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SYSTEMATIC AND DESCRIPTION OF NEW SPECIES OF *MAXOMYS* (MURIDAE)

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ABSTRACT

We review the murid rodents of the genus *Maxomys* from Borneo, and recognise one new species, *Maxomys tajuddinii* sp. nov. The type locality is Empakuq village (1^o 19’ 8.11” S, 120^o 6’ 8” E), Melak District, Kutai, East Kalimantan, Indonesia. Descriptive and multivariate Analyses were used to reveal the variation and distinctive characters of this new species from its closest relatives. Results depicted that the morphology of new species *M. tajuddinii* sp. nov. resembles that of *M. whiteheadi* Thomas, 1894, which occurs throughout the Borneo island. Nine characters distinguish the new species: (1) sharp demarcation on the flanks between the dorsal and ventral pelage; (2) tail slightly similar to longer than head and body length, tapered and bicoloured, brownish black on dorsal surface and creamy white on ventral surface; (3) individual hairs covering head and body long, thick, and spinous, resulting in a dense pelage; (4) brownish orange buff dorsal pelage, with long, dense, spinous, black tipped guard hairs and creamy white ventral pelage; (5) rostrum long and narrow relative to overall skull size; (6) incisive foramina narrow relative to length, with posterior margins located slightly anterior to first molar; (7) first upper molar with three roots; (8) cusp t^4 complete on first and second molars; and (9) 10 – 12 scales per cm on tail. Morphologically, *M. tajuddinii* sp. nov. is unlike any other described species of *Maxomys* known to occur on Borneo. *M. tajuddinii* is the new species occurs in sympatry with *M. whiteheadi* Thomas, 1894 in peat swamp forests, logged mixed dipterocarp forests or waterlogged and periodically inundated sandy clay soil dominated by kerangas vegetation.

Keywords: description, new species, *M. tajuddinii* sp. nov., morphology, Borneo

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 in 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 (*eg*. Corbet & Hill 1992, Musser & 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 & 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 & 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 colour were not quite right with *M. whiteheadi* Thomas, 1894 and suspected as distinct species.

In the present study, we compared morphological characters between these new specimens and all extant species of *Maxomys* from Borneo. The results suggest that the new specimens warrant recognition as a new species, and we formally describe them as such.

MATERIAL AND METHODS

Study Area and Fieldwork

Surveys were conducted in Melak district, East Kalimantan from

Figure 1. 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)

14 to 31 May 2006. Field surveys in Sarawak, Sabah and the Malay Peninsula were conducted from February to November 2008 (Table 1, Fig. 1).

Fifty to 100 cage traps and Sherman traps 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. We 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. Captured specimens were placed in cloth bags, measured using digital callipers (Mitutoyo^{TM}) and weighed using Pesola spring scales. Identification of specimens followed Corbet & 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 70% ethanol solution for permanent storage.

Morphological Data and Analyses

Values (in millimeters) for head and body length (HB), tail length (TL), hind foot length (HF), and ear length were taken from fresh specimens. The following cranial and dental dimensions (Fig. 2, following Musser (1991), Musser & Newcomb (1983) and Musser *et al.* (2005)) were measured on adult specimens (determined by molar wears on the

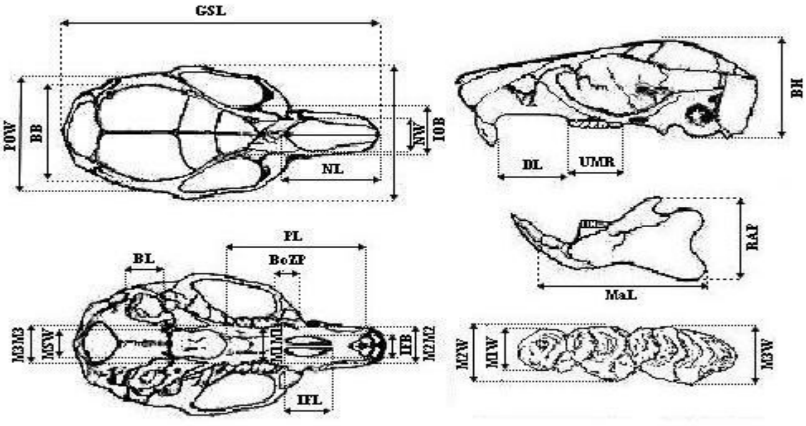

Figure 2. Views of cranium and molars showing limits of cranial and dental measurements. See text for abbreviations and additional information. (adapted and modified from Musser 1991)

