RESEARCH ARTICLE

Taxonomy of the Bornean Slow Loris, With New Species Nycticebus kayan (Primates, Lorisidae)

RACHEL A. MUNDS^{1*}, K. A. I. NEKARIS², AND SUSAN M. FORD³

¹Department of Anthropology, University of Missouri Columbia, Columbia, Missouri
²Department of Anthropology and Geography, Oxford Brookes University, Oxford, Great Britain
³Department of Anthropology, Southern Illinois University, Carbondale, Illinois

More species of nocturnal primates are now recognized than in the past, because many are cryptic species. Subtle morphological disparities, such as pelage pattern and color variation, vocal cues, and genetics have aided in elucidating the number of diagnosable species in a genus. The slow lorises (genus Nycticebus) once included only two species, but recent taxonomic studies resulted in the description of three additional species; further incompletely explored variability characterizes each of the currently described species. The Bornean loris in particular is characterized by pelage and body size variation. In this study, we explored facemask variation in the Bornean loris (N. menagensis). Differing facemask patterns, particularly influenced by the amount of white on the face, significantly clustered together by geographic regions, separated by notable geographic boundaries. Our results support the recognition of four species of Bornean lorises: N. menagensis, N. bancanus, N. borneanus, and N. kayan. Genetic studies are required to support these findings and to refine further our understanding of the marked variability within the Bornean loris populations. Am. J. Primatol. 75:46-56, 2013. © 2012 Wiley Periodicals,

Key words: Nycticebus menagensis; Nycticebus bancanus; Nycticebus borneanus; cryptic species; morphology; sympatric, allopatric

INTRODUCTION

Technological advances have improved our knowledge about the diversity of several nocturnal mammals; many of these nocturnal mammals include cryptic species that were falsely lumped together as one species [Bickford et al., 2006]. With a better understanding of what differentiates these cryptic mammals, new species have been recognized [Bearder, 1999; Jacobs et al., 2006; Munshi-South, 2006; Yoder et al., 2000]. Additional species have been distinguished by their unique calls [Bearder, 1999; Jacobs et al., 2006; Niemitz, 1984], others by variation in sexual anatomy [Anderson, 2000], or subtle and obvious pelage variations [Bearder, 1999; Bradley and Mundy, 2008; Carraway and Verts, 2002; Ford, 1994], and the increased use of genetics has resulted in the exponential recognition of new species [Chen et al., 2006; Merker et al., 2010; Yoder et al., 2000]. Although the number of recognized species of primates has more than doubled in the past 25 years and our understanding of what defines a species has improved, some species, particularly the nocturnal ones, remain hidden to science. Many compounding variables contribute to the poor understanding of these species: difficulty of distinguishing between allopatric species, inability to collect genetic

tissue, highly subtle morphological cues, and disagreements on what defines a species [Bradley and Mundy, 2008; Isaac et al., 2004; Tattersall, 2007]. Here we examine morphological and geographic variation in the Bornean slow loris [Nycticebus menagensis, Lydekker, 1893]. A small taxonomic study on species-level differences in N. menagensis done previously found diversity within this species [Nekaris and Munds, 2010], but no thorough investigation of intraspecific variation has been conducted to date.

Contract grant sponsor: Systematics Research Fund of the Linnaean Society; Contract grant sponsor: Primate Conservation Inc.; Contract grant sponsor: International Animal Rescue Indonesia; Contract grant sponsor: Royal Society; Contract grant sponsor: Primate Society of Great Britain; Contract grant sponsor: Primate Conservation Inc.; Contract grant sponsor: Primate Action Fund; Contract grant sponsor: Margot Marsh Biodiversity Foundation; Contract grant sponsor: SYNTHESYS Project (European Community Research Infrastructure Action, FP6 "Structuring the European Research Area" Programme); Contract grant number: NL-TAF-3491.

*Correspondence to: Rachel A. Munds, Department of Anthropology, 107 Swallow Hall, University of Missouri, Columbia, MO 65203, USA. E-mail: rmunds27@gmail.com

Received 09 April 2012; revised 13 July 2012; revision accepted 19 July 2012

DOI 10.1002/ajp.22071

Published online in Wiley Online Library (wileyonlinelibrary.

