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Borneo yellow muntjac (*Muntiacus atherodes*)
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BORNEO : an Introduction

At almost 750,000 km², Borneo ranks as the world's third largest island. The political division between three nations—Malaysia, Brunei Darussalam and Indonesia—and their contrasting histories, have generated economic and cultural distinctions in human society in different parts of this huge island. Nonetheless, geography, climate, and plant and animal ecology provide a unifying environment to justify the theme of this issue of the Malayan Nature Journal. In these pages, participants from all three nations have presented a remarkable collection of reports on aspects of the natural history of Borneo, or parts of Borneo. Collectively, these papers illustrate the diverse character and fascinating breadth of the subject, and celebrate the endeavours of the community of people and institutions who participate in studies that add to our collective understanding of the diverse and remarkable natural history of Borneo.

The opening contribution draws attention to the Proboscis monkey, the long-nosed colobine endemic to Borneo, frequenting coastal and riparian forest throughout the island. Equally well-known is Borneo's great ape, the Orangutan, whose threatened status has roused international and national support for the rescue and rehabilitation programme at Lamadau, Central Kalimantan. Also generated in Indonesia, in West Kalimantan, the Mastwatch website continues to link observers throughout Borneo in a programme to monitor the phenomenon of mast-flowering and fruiting of dipterocarps, the magnificent giant trees that dominate the lowland and lower montane forest of Borneo. There follows a study of the utilisation of natural resources by an indigenous community of Muslim faith.

Move on to the giant mammals, Asian elephants, at last proven by skilled zooarchaeological detective work to be present in Borneo in the Late Pleistocene era. An archaic group among invertebrates, the Odonata (dragonflies and damselflies) are well represented in Borneo; presented here is an overall review and a linked, first Borneo-wide checklist. The birds of Borneo are perhaps a group more often drawing naturalists to Borneo; several checklists exist and it is more cogent to include, in these pages, an authoritative review of ornithology, an active pursuit throughout the island.

There are two contributions from Brunei based on phototrap images. The first provides previously unknown evidence of colour variation among the Sundaic Horse-tailed squirrel, while the second puts into circulation the first pictures of living Borneo Yellow muntjac, and original evidence of ecological separation of the two species of barking deer in Borneo. On the island Mantanani Besar a study, initiated by the Sabah Society, has investigated the human/bird relationship, and assessed the likelihood of a productive future for the strange, mound-building megapodes. A short essay on the cultural significance of Clouded leopard precedes a careful, well illustrated account of the living legend of Tigers in East and North Kalimantan. In the same area, human ingenuity has invented a mechanical alternative to the blowpipe, the traditional hunting weapon of interior people of Borneo. The second-last features a study of the declining mud crabs in Kuching mangroves, and this issue closes on a report showcasing prey-handling of a venomous Bornean Keeled Pit Viper.

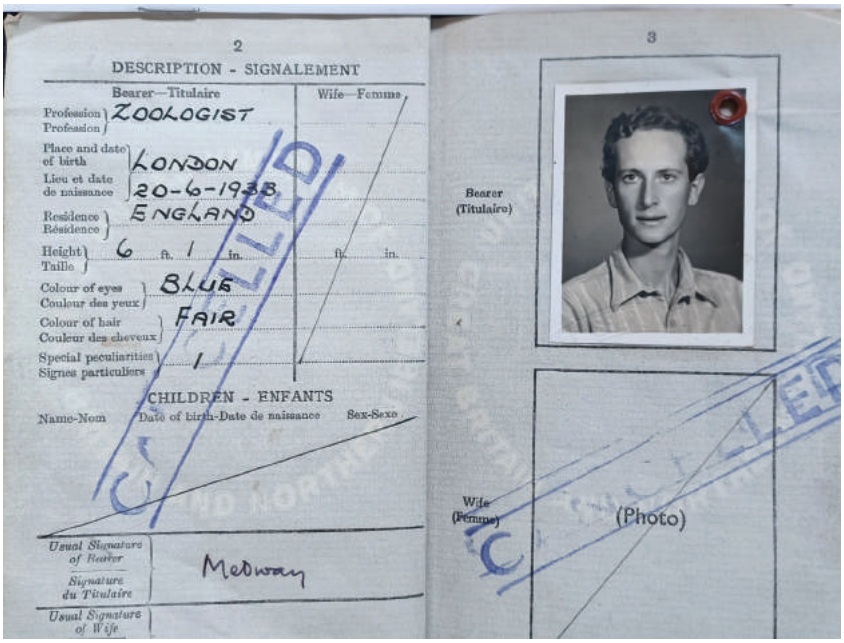
Apologia: lifetime connections with people and places in Borneo

Readers of the Malayan Nature Journal may question my qualification to serve as Guest Editor of this Borneo-themed issue. I hope a few paragraphs can provide satisfactory justification.

Sometimes, in Sarawak, people who half-hear my name, jump to the (wrong) conclusion that I am related to the dynasty of Brooke Rajahs. Dismiss that as the reason why, in March 1956, shortly before graduating at Cambridge, I did not refuse the offer by Tom Harrisson, then Curator of the Sarawak Museum, who offered to give me a job, if I came to Kuching. So, in June 1956, I bought a passage on a cargo steamer of the Blue Funnel Line, from Liverpool to Singapore, where I transhipped to S.S. Rajah Brooke -- and finally arrived at Kuching.

