3.64	4.34	4.66	5.57	3.15	9.96	22.25

Table 1. continued

Species	GSL	BB	ZB	ZP	IOB	NL	NW	POW	HB	D	PL	UMR
Maxomys surifer												
N	13	13	13	13	13	13	13	13	13	13	13	13
Mean	38.74	16.00	16.62	3.22	6.03	13.80	3.96	15.44	10.57	10.57	15.73	6.03
S. D	0.95	0.26	0.36	0.27	0.35	0.10	0.23	0.24	0.31	0.31	0.34	0.15
Minimum	37.45	15.42	15.94	2.81	5.48	13.55	3.66	15.01	10.11	9.92	15.11	5.79
Maximum	39.89	16.45	17.14	3.71	6.58	13.96	4.38	15.82	11.33	11.00	16.16	6.29
Maxomys rajah												
N	12	12	12	12	12	12	12	12	12	12	12	12
Mean	41.44	17.01	18.82	3.65	6.65	15.60	4.60	16.37	11.61	11.38	17.45	6.78
S. D	1.82	0.58	0.81	0.33	0.27	0.89	0.25	0.49	0.27	0.37	0.35	0.26
Minimum	39.09	16.48	17.59	3.23	6.09	13.96	4.31	15.32	11.24	10.71	16.74	6.39
Maximum	44.68	18.14	20.06	4.16	6.99	16.85	5.04	17.04	11.98	12.04	17.85	7.17
Maxomys pagensis												
N	3	3	3	3	3	3	3	3	3	3	3	3
Mean	47.02	17.53	19.89	3.81	7.33	18.09	5.44	16.78	12.10	12.60	18.35	6.69
S. D	0.58	0.59	1.34	0.20	0.08	0.65	0.43	0.41	0.20	0.43	0.19	0.13
Minimum	46.47	16.97	19.01	3.58	7.24	17.34	4.96	16.49	11.91	12.28	18.18	6.54
Maximum	47.63	18.15	21.43	3.96	7.40	18.54	5.77	17.24	12.31	13.08	18.56	6.77
Maxomys hellwaldii												
N	6	6	6	6	6	6	6	6	6	6	6	6
Mean	47.71	18.55	20.82	4.22	7.44	18.63	5.48	18.01	12.51	11.87	17.47	6.91
S. D	1.00	0.42	0.48	0.24	0.26	0.75	0.28	0.44	0.16	0.33	0.59	0.14
Minimum	46.01	17.99	20.29	3.95	7.20	17.46	5.09	17.39	12.27	11.46	16.56	6.74
Maximum	48.92	19.12	21.43	4.64	7.86	19.56	5.82	18.62	12.69	12.29	18.09	7.07
Maxomys bartelsii												
N	11	11	11	11	11	11	11	11	11	11	11	11
Mean	38.46	14.72	16.39	3.27	6.45	13.92	3.93	14.57	10.35	10.47	14.90	5.31
S. D	0.80	0.36	0.38	0.23	0.15	0.40	0.21	0.36	0.35	0.27	0.39	0.13
Minimum	37.49	14.12	15.69	3.01	6.19	13.30	3.60	13.97	9.89	9.86	14.30	5.10
Maximum	39.95	15.25	16.81	3.65	6.76	14.69	4.19	15.09	11.19	10.79	15.41	5.51
Maxomys alticola												
N	6	6	6	6	6	6	6	6	6	6	6	6
Mean	37.76	16.01	16.66	2.62	7.37	14.70	4.24	15.37	11.57	9.95	14.95	5.38
S. D	0.54	0.23	0.61	0.22	0.33	0.60	0.20	0.39	0.40	0.56	0.69	0.09
Minimum	37.08	15.62	15.70	2.35	7.09	13.83	3.87	14.84	10.81	9.12	14.13	5.29
Maximum	38.52	16.31	17.47	2.98	7.85	15.32	4.42	15.94	11.90	10.61	16.21	5.51
Maxomys inas												
N	1	1	1	1	1	1	1	1	1	1	1	1
	33.74	14.16	14.87	3.15	5.76	11.82	3.41	13.69	9.17	7.74	12.83	5.46

