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Report

The mountain giant rat of Borneo *Sundamys infraluteus* (Thomas) and its relations

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Abstract
The genus *Sundamys* comprises the species *Sundamys muelleri*, Müller's rat, which is widespread in the Sundaic biogeographical subregion, and three other taxa, the mountain giant rats of Borneo *S. infraluteus*, Java *S. maxi* and Sumatra *S. atchinensis*. Nine additional specimens of the Borneo Mountain giant rat are reported, and one field record, adding new locations to the known range of the species in the Crocker Range, notably the vicinity of Gn. Alab, and Gn. Lumaku, Sabah, and at Pa Raye, Kalimantan Utara. Measurements of the specimens, and the first from Gn. Mulu, Sarawak, are tabulated with previously published data. Trapping results indicate that this rat is confined to an altitudinal range, 900 – 2350 m, broadly corresponding with the limits of Lower Montane Forest, especially Oak-Laurel forests, and that it occurs both in pristine habitat and in disturbed forests. The topography of the uplands of northern Borneo provides connections between all locations except Mulu, which is surrounded by lowlands. A review of palaeoecological interpretations indicates that favourable habitat for this rat was more extensive in north-western Borneo in the terminal Pleistocene, but may have been more reduced than at present during warm episodes of the Holocene. Consideration of palaeo-environments in the Sundaic subregion suggests that there may have been no genetic contact between mountain giant rats of Sumatra and Borneo during the Quaternary. Although molecular evidence is lacking, it is reasonable to treat *Sundamys infraluteus*, *S. atchinenesis* and *Sundamys maxi* as distinct species, arising independently by vicariant evolution from a Pliocene ancestry.

Keywords: Mammals, Rodents, Murinae, South-east Asia, Distribution, Taxonomy

Introduction
Sundamys infraluteus (Thomas 1888), the Mountain giant rat (Payne et al.,1985: 254) or Mountain Sundamys (Wilson & Reeder, 2005: 1503) is one of three species included in the genus *Sundamys* as defined by Musser & Newcomb (1983). Of the others, Müller's rat (or Müller's Sundamys) *S. muelleri* (Jentink

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1880) is widespread in the Sundaic subregion of Southeast Asia, from southern peninsular Burma and Thailand, through Peninsular Malaysia, Sumatra, Borneo, Palawan and many other islands, excepting Java, ranging from the lowlands to lower montane altitudes. The third, Javan Sundamys *S. maxi* (Sody 1932) is confined to uplands of western Java, 900 – 1350 m (distributions from Wilson & Reeder, 2005).

The type specimen of the Mountain giant rat *Mus infraluteus* (Thomas, 1888; 1889) was prepared by John Whitehead from a carcass "in a very decomposed state and full of maggots" brought to him when camped by the Sungai Kinokok, at 3300 ft (≈1000 m), on the slopes of Gunung (Gn.) Kinabalu, Sabah, Malaysia (Whitehead, 1893: 183). Subsequent additions provided Musser & Newcomb (1983: 451) with a total of 42 specimens, all from Sabah. Collecting localities on the standard route to the summit of Kinabalu extended to above Kamborangah at 7700 ft (≈ 2350 m), and on surrounding high ground south to Bundu Tuhan (6°00'N 116°32'E, 1500 m), and at Kampung (Kg) Kiau on the south-western approach at 3000 ft (≈ 915 m). In addition, two specimens had been obtained at Pampang camp on Gn. Trus Madi (5°33'N 116°33'E), the second highest mountain in Borneo with a summit at 2649 m. The record of Gn. Mulu, Sarawak, was added by Payne et al. (1985) without comment.