occlusal surface) using digital calipers accurate to the nearest 0.1 mm: Greatest Skull Length (GSL), Post Orbital Breadth (POW), Zygomatic Breadth (ZB), Zygomatic Plate (ZP), Inter Orbital Breadth (IOB), Nasal Length (NL), Nasal Width (NW), Braincase Width (BW), Height of Braincase (HB), Diastema (D), Palatal Length (PL), Upper Molar Row (UMR), Incisive Foramina Length (IFL), Incisive Foramina Breadth (IFB), Molar 1Width (M1W), Molar 2 Width (M2W), Molar 3 Width (M3W), Molar 1 to Molar 1 (M1M1), Molar 2 to Molar 2 (M2M2), Molar 3 to Molar 3 (M3M3), Bulla Tymphani Length (BL), Meso Pterygoid Width (MPW), Ramus Angular Process (RAP), Dental Length (DL).

We calculated standard descriptive statistics (mean, standard deviation and range) for each measurement. Anatomical terminology follows Musser (1991), Musser & Newcomb (1983) and Musser *et al.* (2005). We employed multivariate statistical analyses to understand the nature and distribution of morphometric variation. These included for Principal Component Analysis (PCA) by correlation matrix and Discriminant Function Analysis (DFA).

RESULTS

On the basis of the distribution of morphological variation detected in specimens of Bornean *Maxomys*, we compare the definition of *M. whiteheadi* and describe one new species. The following systematics section describes the differences between the geographic groups of *M. tajuddinii* sp. nov. to facilitate the identification and classification of its distinctness.

SYSTEMATICS

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 bicolour, 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 Sumatera. Also present on the Malay Peninsula, possibly extending N of the Isthmus of Kra into Thailand (Corbet & 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^{o} 19’ 8.11” S, 120^{o} 6’ 8” E), East Kalimantan, Indonesia.

Paratypes:

There are 11 adult males and 9 adult females.

Six adult females and one adult male were collected from the same locality with the holotype, by A. S. Achmadi and I. Maryanto: 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. Two adult males were collected from Fraser Hill Forest Reserve (TK153703 and TK153717) on 10 July 2008 with weight 70 and 85 g. Seven adult males and two adult females were collected from Sumatera (MZB 28960 – 28968) by Maharadatunkamsi between 2 – 11 January 2007 (see Appendix 1) with weights 73, 74, 67, NA, 57, 87, 84, 121 and 85 gs. A male (no. 471) was collected from Balambangan Island (Sabah) and a female (no.1618) was collected from Jambusan cave (Sarawak) without field labels and catalog so measurements were not recorded. 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 (Fig. 3).

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.

Figure 3. 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)

The slim, tapered tail is either similar or slightly longer than the 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 (Fig. 4).

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

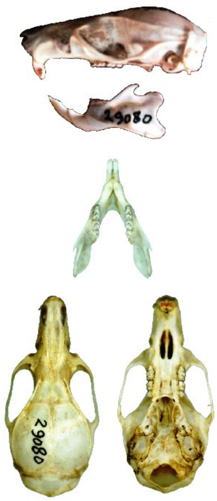

Figure 4. View (x 1) of cranium and dentary of the holotype *M. tajuddinii* sp. nov. (MZB 29080) from East Kalimantan

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 appear 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 & 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 primarily consists of cusp t^8 merged cusp t^9 to form distorted diamond-shaped chewing surface. The occlusal pattern of third upper molar is basically compacted form of that characterizing the second upper molar; a conspicuous cusp t^1, no cusp t^3, and small posterior oblong chunk (Fig. 5). A cusp of t^7 is difficult to detect in all uppermolar, and its possibilities not present in this species.

The lower molars are relatively long compared to the 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.

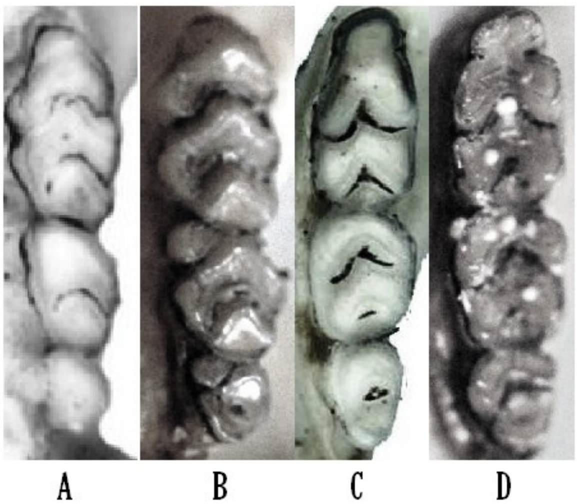

Figure 5. Occlusal view (approximately x 10) of adult upper and lower molars in species of *M. tajuddinii* sp. nov. From left to right; A. Uppermolars of MZB 29080 (Holotype); B. Uppermolars of TK153717 (Malay peninsular); C. Lower molars of MZB 29080 (Holotype); Lowermolars of TK153717 (Malay peninsular)

Distribution and Habitat

Since the first expedition conducted in Melak, Kutai, East Kalimantan and collected the interesting specimens, the following surveys revealed the 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 Malay peninsular (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 Sumatera, 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 starting from Kalimantan, Sarawak, Sabah, Malay peninsular and Sumatera 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).

