MORPHOLOGICAL VARIATION OF WHITEHEAD'S RAT *Maxomys whiteheadi* (Thomas, 1894) (RODENTIA: MURIDAE) FROM KALIMANTAN AND SUMATRA

Martua H. Sinaga[1], Antonia J. Gorog[2] & Alejandro A. Chinen[3]

[1] Museum Zoologicum Bogoriense-Indonesian Institute of Sciences (LIPI)
Cibinong, West Java, Indonesia 16911
e-mail*: usinaga@yahoo.com*
[2]University of Michigan, Museum of Zoology and Department of Ecology and Evolutionary Biology
1109 Geddes Ave., Ann Arbor, MI 48109, USA
[3]Graduate School of Environmental Earth Science
Hokkaido University, Sapporo, Japan 060-0811

ABSTRACT

Sinaga, M.H., A.J Gorog & A.A Chinen. 2007. Morphological variation of Whitehead's rat *Maxomys whiteheadi* (Thomas, 1894) (Rodentia: Muridae) from Kalimantan and Sumatra. Zoo Indonesia 62 (2): 75-86. *We conducted a study of morphological variation in Whitehead's rat (Maxomys whiteheadi) based on specimens available at the Museum Zoologicum Bogoriense. A total of 224 adult specimens from the Indonesian island's of Sumatra and Kalimantan were examined using measurements of 17 skull and four external characters. Multiple analyses of variance demonstrated that 20 of characters measured varied significantly with location. Only breadth of zygomatic plate did not show a significant effect by location. One character, hind foot length, was significantly affected by sex, and the characters head and body length, breadth of braincase, and breadth of molar 1 showed a significant interaction (p< 0,05) between sex and location. Three distinct morphological groups of M. whiteheadi were recognized within Kalimantan using discriminant function analysis. These were: a West and East Kalimantan group; a Central Kalimantan group; and a North East Kalimantan group. No distinct morphological groups were observed among the Sumatra specimens. The discriminant analysis indicated that most of the variation (79,9%) distinguished the Kalimantan and Sumatra populations from one another.*

Keywords: *Whitehead's rat, Maxomys whiteheadi, Sumatra, Kalimantan*

ABSTRAK

Sinaga, M.H., A.J Gorog & A.A Chinen. 2007. Variasi morfologi tikus Whitehead *Maxomys whiteheadi* (Thomas, 1894) (Rodentia: Muridae) dari Kalimantan dan Sumatra. Zoo Indonesia 62 (2): 75-86. *Penelitian mengenai variasi morfologi tikus* Whitehead (*Maxomys whiteheadi*) berda*satrkan specimen koleksi yang ada di Museum Zoologicum Bogoriense telah dilakukan. Sejumlah 224 spesimen dewasa berasal dari Sumatera dan Kalimantan dianalisa berdasarkan pengukuran 17 karakter tengkorak dan empat karakter mrfologi. Hasil multiple analyses of variance menunjukkan bahwa 20 karakter yang diuji berbeda nyata berdasarkan tipe lokasi. Hanya karakter breadth of zygomatic plate yang tidak berbeda. Satu karakter lainnya, kaki belakang, sangat nyata dipengaruhi oleh jenis kelamin dan karakter panjang kepala hingga badan, breadth of braincase, dan lebar molar ke 1 menunjukkan interaksi yang nyata (p< 0.05) antara jenis kelamin dan lokasi. Tiga kelompok berdasarkan karakter morfologi yang sangat nyata dari M. whiteheadi dari wilayah Kalimantan adalah kelompok Kalimantan Barat dan Timur; kelompok Kalimantan*

Tengah; dan kelompok Timur Laut Kalimantan. Tidak dijumpai hal yang serupa untuk wilayah Sumatera. Hasil discriminant analysis menunjukkan bahwa kebanyakan variasi (79.9%) dapat membedakan antara populasi tikus whithead Kalimantan dengan Sumatra.