Table 1. continued

Species	IFL	IFB	M^1W	M^2W	M^3W	M^1M^1	M^2M^2	M^3M^3	BL	MSW	RAP	DL
Maxomys surifer												
N	13	13	13	13	13	13	13	13	13	13	13	13
Mean	5.41	2.92	1.83	1.71	1.44	3.60	3.61	3.78	4.78	2.53	8.67	19.46
S. D	0.25	0.21	0.08	0.09	0.06	0.15	0.14	0.21	0.13	0.15	0.30	0.37
Minimum	5.08	2.56	1.69	1.56	1.36	3.31	3.34	3.29	4.43	2.34	8.17	18.81
Maximum	5.87	3.28	1.95	1.85	1.57	3.85	3.79	4.04	4.95	2.93	9.42	19.97
Maxomys rajah												
N	12	12	12	12	12	12	12	12	12	12	12	12
Mean	5.80	3.04	2.08	2.00	1.58	4.08	4.25	4.58	4.61	2.85	10.58	21.18
S. D	0.28	0.20	0.08	0.09	0.10	0.20	0.24	0.25	0.31	0.13	0.56	1.14
Minimum	5.50	2.81	1.96	1.87	1.43	3.79	3.88	4.07	4.09	2.56	9.81	19.54
Maximum	6.52	3.44	2.22	2.17	1.73	4.46	4.62	4.88	5.06	3.11	11.58	22.67
Maxomys pagensis												
N	3	3	3	3	3	3	3	3	3	3	3	3
Mean	6.74	3.31	2.24	2.02	1.57	4.19	4.47	5.03	5.17	3.02	10.92	23.61
S. D	0.55	0.19	0.05	0.03	0.10	0.25	0.11	0.15	0.57	0.33	0.43	0.74
Minimum	6.27	3.19	2.19	1.99	1.48	3.90	4.34	4.89	4.52	2.82	10.59	22.95
Maximum	7.35	3.52	2.29	2.04	1.68	4.35	4.55	5.18	5.51	3.40	11.41	24.41
Maxomys hellwaldii												
N	6	6	6	6	6	6	6	6	6	6	6	6
Mean	7.05	3.37	2.07	1.87	1.33	4.18	4.55	5.17	7.28	3.41	11.35	23.86
S. D	0.38	0.12	0.09	0.11	0.12	0.29	0.29	0.31	1.29	0.11	0.35	0.80
Minimum	6.38	3.18	1.95	1.74	1.19	3.90	4.20	4.85	6.21	3.29	10.69	23.12
Maximum	7.57	3.52	2.20	2.06	1.52	4.63	4.99	5.73	9.38	3.57	11.7	24.87
Maxomys bartelsii												
N	11	11	11	11	11	11	11	11	11	11	11	11
Mean	6.17	2.62	1.63	1.51	1.09	3.58	3.78	4.14	5.13	2.40	7.96	19.02
S. D	0.26	0.14	0.07	0.05	0.04	0.26	0.20	0.16	0.20	0.15	0.24	0.34
Minimum	5.76	2.39	1.51	1.42	1.03	3.31	3.56	3.91	4.66	2.17	7.58	18.61
Maximum	6.62	2.82	1.74	1.58	1.18	4.27	4.25	4.54	5.32	2.70	8.23	19.56
Maxomys alticola												
N	6	6	6	6	6	6	6	6	6	6	6	6
Mean	5.63	2.73	1.76	1.69	1.24	4.04	4.01	4.19	4.47	2.97	9.07	18.46
S. D	0.29	0.12	0.09	0.04	0.06	0.19	0.25	0.14	0.26	0.08	0.40	0.52
Minimum	5.20	2.60	1.68	1.65	1.16	3.69	3.60	4.04	4.22	2.83	8.64	17.88
Maximum	5.97	2.93	1.88	1.77	1.32	4.21	4.28	4.40	4.82	3.06	9.79	19.35
Maxomys inas												
N	1	1	1	1	1	1	1	1	1	1	1	1
	4.77	2.27	1.55	1.46	1.03	3.09	3.35	3.93	4.89	2.30	8.35	16.45

Table 2. Multiple regression on sex, locality and interactions among these factors in *Maxomys* for skull and dentary characters. F values are presented for main effects with significance levels are *) 0.05>p>0.01; **) 0.01>p>0.001; and ***) P>0.001.

Dependent Variable	**Sex**	**Locality**	**Interaction**
GSL	1.297	12.062***	0.260
BB	0.099	9.372***	0.414
ZB	0.504	12.616***	0.365
ZP	1.711	8.983***	0.971
IOB	1.540	16.442***	0.430
NL	0.433	13.686***	0.302
NW	0.964	11.050***	0.107
POW	0.770	0.858***	0.592
B	0.679	11.679***	0.586
D	0.523	8.980***	0.158
PL	0.955	7.474***	0.183
UMR	1.878	11.147***	1.141
IFL	0.547	15.472***	0.320
IFB	2.291	4.879***	0.634
M1W	1.398	12.826***	0.449
M2W	0.827	9.988***	0.541
M3W	0.224	4.171***	0.873
M1M1	0.157	6.658***	0.502
M2M2	0.336	6.775***	0.814
M3M3	1.150	11.148***	0.697
BL	0.036	14.501***	0.613
MSW	0.027	13.255***	0.899
RAP	0.725	10.766***	0.266
DL	0.362	12.986***	0.497

Table 3. Total variation accounted for 24 measurements on five principal components (PCs**)**

	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	**% of variance**	**Cumulative %**	**Total**	**% of variance**	**Cumulative %**
1	17.71	73.80	73.80	17.71	73.80	73.80
2	1.44	6.01	79.81	1.44	6.01	79.81
3	1.08	4.52	84.32	1.08	4.52	84.32
4	0.82	3.41	87.73	0.82	3.41	87.73
5	0.54	2.27	90.00	0.54	2.27	90.00

Extraction Method: Principal Component Analysis.

Table 4. Standardised and unstandardised (in the brackets) canonical variate function coefficients derived from analysis of five characters

	Function				
	1	2	3	4	5
GSL	0.017(0.013)	0.830(0.653)	-0.603(-0.474)	1.100(0.866)	-0.794(-0.625)
BB	0.461(0.984)	-0.108(-0.230)	-0.496(-1.059)	0.423(0.904)	0.762(1.626)
ZB	0.005(0.010)	0.091(0.164)	1.436(2.581)	-0.176(-0.316)	0.253(0.454)
NL	0.477(0.754)	0.433(0.686)	-0.196(-0.311)	-0.963(-1.524)	0.149(0.236)
PL	0.476(0.886)	-1.212(-2.254)	-0.048(-0.090)	-0.290(-0.539)	-0.236(-0.439)
(Constant)	(-36.865)	(0.182)	(-3.679)	(-12.610)	(-5.679)

Table 5. Total explained variation for 24 measurements on five Discriminant functions (DFs)

Function	**Eigenvalue**	**% of Variance**	**Cumulative %**	**Canonical Correlation**
1	21.38(a)	88.49	88.49	0.98
2	1.19(a)	4.92	93.41	0.74
3	0.78(a)	3.23	96.63	0.66
4	0.45(a)	1.88	98.51	0.56
5	0.36(a)	1.49	100.00	0.51

a. First 5 canonical discriminant functions were used in the analysis.

Table 6. Total explained variation for 24 measurements on two Discriminant functions (DFs)

Function	Eigenvalue	% of variance	Cumulative %	Canonical Correlation
1	3.35 (a)	94.04	94.04	0.88
2	0.21(a)	5.96	100.00	0.42

a First 2 canonical discriminant functions were used in the analysis.