Until recently, the genus *N. ycticebus* Boddaert 1785 comprised two species, the pygmy loris (N. pygmaeus) and the polytypic slow loris (N. coucang), which consisted of four subspecies [Groves, 1971]. Only in 1998 was one of the subspecies of N. coucang recognized as a distinct species (*N. bengalensis*) [Groves, 1998]. More than a decade after the first split in the original *N. coucang*, the three remaining subspecies of N. coucang (N. javanicus, N. menagensis, N. coucang) have been elevated to species level, based on genetic and morphological research [Nekaris et al., 2008; see also Chen et al., 2006; Ravosa, 1998; Roos, 2003]. More taxonomic research is required, as there is clear variation within each of the currently recognized slow loris taxa [Groves and Maryanto, 2008; Nekaris and Jaffe, 2007; Nekaris and Munds, 2010].

Nycticebus menagensis is found on the island of Borneo, some of the small Philippine islands to the northeast of Borneo, and some small islands to the southwest of Borneo. Historically, four subspecies have been recognized across this region: N. m. bancanus, N. m. borneanus, N. m. menagensis, and N. m. philippinus. These distinctions were not only based on distinct pelage characteristics, but also body size differences with adult body weights (in the same season) ranging from 265-610 g (based on museum specimens), with reports of up to 800 g from animals rescued from trade. Across Borneo and on the small islands, slow lorises are actually scarce, with what may be a disjunct distribution; as field studies are still lacking, no overlap between subspecies is known [Nijman and Nekaris, 2010; Wells et al., 2004].

Slow lorises are found in a multitude of habitats from heavily degraded to pristine rainforests, plantations, and lowland and montane forests [Nekaris et al., 2008; Thorn et al., 2008; Wiens and Zitzmann, 2003]. Although they are most common at an altitudinal limit of approximately 1000 m asl [Thorn et al., 2008, some Bornean specimens in museum collections come from about 1300 m, and in Java, they are found at nearly 1500 m]. The Bornean slow loris is listed as vulnerable by the IUCN. Habitat loss and the illegal wildlife trade are affecting their survival = [IUCN 2010; Nekaris and Nijman 2007]. In addition, Borneo has lost a third of its forest in less than 25 years [Rautner and Hardino, 2005]. Much phenotypic variation has been detected within N. menagensis [Nekaris and Munds, 2010], and studies are needed to determine if this variation differentiates additional discrete taxa, as such research would assist conservationists in creating appropriate action plans to protect these primates.

Here we examine the external pelage variability of *N. menagensis*. Studies on other nocturnal primates have indicated that differences in pelage, particularly the amount of white, have an influence on species recognition [Bearder, 1999; Bradley and Mundy, 2008; Ford, 1994]. By examining pho-

tographs and museum specimens of N. menagensis, we hope to reveal a greater diversity within this species than originally presumed. We propose that, as in other Bornean mammals and nocturnal primates, morphological disparities differentiate multiple taxa within the N. menagensis group.

METHODS

Twenty-three photographs and twenty-seven museum specimens of N. menagensis were examined for facemask differences. This sample included the type specimens for the subspecies N. coucang bancanus (= N. menagensis bancanus) and N. coucang borneanus (= N. m. borneanus), as well as specimens that have been designated as topotypes of N. coucang menagensis (= N. m. menagensis, whose type skin is missing; [Timm and Birney, 1992]). Unfortunately, we have been unable to locate the type of N. m. philippinus. Requirements for using images and specimens were: a color image (photographs); general locale is known either by museum tag or personal communication from photographer or source stating where image was photographed; a clear view of the facemask; and a clear view of the top of the head (crown). Features analyzed included those shown elsewhere to provide meaningful discrimination between slow lorises [Nekaris and Jaffe, 2007; Nekaris and Munds, 2010]. These included 13 features clustered into four groups based on cranial region: (1) Circumocular patch traits (patch top, presence of eye rim, eye rim color, patch middle, patch bottom); (2) Interocular stripe traits (width, shape); (3) Crown traits (crown and fork shape, ear fur coverage, preauricular hair width); and (4) Miscellaneous traits (mask color, nose color, black and white "shade" in a black and white image) [Nekaris and Jaffe, 2007; Nekaris and Munds, 2010]. A guide was created for future researchers to replicate or expand upon this study easily (see Appendix A). A complete list of the 27 museum specimens examined is included in Appendix B. We were granted permission from the listed museums to study their collections for this project. We adhered to the American Society of Primatologists principles for the ethical treatment of primates.