Kata kunci: *tikus Whitehead, Maxomys whiteheadi, Sumatera, Kalimantan.*

INTRODUCTION

The genus *Maxomys* was originally assigned to the species *Maxomys bartelsii*. Subsequently, *Maxomys* was subsumed into the genus *Rattus* as a subgenus containing several species, including some species now placed in the genus *Niviventer* (Musser & Carleton 1993). Most of the currently-recognized species of *Maxomys* and *Niviventer* were placed in *Lenothrix*, which also was treated as a subgenus of *Rattus* (Ellerman & Morrison-Scott 1966; Laurie & Hill 1954; Musser et al. 1979). Finally, Musser and Newcomb (1983) confirmed that *Maxomys* is not closely related to *Rattus* and restored the genus-level ranking of *Maxomys.*

Maxomys comprises small to medium-sized rats of a generalized appearance. Key characters of the genus include a long and slender hind foot with smooth and naked plantar surfaces, a tail usually shorter or only slightly longer than head and body, a broad and inflated braincase, broad incisive foramina and small bullae (Musser & Carleton 1993).

Maxomys whiteheadi is a small spiny rat has a sharply bicolored tail that is shorter than head and body. Dark brown dorsally, and the venter gray, ochraceous color on the anterior flanks. The skull has small bulae, broad incisive foramina, and larger teeth. This species is found on Borneo, Sumatra and the Malay Peninsula south of the Isthmus of Kra, but absent from Java (Musser & Carleton 1993),

In Indonesia, six subspecies *M. whiteheadi* are recognized (Musser & Newcomb 1983; van Strien, 1986; Corbet & Hill 1992). These are: *M. w. whiteheadi* (Thomas 1894) on Middle East Kalimantan; *M.w. melanurus* (Shamel 1940) on the east coast of Kalimantan; *M. w. coritzae* (Sody 1941) in Riam Kotawaringin Southwest Kalimantan; *M. w. batamanus* (Lyon 1907) in the Riau Archipelago; *M. w. batus* (Miller 1911) in Aceh, North Sumatra; *M. w. subitus* (Chasen 1940) on the Natuna Island. A seventh putative subspecies (*M. whiteheadi subsp.* incert) was recorded by Sody (1941) in South Sumatra.

In this study, we used a suite of external and skull morphological characters to (1) test for morphological differentiation among the seven named subspecies of *M. whiteheadi*, and (2) examine the effect of sex and location on morphology of *M. whiteheadi.*

MATERIALS & METHODS

A total 224 adult specimens of *M. whiteheadi* deposited at the Museum Zoologicum Bogoriense (MZB) were examined. Adult specimens were selected based on the criteria of having a fused basioccipital-basissphenoid suture and fully erupted alveolar molars.

Table 1. Raw data of external and cranial measurements (mm) for *Maxomys whiteheadi* from Sumatra and Kalimantan. Sd = standard deviation; Min = minimum; Max = maximum.

Var.	Sumatra (n = 73)				Kalimantan (n = 224)			
	Mean	sd.	Max.	Min.	Mean	sd.	Max.	Min.
HB	112,93	± 23,58	148	84	122,86	± 11,69	158	95
T	100,96	± 19,33	129	86	114,38	± 9,87	141	92
HF	26,45	± 4,80	30	25	28,34	± 2,05	32	24
E	16,33	± 2,91	19	15	17,91	± 0,90	20	15
GSL	32,74	± 1,58	36,35	29,60	33,07	± 1,68	36,83	29,36
HBC	9,13	± 0,35	10,17	8,59	9,31	± 0,37	10,24	8,40
BZP	2,97	± 0,22	3,58	2,61	2,99	± 0,21	3,54	2,51
LR	9,88	± 0,63	11,41	8,52	10,23	± 0,68	11,84	8,46
BR	5,86	± 0,36	6,69	4,75	5,76	± 0,35	6,89	4,87
IB	5,81	± 0,29	6,58	5,10	5,67	± 0,26	6,34	4,95
BBC	13,83	± 0,48	14,90	12,62	14,95	± 0,68	14,70	12,52
ZB	14,82	± 0,55	16,09	13,57	14,95	± 0,68	16,66	13,10
LD	7,77	± 0,53	8,98	6,60	7,9	± 0,64	9,34	6,50
LBP	5,83	± 0,37	6,73	4,89	5,78	± 0,40	6,60	4,82
PPL	12,00	± 0,69	13,50	10,32	12,21	± 0,79	13,84	10,45
BMF	2,53	± 0,19	3,03	2,00	2,52	± 0,18	3,00	2,10
CLM1-3	5,42	± 0,27	5,97	4,94	5,38	± 0,23	6,00	4,57
LIF	4,24	± 0,38	5,46	3,54	4,41	± 0,34	5,21	3,30
BM1	1,58	± 0,07	1,73	1,40	1,56	± 0,06	1,69	1,41
BM2	1,48	± 0,10	1,76	1,28	1,45	± 0,07	1,62	1,26
BM3	1,09	± 0,07	1,29	0,90	1,06	± 0,06	1,22	0,95