Table 7. Standardised and unstandardised (in the brackets) canonical variate function coefficients derived from analysis of seven characters

	Function	
	1	2
BB	1.034(2.558)	0.059(0.145)
IOB	-0.691(-2.522)	-0.462(-1.684)
NL	0.820(1.413)	0.119(0.205)
NW	0.334(1.663)	0.143(0.714)
M1M1	-0.390(-2.044)	0.551(2.890)
M3M3	-0.509(-2.000)	0.580(2.282)
RAP	0.009(0.019)	-0.944(-2.089)
(Constant)	(-28.725)	(1.922)

Table 8. Total explained variation for 24 measurements on four Discriminant functions (DFs)

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	191.54(a)	92.05	92.05	1.00
2	12.57(a)	6.04	98.09	0.96
3	3.01(a)	1.44	99.53	0.87
4	0.97(a)	0.47	100.00	0.70

a First 4 canonical discriminant functions were used in the analysis.

Table 9. Standardised and unstandardised (in the brackets) canonical variate function coefficients derived from analysis of eight characters

	Function			
	1	**2**	**3**	**4**
BB	0.109(0.243)	-1.681(-3.747)	0.816(1.819)	0.638(1.421)
ZP	3.814(22.640)	0.006(0.034)	0.818(4.858)	-0.351(-2.083)
IOB	0.068(0.271)	1.913(7.664)	0.273(1.095)	0.296(1.186)
D	-4.702(-8.325)	-1.367(-2.420)	0.505(0.895)	-0.342(-0.606)
UMR	2.969(13.792)	-0.467(-2.171)	0.054(0.251)	0.477(2.216)
IFL	3.728(10.776)	1.514(4.377)	-1.129(-3.263)	0.398(1.151)
MSW	2.477(8.892)	1.514(-0.404)	0.308(1.106)	-1.045(-3.750)
RAP	-2.401(-5.631)	-0.112(2.112)	-1.336(-3.134)	0.086(0.201)
(Constant)	(-111.376)	(2.196)	(-17.022)	(-26.249)

Table 10. Descriptive analysis : mean, number of specimens, standard deviation, maximum and minimum values of dorsal color measurements.

Species		SCI			SCE		
		L*	a*	b*	L*	a*	b*
Maxomys hellwaldii	Mean	28.98	6.56	12.64	28.81	6.60	12.77
	Min	25.73	4.35	8.88	25.54	4.36	8.98
	Max	34.49	9.76	19.17	34.52	9.82	19.33
	Stdev	2.41	1.85	3.30	2.48	1.86	3.31
Maxomys musschenbroekii	Mean	26.17	4.23	9.08	26.16	4.24	9.16
	Min	20.43	2.25	4.38	21.19	2.29	4.47
	Max	33.42	7.97	18.88	33.34	7.96	18.85
	Stdev	3.08	1.31	3.36	2.86	1.31	3.34
Maxomys pagensis	Mean	28.37	6.46	11.78	28.29	6.48	11.86
	Min	21.74	2.92	5.04	21.71	2.93	5.12
	Max	36.33	11.06	20.19	36.19	11.07	20.44
	Stdev	4.19	2.25	4.38	4.19	2.27	4.39
Maxomys bartelsii	Mean	28.37	5.85	10.00	28.31	5.86	10.06
	Min	19.49	2.20	3.71	19.39	2.31	3.82
	Max	35.03	8.42	17.28	35.06	8.63	17.58
	Stdev	3.61	1.30	2.77	3.62	1.33	2.82
Maxomys dollmani	Mean	27.72	3.78	7.51	27.64	3.80	7.56
	Min	24.23	2.90	5.84	24.20	2.91	5.91
	Max	31.19	5.05	9.57	31.01	5.11	9.60
	Stdev	2.72	0.79	1.34	2.59	0.81	1.33
Maxomys baeodon	Mean	25.49	6.03	10.04	25.46	6.04	11.71
	Min	18.19	4.05	5.78	18.67	3.98	5.79
	Max	32.69	8.64	14.74	32.49	8.63	71.05
	Stdev	3.17	1.29	2.60	3.01	1.31	9.97
Maxomys alticola	Mean	26.04	6.74	11.84	25.97	6.76	11.89
	Min	22.15	5.11	8.49	22.19	5.13	8.55
	Max	33.65	8.78	18.07	33.66	8.93	18.16
	Stdev	3.61	1.13	2.93	3.58	1.16	2.95
Maxomys ochraceiventer	Mean	26.93	5.72	9.81	26.87	5.75	9.91
	Min	22.89	4.05	6.62	22.72	4.08	6.57
	Max	32.69	7.66	13.94	32.49	7.69	14.01
	Stdev	3.05	1.16	2.57	3.06	1.20	2.66
Maxomys rajah	Mean	29.67	7.31	13.12	29.59	7.33	13.18
	Min	23.45	4.23	7.49	23.42	4.21	7.71

Table 10. continued

	Max	38.10	12.37	23.36	38.03	12.35	23.33
	Stdev	3.63	1.97	3.83	3.64	1.98	3.84
Maxomys surifer	Mean	31.46	7.84	14.61	31.40	7.87	14.70
	Min	25.90	4.01	7.63	25.83	4.00	7.71
	Max	36.68	11.86	22.94	36.66	11.85	22.91
	Stdev	3.06	2.03	3.40	3.02	2.03	3.39
Maxomys whiteheadi	Mean	24.53	5.91	9.84	24.55	5.91	9.79
	Min	13.93	2.04	2.99	17.05	2.13	3.22
	Max	32.53	10.84	27.39	32.41	10.87	18.29
	Stdev	3.79	2.22	4.23	3.66	2.23	3.91

Table 11. Descriptive analysis : mean, number of specimens, standard deviation, maximum and minimum values of ventral color measurements.