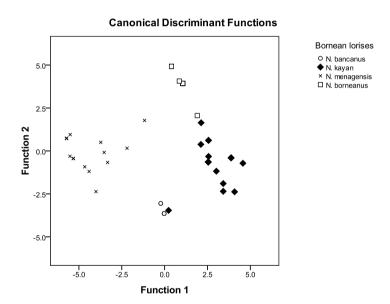
Of the original 13 features, only eight showed variation across the sample of Bornean lorises. Thus we used the following features in further analyses: two Circumocular patch traits (patch top, patch bottom); two Interocular stripe traits (width, shape); three Crown traits (crown and fork shape, ear fur coverage, preauricular hair width); and one miscellaneous trait (black and white shade). We used several multivariate and univariate analyses to test for differences between groups of Bornean lorises; all analyses were done using SPSS v. 17.0. After coding the features with numeric scores that reflect distinctly recognized stages along a continuum of variation, a

cluster analysis (CA) was used to divide the Bornean lorises into separate groups. To strengthen the CA findings, a discriminant analysis (DA) was run on the identified groups. The DA determined how distinctive the groups are and which of the eight facial features are most important in distinguishing between the groups identified in the CA. We used GoogleEarth 2010 to obtain and map the precise decimal latitude and longitude (GPS points) localities of all analyzed loris specimens/photos, which allowed us to assess if groups were clustered by geographic regions. Outlier lorises (those not falling into any of the main clusters in the CA) were re-examined and placed into appropriate groups based on the DA of facial features and geographic location. Once we were confident with the groupings, Pearson's Chi-squares were used to test for significance between groups for

analyzed facial features. We used a 95% confidence level.

RESULTS

A hierarchical cluster analysis (CA) divided the 50 lorises into four groups. The discriminant analysis (DA) supported the CA division as significant (p < 0.0001) and only misclassified one specimen (as Group 1 rather than group 2) (Fig. 1). The groups are broadly discriminated geographically as well. Group 1 is on the island of Bangka and in the southwestern portion of Borneo south of the Kapuas River and east to the Barito River; this group's boundaries appear not to extend all the way east to Barito River. Group 2 is found in central Borneo, north of the Kapuas



Classification Results

		Predicted Group Membership				
		N. bancanus	N. kayan	N. menagensis	N. borneanus	Total
Original Count	N. bancanus	6	0	0	0	6
	N. kayan	1	19	0	0	20
	N. menagensis	0	0	15	0	15
	N. borneanus	0	0	0	9	9
%	N. bancanus	100.0	.0	.0	.0	100.0
	N. kayan	5.0	95.0	.0	.0	100.0
	N. menagensis	.0	.0	100.0	.0	100.0
	N. borneanus	.0	.0	.0	100.0	100.0

a. 98.0% of original grouped cases correctly classified.

Fig. 1. Canonical discriminant function and classification results showing the clustering of the four groups of slow lorises on Borneo.

and Mahakam Rivers. It is often found in higher elevations, but is not restricted to them. The boundary of Group 3 overlaps in part with Group 1, as it is found north of the Kapuas River, but its range extends as far east as the Barito River. Finally, Group 4 inhabits the southern Philippines and northern and eastern Borneo, primarily in coastal and lowland areas. It does not range south of the Mahakam River. One specimen (#30, from Mt. Kinabalu in extreme northern Borneo) was misclassified with the extreme southwestern Group 1, based primarily on its light black-white shade. We left it with the group in which it was originally placed by the cluster analysis, Group 2, reflecting its great geographic separation from the members of the group that is located in the extreme southwest. Thus, our data discriminate four groups, each with members found on the island of Borneo.