The 'job' was termed 'Technical Assistant to the Curator', and had no fixed duties. The Museum was engaged in a programme of amassing bird skins, funded by the eminent businessman and ornithologist Dato Loke Wan Tho. Young men from rural longhouses were given basic training in skinning and specimen preparation, and sent home with a supply of cartridges, museum labels, cotton wool and preservative. At the Museum, I sorted and identified the resulting skins. This task -- a valuable introduction to the avifauna -- was supplemented by proof-reading B. E. Smythies' new checklist of the birds of Borneo (1957). The text went back and forth (seven times, I remember) between Museum and the Government printer, whose staff were seriously challenged by Latin nomenclature and the arcane rules on the use of italics in zoology. In the same year, I was issued a Sarawak international passport, no. 4553, valid in 'The British Commonwealth and all Foreign Countries'. On this document, I travelled the world for ten years until it expired in February 1967.

Plate 1 - Sarawak International Passport



In 1958, promoted to Archaeological Assistant, I became responsible for the identification of animal remains excavated at Niah caves, and elsewhere in Sarawak and Sabah. As a personal project, the Curator also encouraged me to study the edible-nest swiftlets -- a group of birds with unique adaptations to life in caves. Two years later, my fieldwork on swiftlets became the foundation of a PhD dissertation at the University of Birmingham, U.K. In 1960-1961, a post-doc fellowship with Yayasan Siswa Lokantara (as ahli burung walet) extended my research to Indonesia; Here I found other managed populations of cave swiftlets, and met other scientists prepared to share their experience in the taxonomy and behaviour of these fascinating birds.

In 1961, appointed to the Zoology Department at the University of Malaya, I was well placed to resume research on the animal remains excavated in Malaysian caves, notably at Niah, Sarawak. Discoveries included the foot bones of Malayan tapir, a large mammal now extinct in Borneo, but I failed to find evidence of the past presence of elephant in any Late Pleistocene context.

Most identifiable animal remains in these cave sites consisted of teeth and bones of mammals, encouraging me to study extant Borneo species. In 1965, a grant from U.S. sources funded a round-the-world air ticket. Starting at the B.P. Bishop Museum, Honolulu, and progressing across mainland USA from San Francisco, via Chicago and Washington, D.C., to the Peabody Museum, Yale, and then to museums in London, Paris and Frankfurt, and finally at the India Museum, Calcutta, I managed to see all historic mammal collections from Borneo. During this circumglobal tour, I discovered two undescribed species of small mammal—not in the upland localities they inhabit, but in the museum cabinets where they lay, overlooked: the Grey-bellied pencil-tailed tree-mouse, in the U.S. National Museum, Washington. D.C., USA, and the Black shrew, in the Museum of Comparative Zoology, Cambridge, Mass., USA. The resulting annotated checklist of mammals of Borneo was published by the Malaysian Branch of the Royal Asiatic Society, first in 1965 and, later, as a revised edition, in 1977.

In the 1990s, invited by the Director of Forests and Wildlife, Sarawak, to review the edible birds'-nest industry. I looked for a student-assistant to cooperate in the research. Luckily, Lim Chan Koon, a graduate student at Universiti Malaysia Sarawak (Unimas) was willing to transfer to the topic, He was awarded a Government scholarship to the University of Kent, U.K., and I became external supervisor for his Ph.D. I remembered my 1957 visit to Salai Cave, in the Middle Baram above Long Laput, site of an accessible colony of White-nest swiftlets. We approached YB Kebing Wan, head of the family of hereditary owners of the cave rights, and were pleased by his generous offer to provide facilities for a year's research on site, alongside his relative Usong Wan, as cave manager. This unprecedented opportunity for a dedicated and assiduous student, and for shared learning by myself as supervisor, resulted in a successful graduation by Dr Lim..

In 2001, a grant from Flora and Fauna International helped Dr Lim and myself, with friends from the community of Sarawak birds'-nest cave owners, including George Nawan, to undertake an investigation of birds'-nest operators and island sites in North Kalimantan, and the extensive complex of caves occupied by Black-nest swiftlets in the upper Kayan river, East Kalimantan, managed by a local cooperative. In 2002, our experiences were recounted in a jointly authored book: *Swiftlets of Borneo: builders of edible nests*, produced in a lavishly illustrated edition by Natural History Publications (Borneo) and reissued with revisions in 2014.

In 2009, I was appointed a member of Yayasan Ulin, an Indonesian foundation dedicated to conservation of natural habitat and wildlife in areas unprotected by legislation. I traversed the southern breadth of Borneo by mixed transport modes from Pontianak to Pangkalan Bun, West Kalimantan, across Central Kalimantan, to Banjarmasin and Martapura, South Kalimantan, and later, from Balikpapan to Samarinda and Tenggarong, East Kalimantan, and— later still — from Bandarbaru on the great Mahakam river, by speed boat up the tributary, Sg Belayan, to the oil palm plantations operated by REA Kaltim. The director and staff of REAKon, the conservation arm of this British-owned company, provided valuable insights of the potential for good environmental management on a large commercial plantation.

In 2014, I was invited to participate in the Heart of Borneo initiative, as operated in Brunei Darussalam under Royal patronage and ministerial support. Recipient of a

Merdeka Award in the same year, among other projects, I was able to fund a Sabah graduate of the University of Malaya, for his M Sc research into the Philippine megapodes of the Mantanani archipelago, Kota Belud District, Sabah. In the following years, until the Covid-19 Pandemic closed international travel, I have made at least one visit to a destination in Borneo, and thereby renewed or extended my personal contacts among colleagues who share enthusiasm for all aspects of natural history.