Species		SCI			SCE		
		L*	a*	b*	L*	a*	b*
Maxomys hellwaldii (n= 3)	Mean	66.99	2.48	18.95	67.10	2.45	19.10
	Min	45.81	0.01	5.43	46.23	-0.08	5.47
	Max	81.72	6.11	34.79	81.46	6.12	34.84
	Stdev	10.61	1.66	8.25	10.33	1.66	8.21
Maxomys musschenbroekii (n= 4)	Mean	67.22	5.73	28.76	67.08	5.79	28.96
	Min	55.82	1.33	19.54	55.70	1.35	19.72
	Max	82.32	11.53	39.11	82.26	11.59	39.22
	Stdev	6.33	2.33	4.49	6.40	2.39	4.60
Maxomys pagensis (n= 4)	Mean	47.40	6.46	17.71	47.39	6.46	17.81
	Min	41.06	4.41	12.09	41.35	4.41	12.18
	Max	56.21	8.17	24.46	56.16	8.18	24.61
	Stdev	4.38	1.37	3.77	4.28	1.38	3.77
Maxomys bartelsii (n= 7)	Mean	65.73	1.62	13.17	65.67	1.60	13.25
	Min	46.82	-0.77	4.06	47.40	-0.78	4.15
	Max	85.12	5.60	26.67	84.90	5.05	26.62
	Stdev	9.25	1.28	5.62	9.12	1.21	5.65
Maxomys dollmani (n= 1)	Mean	70.16	1.10	13.41	69.98	1.11	13.52
	Min	62.34	0.39	11.47	62.01	0.40	11.71
	Max	77.74	2.25	14.85	77.68	2.29	14.94
	Stdev	7.23	0.77	1.35	7.26	0.79	1.31
Maxomys baeodon (n= 6)	Mean	59.67	2.29	13.50	58.40	2.30	13.64
	Min	50.82	0.57	7.64	12.51	0.58	7.74
	Max	68.32	5.47	21.65	68.26	5.47	21.73
	Stdev	5.22	1.14	3.62	9.96	1.16	3.72
Maxomys alticola (n= 2)	Mean	57.89	7.08	29.37	57.82	7.12	29.50
	Min	50.75	5.30	24.81	50.78	5.33	24.94
	Max	64.81	9.07	30.72	64.66	9.14	30.95
	Stdev	4.23	1.16	1.81	4.18	1.17	1.82
Maxomys ochraceiventer (n= 1)	Mean	52.54	8.07	20.88	52.63	8.10	21.02
	Min	44.08	4.39	14.77	44.58	4.55	15.26
	Max	59.05	10.72	25.37	58.86	10.73	25.41
	Stdev	4.27	2.38	3.11	4.19	2.37	3.06
Maxomys rajah (n= 7)	Mean	80.68	1.20	17.40	80.67	1.20	17.50
	Min	72.12	-0.40	12.77	72.35	-0.38	12.89

Table 11. continued

	Max	87.10	2.83	25.97	86.90	2.84	26.12
	Stdev	3.35	0.81	3.47	3.20	0.80	3.46
Maxomys surifer (n= 5)	Mean	74.55	3.55	24.21	74.50	3.56	24.35
	Min	59.62	-0.09	14.60	59.76	-0.07	14.71
	Max	86.17	15.02	35.18	85.96	15.06	35.32
	Stdev	7.43	3.59	6.11	7.38	3.60	6.13
Maxomys whiteheadi (n= 23)	Mean	60.32	3.67	14.64	60.26	3.85	14.88
	Min	42.38	0.05	5.97	43.11	0.09	6.06
	Max	78.44	12.64	30.37	78.13	20.14	30.43
	Stdev	6.68	2.56	5.10	6.56	2.99	5.11

Table 12. Total variance explained for dorsal color measurements of *Maxomys* from PCA analysis using correlation matrix.

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	6.03	75.38	75.38	6.03	75.38	75.38
2	1.85	23.07	98.45	1.85	23.07	98.45
3	0.07	0.83	99.28	0.07	0.83	99.28

Only cases for which Species_no = 12 are used in the analysis phase.

Table 13. Total variance explained for ventral color measurements of *Maxomys* from PCA analysis using correlation matrix.

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	6.58	82.22	82.22	6.58	82.22	82.22
2	1.19	14.83	97.06	1.19	14.83	97.06
3	0.16	2.04	99.10	0.16	2.04	99.09

Only cases for which Species_no = 12 are used in the analysis phase.

Table 14. Total explained variation for dorsal color measurements on two discriminant functions (DFs) using stepwise methods.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.741(a)	71.2	71.2	0.797
2	.428(a)	17.5	88.7	0.548
3	.276(a)	11.3	100	0.465

a. First 2 canonical discriminant functions were used in the analysis.

Table 15. Total explained variation for ventral color measurements on two discriminant functions (DFs) using stepwise methods.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	4.862(a)	76.5	76.5	0.911
2	1.493(a)	23.5	100	0.774

a. First 2 canonical discriminant functions were used in the analysis.

Table 16. Mean uncorrected genetic distances (*p-distances*) between species of *Maxomys* and *Crunomys* (below diagonal) and maximum intraspecific uncorrected genetic distances (bold font on diagonal). Intraspecific distances are only shown for those species sampled from multiple localities.