The following standard external measurements (in mm) were recorded from collectors specimen labels: head and body length (HB) by subtracting tail length (T) from total length (TL); hind foot length (HF); and ear length (E). Seventeen cranial measurements (in mm) were used in this study: greatest skull length (GSL); height brain case (HBC); breadth of zygomatic plate (BZP); length of rostrum (LR); breadth of rostrum (BR); interorbital breadth (IB); breadth of brain case (BBC); zygomatic breadth (ZB); length of diastema (LD); length of bony palate (LBP); post palatal length (PPL); breadth of mesopterygoid fossa (BMF); crown length of molars 1-3 (CLM1-3); length of incisive foramina (LIF); breadth of molar 1 (BM1); breadth of molar 2 (BM2); and breadth of molar 3 (BM3). All measurements were made by MHS using Vernier calipers and recorded to two decimal places.Variation due to the factors sex and location, and the

interaction between these factors was examined by Multiple Analysis of Variance (MANOVA).

Morphological differences among subspecies and species were examined using discriminant function analysis (DFA). External characters were not used for the DFA because they might be affected by minor methodological differences among collectors. Seventeen cranial characters were entered into the DFA. The analysis was also run on a reduced set of eleven characters that maximized F values (minimizing Wilks' lambda values). The DFA plot based on the reduced set of characters reflected that obtained from the full set of seventeen characters. Consequently, we present only the analysis of the reduced set characters. Computations for all analyses were undertaken with the SPSS statistical package.

RESULTS

Univariate analysis

Descriptive statistics of external and skull characters for each locality are presented in Table 1. These demonstrate that *M. whiteheadi* from Kalimantan are larger for most characters than specimens from Sumatra with the exception of BR, IB, LBP, BMF, CLM 1-3, BM1, BM2 and BM3.

Multiple Analysis of Variance (MANOVA)

The MANOVA was used to test for the main effect of sex and location, and to examine potential interaction between these factors, on morphological characters. All characters values presented in the following MANOVA are raw values (Table 2). Location was found to have a significant effect on most characters ($0{,}05 \geq p \geq 0{,}01$). The exceptions were BZP, and BMF.

Table 2. MANOVA of skull and external body characters of *Maxomys whiteheadi* by location, sex and interaction.

Variables	Location		Sex		interaction	
	F	Sig.	F	Sig.	F	Sig.
HB	10,319	0,000	0,008	0,927	4,598	0,001
T	42,312	0,000	1,603	0,207	2,053	0,072
HF	72,001	0,000	7,577	0,006	2,150	0,061
E	27,714	0,000	0,716	0,398	0,561	0,730
GSL	9,058	0,000	0,259	0,611	0,454	0,810
HBC	21,896	0,000	0,634	0,427	1,726	0,130
BZP	2,224	0,053	0,053	0,818	0,788	0,559
LR	12,426	0,000	0,031	0,861	1,563	0,172
BR	4,815	0,000	0,188	0,665	0,761	0,579
IB	6,932	0,000	0,122	0,727	2,131	0,063
BBC	9,190	0,000	0,797	0,737	2,959	0,013
ZB	12,623	0,000	0,219	0,640	1,946	0,088
LD	10,931	0,000	0,224	0,637	0,860	0,509
LBP	21,932	0,000	2,067	0,152	1,799	0,114
PPL	6,579	0,000	0,101	0,751	1,307	0,262
BMF	2,335	0,043	0,290	0,590	0,849	0,516
CLM1-3	15,310	0,000	0,327	0,568	1,859	0,103
LIF	4,384	0,001	0,488	0,485	0,764	0,576
BM1	12,952	0,000	3,698	0,056	2,509	0,031
BM2	13,836	0,000	2,233	0,136	1,027	0,403
BM3	12,809	0,000	0,231	0,631	1,114	0,354

Only HF was significantly affected by sex ($0,05 \geq p \geq 0,01$). A significant interaction between sex and location was observed for HB, BBC, and BM1 ($p<0,05$).