It is important to note that our Group 4 includes members of two of the currently described subspecies: N. m. menagensis and N. m. philippinus. Cabrera's [1908] recognition of the southern Philippine slow lorises as a distinct subspecies from those found on Borneo indicates that he also recognized the variation within this region, but one of our groups of northern Bornean lorises is indistinguishable from those in the Philippines [see also Timm and Birney, 1992]. The syntype specimens of N. menagensis Lydecker 1893 are from the Philippine island of Tawi Tawi and thus this name takes precedence for this group. However, we note that we were unable to examine the type of *N. m. philippinus*, which is apparently missing, and the syntypes of *N. menagensis* do not include skins. We did examine skins from the nearby Bungao Island.

From the DA, 58% of variance was described by Canonical Discriminant Function 1, another 28% (86% cumulative) by Function 2, and the final 14% (100% cumulative) by Function 3. The characters' weights for each of these functions are given in Table I; while a few characters have stronger weights (e.g. ear coverage for Function 1, PA width for Function 2, and interwidth for Function 3), all eight variables contribute considerably to at least one function (Table I).

TABLE I. Standardized Canonical Discriminant Function

Facial feature	Function 1	Function 2	Function 3
Patch top	0.581	- 0.449	- 0.089
Patch bottom	0.144	-0.422	-0.178
Interwidth	0.277	-0.197	0.787
Intershape	0.282	-0.551	-0.465
Crown forks	0.008	0.634	0.491
Ear coverage	0.837	-0.315	0.353
PA width	-0.738	0.824	-0.217
BW shade	0.654	0.509	-0.229

Pearson's chi-square tests found all eight variables were highly significant between the four groups $(x^2 = p \le 0.002)$. Therefore, chi-squares were computed to determine the significance of differences between paired group comparisons (Table II). Frequencies of pelage variation in the four groups are provided in Table III. Based on the level of significance, the existence of significant geographic barriers between groups, and some important geographic range overlaps [see below], we recognize four distinct species of lorises on Borneo (Table IV).

DISCUSSION

Our results found that facial masks are a significant marker in distinguishing species differences in Bornean lorises (Fig. 2). Four groups are distinguishable based on cluster analyses, discriminant analyses, and chi-square tests, supporting a strong distinction between the groups. Slow lorises, like other nocturnal primates, possess dichromatic vision: therefore white, contrasting colors and patterns are easily distinguishable for individuals [Bradley and Mundy, 2008; Surridge et al., 2003]. These contrasting patterns are seen in the facial masks of lorises. Thus it is not surprising that facial mask variety is useful in distinguishing between species, as vision may have a greater role in the lives of nocturnal primates than originally presumed [Bearder et al., 2006], aiding these animals in identifying potential mates and con-specifics. The observed differences within Bornean lorises may be a result of mate recognition or an anti-predator strategy by deceptively appearing to have larger eyes and larger size [Bradley and Mundy, 2008; Brockelman, 2004]. Our results on the Bornean slow lorises are consistent with past nocturnal primate taxonomic studies [Bearder, 1999; Bearder et al., 2006; Ford, 1994; Yoder et al. 2000], as the significant features influencing the division of these groups are ones describing the amount of white on the face, which enhance visual contrast cues.

Taxonomy

Based on known geographical boundaries of Borneo and the facemask variations discerned, we recognize four species (Table IV). Three of the four species of Bornean lorises proposed here have been previously recognized as subspecies [reviewed in Osman Hill, 1953]. One new species is named and described. The Bornean and Bangka population of lorises were also previously supported as distinct [Nekaris and Munds, 2010]. Appendix A will provide further understanding of the facial mask features that distinguish the four species described below.