Nine further specimens, and one field record, are reported below, extending the known range of the Mountain giant rat in western Sabah and adding the first record in North Kalimantan, Indonesia. Details of an individual trapped on Gn. Mulu, Sarawak, are given for the first time. Specimens discussed are in the collections of the Institute for Tropical Biology & Conservation, Universiti Malaysia Sabah (UMS) and the Sabah Museum, Kota Kinabalu (SM), Malaysia; LIPI Zoological Museum, Cibinong (MZB), Indonesia, and the Natural History Museum, London (BMNH), United Kingdom. Measurements follow the conventions of Musser & Newcomb (1983).

New Borneo records of Mountain giant rat

The Crocker Range in Sabah is a SSW-NNE trending highland area exceeding 1000 m in elevation geologically connected with Kinabalu (the type locality of the Mountain giant rat). Some 40 km from Kinabalu, a prominent peak in this range is Gn. Alab (5°30'N 116°21'E, 1762 m) in the vicinity of which Mountain giant rats have been collected. New records are: four specimens collected in 1971 (SM 1984 – 1987) at a locality noted as 'Kampung Togudon, Ulu Tuaran', which we conclude is an alternative designation of the village of this name on what is now the Tambunan road, near Gn Alab; from the entrance to the transmitter station at Km 28 Jalan Tambunan, Kampung Togudon (SM NH3504); and Gn. Alab itself (UMS 5964) (Figure 1). Also reported is the live capture of an adult female (weight 470 g) taken at Mahua Waterfalls, Mountain trail (5°48'N 116°24'E, 1310 m) (5 December 2008, Konstans Wells, unpublished).

The southern end of the Crocker Range is cut through by the Padas gorge below Tenom but, after this comparatively narrow interruption, high ground, much of it above 1500 m, continues southwards to merge with the 'Spinal Chain' of the northern half of Borneo (Smythies, 1999: 12-13). One specimen of Mountain giant rat (SM NH3496) has been taken at 1365 m elevation on Gn. Lumaku (4°52' N 115°38' E, summit 1966 m) which stands to the west of the spinal chain, but is connected by high ground.

The long, north-south trending valley of Sungei Pegalan running through Keningau to Tambunan forms the east flank of the southern limb of the Crocker Range. The east-west watershed runs further inland, through the Interior (Pendalaman) Division of Sabah, with Gn. Trus Madi a prominent feature at about 75 km from Kinabalu (summit to summit). The southern continuation becomes the international border which at this point bisects a large block of

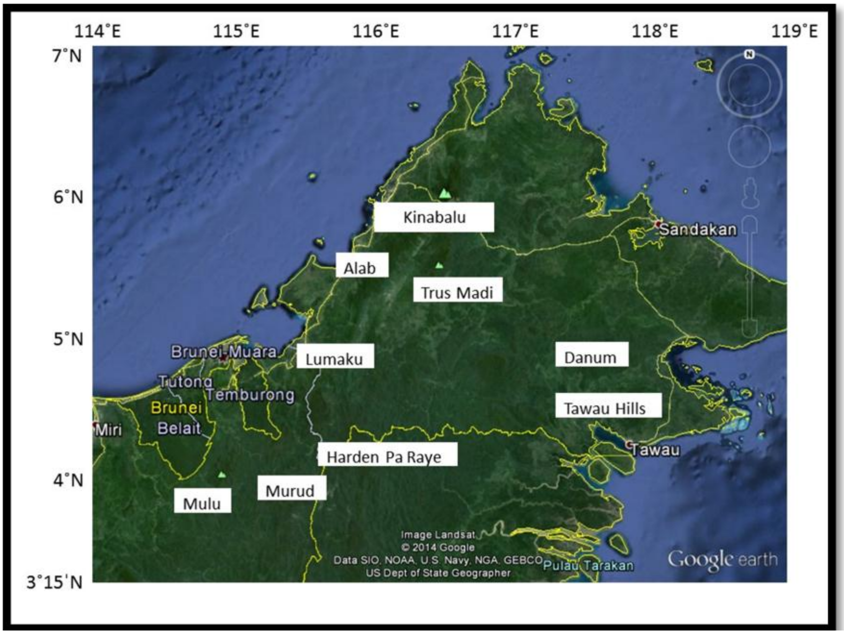

Figure 1. Map of northern Borneo, showing locations mentioned in the text. Source Google Earth.