Through the Pandemic years 2020 and 2021, and into 2022, contact has been limited to digital exchanges. As Guest Editor of this Borneo-themed issue of the Malayan Nature Journal, I am supremely grateful to all contributors -- and especially those whom I invited to submit their own stories and discoveries. The subject matter is unlimited. The combination of submissions in this issue indicates the wealth and variety of topics available for research. The published articles demonstrate, emphatically, the assiduity and scrupulous ardour of the diverse community of people whose lives and careers have led them into these fields of research. There is still much more to be discovered. I sincerely hope that this themed issue of MNJ will stimulate further research into the diverse aspects of the natural history of Borneo.

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Unexpected variability in pelage colouration of Horse-tailed Squirrels *Sundasciurus hippurus* in Brunei Darussalam

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Abstract : The WWF-sponsored Heart of Borneo initiative received high level support in Brunei Darussalam during 2009-2016. Mammal studies were carried out successively by Charles and Ang. The subject of this study, Horse-tailed squirrel *Sundasciurus hippurus* was photographed by camera traps, or after capture in small mammal cage traps. Previously unrecorded variation in pelage coloration did not match those for the four described subspecies in Borneo. Analysis of color variation identified five distinct forms from different localities, which are described and tabulated, and illustrated by selected photographs, and compared with images of Type specimens in the Natural History Museum, London. The pelage variation as encountered in *S. hippurus* in Brunei defies a conventional solution but, in the absence of DNA analyses, we refrain from nomenclatural acts.

Keywords: Heart of Borneo, Brunei Darussalam, Sciuridae, Horse-tailed squirrel, *Sundasciurus hippurus*, pelage coloration, variability.

INTRODUCTION

The Heart of Borneo (HoB) project was a World Wildlife Fund (WWF) programme initiated by a joint declaration signed in Bali, Indonesia, in 2007, by the governments of Brunei Darussalam, Indonesia and Malaysia. The objective was to conserve the biodiversity of Borneo through a network of protected areas, sustainable management of forests, and other sustainable land uses. In Brunei Darussalam, HoB received high-level support under the committed patronage of HRH the Crown Prince Haji Al-Muhtadee Billah Ibni Sultan Haji Hassanal Bolkiah Mu'izzaddin Waddaulah, and through overall management by the former Ministry of Industry and Primary Resources (at present Ministry of Primary Resources & Tourism), with the personal dedication of the former Minister, Pehin Dato Hj Yahya. We present here one outcome of mammal surveys in existing conservation areas and other natural habitats across the country, notably in Sungei Ingei Conservation Forest (18,491 ha), a totally protected area in Ulu Belait, Belait District, ,where a temporary field station was established in 2010 for close investigation of pristine lowland mosaic forest.

The Horse-tailed squirrel *Sundasciurus hippurus* (Geoffroy,1831) is a Sundaland endemic found in southern Vietnam, southern Thailand, Peninsular Malaysia, Sumatra and Borneo (Lyon, 1907; Corbet & Hill, 1992; Lekagul & McNeely, 1977; Medway, 1978; Wilson & Reeder, 2005). In Borneo it is 'patchy or rare' in lowland forests (Phillipps & Phillipps, 2018) with upland records on Mt Penrisen, Mt Dulit and Usun Apau in Sarawak (Banks 1931, Medway 1977, Cranbrook 2020, 2021). *Sundasciurus hippurus* is distinguished by a thick, bushy tail, all black in the nominate subspecies *S. h. hippurus*, thereby giving the species its descriptive English vernacular name.

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Previous small mammal studies in Brunei Darussalam have confirmed that Horse-tailed squirrels are diurnally active between 0600-1600 hrs (Ang, J. M. A., 2014), and have found the species in large, pristine, undegraded lowland forests, but not in fragmented forests (Charles & Ang, B.B. 2006, 2010; Ang, B. B., 2010). In Borneo, four geographical subspecies are currently recognized, based on variation in pelage colour (Phillipps & Phillipps, 2020) namely: *S. h. borneensis* (Gray, 1867), distinguished by a rich chestnut red venter and a black bushy tail, occurring in Sarawak north of the river Rajang, and in North, East, South, Central and most of West Kalimantan; *S.h. pryeri* (Thomas, 1892) characterised by white underparts (venter) and a banded black and grey bushy tail, occurring throughout the Malaysian State of Sabah; *S. h. hippurellus* (Lyon, 1907), occurring in south-west Borneo from West Kalimantan at Sungei Kapuas and Sg Landak, through Sarawak to the lower Rajang, which forms a riverine boundary between this subspecies and *S. h. borneensis*; and *S. h. inquinatus* (Thomas, 1908), a distinctive form with pale chestnut (or orange-brown) venter, apparently intervening geographically between the white-bellied *S. h. pryeri* and deep chestnut red-bellied *S. h. borneensis*. Existing known localities of *S.h inquinatus* include Sarawak, in Lawas district (the type locality), and in North Kalimantan in the border region of rivers Sembakung and Sembuku (Medway, 1977).

Four criteria were used by Corbet & Hill (1992) to distinguish the subspecies of *S. hippurus* in Borneo, namely: colour of the dorsal pelage, venter, hind legs and tail[1]. To these, we added: head, shoulders, forelimbs and thigh (Table 1). To check the original descriptions, photographs were also made, with permission, of skins in the collection of the Natural History Museum, London, UK., abbreviated below to 'BMNH'.