TABLE II. Chi-Square and Pair-Wise Comparison Results

Pairwise comparisons	Relationship	Patch top	Patch bottom	Inter width	Intershape	Crown fork	Ear coverage	PA width	BW shade
Grp1vsGrp4	Allopatric	0.04	NS	0.000	NS	NS	0.002	0.001	NS
Grp1vsGrp2	Allopatric	0.000	0.004	0.000	0.054	NS	NS	0.000	0.000
Grp4vsGrp3	Allopatric	NS	NS	NS	NS	0.000	0.000	NS	0.000
Grp1vsGrp3	Sympatric	0.01	NS	0.000	NS	0.001	NS	0.001	0.000
Grp4vsGrp2	Sympatric	0.001	0.024	NS	0.004	NS	0.000	0.043	0.000
Grp2vsGrp3	Sympatric	0.015	0.001	NS	0.021	0.000	NS	0.003	NS
All groups	N/A	0.000	0.001	0.000	0.002	0.000	0.000	0.000	0.000

TABLE III. Frequencies of Pelage Features in Four Groups of Bornean Slow Lorises

Characters	Group 1 N. bancanus	Group 2 N. kayan	Group 3 N. borneanus	Group 4 N. menagensis
Circumocular Patch				
Patch top	D: 100%	D: 0%	D: 33%	D: 53%
•	R: 0%	R: 79%	R: 67%	R: 47%
	P: 0%	P: 21%	P: 0%	P: 0%
Patch bottom	BE: 33%	BE: 16%	BE: 33%	BE: 40%
	AZ: 67%	AZ: 11%	AZ: 67%	AZ: 33%
	UZ: 0%	UZ: 74%	UZ: 0%	UZ: 27%
Interocular stripe				
Width	N: 0%	N: 90%	N: 67%	N: 93%
	W: 100%	W: 10%	W: 33%	W: 7%
Shape	B: 0%	B: 42%	B: 0%	B: 0%
•	R: 100%	R: 58%	R: 100%	R: 100%
Crown				
Crown/fork	D: 100%	D: 58%	D: 0%	D: 87%
	R: 0%	R: 11%	R: 89%	R: 0%
	B: 0%	B: 32%	B: 11%	B: 13%
Ear fur coverage	A: 0%	A: 0%	A: 0%	A: 73%
	P: 100%	P: 100%	P: 100%	P: 27%
Preauricular hair width	N: 100%	N: 11%	N: 0%	N: 13%
	M: 0%	M: 68%	M: 11%	M: 27%
	W: 0%	W: 21%	W: 89%	W: 60%
Miscellaneous				
Black and white shade	D: 0%	D: 95%	D: 100%	D: 7%
	L: 100%	L: 5%	L: 0%	L: 93%

Patch top: D-diffused, P-pointed, R-round; Patch bottom: BE-below eye, AZ-above zygomatic arch; UZ-under zygomatic arch; Interocular width: N-narrow, W-wide; Interocular shape: B-bulb, R-rectangular; Crown/fork: B-band, D-diffused, R-round; Ear fur coverage: A-absent, P-present; Preauricular hair width: N-narrow, M-medium, W-wide; Black and white shade: L-light, D-dark.

Nycticebus kayan [New Species]

Holotype

Adult male skin, and skull, AMNH 106012 (Fig. 3), deposited in the American Museum of Natural History, New York, New York. Collected 8 October 1935 by Baron V. von Plessen. Head and body length measured from skin is 257.3 mm.

Allotype

Adult female skin, and skull, AMNH 106013, deposited in the American Museum of Natural History, New York, New York. Collected 8 October 1935 by Baron V. von Plessen. Head and body length measured from skin is 269.5 mm.

Type locality

Peleben, East Kalimantan, Borneo, Indonesia. Latitude 2.78 ($2^{\circ}46'60$ N) and a longitude of 116.58 ($116^{\circ}34'60$ E). (The town is 132 meters above sea level. Elevation of collecting point is unknown).