dissected uplands generally exceeding 1000 m elevation, being the headwaters of the rivers Padas (Sabah), Trusan, Limbang and Baram (Sarawak) and Melinau (Kalimantan Utara). On the western side of this block, i.e., the Kelabit uplands of Sarawak and Gn. Murud (summit 2438 m), mammal collectors have failed to find specimens (Davis, 1958, Abdul Rahman et al.1998; 1999, Faisal et al. 2007, Wiantoro et al. 2009). On the eastern flank, in Kalimantan Utara, Indonesia, Gn. Harden (=Harun) peaks at 2160 m. On the southern approaches to this mountain, one specimen (MZB 23609) has been collected at Pa Raye (4°52'N 116°00'E, 960 m). Some 60 km to the west, and surrounded by dissected lowlands dropping to 350 m elevation, is Gn. Mulu, Sarawak (4°N 115°E, summit 2376 m). Here, at 1850 m, an aged male, with exceedingly worn dentition, entered Camp IV site by night and was collected (BMNH 78.1549). Although details have not previously been published, the record was reported by Payne et al. (1985: 254).

In other upland areas towards the east coast of Sabah, mammal-trapping surveys have failed to find specimens in the Tawau Hills (Stuebing & Shukor, 1995), where three summits exceed 1000 m, namely Magdalena (1310m), Lucia (1189 m) and Maria (1067 m).There has also been an equal lack of results on Bukit Danum (1093 m) in the Danum Valley Conservation Area.

Named localities are shown on the map (Table 1 and Figure 1), and measurements are given in Table 2. Measurements of the holotype of *S. infraluteus* (BMNH 95.10.4.22) were apparently not included in the means and ranges given by Musser and Newcomb (1983: Table 24), for which the number of samples was 10 - 14 for each measurement. Also added are measurements of BMNH 71.246, a juvenile collected by J. L. Harrison at Pampang camp on Trus Madi, which was listed by Musser & Newcomb (1983: 451) but evidently not included in their table. A later specimen from this mountain, collected in 1996 (UMS 1081, elevation not recorded) extends the range of several anatomical measurements.

Discussion

Present and past distribution of Borneo Mountain giant rat

The previously unreported locations presented here enlarge the known distribution of Mountain giant rat in Borneo. Elevations extend from 900 m to

Table 1. Museum specimens of mountain giant rats, including source reference or specimen number, and collection data.

No.	Museum Registration Number	Specimens Information			
		Island, Province, Locality, Location	Elevation (m)	Date	Sex / Age
1	Holotype BMNH 1895.10.4.22	BORNEO, Sabah, Kinabalu, Kinokok	1000	22-Mar-1888	o / -
2	Musser & Newcomb (1983)	BORNEO, Sabah, Kinabalu etc.	915-2350		
3	BMNH 71.2846	BORNEO, Sabah, Trus Madi, Pampang		22-Jul-1953	o / juv.
4	UMS 1081	BORNEO, Sabah, Trus Madi,		15-Sep-1996	f / ad.
5	SM NH1984	BORNEO, Sabah, Kg Togudon, Ulu Tuaran		16-Aug-1971	f / juv.
6	SM NH1985	BORNEO, Sabah, Kg Togudon, Ulu Tuaran		16-Aug-1971	m / juv.
7	SM NH1986	BORNEO, Sabah, Kg Togudon, Ulu Tuaran		11-Dec-1971	f / ad.
8	SM NH1987	BORNEO, Sabah, Kg Togudon, Ulu Tuaran		16-Aug-1971	m / ad.
9	UMS 5964	BORNEO, Sabah, Mt Alab		05-Mar-1996	f / ad.
10	SM NH3504	BORNEO, Sabah, Kg Togudon, Tambunan Rd, Mi 28		01-Feb-1993	m / ad.
11	SM NH3976	BORNEO, Sabah, Mt Lumaku	1365	30-Jun-1995	m / ad.
12	BMNH 78.1549	BORNEO, Sarawak, Mulu, Camp 4	1850	06-Sep-1977	m / aged.
13	MZB 23609	BORNEO, Kaltara, Pa' Raye, Long Bawan	960	17-Apr-1903	f / ad.
14	MZB 5084	SUMATRA, Aceh, Atang Putar, Lempelam	1000	14-Apr-1917	f / ad.