In a brief review of the variability among Horse-tailed squirrels in Borneo, Phillipps & Phillipps (2020) have allocated all white-bellied forms (throughout Sabah) to the subspecies *Sundasciuirus hippurus pryeri* [2] and those with rufous to dark red venter (found in much of Sarawak and the Kalimantan provinces, Indonesia) to *S. h. borneensis* or, locally, to *S. h. hippurellus*. They have pointed out that *S. h. inquinatus* occurs in a biogeographical zone extending from Lawas district, Sarawak, to Tawau, Sabah, which they have previously named the South Sabah Zoological Boundary (SSZB) zone (Phillipps & Phillipps, 2018), identified as an important zoogeographical boundary stretching from Lawas to Tawau, along the political border of Sabah to the north and Sarawak and North Kalimantan to the south. Lowland birds and mammals tend to be represented by different species or subspecies north and south of the SSZB. Geographically, it may be contemplated that the described subspecies of Horse-tailed squirrel fit this pattern, with white-bellied *Sundasciurs hippurus pryeri* in Sabah and brick red-bellied *Sundasciurus hippurus borneensis* in northern Sarawak and all Indonesian provinces. Medway (1977) interpreted the pale orange-bellied *S. h. inquinatus* as a clinal intermediate between *S. h. pryeri* and *S. h. borneensis*. This interpretation was proposed in an early edition, by Phillipps & Phillipps (2016). These interpretations are challenged by our new observations of variation in pelage coloration among Horse-tailed squirrels in Brunei Darussalam, arising from photographic and live-trapping records obtained during our participation in HoB faunal surveys.

[1]There is an error in the colour of the venter of *S. inquinatus* and *S. pryeri* in Table 188 of Corbet & Hill (1992).
[2]Phillipps & Phillipps (2020) have also suggested that there may be grounds to separate *S. pryeri* as a full species, endemic to Sabah

MATERIALS AND METHODS

Declaration

The Forestry Department, Ministry of Primary Industries & Tourism (formerly Ministry of Industry & Primary Resources), Bandar Seri Begawan, Brunei Darussalam and the Use Permit Section have reviewed all our sampling procedures and approved permits for the research conducted. Every animal that was trapped and etherized was revived and released in the field. No animals were killed, and none collected as conventional skins and skulls.

Data collection

Camera traps used were the passive infra-red motion sensitive incandescent flash type (Wild-Eye Remote Camera Trap System by Wildtrack Services): trigger speed 0.3sec, detection angle 60 degrees, detection range 30 ft, interval 10 secs between events. These camera traps were set in Sungai Ingei Conservation Forest, Belait District, 2009-2012 (Charles, 2012), and Tasek Merimbun Heritage Park, 2014-2015. Our small mammal cage traps, of the design used extensively in our previous studies (Charles & Ang, B.B. 2006) were deployed in Bang Nalud, Tutong District in 2007, Bukit Patoi in Peradayan Forest Reserve in 2008 and in Ulu Temburong National Park in 2015 (Fig 1). In a total of 51,202 camera trap-nights in the Sungai Ingei Conservation Forest over three years, 32,553 digital images were obtained. Of these, 16,986 images showed identifiable mammals including 22 independent camera trap images of Horse-tailed squirrels. An independent event was defined as consecutive images of the same mammal species at the same trap station within an hour interval. In a total of 1709 camera trap images at Tasek Merimbun Heritage Park, seven independent images of Horse-tailed squirrel were used for this study.

Small mammal cage traps were also set in appropriate locations. Captured Horse-tailed squirrels were photographed in the trap or, sometimes, etherized and measured and photographed while insensible, as follows: two individuals at Bang Nalud and one at Bukit Patoi, Tutong District, and one in Ulu Temburong National Park. Additionally, four individuals were observed in the wild in Ulu Temburong. All images of Horse-tailed squirrels from camera traps and photographs of trapped squirrels were carefully examined and compared with one another; none of the images was enhanced.

The Horse-tailed squirrel populations sampled across the national territory of Brunei Darussalam showed greater phenotypic variability in pelage coloration than was previously known. Many of the examples illustrated in our Tables and Figures, as presented below, do not match the descriptions of named subspecies. The variations in coloration at different localities therefore defy a conventional interpretation. We use the term 'form' as a neutral expression.

RESULTS

Eight colour varieties were distinguishable (Table 1), and are described below:

Temburong form. Ulu Temburong National Park. Five images:- one was trapped, and four separate individuals were observed in the field. Description: head, shoulders, forelimbs, hindlimbs and thighs are heavily grizzled grey, with a black tail and brown dorsal pelage. The sides of body are tinged with brown on the grey pelage. The venter is brick red in colour. By comparison, the BMNH specimens of *S. h. borneensis* 49.3.2.3b and 93.6.1.8b have, a reddish-brown dorsal pelage, but otherwise resemble the Temburong form (Figs. 2a-c).

Patoi form. Bukit Patoi, Temburong District, one photographic image. This differs from the BMNH specimens of *S. h. borneensis* by the tail being infused with grey, rather than pure black.