Multivariate analysis

1.Kalimantan group

Sody (1941) described a new subspecies from Riam Kotawaringin southwest Kalimantan as *coritzae* based the paler pelage of these samples than any other material from Borneo and Sumatra, and the pure light grey belly compared with *M. w. whiteheadi* from Middle East Kalimantan. We observed similar differences in pelage in our specimens.

DFA was carried out for a reduced set of 11 characters to examine geographic variation among samples from Kalimantan. This analysis reflected similar configuration in discriminant function space to that using the complete character set.

The cumulative variation explained by the first three canonical variate functions was 100%, with function 1,2 and 3 explaining 72,7; 16,3 and 11,0% respectively (Table 3) The overall percentage of cases correctly classified to their location was 81,3% for West Kalimantan, 93,8% for Central Kalimantan, 89,7% for East Kalimantan, and 81,3% for North East Kalimantan group.

Misclassifications resulted when specimens from West Kalimantan population were classified in the Central Kalimantan group (3,1%), and in the East Kalimantan group (15,6%). Some specimens from Central Kalimantan were misclassified in the East Kalimantan group (3,1%), and in the North East Kalimantan group (3,1%). Several East Kalimantan specimens are classified incorrectly to West Kalimantan (7,7%) and, to Central Kalimantan (2,6%). Finally, some North East Kalimantan specimens are incorrectly grouped with West Kalimantan samples (6,3%), and Central Kalimantan samples (12,5%).

This study clearly showed that there are three distinct groups of *M. whiteheadi* within Kalimantan.

Table 3. Standardized and unstandardized (in bracket) canonical variate function coefficients for Kalimantan *Maxomys whiteheadi* (Gunung Palung and Tanjung Puting, West Kalimantan; Sebangau and Barito Ulu, Central Kalimantan; Bukit Bangkirai, East Kalimantan; and Kayan Mentarang, North East Kalimantan).

Character	Function 1	Function 2	Function 3
HBC	0,802 (3,343)	-0,201 (-0,838)	-0,227 (-0,945)
BZP	-0,293 (-1,489)	-0,120 (-0,610)	0,482 (2,450)
BR	-0,082 (-0,263)	-0,821 (-2,621)	-0,283 (-0,904)
IB	-0,185 (-0,771)	0,895 (3,725)	-0,664 (-2,762)
ZB	0,121 (0,228)	1,157 (2,181)	0,141 (0,266)
LD	0,385 (0,741)	-0,285 (-0,550)	-0,435 (-0,837)
LBP	0,327 (1,169)	-0,161 (-0,577)	0,077 (0,274)
PPL	-0,295 (-0,427)	-0,560 (-0,811)	0,903 (1,307)
CLM1-3	0,463 (2,775)	0,125 (0,747)	0,599 (3,589)
BM1	0,369 (-6,562)	0,463 (8,242)	-0,177 (-3,153)
BM2	0,537 (8,382)	-0,208(-,3,247)	-0,155 (-2,418)
Constant	-48,437	-23,543	-3,415
Variation explained (%)	72,7	16,3	11,0

These are: a Central Kalimantan group, described as *M. w. whiteheadi* by Thomas (1894); a North East Kalimantan group (previously unnamed);, and a West and East Kalimantan group, described as *M. w. coritzae* (Sody 1941) from Riam Kotawaringin that close with Gunung Palung location that specimens examined and we assumed as representative of West Kalimantan, and *M. w. melanurus* (Shamel 1940) from east coast Kalimantan as representing East kalimantan were clustered together as a group. The plots of function 1 and 2 indicates that specimens from West Kalimantan and East Kalimantan overlap in 11 selected characters analyzed (Figure 1).

2.Sumatra group

Within Sumatra, three subspecies of *M. whiteheadi* were recognized by Chasen: *M. w. batus* from Aceh, North Sumatra; *M. w. batamus* from the Riau Archipelago and central East Sumatra; and a group from South Sumatra recognized by Sody (1941) as distinct subspecies (*M. whiteheadi subsp.* incert.).