2350 m. The natural vegetation expected within these altitudinal limits is mainly Lower Montane Tropical Rainforest, characteristically occurring between 750 m and 1500 m, with a break around 1200 m marking the ecotone between Upper Dipterocarp and Oak-Laurel forest types (Whitmore, 1975: 199-201, Smythies, 1999: 26-27). At higher elevations, the occurrences of Upper Montane and Montane Ericaceous facies are influenced by topography and exposure. On the highest mountain, Kinabalu, vegetational zonation is extended. Here Kitayama (1992) recognised two montane forest zones: Lower Montane 1200 to 2000-2350 m, and Upper Montane, 2000-2350 m to 2800 m. The variability of zonation on this mountain is illustrated by the occurrence of the oak forests. These lie between 1220 m and 1830 m (4000 – 6000 ft) in the south-western slopes while, on the east ridge, an oak *Lithocarpus havilandii* forms forest at 3000 m (10 000 ft) (Corner, 1978).

Field data, as noted on specimen labels or elsewhere, provide little information on the habitat of Mountain giant rats. On the higher slopes of Kinabalu (as on Trus Madi and Mulu) the rats would have inhabited undisturbed Montane forest. But at lower elevations on the Kinabalu foothills, near the settlements of Bundu Tuhan or Kiau, the forests were likely to have been subject to some degree of disturbance – even when the first specimens were taken in the late 19th century. Kg Togudon, Sabah, is a village surrounded by secondary forest, and collecting information confirms that all Sabah Museum specimens were taken in logged or secondary forests. Wells et al. (2007) have shown that, while the catch of rarer non-volant small mammas declines in logged forest by comparison with unlogged, the density of commoner species is unaffected. On Kinabalu, Mountain giant rats are among the commoner small mammas trapped within relevant altitudinal limits (Md Nor, 2001). The distribution of this rat over its wider range supports the conclusion of Wells et al. (2007: 1095-6) that, more that the vegetational differences between logged and unlogged forest, abiotic features of the biome (in this case characters controlled by altitude) are significant factors. In short, altitude appears to be a more reliable predictor of the occurrence of this rat than the presence of undisturbed Montane forest habitat.

It is notable that all trapping localities at lower altitudes are connected to higher ground. From Kg Kiau or Bundu Tuhan, for instance, continuous upland merges with a large area of montane habitat on Kinabalu. Similarly, from the neighbourhoods of Kg Togudon and Pa Raye there is connection with the high ground and montane habitat of Gn. Alab and Gn. Harden (Harun), respectively. The summits of hills of eastern Sabah exceed the lower elevation at which

Table 2. Available measurements of specimens of mountain giant rats. Skull measurements follow Musser & Newcomb (1983), to nearest 0.1 mm.