	celebensis	*melanius*	*suncoides*	*bartelsii*	cf. *hellwaldii*	*dollmani*	*hellwaldii*	*hylomyoides*	*moi*	*musschenbroekii*	*ochraceiventer*	*pagensis*	*panglima*	*rajah*	sp. (Sulawesi)	*surifer*	*tajuddinii* sp. nov	*whiteheadi*
celebensis	-																	
melanius	0.07	-																
suncoides	0.07	0.04	-															
bartelsii	0.14	0.12	0.12	**0.01**														
cf. *hellwaldii*	0.12	0.12	0.13	0.12	-													
dollmani	0.13	0.12	0.13	0.13	0.13	**0.02**												
hellwaldii	0.12	0.11	0.11	0.13	0.12	0.09	-											
hylomyoides	0.13	0.13	0.13	0.13	0.13	0.12	0.13	**0.07**										
moi	0.12	0.11	0.12	0.12	0.13	0.14	0.13	0.12	-									
musschenbroekii	0.14	0.13	0.12	0.13	0.13	0.14	0.14	0.14	0.14	**0.07**								
ochraceiventer	0.12	0.10	0.11	0.12	0.11	0.13	0.13	0.11	0.13	0.11	-							
pagensis	0.12	0.11	0.11	0.14	0.12	0.14	0.13	0.12	0.13	0.14	0.13	-						
panglima	0.13	0.12	0.12	0.14	0.13	0.14	0.13	0.13	0.12	0.14	0.12	0.12	**0.04**					
rajah	0.12	0.10	0.11	0.13	0.11	0.13	0.12	0.12	0.11	0.14	0.11	0.06	0.12	**0.01**				
sp. (Sulawesi)	0.13	0.12	0.12	0.13	0.11	0.10	0.12	0.13	0.13	0.15	0.12	0.13	0.13	0.13	-			
surifer	0.14	0.12	0.12	0.13	0.13	0.14	0.14	0.12	0.12	0.13	0.11	0.12	0.14	0.12	0.13	**0.08**		
tajuddinii sp. nov	0.11	0.12	0.12	0.13	0.13	0.13	0.13	0.08	0.12	0.09	0.12	0.14	0.13	0.13	0.12	0.15	-	
whiteheadi	0.10	0.14	0.11	0.14	0.12	0.13	0.15	0.09	0.13	0.09	0.09	0.11	0.13	0.12	0.12	0.13	0.10	**0.08**

Table 17. The selected sampling sites. date of visits and habitat type in Borneo Island

No	Sampling Locality	GPS Reading	Date	Habitat Type
1	Kinabalu Park. Sabah	N 06^{0} 00’27” E 116^{0}33’05”	13 - 26 February 2008	Mixed dipterocarp and sub-montane forest
2	Fraser's Hill Forest reserve	N 03^{o}42’57” E 101^{o} 44’23”	8 - 12 July 2008	Mixed dipterocarp forest
3	Lanjak Entimau Wildlife Sanctuary	N 01°00’22” E 112°00’07”	14 - 26 June 2008	Mixed dipterocarp forest. Kerangas
4	Niah National Park	N 3° 47' 54" E 113°46'54"	2 - 7 August and 14 - 20 November 2008	Mixed dipterocarp forest. Kerangas
5	Melak. Kutai Barat. East Kalimantan	S 0°16’53” E 115°51’21”	14 - 30 May 2006	Mixed dipterocarp forest. Kerangas

Table 18. Comparisons of selected traits and measurements between *M. tajuddinii* sp. nov. and *M. whiteheadi* Thomas. 1894

	M. tajuddinii sp. nov.	*Maxomys whiteheadi*		
		Present Study	Thomas (1894)	Corbet and Hill (1992)
Head and Body Length (mm)	106.84	101.18	102	112.5
	(95.36 - 121.5)	(91.2 - 111.08)		(100 - 125)
Tail (% of H and B)	90 - 100	105 - 120	107	85 - 90
Hindfoot (mm)	28.64	24.76	27	26
	(27.62 - 30.04)	(23.49 - 25.92)		(24 - 28)
Dorsal pelage with flat spines	√	√	√	√
Flanks with sharp delimitation Between dorsal and ventral color	√	No	No	No
Ventral pelage	Creamy white	Dark orange with black tips	Ochraceous	Dark grey
Mammae	2 + 2	2 + 2	2 + 2	
Skull Traits				
Greatest Scale Length (mm)	36.38	32.4	33.6	29 - 38
	(34.19 - 39.71)	(29.08 - 35.13)		
Zygomatic Breadth (mm)	16.35	14.75	16	
	(15.31 - 18.21)	(13.31 - 15.92)		
Zygomatic Plate Length (mm)	3.22	2.87	3.2	
	(2.79 - 3.72)	(2.4 - 3.52)		
Upper Molar Row (mm)	5.89	5.36	5.1	5.1 - 6.2
	(5.23 - 6.44)	(4.84 - 6.14)		
Incisive Foramina Length (mm)	5.18	4.58	4.8	4.0 - 5.4
	(4.52 - 5.94)	(3.95 - 5.30)		
Diastema (mm)	9.36	8.1	8.9	
	(8.17 - 10.93)	(7.27 - 9.35)		
Nasal Length (mm)	12.29	10.86	11.4	
	(11.20 - 13.83)	(9.12 - 12.36)		

Table 19. Comparisons of skull measurements between *M. tajuddinii* sp. nov. and *M. whiteheadi* Thomas. 1894 (in mm)

	Maxomys tajuddinii sp. nov.			*Maxomys whiteheadi*		
	N	Mean	Std. Deviation	N	Mean	Std. Deviation
Greater Scale Length	21	36.38	1.39	90	32.40	1.32
Post Orbital Breadth	21	14.67	0.52	90	13.69	0.49
Zygomatic Breadth	21	16.35	0.64	90	14.75	0.53
Zygomatic Plate	21	3.22	0.29	90	2.87	0.22
Inter Orbital Breadth	21	6.21	0.48	90	5.62	0.29
Nasal Length	21	12.29	0.66	90	10.86	0.62
Nasal Width	21	3.98	0.26	90	3.71	0.25
Braincase Width	21	14.44	0.44	90	13.44	0.47
Heigth of Braincase	21	9.93	0.46	90	9.26	0.36
Diastema	21	9.36	0.65	90	8.10	0.46
Palatal Length	21	14.34	0.72	90	12.38	0.52
Upper Molar Row	21	5.89	0.31	90	5.36	0.26
Incisive Foramina Length	21	5.18	0.42	90	4.58	0.30
Incisive Foramina Breadth	21	2.80	0.27	90	2.40	0.18
Molar 1Width	21	1.64	0.10	90	1.55	0.09
Molar 2 Width	21	1.56	0.09	90	1.46	0.09
Molar 3 Width	21	1.18	0.09	90	1.14	0.09
Molar 1 to Molar 1	21	3.53	0.32	90	2.95	0.22
Molar 2 to Molar 2	21	3.85	0.23	90	3.35	0.26
Molar 3 to Molar 3	21	4.30	0.23	90	3.81	0.27
Tympanic Bulla Length	21	4.76	0.46	90	4.51	0.24
Meso Pterygoid Width	21	2.78	0.30	90	2.49	0.17
Ramus Angular Process	21	8.97	0.44	90	7.85	0.44
Dental Length	21	17.41	0.91	90	15.66	1.19