The DFA for the Sumatra population was run using two selected characters (LBP & BM2). A total of 57,5% of original grouped cases were correctly classified. The DFA also extracted two significant functions that explained 100% of variation. Function 1 explained 59,6% of the variance, and function 2 explained 40,4% (Table 4).

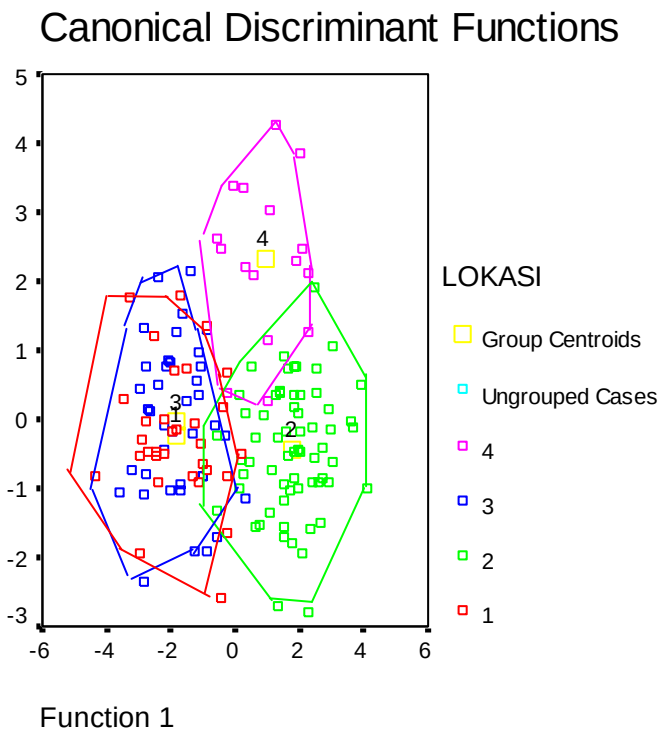

Figure 1. Plot of function 1 against 2 from canonical variate analysis of *M. whiteheadi* Kalimantan group. (1) Gunung Palung and Tanjung Putting (West Kalimantan); (2) Sebangau and Barito Ulu (Central Kalimantan); (3) Bukit Bangkirai (East Kalimantan) and (4) Kayan Mentarang (North East Kalimantan).

Table 4. Canonical variate function coefficient in the Sumatra populations of *M. whiteheadi*. Standardized values followed by unstandardized values (in brackets) for two cranial characters (LBP and BM2).

Characters	Function 1	Function 2
LBP	0,931 (2,383)	-0,510 (-1,306)
BM2	0,167 (2,417)	1,049 (15,187)
Constant	-16,601	-8,916
Variation explained (%)	59,6%	40,4%

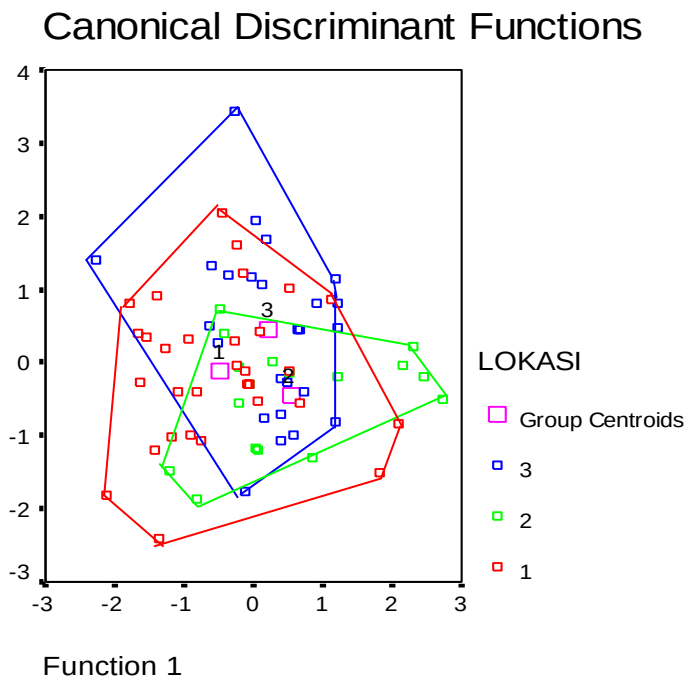

Figure 2. Plot of functions 1 and 2 from canonical variate analysis of Sumatra *M. whiteheadi* samples. (1) Aceh, Tapanuli Selatan (North Sumatra); (2) Jambi (Central Sumatra), and (3) Bengkulu, Lampung, Palembang (South Sumatra).