Ingei forms. Sungei Ingei Conservation Forest, Belait District (Figs. 3 a-f, Table 2). A total of 22 images: - Ingei form (i). 18 images: Head, shoulders, forelimbs, hindlimbs and thighs are heavily grizzled grey; mid-dorsal pelage is bright orange, while sides of the body to the base of the tail are cinnamon brown. The venter is pale orange. The tail is black-grey (Fig. 4b). Ingei form (ii). Four images: similar to the above, but differing in a heavily grizzled grey tail (Fig. 4a) with a black region. The similarity with skins collected at Lawas, Sarawak, and identified as *Sundasciurus hippurus inquinatus* (BMNH 8.25.1c, 1.8.25.1b and 1.8.25.1d) is the pale orange ventral region; but there are strong differences in five features, namely coloration of dorsal pelage, forelimbs, hind limb, thigh and tail.

Merimbun forms. Tasek Merimbun, Tutong District. Seven images were obtained, of which three (form i) were similar to the BMNH comparison skins of *S. h. borneensis*, while four (form ii) differed in having a black-grey tail.

Nalud forms. Bang Nalud, Tutong District. Two images: one comparable to Merimbun (form i, Fig. 5c), while the other (form ii) varied in three features: colour of the neck, the venter, and black-grey tail (Figs. 5a-b). Form (ii) is a Horse-tailed squirrel with an orange-brown colour of the venter and intermediate between the rich brick red of *S. h. borneensis* and the pale orange of Ingei forms (Table 2). Dorsally, it has an orange tinge on the neck, and reddish-brown mid-back (Figs. 5a, b).

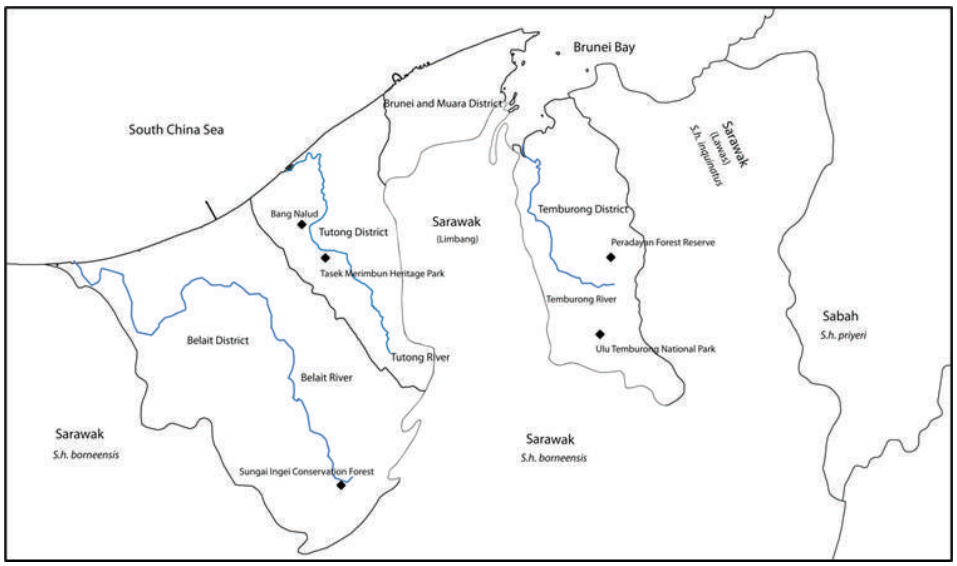

Fig.1. Outline map of Brunei Darussalam showing collection sites of images of Horse-tailed squirrels, and surrounding territory of Sarawak with distribution of named subspecies *S. h. borneensis* and *S. h. inquinatus*, and adjacent Sabah territory presumably, occupied by *S.h. pryeri.*

Table 1. Pelage colour comparisons between the eight varieties of *S. hippurus* from Brunei Darussalam with skins of *S. h. borneensis* BMNH 49.3.2.3b and 93.6.1.8b.

	Temburong Form	Patoi form	Merimbun form		Bang Nalud form		Ingei form		BMNH
			(i)	(ii)	(i)	(ii)	(i)	(ii)	
dorsal pelage	Brown	Brown	Brown	brown	brown	reddish brown orange on neck	orange mid-back cinnamon brown sides	orange mid-back cinnamon brown sides	brown/mid-back reddish brown
venter	brick red	brick red	Reddish	reddish	brick red	orange brown	pale orange	pale orange	brick red
head	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey
forelimbs	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey
shoulders	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey
hind limbs	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey
thigh	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey
tail	Black	black-grey	Black	black-grey	Black	black-grey	black-grey	grizzled grey with black patch	black
identity	*S.h. borneensis*	Variant	*S.h. borneensis*	variant	*S.h. borneensis*	variant; intermediate	*	*	-

* Cannot be matched with any described subspecies of *Sundasciurus hippurus.*

Table 2. Pelage colour comparisons between the Ingei forms (i, ii), Nalud form (ii) and the Type skins BMNH *Sundasciurus inquinatus* 1.8.25.1b and 1.8.25.1c, BMNH Type *S. h. borneensis* 49.3.2.3b and BMNH Type *S.h.pryeri* 92.7.19.1

	BMNH Type 49.3.2.3b *S. h. borneensis*	BMNH Type 92.7.19.1 *S.b.pryeri*	BMNH Type 1.8.25.1b *S.h. inquinatus*	Ingei Form (i)	Ingei Form (ii)	Nalud Form (ii)
dorsal pelage	brown/mid-back reddish brown	Brown	Brown	orange mid-back cinnamon brown sides	orange mid-back cinnamon brown sides	reddish brown orange on neck
venter	brick red	White	pale orange-brown	pale orange	pale orange	orange brown
head	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey
forelimbs	grizzled grey	Brown	Brown	grizzled grey	grizzled grey	grizzled grey
shoulders	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey	grizzled grey
hind limbs	grizzled grey	Brown	Brown	grizzled grey	grizzled grey	grizzled grey
thigh	grizzled grey	Brown	Brown	grizzled grey	grizzled grey	grizzled grey
tail	Black	banded black and grey	banded black and grey	black-grey	grizzled grey	black-grey
identity	-	-	-	-	-	intermediate