DISCUSSION

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 colour 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 & Hill (1992) appears slightly different because they 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 2).

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 colour on ventral fur. A shorter tail percentage (90 – 100 %) seemed 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 is larger in range either breadth or length on each trait as show in Table 3. The molar size of *M. tajuddinii* sp. nov. is slightly larger than the other one.

Crania and dentaries of the two species are in contrast as seen in Figs. 6-8. 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 was carried out to distinguish and strengthen the descriptive analyses as mentioned earlier that the morphology of *M. tajuddinii* sp. nov. and *M. whiteheadi* Thomas, 1894 are clearly distinct. Cranial, dentary and dental measurements were analysed, and in addition the skull measurements of *M. ochraceiventer* Thomas, 1894 and *M. baeodon* Thomas, 1894 also analysed and 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,

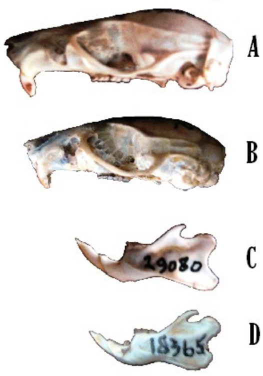

Figure 6. Lateral view (x 1) of head skulls showing differences between *M. tajuddinii* sp. nov. (A & C; holotype; MZB 29080) and *M. whiteheadi* Thomas, 1894 (B & D; MZB 18365)

Figure 7. Dorsal view (x 2) comparing adult crania of species *Maxomys*. From left to right; A. *M. tajuddinii* sp. nov (TK153703); B. *M. tajuddinii* sp. nov (MZB 29080, Holotype); C. *M. whiteheadi* Thomas, 1894 (MZB 14749); D. *M. whiteheadi* Thomas, 1894 (MZB 18365)

Figure 8. Ventral view (x 2) comparing adult crania of species *Maxomys*. From left to right; A. *M. tajuddinii* sp. nov (TK153703); B. *M. tajuddinii* sp. nov (MZB 29080, Holotype); C. *M. whiteheadi* Thomas, 1894 (MZB 14749); D. *M. whiteheadi* Thomas, 1894 (MZB 18365)

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 4). 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 (Fig. 9 and Table 5).

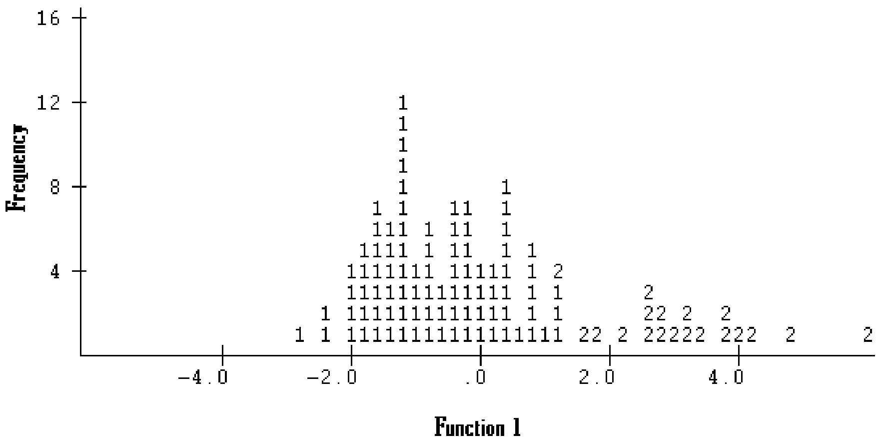

Figure 9. Plot of a number of function 1 and frequency of variables skull measurements from (1) *M.whiteheadi* Thomas, 1894 and (2) *M. tajuddinii* sp. nov.

Table 5. 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	0
			100%	0%
2	*M. tajuddinii* sp.nov	19	0	19
			0%	100%

Percent of "grouped" cases correctly classified : 100 %

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 (Figs. 10, 11 and Table 6, 7).