Table 20. Standardised and unstandardised canonical discriminant function coefficients of selected skull characters from *M. tajuddinii* sp. nov. and *M. whiteheadi* Thomas. 1894

	Function 1	
	Standardised	Unstandardised
BB	0.32	0.66
PL	0.67	1.19
RAP	0.34	0.77
(Constant)		-30.44

Table 21. Classification results of Discriminant Function Analyses between *M. tajuddinii* sp. nov. and *M. whiteheadi* Thomas. 1894

Actual Group		No. of Cases	Predicted Group Membership	
			1	2
1	*M. whiteheadi*	90	90 100%	0 0%
2	*M. tajuddinii* sp.nov	19	0 0%	19 100%

Percent of "grouped" cases correctly classified : 100 %

Table 22 Classification results of Discriminant Function Analyses between *M. tajuddinii* sp. nov. and *M. baeodon*

Actual Group		No. of Cases	Predicted Group Membership	
			1	2
1	*M. tajuddinii* sp.nov	21	21 100%	0 0%
2	*M. baeodon*	6	0 0%	6 100%

Percent of "grouped" cases correctly classified : 100 %

Table 23. External measurements from four known species of *Maxomys* (*hellwaldii*. *tompotika* sp. nov. *dollmani* and *musschenbroekii*) from Sulawesi. Abbreviated external measurements are as follows: TTL (Total Length of the Body). TL (Tail Length). Length of Hindfoot. and Ear Length. All measurements in mm except Mass (g).

Species	TTL	TL	HF	Ear	Mass
Maxomys hellwaldii					
N	10	10	10	10	10
Mean	375.67	166.33	45.50	26.89	218.50
STDev	28.42	28.96	1.90	1.05	34.61
Min	326	110	42	25	170
Max	415	195	48	28	267
Maxomys tompotika sp. nov					
N	6	6	6	6	6
Mean	348.83	170.83	44.83	28.67	165.50
STDev	16.99	9.41	1.72	1.37	11.55
Min	323	153	42	27	150
Max	369	180	47	31	186
Maxomys dollmani					
N	4	4	4	4	4
Mean	373.75	207.75	40.50	22.75	84.25
STDev	24.19	11.09	4.80	2.22	28.50
Min	343	195	36	21	70
Max	401	222	46	26	127
Maxomys musschenbroekii					
N	7	7	7	7	7
Mean	275.50	133.83	35.50	21.17	92.50
STDev	20.54	8.70	1.87	1.17	19.50
Min	252	119	32	20	65
Max	306	141	37	23	118
Maxomys wattsi (taken from Musser 1991)					
N	7	8	10	7	
Mean	314.0	137.0	36.5	23.9	
STDev		9.2	1.1	1.8	
Min	289	125	35	20	
Max	339	154	38	25	

Table 24. Cranial and dental measurements from all known species of *Maxomys* from Sulawesi. Abbreviated cranial dimensions are defined in Materials and Methods.

Species	GSL	POW	ZB	ZP	IOB	NL
Maxomys hellwaldii						
N	9	10	10	10	10	10
Mean	47.45	18.76	21.13	4.24	7.56	18.47
Std Dev	1.06	0.46	0.92	0.36	0.30	0.83
Max	48.92	19.54	23.18	4.89	7.99	19.56
Min	45.76	17.99	20.09	3.56	7.20	16.89
Maxomys tompotika sp. nov						
N	6	6	6	6	6	6
Mean	44.37	17.56	20.64	4.07	7.06	16.19
Std Dev	1.04	0.57	0.37	0.15	0.36	0.33
Max	45.77	18.09	21.02	4.35	7.64	16.72
Min	43.15	16.74	20.07	3.92	6.72	15.89
Maxomys dollmani						
N	4	4	4	4	4	4
Mean	41.18	16.73	18.80	3.10	7.19	14.90
Std Dev	2.08	0.36	0.69	0.32	0.21	1.60
Max	42.94	17.13	19.34	3.54	7.50	15.98
Min	38.16	16.40	17.91	2.83	7.06	12.53
Maxomys musschenbroekii						
N	7	7	7	7	7	7
Mean	37.73	15.19	17.32	3.32	6.43	13.55
Std Dev	1.66	0.40	0.89	0.24	0.19	0.92
Max	39.55	15.55	18.62	3.59	6.64	14.48
Min	35.72	14.54	16.53	2.93	6.11	12.37
Maxomys wattsi						
N	2	2	2	2	2	2
Mean	41.32	15.82	18.43	3.46	7.37	17.43
Std Dev	2.12	0.04	0.67	0.14	0.16	0.43
Max	42.82	15.85	18.90	3.56	7.48	17.73
Min	39.82	15.79	17.95	3.36	7.25	17.12