Diagnosis

Nycticebus kayan exhibits a distinctive suite of pelage characteristics that distinguish specimens, particularly from its nearest neighbors. In contrast to all other Bornean lorises, most specimens have a dark circumocular patch that extends below the zygomatic arch, often to the bottom of the jaw. The top of the dark circumocular patch is either round or pointed, in contrast to other Bornean lorises

TABLE IV. Taxonomy of the Lorises of Borneo

Study ID	Taxonomic nomenclature	Range	Type specimen location and cat. number
Group 1	N. bancanus (Lyon 1906)	Southwestern Borneo (West and South Kalimantan) and the island of Bangka	USNM 124907
Group 3	N. borneanus (Lyon 1906)	Central south Borneo, excluding the far west (South, West, and Central Kalimantan)	USNM 142234
Group 2	N. kayan	Central North Borneo (Sarawak, Sabah, East and South Kalimantan)	AMNH 106012
Group 4	N. menagensis (Lydekker 1893)	Philippine islands, coastal northern Borneo (East Kalimantan, Sabah, Brunei)	MMNH or FMNH Type not available ^a

USNM, United States National Museum (Smithsonian).

^aSixteen syntypes (cotypes) were named and are housed at the Bell Museum of Natural History, Minneapolis (MMNH) and the Field Museum of Natural History, Chicago (FMNH); none of these specimens include skins. The specimens with pelage are only at FMNH. The types of both *N. menagensis menagensis* and *N. menagensis philippinus* are both missing.



Fig. 2. Facial masks of the lorises of Borneo: A. Group 1 (Nycticebus bancanus); B. Group 3 (N. borneanus); C. Group 2 (N. kayan); D. Group 4 (N. menagensis).

whose circumocular patches are never pointed and instead are a mixture of round or diffuse bordered (*N. menagensis* and *N. borneanus*) or entirely diffuse at edge (*N. bancanus*). The interocular stripe is bulb shaped in approximately half of individuals, whereas it is never bulb shaped in any other Bornean

lorises, being always rectangular. The light band of preauricular hair varies but is predominantly of medium width, whereas it is always narrow in *N. bancanus*, and predominantly wide in *N. borneanus* and *N. menagensis*. In particular, *N. kayan* contrasts with the partly sympatric *N. menagensis* in having



Fig. 3. (Clockwise starting left hand side) Skull of 106012 AMNH, facial mask (note the circumocular patch extending to the jaw line) and full dorsal view.

a sharply contrasting dark black and white facemask (as in neighboring *N. borneanus*) vs. the more blended and markedly less sharp contrasts in the facemask of *N. menagensis*, and the ears of *N. kayan* are always covered with hair (as in the other southwestern species) whereas those of *N. menagensis* are predominantly naked (although a small percentage of specimens do have hairy ears).

Although Bornean lorises have similar head and body lengths, *N. kayan* have longer, fluffier body hair, especially in comparison to the short, unfluffed body hairs of *N. menagensis*, who also appear to have leaner bodies (Fig. 4). The fluffiness of hair is not attributed to seasonal responses, as museum specimens observed in this study were collected throughout various times of the year for both species.



Fig. 4. Comparison of fluffiness between *Nycticebus menagensis* (left FMNH 8964 & 89466) and *N. kayan* (right FMNH 85926 & 108856).

Description

Nycticebus kayan is characterized by typically having a dark, highly contrasting facemask. Its dark circumocular patch is either round or point edged along its upper margin, and the lower circumocular patch commonly extends below zygomatic arch, often as far as the base of the lower jaw. The interocular stripe is almost always narrow and is either rectangular or bulb shaped. The crown patch is variable but mainly diffuse along edges. The ears are hairy, and the light preauricular hair band is variable but primarily of moderate width. The average head and body length of N. kayan is 273.4 mm (10 specimens) and average body weight 410.5 g (two specimens).

Etymology

The specific name *kayan* comes from the Kayan River, which flows through the range of the species, close to the type locality of Peleben.

Distribution

Nycticebus kayan is located in central and northern Borneo (Sarawak, Sabah, and East Kalimantan). Its southern range extends to the Mahakam River in East Kalimantan and the Rajang River in Sarawak. It is found as far north as the base of the southern part of Mt. Kinabalu in Sabah. It spans the width of Borneo, east to west, but unlike its neighbor (N. menagensis), it appears not to be found along the coast. It is sympatric with N. menagensis in East Kalimantan and Sabah.

OTHER BORNEAN SPECIES

Nycticebus bancanus [Lyon, 1906]

Type locality-

Klabat Bay, Bangka, Indonesia. Type specimen USNM 124907.