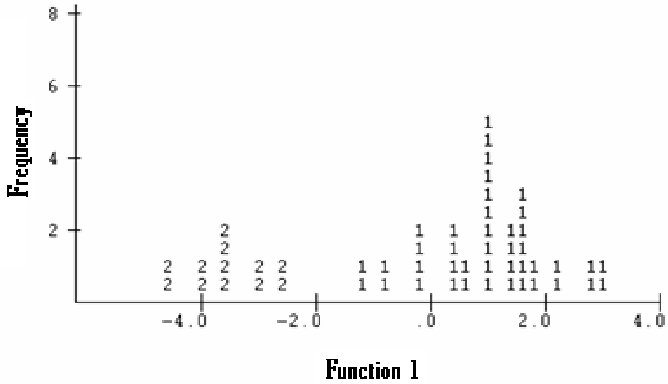

Figure 10. Plot of a number of function 1 and frequency of variables skull measurements from (1) *M. tajuddinii* sp. nov. and (2) *M. baeodon*

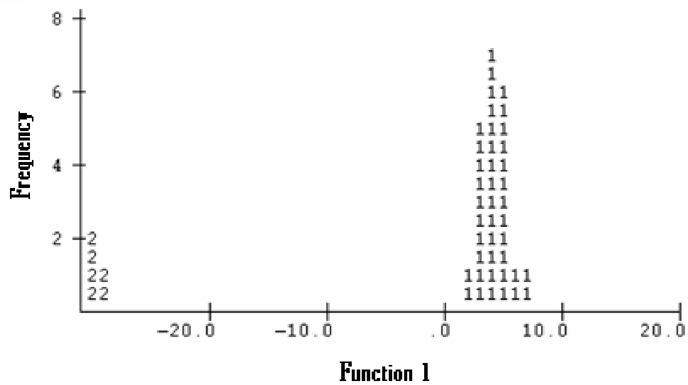

Figure 11. Plot of a number of function 1 and frequency of variables skull measurements from (1) *M. tajuddinii* sp. nov. and (2) *M. ochraceiventer* Thomas, 1894

Table 6. 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 %

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* (Fig. 12). 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* (Fig. 13).

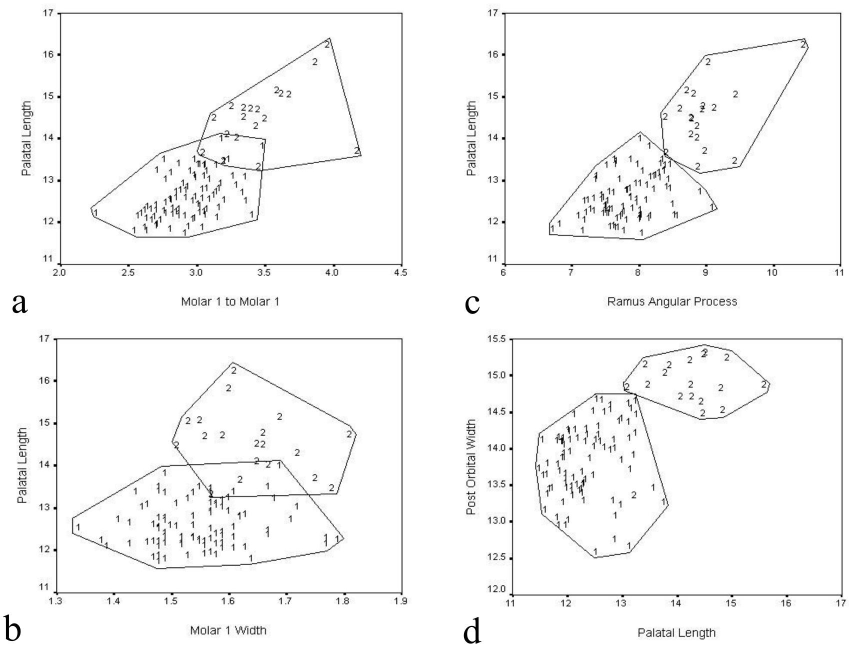

Figure 12. Bivariate plots of : a. palatal length against molar 1 to molar 1; b. palatal length against molar 1 width; c. palatal length against ramus angular process and d. palatal length against post orbital width. (1) *M. whiteheadi*; (2). *M. tajuddinii* sp. nov.