	Specimen No. (See Table 1)													
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
BODY														
H&B	285	229-282	210	221	190	180	255	260	230	255	220	275	245	259
Tail	235	289-343	250		240	140	300	270	240	266	265	300	260	298
T/HB%		122	119	120								109	106	115
Ear		22-27	24	26	20	15	23	24	19	24	20	29	-	29
Hind foot	51	55-61	53	55	50	50	45	60	50	62	42	57	52.9	57
Wt (g)			245	317			478	340		503	290		339	
SKULL														
GL Lmbd-Nas	51.8	55.9-63.3	N/A	56.8					60.3			62.6	58.3	N/A
GL.Cond-I	N/A		N/A	52.3					56.5			60.0	54.4	57.7
Zyg bdth	28.9	28.2-32.8	25.5	26.5					29.4			30.3	24.8	N/A

(*continued on next page*)

Table 2. (continued)

I-O bdth	8.7	7.8-9.1	7.8	9.3	9.2	8.7	8.4	8.6
Nasal L	22.4	22.3-26.4	20	23.1	23.9	25.1	22.4	N/A
Braincase bdth	23.1	20.2-22.5	19.3	17.8	21.6	22.5	20.5	22.8
Incisor tip bdth	5.9	3.9-4.9	4.6	3.9	5.9	5.5	4.3	5.6
Diastema L	17.1	14.6-18.7	13.6	16.6	16.3	19.5	15.7	18.1
Incisive foram L	8.2	8.8-10.1	7.4	8.2	8.7	9.2	9.0	10.2
Palate at M^1 bdth	4.8	4.7-5.7	4.3	5.0	6.1	5.6	5.5	6.7
Palate at M^3 bdth	6.6	6.5-7.7	5.2	6.0	7.2	7.7	6.5	7.3
M^1-M^3 alveoli	10.6	10.6-11.6	10.3	9.9	11.0	10.9	10.9	11.6
M^1 bdth	3.3	3.0-3.5	3.4	2.9	3.4	3.0	3.2	3.5
M_1-M_3 alveoli	10.3		10.4	9.5	11.2	11.3	10.5	11.8
M_1 bdth	3.3		2.9	2.9	3.8	3.0	3.0	3.2
Nasal bdth							7.5	6.7
Zyg plate							6.6	

Mountain giant rats have been trapped, but the absence of records may reflect the fact that none of these peaks connect with extensive upland exceeding 1200 m. A reasonable conclusion is that the Oak-Laurel forest zone, typically 1200 – 1500 m, is the optimal habitat of the Mountain giant rat of Borneo and that specimens obtained above or below these limits (except on Gn. Kinabalu) probaby represent excursions or dispersing emigrants.

A topographical chart (Ministry of Defence, 1976) confirms that dissected uplands, mostly above 1000 m elevation, connect Kinabalu with Trus Madi to the south and with Alab, in the Crocker Range, to the southwest, although these two locations are separated by the long Keningau – Tambunan valley. From Lumaku towards the west coast and Trus Madi in the interior, upland terrain continues to the Kelabit-Kerayan highlands of Sarawak and Kalimantan Utara, respectively. East of the international border, Gn. Harden (also known as Gn. Harun) is directly connected while, to the west, Murud is flanked by river valleys dropping below 600 m. Some 60 km further west, Gn. Mulu is surrounded by dissected lowlands *ca*. 350 m. This is the only truly isolated upland area on which Mountain giant rat has been found, so far only at high elevation. Given that no occurrences are known below 900 m (Table 1), the present extent of lowland habitat between Mulu and other populations is probably a formidable barrier to movement of the Mountain giant rat. Under prevailing environmental conditions, the Mulu population is unlikely to receive new recruits.