Table 24. continued…

Species	NW	WB	HB	D	PL	UMR
Maxomys hellwaldii						
N	10	10	9	10	10	10
Mean	5.41	18.06	12.69	12.03	17.90	6.85
Std Dev	0.27	0.36	0.30	0.44	0.87	0.17
Max	5.82	18.62	13.13	12.91	19.54	7.07
Min	5.08	17.39	12.27	11.46	16.56	6.56
Maxomys tompotika sp. nov						
N	6	6	6	6	6	6
Mean	4.86	17.13	12.47	11.04	17.22	6.93
Std Dev	0.21	0.50	0.36	0.30	0.36	0.19
Max	5.22	17.53	12.95	11.39	17.73	7.24
Min	4.67	16.45	11.93	10.55	16.84	6.73
Maxomys dollmani						
N	4	4	4	4	4	4
Mean	4.90	16.37	11.82	10.48	15.83	6.11
Std Dev	0.58	0.11	0.09	0.60	0.65	0.25
Max	5.54	16.50	11.89	11.11	16.59	6.35
Min	4.14	16.26	11.69	9.72	15.01	5.78
Maxomys musschenbroekii						
N	7	7	7	7	7	7
Mean	4.10	15.10	10.32	9.49	14.33	5.77
Std Dev	0.42	0.52	0.26	0.68	0.73	0.24
Max	4.86	15.71	10.72	10.15	15.17	6.03
Min	3.73	14.29	9.97	8.47	13.26	5.32
Maxomys wattsi						
N	2	2	2	2	2	2
Mean	5.11	15.15	11.21	10.09	16.25	6.45
Std Dev	0.28	0.01	0.49	0.60	0.74	0.09
Max	5.30	15.16	11.56	10.51	16.77	6.51
Min	4.91	15.14	10.86	9.66	15.72	6.38

Table 24. continued…

Species	IFL	IFB	M1W	M2W	M3W	M1M1
Maxomys hellwaldii						
N	10	10	10	10	10	10
Mean	7.19	3.44	2.10	1.91	1.40	4.23
Std Dev	0.57	0.18	0.09	0.10	0.13	0.26
Max	8.11	3.78	2.22	2.06	1.55	4.64
Min	6.25	3.18	1.95	1.74	1.19	3.90
Maxomys tompotika sp. nov						
N	6	6	6	6	6	6
Mean	6.65	3.39	2.18	1.98	1.47	3.75
Std Dev	0.36	0.25	0.07	0.09	0.09	0.18
Max	7.15	3.71	2.27	2.07	1.61	4.12
Min	6.09	3.03	2.09	1.88	1.38	3.61
Maxomys dollmani						
N	4	4	4	4	4	4
Mean	6.15	3.44	1.91	1.75	1.36	3.88
Std Dev	0.47	0.30	0.16	0.11	0.05	0.30
Max	6.63	3.83	2.14	1.89	1.41	4.18
Min	5.50	3.11	1.81	1.63	1.31	3.61
Maxomys musschenbroekii						
N	7	7	7	7	6	7
Mean	5.47	2.75	1.82	1.68	1.26	3.51
Std Dev	0.17	0.44	0.06	0.11	0.16	0.38
Max	5.60	3.36	1.89	1.80	1.54	3.94
Min	5.11	2.22	1.73	1.50	1.09	2.98
Maxomys wattsi						
N	2	2	2	2	2	2
Mean	6.02	3.48	2.15	1.99	1.47	3.29
Std Dev	0.00	0.19	0.03	0.03	0.01	0.37
Max	6.02	3.61	2.17	2.01	1.47	3.55
Min	6.02	3.34	2.13	1.97	1.46	3.02

Table 24. continued…

Species	M3M3	BL	MSW	RAP	DL
Maxomys hellwaldii					
N	10	9	10	10	10
Mean	5.19	7.02	3.61	11.32	23.62
Std Dev	0.28	1.14	0.40	0.49	0.88
Max	5.73	9.38	4.44	12.09	24.87
Min	4.85	5.81	3.29	10.49	22.30
Maxomys tompotika sp. nov					
N	6	6	6	6	6
Mean	4.51	5.40	3.10	10.27	21.79
Std Dev	0.35	0.17	0.23	0.23	0.83
Max	4.98	5.60	3.35	10.56	22.52
Min	4.13	5.13	2.73	9.97	20.30
Maxomys dollmani					
N	4	4	4	4	4
Mean	4.74	5.59	2.91	9.75	20.36
Std Dev	0.06	0.17	0.33	0.66	0.78
Max	4.77	5.78	3.20	10.51	21.21
Min	4.65	5.43	2.46	8.92	19.48
Maxomys musschenbroekii					
N	7	7	7	7	7
Mean	4.39	4.64	2.85	9.34	18.72
Std Dev	0.24	0.15	0.18	0.42	0.59
Max	4.67	4.92	3.11	9.80	19.32
Min	4.05	4.46	2.61	8.77	17.70
Maxomys wattsi					
N	2	2	2	2	2
Mean	4.33	5.31	3.13	9.30	20.10
Std Dev	0.42	0.25	0.19	0.54	1.80
Max	4.62	5.49	3.26	9.68	21.37
Min	4.03	5.13	2.99	8.91	18.83

Table 25. Total variance explained in principal components analysis of five external characters of all known species of *Maxomys* from Sulawesi.

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	3.41	68.16	68.16	3.41	68.16	68.16
2	1.11	22.14	90.31	1.11	22.14	90.31
3	0.33	6.59	96.90			
4	0.09	1.86	98.76			
5	0.06	1.25	100.00			

Table 26. Total variance explained in principal components analysis of 24 skull and dental characters of all known species of *Maxomys* from Sulawesi.

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	17.08	71.15	71.15	17.08	71.15	71.15
2	2.54	10.60	81.75	2.54	10.60	81.75

Table 27. External measurements from additional museum collections. it includes *Maxomys inas*. *M. moi* and *M. inflatus*. Abbreviated external measurements are as follows: TTL (Total Length of the Body). TL (Tail Length). Length of Hindfoot. and Ear Length. All measurements in mm except Mass (g).