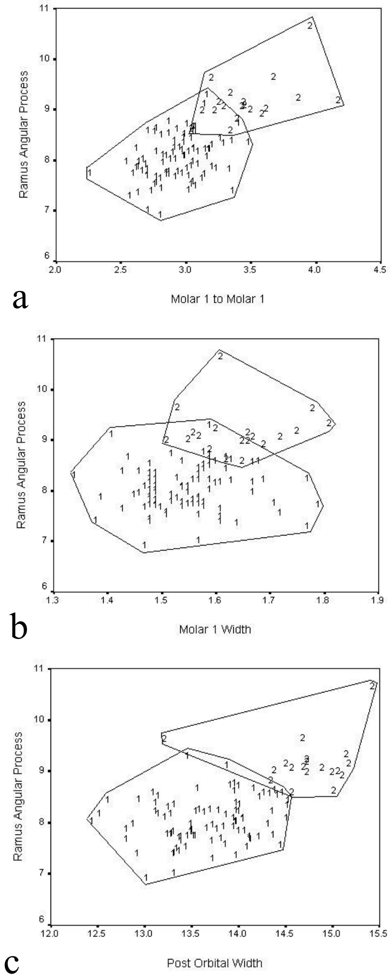

Figure 13. Bivariate plots of : a. ramus angular process against molar 1 to molar 1; b. ramus angular process against molar 1 width and c. ramus angular process against post orbital width. (1) *M. whiteheadi*; (2). *M. tajuddinii* sp. nov.

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Table 1. 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°42'57" E 101° 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 2. 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 & 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 colour	√	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 3. 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
Bulla Tymphani 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 4. 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

APPENDIX 1. Samples used for morphometric analyses

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	

NO	SPESIES	Museum No.	SEX	LOCALITY	Depository	Notes
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, Sumatera	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, Sumatera Utara	MZB	
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	

NO	SPESIES	Museum No.	SEX	LOCALITY	Depository	Notes
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, Sumatera	MZB	
58	*M. whiteheadi*	24957	Female	Tapanuli Selatan, Sumatera	MZB	
59	*M. whiteheadi*	2071	Female	Deli, Sumatera Utara	MZB	
60	*M. whiteheadi*	24931	Female	Tapanuli Selatan, Sumatera	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, Sumatera Utara	MZB	
76	*M. whiteheadi*	24898	Male	Kawasan Tesso Nilo, Riau	MZB	
77	*M. whiteheadi*	13,031	Female	Bukit Bawang, Kec. Bohorak, Sumatera 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	

NO	SPESIES	Museum No.	SEX	LOCALITY	Depository	Notes
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	
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*	29,058	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
92	*M. tajuddinii*	29,062	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
93	*M. tajuddinii*	29,066	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
94	*M. tajuddinii*	29,068	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
95	*M. tajuddinii*	29,070	Female	Intulingau, Maruwai, Kalimantan Timur	MZB	Paratype
96	*M. tajuddinii*	29,077	Male	Melak, Maruwai, Kalimantan Timur	MZB	Paratype
97	*M. tajuddinii*	29,080	Male	Melak, Maruwai, Kalimantan Timur	MZB	Holotype
98	*M. tajuddinii*	18,482	NR	Gn.Kerinci, Sungai Penuh, Jambi	MZB	
99	*M. tajuddinii*	29,086	Female	Melak, Maruwai, Kalimantan Timur	MZB	Paratype
100	*M. tajuddinii*	28,961	Male	Hutan gambut awang, Kec.Sungai Rawa, Inderapura, Riau	MZB	Paratype
101	*M. tajuddinii*	28,962	Female	Hutan gambut awang, Kec.Sungai Rawa, Inderapura, Riau	MZB	Paratype
102	*M. tajuddinii*	28,960	Female	Hutan gambut awang, Kec.Sungai Rawa, Inderapura, Riau	MZB	Paratype
103	*M. tajuddinii*	28,963	Male	Hutan gambut awang, Kec.Sungai Rawa, Inderapura, Riau	MZB	Paratype
104	*M. tajuddinii*	28,967	Male	BKM KM 70 Pangkalan Kerinci,Kab.Palalawan, Riau	MZB	Paratype
105	*M. tajuddinii*	28,968	Male	BKM KM 70 Pangkalan Kerinci,Kab.Palalawan, Riau	MZB	Paratype

NO	SPESIES	Museum No.	SEX	LOCALITY	Depository	Notes
106	*M. tajuddinii*	TK153703	Male	Fraser's Hill, Malay Peninsula	UNIMAS	Paratype
107	*M. tajuddinii*	TK153717	Male	Fraser's Hill, Malay Peninsula	UNIMAS	Paratype
108	*M. tajuddinii*	TK152349	NR	Kubah National Park, Sarawak	UNIMAS	Paratype
109	*M. tajuddinii*	TK152861	NR	Kubah National Park, Sarawak	UNIMAS	Paratype
110	*M. tajuddinii*	471	Male	P. Balambangan, Sabah	UNIMAS	
111	*M. tajuddinii*	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	

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