Past regional environments were different. Palaeogeographical and palaeoecological data show that the present regional geography and environment of island South-east Asia is untypical, representing an extreme state in the latest of a succession of interglacial episodes that may cumulatively amount to no more than 2 % of the Quaternary period (Woodruff, 2010). The local environment of north-western Borneo during the terminal Pleistocene is illustrated by palynology from exposures in nearby Niah caves, Sarawak (3°48'N 113°47'E), spanning a period from *ca*. 52 000 to 9000 BP (Hunt et al. 2012). Vegetation was climate-driven and often highly unstable. At Niah, now only a few metres above mean sea level, warm interstadials are marked by lowland forest, sometimes rather dry, and at times by mangroves. Cool stadials are characterised by taxa now restricted to 1000 - 1600 m above sea level, suggesting temperature declines of *ca*. 7 - 9° C relative to present. In an extreme case (RS-5, dated 23 086 – 23 859 cal. BP, i.e., height of the Last Glacial Maximum) the lowland trees present (*Palaquium, Santiria, Elaeocarpus* and *Euonymus*) are all tolerant of relatively high altitudes, while high numbers of altitudinally-restricted upland taxa such as *Acer, Albizzia, Alnus* and *Prunus*, suggest depressed temperatures relative to the present, perhaps averaging 21° C or lower. Relatively high counts for dry-land taxa, such as *Casuarina, Myrica* and Ericaceae, point to lowered effective precipitation. Some open-ground taxa and very high counts for *Callicarpa* point to climatically disrupted and unstable vegetation, but there is little evidence for deforestation. This phase may have lasted from about 38 000 until 18 000 years BP (Hunt et al. 2012: Fig. 11). During these twenty millennia, habitat suitable for Mountain giant rats, i.e., vegetation of comparable composition to present Lower Montane forest, could have prevailed widely across the lowlands of northern Borneo eliminating a barrier to colonisation of Mulu. It is possible that the distribution of this rat expanded further but, with the lack of evidence, wider occurrence of the species during the terminal Pleistocene remains conjectural. It can be hoped that future archaeological excavations may provide evidence of former distributions.

For the final millennia of the Quaternary (the Holocene), additional evidence of the environment of north-eastern Sarawak has been obtained from a 40 m lake-bed core at Loagan Bunut (Hunt & Premathilake, 2012). A climate warmer than present is indicated by heightened sea-level, shown as mangroves at this interior locality, associated with rising rainfall. Palynological analysis confirmed the presence of relatively stable lowland tropical rainforest throughout the period. Signals at 9250-8890, 7900 and 7600-7545 cal. BP indicate episodes of drier climate and weakening monsoonal activity, but no significant cooling Together these samples confirm that, during the post-glacial warming phase, plant communities occurring at lowland elevations in north-western Borneo during the terminal Pleistocene (including the Last Glacial Maximum) retreated to the higher elevations where they are now symptomatic of 'Lower Montane' forest types. Since trapping results reported above indicate that the present Lower Montane (oak-laurel) forest is the optimal habitat for the Mountain giant rat, it can be concluded that the distribution of this species would have shrunk in phase with rising ambient temperatures. Subsequently, during the warm past 11 000 years there has been no downward re-expansion of montane forest plant communities to re-invest the lowlands where they were formerly widespread. As a result, the present known occurrences of Mountain giant rat in Borneo offer a typical example of relict distribution. Local populations apparently now exist only in upland locations where there is a sufficient area of optimal habitat, including logged or otherwise disturbed forest. None the less, in northern Borneo the extent of connected uplands above 900 m (the lowest elevation at which Mountain giant rats have been found) suggests that, with the exception of Gn. Mulu, occasional genetic exchange may still be possible between most populations.