	TTL	**TL**	**HF**	**Ear**	**Mass**
Maxomys inas					
N	11	11	11	11	8
Mean	145.36	145.18	31.73	20.50	79.06
Std. Deviation	12.11	12.68	1.19	0.97	12.57
Minimum	124.00	122.00	29.00	19.00	60.00
Maximum	162.00	167.00	33.00	22.00	92.00
Maxomys moi					
N	14	14	14	14	4
Mean	345.73	176.07	38.27	24.73	100.50
Std. Deviation	23.60	13.30	1.58	1.49	23.75
Minimum	297.00	146.00	36.00	22.00	64.00
Maximum	390.00	197.00	41.00	27.00	130.00
Maxomys inflatus					
N	5	5	5	5	
Mean	175.20	152.40	38.80	22.60	
Std. Deviation	8.79	6.88	1.48	0.89	
Minimum	163.00	144.00	37.00	22.00	
Maximum	169.00	147.00	37.00	22.00	

Table 28. Cranial and dental measurements from additional museum collections. it includes *Maxomys inas*. *M. moi* and *M. inflatus*. Abbreviated cranial dimensions are defined in Materials and Methods in Chapter 1.

	GSL	**POW**	**ZB**	**ZP**	**IOB**	**NL**	**NW**
Maxomys inas							
N	11	11	11	11	11	11	11
Mean	36.89	15.23	16.22	3.43	6.83	12.23	3.97
Std. Deviation	1.69	0.66	0.76	0.24	0.27	0.96	0.28
Minimum	34.09	14.14	14.62	3.15	6.40	11.19	3.58
Maximum	40.25	16.73	17.66	3.86	7.17	14.59	4.49
Maxomys moi							
N	14	14	14	14	14	14	14
Mean	42.38	16.25	18.43	4.94	6.65	15.33	4.57
Std. Deviation	3.38	0.64	2.23	3.70	0.41	1.41	0.39
Minimum	35.81	15.03	11.66	2.90	5.63	12.32	3.69
Maximum	45.83	17.29	21.01	19.15	7.27	17.60	5.27
Maxomys inflatus							
N	5	5	5	5	5	5	5
Mean	42.96	16.42	18.59	3.57	7.55	15.96	4.99
Std. Deviation	1.42	0.85	0.51	0.36	0.47	0.30	0.32
Minimum	40.65	15.58	17.93	3.10	6.97	15.66	4.44
Maximum	44.30	17.58	19.13	3.92	8.05	16.40	5.30

Table 28. continued.

	WB	**HB**	**D**	**PL**	**UMR**	**IFL**	**IFB**
Maxomys inas							
N	11	11	11	11	11	11	11
Mean	14.84	10.28	8.97	14.02	6.14	5.43	2.79
Std. Deviation	0.48	0.39	0.63	0.62	0.16	0.54	0.18
Minimum	14.00	9.69	7.99	13.04	5.89	4.98	2.43
Maximum	15.56	10.85	10.33	15.06	6.42	6.52	3.04
Maxomys moi							
N	14	14	14	14	14	14	14
Mean	16.41	11.47	11.75	17.06	5.95	6.90	3.33
Std. Deviation	0.67	0.58	1.29	1.37	0.30	0.66	0.47
Minimum	14.84	9.67	9.34	14.57	5.43	5.33	2.37
Maximum	17.19	11.99	13.56	18.78	6.58	7.95	4.34
Maxomys inflatus							
N	5	5	5	5	5	5	5
Mean	16.67	11.73	12.26	17.53	6.15	7.02	3.73
Std. Deviation	0.40	0.43	1.01	0.70	0.13	0.33	0.28
Minimum	16.17	11.16	10.92	16.51	5.98	6.65	3.40
Maximum	17.20	12.11	13.67	18.30	6.33	7.51	4.16

Table 28. continued.

	M1W	**M2W**	**M3W**	**M1M1**	**M2M2**	**M3M3**
Maxomys inas						
N	11	11	11	11	11	11
Mean	1.79	1.68	1.27	3.45	3.71	4.19
Std. Deviation	0.07	0.11	0.14	0.42	0.39	0.41
Minimum	1.71	1.46	1.13	2.70	2.95	3.30
Maximum	1.89	1.78	1.56	4.03	4.32	4.85
Maxomys moi						
N	14	14	14	14	14	14
Mean	1.97	1.84	1.38	4.26	4.47	4.80
Std. Deviation	0.11	0.09	0.08	0.48	0.45	0.41
Minimum	1.76	1.64	1.19	3.35	3.81	4.02
Maximum	2.13	1.93	1.50	5.24	5.27	5.55
Maxomys inflatus						
N	5	5	5	5	5	5
Mean	1.94	1.87	1.37	4.50	4.43	4.81
Std. Deviation	0.05	0.05	0.11	0.35	0.35	0.26
Minimum	1.87	1.83	1.28	4.06	3.92	4.49
Maximum	2.01	1.93	1.55	4.86	4.75	5.15

Table 28. continued.

	BL	BlH	MSW	RAP	DL
Maxomys inas					
N	11	11	11	11	11
Mean	5.33	3.54	2.76	9.04	18.08
Std. Deviation	0.22	0.20	0.24	0.51	0.68
Minimum	4.99	3.24	2.13	8.18	16.79
Maximum	5.67	3.82	3.00	10.01	19.29
Maxomys moi					
N	14	14	14	14	14
Mean	5.52	3.93	2.79	9.29	21.49
Std. Deviation	0.24	0.23	0.19	0.77	1.55
Minimum	5.03	3.47	2.46	7.43	18.26
Maximum	5.88	4.29	3.23	10.53	23.68
Maxomys inflatus					
N	5	5	5	5	5
Mean	5.00	3.51	3.02	8.88	21.13
Std. Deviation	0.13	0.25	0.29	0.40	0.65
Minimum	4.86	3.21	2.75	8.47	20.30
Maximum	5.13	3.86	3.41	9.42	21.83