DISCUSSION

The related genera of Indo-Malayan squirrels, *Sundasciurus* and *Callosciurus* ('beautiful squirrels'), are well known for colorful regional or local variarion in coat colouration (Tex *et al*,, 2010). In some variable species, such as Finlayson's squirrel *Callosciurus finlaysoni*, molecular studies have tested the genetic basis of coat colour (Boonkhaw *et al.* 2017). The HoB project in Brunei Darussalam was not resourced to conduct comparable studies. Not was it our intention to create a collection of museum-standard skins and skulls for conventional taxonomic descriptions. In line with the objectives of HoB, our survey was designed to sample the biodiversity of existing protected areas, and some unscheduled localities with as little impact as possbile on individual animals. In doing so, we gathered records of Horse-tailed squirrels that greatly enhanced comprehension of the distribution of this squirrel within Brunei Darussalam, and also discovered unexpected variation in coat colour of this variable species. For the sake of conformity, as far as possible, we have matched our records with the existing picture of geographic variation in terms of subspecific taxonomy within *Sundasciurus hippurus*. Based on geography, and present understanding of regional climatic changes during the terminal Pleistocene and early Holocene, we venture a possible explanation for some of the variability demonstrated by our results.

Geographically, the two parts of Brunei Darussalam are enclosed by Sarawak territory. Since the subspecies of Horse-tailed squirrel *Sundasciurus hippurus borneensis*, characterised by a deep brick-red venter, occurs in adjoining parts of Sarawak, it would not be surprising that the range of this subspecies extended to Brunei. On the other hand, Temburong District adjoins the Lawas District of Sarawak, type locality of the orange-bellied *S. h. inquinatus*. Temburong District of Brunei Darussalam, therefore, might alternatively be expected to be included in the range of this intermediate colour variant. Our observations of the variable coloration of the pelage of Horse-tailed squirrels in Brunei Darussalam, summarised below, do not fit either expectation:

a) Temburong District forms. All were characterized by the dark, brick-red venter comparable with *S. h. borneensis*, but differed in tail coloration, black as in typical *S. h. borneensis* in most cases at Temburong National Park (nearer the Sarawak border) and black-grey at Bukit Patoi (Table 1).

b) Merimbun forms. Seven images, of which three (Form i, Fig. 5c) resembled skins of *S. h. borneensis* in BMNH, while four (Form ii) differed in a black and grey mixed tail.

c) Nalud forms. Tutong District. Two images, one comparable to Merimbun (form i, Fig. 5c), the other Nalud form (ii), differs from *S. h. borneensis* in three features – a black-grey tail, orange-brown underparts and reddish-brown mid-dorsum with an orange-tinged neck. In these features, it is intermediate between *S. h. borneensis* and the Ingei form (Table 2; Figure 5).

d) Ingei forms. At Ingei Conservation Forest, Belait District, there were two forms, identical with each other in seven features, except for tail colour (Table 2): 18 individuals had black-grey tails while four had grizzled-grey tails (Figs. 4a-b). The only difference between the two Ingei forms is the presence of a grizzled grey tail with a black patch in Ingei form (ii), a colour shift from the black-grey tail of form (i). Three features were shared with BMNH skins of subspecies *Sundasciurus hippurus inquinatus*, i.e., pale orange brown underparts, grizzled grey shoulders and grizzled grey head. Five other features, colour of dorsal pelage, hind limbs, thighs, forelimbs and tail, emphasise the distinctiveness of the Ingei forms (Table 2), which cannot be matched with any described subspecies of *Sundasciurus hippurus.*

Analysis of these eight forms or colour varieties (Tables 1 & 2) suggests that they can be reduced to five phenotypes in Brunei:

1) the Temburong form, with Merimbun form(i) and Nalud form (i), identifiable by venter coloration as *S.h.borneensis*
2) the Patoi form and Merimbun form (ii) having a black-grey tail, but venter coloration of *S.h.borneensis.*
3) Nalud form (ii) an intermediate between *S. h. borneensis* and the Ingei forms
4) Ingei form (i)
5) Ingei form (ii)

A brick-red venter (1) is a common feature of all Horse-tailed squirrels in Temburong District, at Ulu Temburong National Park and at Bukit Patoi in Peradayan Forest Reserve. This character places both forms within the prevailing classification of *S.h.borneensis* by Phillipps & Phillipps (2020). Venter coloration (2), the Patoi form and Merimbun form (ii), would again place these phenotypes in *S.h.borneensis*. Nonetheless, both differ from typical *S.h.borneensis* in one character: black-grey tail, as a variant of all black tail.

In Tutong District four colour forms are recognisable – two at Tasek Merimbun Heritage Park, and two at Bang Nalud (Forms i, ii). The Merimbun Form (i) and Nalud Form (i) share the brick red venter characteristic of *S. h. borneensis* while Merimbun form (ii) differs with black and grey tail, also a feature of the Patoi form, Temburong District. Examples of deep brick-red venter coloration were also found in Tutong District - Tasek Merimbun Heritage Park and Bang Nalud. Yet, in Sungai Ingei Conservation Forest, Belait District, closer to the border with Sarawak than these localities in Tutong District, this venter coloration was not found in any of the 22 examples camera-trapped, trapped and photographed or otherwise recorded at this locality (Table 1).