Table 5. Standardized and unstandardized (in the bracket) canonical variate function coefficients of *M. whiteheadi* from Kalimantan and Sumatra.

Characters	Discriminant function	Group Centroids
HBC	-0,807 (-2,210)	Kalimantan -0,539
LR	-1,003 (-1,511)	Sumatra 1,115
BR	0,402 (1,141)	
IB	0,463 (1,676)	
BBC	0,388 (0,884)	
LBP	0,533 (1,381)	
BM2	0,313 (3,858)	
Constant	-6,239	
Variation explained (%)	100	

Subspecies designations by previous taxonomists (Chasen 1940; Sody 1941) indicating that the North Sumatra form differed from Riau Archipelago and South Sumatra were not upheld with this study as demonstrated by a plot of function 1 against 2 (Figure 2). The plot shows that all specimens from North, Central, and South Sumatra are clustered tightly together, indicating that samples from different localities in Sumatra were morphologically similar.

3. Kalimantan and Sumatra group

We compared the Kalimantan samples with the Sumatra samples using a DFA was run using seven selected characters, these are: HBC, LR, BR, IB, BBC, LBP, and BM2. A total of 79,9% of original grouped cased correctly classified. 18,5% or 28 specimens of Kalimantan were misclassified into Sumatra population. Some specimens from Sumatra are classified incorrectly to Kalimantan (23,3%, or 17 samples; Table 5).

DISCUSSION

Our examination of 21 morphological characters from 224 specimens of Indonesian *M. whiteheadi* demonstrated a clear morphological division between Kalimantan and Sumatran populations. This result is consistent with those of a previous phylogenetic analysis of *M. whiteheadi* using mitochondrial DNA (Gorog et al. 2004). In this earlier study, rats from Kalimantan represented a well-supported lineage distinct from animals in the Malay Peninsula and Sumatra. This is consistent with the hypothesis that rainforest habitats on Kalimantan have been long isolated from rainforests to the west, even during periods of low sea level when land bridges among islands were formed.

Within the island of Kalimantan, three distinct morphological groups of *M. whiteheadi* were found among the samples examined (N=151). One is represented by samples from West and East Kalimantan, the second is represented by samples from Central Kalimantan, and the third by specimens from Northeast Kalimantan (Figure 3). Considerable phylogeographic structure within-species variation on Kalimantan has been found for many other taxa, including the red spiny rat *Maxomys surifer* (Gorog, Sinaga & Engstrom, 2004), orangutan *Pongo pygmaeus* (Warren et al. 2001), and the white-crowned forktail *Enicurus leschenaulti* (Moyle et al. 2005). These patterns are most likely the result of historical isolation caused by the island's multiple mountain ranges, large rivers, the formation of rain forest refugia during cooler periods of the Pleistocene, or previously higher sea levels.

The morphological groups of *M. whiteheadi* identified on Kalimantan differ from the recognized geographic subspecies in the following way: *M. w. melanurus* (Shamel 1940) from East Kalimantan and *M. w. coritzae* (Sody 1941) from West Kalimantan are same subspecies. A new subspecies recognized in this study is from North East Kalimantan (Kayan Mentarang) and *M. w. whiteheadi* (Thomas 1894) is valid representing Central Kalimantan.

Our morphological analysis of *M. whiteheadi* on Sumatra (N=73) revealed no distinct morphological groups on this island (Figure 4). Few previous studies of other taxa have used adequate sampling of Sumatran populations to test for geographic differentiation within the island. One, however, similarly demonstrated no genetic structure among populations of a primate, *Macaca nemestrina*, on Sumatra (Rosenblum et al. 1997). These results may be indicative of little

historical isolation of Sumatran populations, or, alternatively, recent expansion from a single rain forest refugium.

This result is not consistent with previous subspecies taxonomy of Sumatran *M. whiteheadi*. Miller (1911) recognized *M. w. batus* from North Sumatra; Lyon (1907) named *M. w. batamus* from Riau and Central Sumatra; and Sody (1941) described a population from South Sumatra that he considered to be unique. However, our analysis found no morphological differentiation in populations throughout the length of Sumatra.