Other Sundaic mountain giant rats, *Sundamys*

The congeneric giant rat *Sundamys maxi* is endemic to Java. This rat was included in the species *S. infraluteus* by Chasen (1940), who regarded it as one of several other post-Pleistocene montane relict murine taxa of the Sunda biogeographical subregion. Most of these are now recognised as distinct species endemic to upland localities in their respective islands. For instance "*Rattus rapit*" of Chasen (1940) included not only *Niviventer rapit* (Bonhote 1903) known from Gn. Kinabalu and Bukit Baka, Kalimantan Barat, but also the species *N. cameroni* (Chasen 1940) from 1524 – 2012 m, Cameron Highlands, Peninsular Malaysia, *N. fraternus* (Robinson & Kloss 1916) of Sumatran mountains, and *N. lepturus* (Jentink 1879) of western Javan mountains. Similarly, Chasen's "*Rattus alticola*" included not only *Maxomys alticola* (Thomas 1888) of Kinabalu and Trus Madi, but also *M. hylomyoides* (Robinson & Kloss 1916) of the Sumatran spinal mountain chain, and *M. inas* (Bonhote 1906) of highland elevations of the Thai-Malay peninsula; and Chasen's Summit rat "*Rattus baluensis*" included both *Rattus baluensis* (Thomas 1894) of the summit of Gn. Kinabalu, and *R. korinchi* (Robinson & Kloss 1916) of Gn. Kerinci and Gn. Talakmau, Sumatra (updated nomenclature and distributions from Wilson & Reeder, 2005). The one remaining potential instance of Sundaic montane relict distribution among Chasen's list is the Mountain giant rat of Sumatra, *Sundamys atchinensis*, treated by Musser & Newcomb (1983) as a geographical subspecies of *Sundamys infraluteus* on the evidence of four specimens. No new examples are known (Table 1) and the relationship has not been tested by genetic evidence.

In Chasen's time, it was already recognised that lowered sea-levels during Pleistocene stadia provided land bridges linking the present islands of the Sunda Shelf (Beaufort, 1951). There was, however, little knowledge of the nature of the vegetation of exposed land at such times. Assembled evidence now points to the existence of a central corridor of drought-induced savannah or dry forest dividing eastern from western forest refugia at the Last Glacial Maximum and, by inference, at preceding stadial maxima (Bird et al., 2005). Supportive evidence for an environmental barrier between forest habitats of Borneo and Sumatra since the Middle Pleistocene is given by genetic studies dating the last common ancestor of the two orang-utan species, *Pongo pygmaeus* and *Pongo abelii* at 400 ka (Locke et al., 2011). Although distribution modelling with extrapolation over different time areas suggests the possibility of periodic forest corridors between east and west parts of the Sundaic subregion during the Pleistocene (Cannon et al., 2009), only at extreme glacial maxima could the climate of the lowlands have been cool enough to maintain the temperature-dependent forest habitat required by mountain giant *Sundamys* rats. At such times, the central drought-induced corridor would have been at its widest (Wurster et al., 2010). Phylogenetic studies of three other murine rats, *Maxomys surifer* (Miller 1900), *Maxomys whiteheadi* (Thomas 1894) and *Leopoldamys sabanus* (Thomas 1887), indicate that these species dispersed throughout their current ranges in the early Pliocene and subsequently, without genetic contact, have diverged by vicariant evolution (Gorog et al., 2004). It seems likely that this model applies also to the mountain giant rats, in which case it is reasonable to recognise the Sumatran *Sundamys atchinensis* as a third species, along with Javan *Sundamys maxi* and the Borneo Mountain giant rat *Sundamys infraluteus*.

In the absence of targeted field studies, understanding of the ecology of these rats is based on little more than capture data. Extrapolation from trapping frequency in Borneo, as reported by Md Nor (2001) on Kinabalu, suggests that mountain giant rats *Sundamys* may not be rare in optimal habitat in their respective upland locations on each of the three Greater Sunda islands. All three species must be equally at risk from habitat loss. The immediate threat in the uplands of Sumatra, Java and Borneo is human intervention by land clearance for permanent agriculture, especially vegetable growing. If sufficient areas of suitable habitat can be protected, including logged forest within altitudinal limits, the longer term threat remains from climate change. The evidence from post-glacial warming a few millennia ago (above) indicates that increasing global temperature will affect tropical forest zonation, uplifting altitudinal ecotones. Monitoring ambient temperature profiles at montane stations would help to assess the risk, but knowledge of the ecology of these rats urgently needs to be improved. Without positive action, it must be feared that the long-term survival of the rare endemic mountain giant *Sundamys* rats of the Sunda subregion is severely threatened.

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