(3): The Nalud Form (ii) has a reddish-brown mid-back, an orange tinge on neck and orange brown venter. In these characters, it seems to be an intermediate, trending to the extreme variety of the Ingei forms (i, ii) with six additional common characters. It also shares three characters of a pale orange-brown venter and grizzled head and shoulders to subspecies *Sundasciurus hippurus inquinatus*.

(4), (5): Three features of the forms recorded in Sungei Ingei Conservation Forest, Belait District, set them apart from other Brunei forms, and five cannot be matched with any described subspecies of *S.hippurus*. A pale orange venter is a distinctive character shared with typical *S.h.inquinatus* but, in the absence of connecting forms, cannot be taken as common genetic feature. It is interesting that in the absence of *S.h.pryeri* and *S.h. inquinatus* anywhere in the region of Belait District, the Ingei forms have acquired a pale orange venter as one of their distinct features which probably has led to reproductive isolation in this population. Creating further complexity, (3) Nalud form (ii) appears to be intermediate between *S.h.borneensis* and the Ingei forms, suggesting a transition or zone of hybridisation of populations previously separated by a geographic barrier.

The remarkable phenotypes (4) and (5) were found only in the Sungei Ingei Conservation Forest, in the southern extremity of Belait District, not far from the Sarawak border with the Belait river and hilly southern border forming a geographical barrier to gene flow from Tutong and Sarawak respectively, leading to geographical isolation. Lacking comparative material from this area of Sarawak, and in the absence of genetic data or DNA analyses that can explain the variability of phenotypes in Brunei Darussalam we conjecture tentatively that Late Pleistocene cold temperatures increased the geographical barrier to gene flow across the hills of this border. The following early Holocene high sea levels (Voris, 2000) would have flooded much of the present Belait catchment, intensifying the

isolation of separated populations, potentially leading to geographical isolation and vicarious non-selective genomic changes (genetic drift). When conditions ameliorated and separated populations could meet again, perhaps only in the past 5000 years or so, their multiple encounters produced this array of different phenotypes.

By comparison, variability in pelage coloration in another forest-dwelling diurnal squirrel in Borneo, Prevost's squirrel *Callosciurus prevostii* (Desmaest, 1822), has also revealed great complexity. Thirteen named subspecies were mapped by Phillipps & Phillipps (2016), but subsequently these authors have concluded that the presence of polychromatic populations with a mixture of phenotypes and intermediates at the contact zones between the described variants have made it difficult to justify that taxonomy; especially when photographs from different locations in Borneo have shown that the differences were too variable (Phillipps & Phillipps, 2020).

Our findings, within the much smaller geographical area of Brunei Darussalam, show an equally great diversity of phenotypes, equally impossible to match with existing subspecific nomenclature of Horse-tailed Squirrels. We submit this challenge to future investigators who may have the inclination and funding to pursue the problem.

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Fig 2a. *Sundasciurus hippurus* (lateral view; etherised) in Temburong (S. Hogg)

Fig 2b. *Sundasciurus hippurus* (side view) in Temburong (S. Hogg)

Fig 2c. *Sundasciurus hippurus* (etherised) in Temburong showing brick-red venter and all-black tail. (S. Hogg)

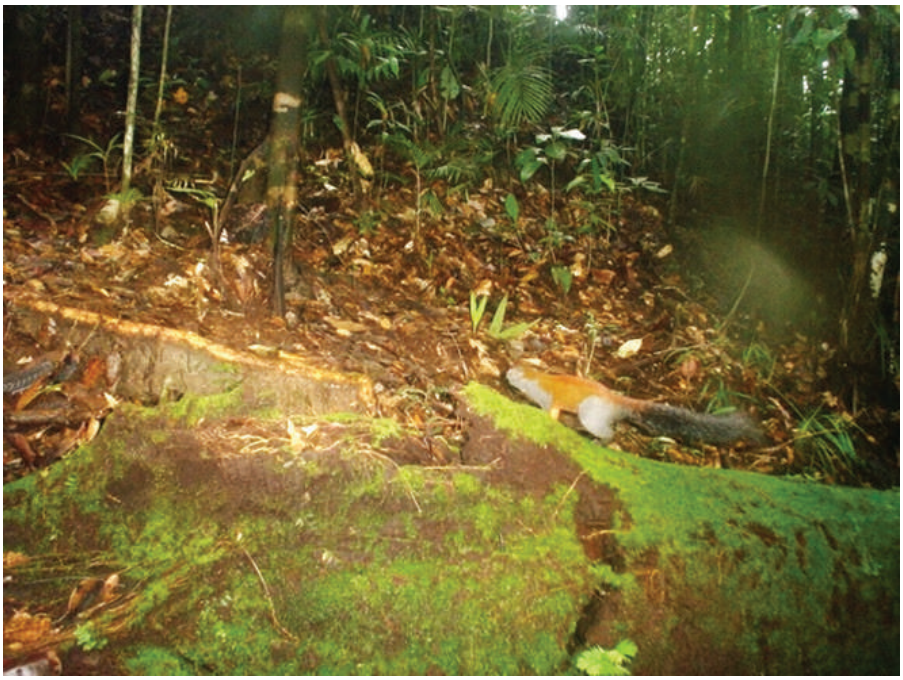

Fig 3a. Camera trap *S. hippurus* (side view) Sungai Ingei Conservation Forest, Ulu Belait