The comparison of patterns of morphological and genetic differentiation from multiple taxa sampled from the same localities throughout Kalimantan and Sumatra would shed greater light of patterns of vicariance and faunal evolution in the region.

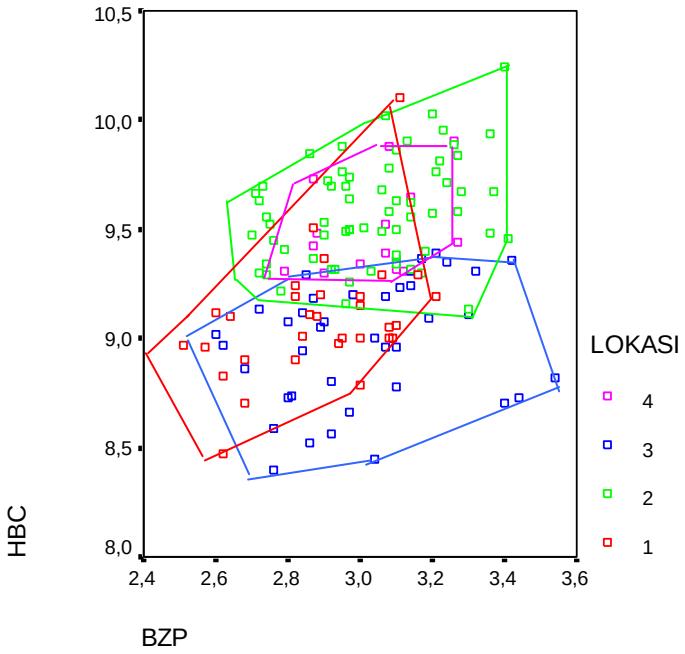

Figure 3. Bivariate plot of HBC and BZP of *Maxomys whiteheadi* from Kalimantan. (1) Gunung Palung and Tanjung Putting (West Kalimantan); (2) Sebangau and Barito Ulu (Central Kalimantan); (3) Bukit Bangkirai (East Kalimantan) and (4) Kayan Mentarang (North East Kalimantan).

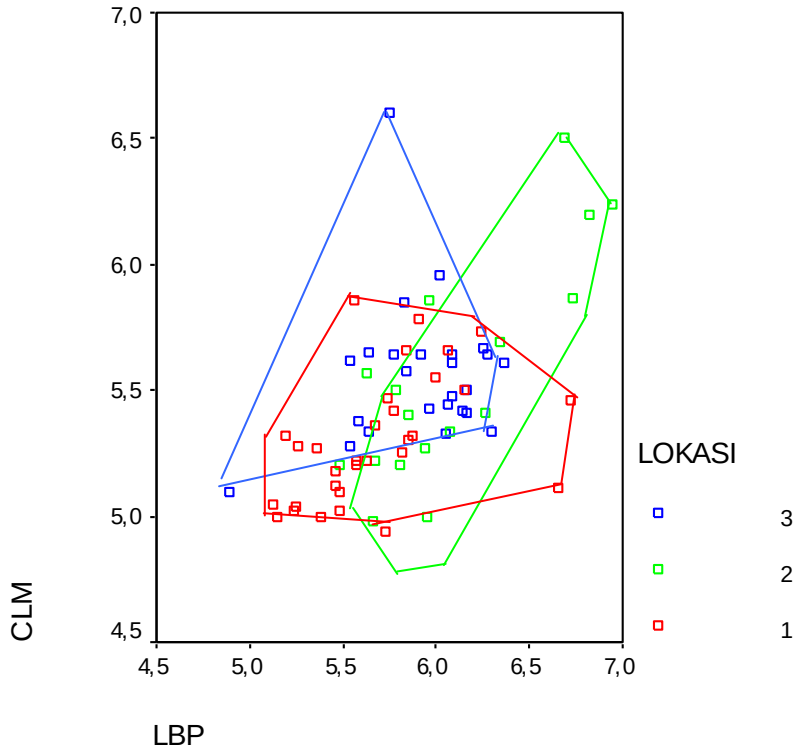

Figure 4. Bivariate plot of CLM and LBP of *M. whiteheadi* from Sumatra group. 1) Aceh, Tapanuli Selatan (North Sumatra); (2) Jambi (Central Sumatra), and (3) Bengkulu, Lampung, Palembang (South Sumatra).