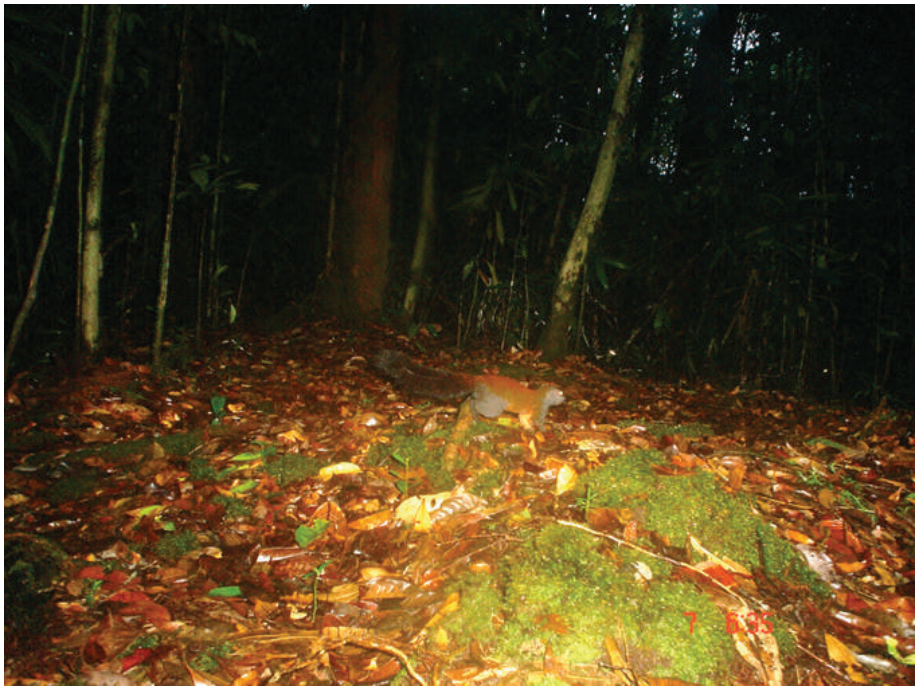

Fig 3b. Camera trap. *S. hippurus* showing the pale orange underparts Sungai Ingei Conservation Forest, Ulu Belait

Fig 3c. Camera trap. *S. hippurus* showing orange midback. Sungai Ingei Conservation Forest

Fig. 4a. Camera trap. (Ingei form ii) Grizzled grey tail with a patch of black, orange mid-back, cinnamon brown sides and pale orange venter.

Fig. 4b. Camera trap. (Ingei form i) A black-grey tail (Ingei form i). Other pelage characters as in Fig. 4a.

Fig 5a. Nalud form ii. Dorsal pelage, reddish brown mid back; shading to orange tinge on neck.

Fig 5b. Nalud form (ii) Ventral view showing the orange-brown venter.

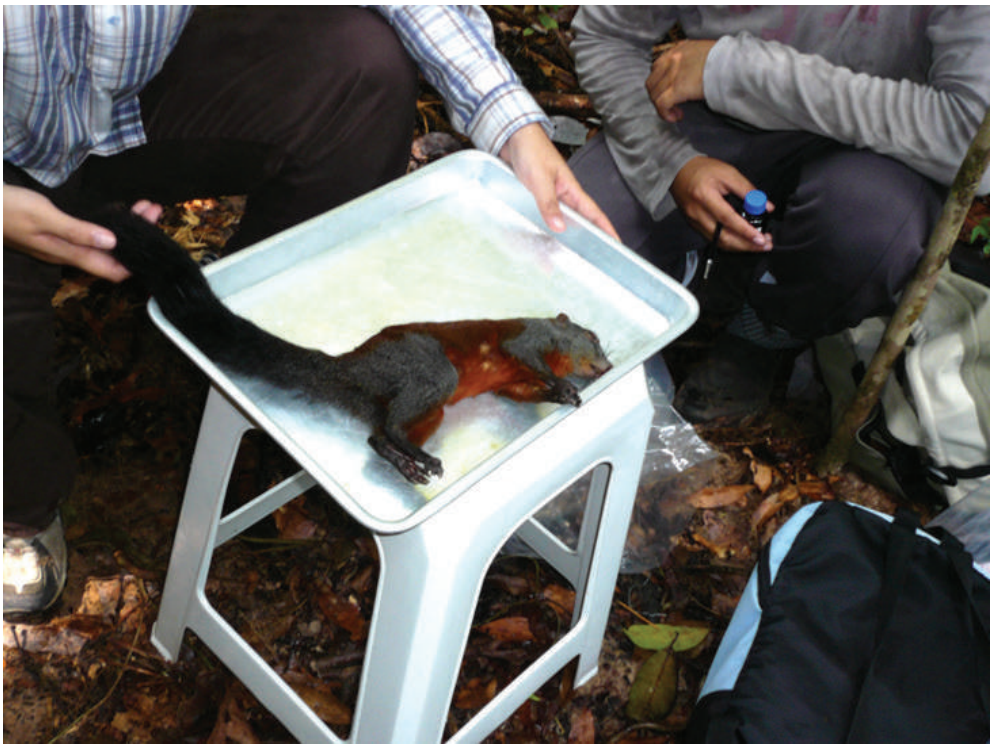

Fig. 5c Nalud form (i) showing brick red venter and black tail, characters of *S.h. borneensis*