ACKNOWLEDGEMENTS

The authors wish to express their gratitude to Achmad Saim B.Sc. for his collection from Sebangau Central Kalimantan that examined, Nanang and Wahyu for prepared many skulls for this study. Thanks are also due to Drs. A. Suyanto, M.Sc. for permission to examine specimens under his care.

REFERENCES

Chasen, F. N. 1940. A handlist of Malaysian Mammals. Bull. Raffles Mus., 15. 209pp.

Corbet, G.B. & J.E. Hill. 1992. The Mammals of the Indo-Malayan region: A Systematic review. Oxford Univ. Press. 488pp.

Ellerman, J. R. & T. C. S. Morrison-Scott. 1966. Checklist of Palaeartic and Indian Mammals. British Mus. (Nat. Hist.) London. 810pp.

Gorog, A.J., M.H. Sinaga & M.D. Engstrom. 2004 Vicariance or Dispersal? Historical Biogeography of Three Sunda Shelf Murine Rodents (*Maxomys surifer, Leopoldamys sabanus* and *Maxomys whiteheadi*). Biological Journal of the Linnean Society 81: 91-109.

Kitchener, D. J. & A. Suyanto. 1996. Intraspecific Morphological Variation Among Island Populations of Small Mammals in Southern Indonesia. In: Kitchener & Suyanto (eds)

Proceeding of the First International conference on Eastern Indonesian-Australian Vertebrate Fauna, Manado, Indonesia, November 22-26.

Laurie, E. M. O. & J. E. Hill. 1954. List of Land Mammals of New Guinea, Celebes and Adjacent Islands. British Mus. (Nat. Hist.) London. 175pp.

Moyle, R.G., M. Schilthuizen, M.A. Rachman & F.H. Sheldon. 2005. Molecular Phylogenetic Analysis of the White-Crowned Forktail *Enicurus leschenaulti* in Borneo. Journal of Avian Biology 36: 96-101.

Musser G.G. & M. D. Carleton 1993. Family Muridae. In: Wilson D. E. & D. M. Reeder. Mammals Species of the World: A Taxonomic and Geographic reference. Washington Smithsonian University Press. 501-755.

Musser, G.G., J.T. Marshall & Boeadi. 1979. Definition and Contents of the Sundaic Genus Maxomys (Rodentia, Muridae). Journal of Mammalogy 60: 592-606.

Musser, G.G. & C. Newcomb. 1983. Malaysian Murids and the Giant Rat of Sumatra. Bulletin of the American Museum of Natural History 174: 329-598.

Myer, E. & P.D. Ashlock. 1991 Principles of Systematic Zoology. 2nd, edition McGraw Hill International.

Rosenblum L.L., J. Supriatna & D.J. Melnick. 1997. Phylogeographic Analysis of Pigtail Macaque Populations (*Macaca nemestrina*) Inferred from Mitochondria DNA. Amer. Jour. of Phys. Anthrop. 104: 35-45.

Sody, H. J. V. 1941. On a Collection of Rats From the Indo-Malayan and Indo-Australian Region (with descriptions of 43 new genera, species and sub species). Treubia 18: 255-325.

Thomas, O. 1894. A Preliminary Revision of the Bornean Species of the Genus Mus. Annals Mag. Nat. Hist. 14: 449-460.

van Strien, N. J. 1986. Abbreviated Checklist of the Mammals of the Australian Archipelago. School of Environmental Conservation Management, Bogor.

Warren, K. S., E.J. Verschoor, S. Langenhuijzen, Heriyanto, R.A. Swan, L. Vigilant & J.L. Heeney. 2001 Speciation and Intrasubspecific Variation of Bornean Orangutans, *Pongo pygmaeus pygmaeus.* Mollecular Biology & Evolution 18: 472-480.

MORPHOLOGICAL VARIATION OF WHITEHEAD'S RAT *Maxomys whiteheadi* (Thomas, 1894) (RODENTIA: MURIDAE) FROM KALIMANTAN AND SUMATRA: Zoo Indonesia 2007. 16(2): 75-86