Description

Nycticebus bancanus is characterized by a light colored facemask and a diffuse-edged upper circumocular patch. The lower part of the circumocular patch never extends below the zygomatic arch, it has a wide interocular stripe, the crown patch is also diffused, the ears are hairy, and the preauricular hair band is narrow. The species is also characterized by a distinct crimson red dorsal pelage. The average head and body length is 258.05 mm (6 specimens).

Distribution-

Nycticebus bancanus (Group 2 in this study) is found in the far southwestern parts of Borneo (West and South Kalimantan) south of the Kapuas River and east to the Barito River (appears not to extend all the way east to the Barito River) and on the island of Bangka. The Bangka population is allopatric to all

other slow lorises, but the Bornean population has some possible sympatry in West Kalimantan with N. borneanus (Group 3 in this study). We are not certain, as the Kapuas River could be a barrier dividing these two species and field studies are required to confirm this on the ground.

Nycticebus borneanus [Lyon, 1906]

Type locality-

Sanggau District, Sakaiam River, western Kalimantan, Borneo, Indonesia. Type specimen USNM 142234.

Description-

Nycticebus borneanus has a dark contrasting facemask and predominantly round but sometimes a diffuse-edged upper circumocular patch. The lower circumocular patch never extends below the zygomatic arch, variable width interocular stripe, the crown patch is often round but sometimes a band (never diffuse), the ears are hairy, and the preauricular hair band is wide. The average head and body length is 260.1 mm (four specimens).

Distribution-

Found in central south Borneo (West, South, and Central Kalimantan, but excluding the extreme southwest), south of the Kapuas River, extending as far east as the Barito River. *N. borneanus* (Group 3 in this study) is sympatric to *N. bancanus* (Group 1).

Nycticebus menagensis [Lydekker, 1893] (includes N. m. philippinus Cabrera 1908)

Type locality-

Vicinity of Tataan, Tawi-tawi Island, Philippines. Topotype specimen series of 15 specimens in Minnesota Bell Museum and one in Western New Mexico University, none with skins (Timm and Birney, 1992). (Type specimen, collected between 5 October and 5 November 1891, no longer exists. See review and naming of topotypes in Timm and Birney, 1992).

Description-

Nycticebus menagensis is very pale with a light contrasting facemask and round or diffuse-edged upper circumocular patch. Lower circumocular patch is variable and sometimes extends below the zygomatic arch, it has a narrow interocular stripe, crown patch is mostly diffused, the ears are usually naked, and the preauricular hair band is variable but mainly wide. The average head and body length is 274.2 mm (six specimens).

Distribution-

Nycticebus menagensis (Group 4 in this study) inhabits north and east coastal Borneo (Brunei, Sabah, and East Kalimantan) and the southern Philippine Islands. It is sympatric with N. kayan (Group 2 in this study).

CONCLUSION

Some researchers claim there is no significant diversity within Bornean lorises because they share a similar cranial morphology and the absence of an upper second incisor, and pelage variability within taxa is minor and should not be a major basis for recognizing different species [Groves, 1971; Groves and Maryanto, 2008]. Yet it is known that many small primates exhibit shared cranial features and therefore this may not be important when recognizing species [Masters and Bragg, 2000]. Pelage color and pattern or other external morphological features have been considered more important in distinguishing species within small primates [Charles-Dominique et al., 1980; Masters and Bragg, 2000]. Our study verifies that pelage (particularly facemask) features are significant in distinguishing the Bornean lorises.

ACKNOWLEDGMENTS

We thank the following museums and curators: L. Heaney, W. Stanley (Field Museum of Natural History), R. Thorington, L. Gordon (National Museum of Natural History), G. Musser (American Museum Natural History), H. Van Grouw (Naturalis Leiden), D. Hill and P. Jenkins (Natural History Museum London), A. Rol and V. Nijman (Zoological Museum Amsterdam), and M. Nowak-Kemp (Natural History Museum Oxford). H. Schulze provided the illustrations and D. Stark and L. Schein provided useful comments. We adhered to all ethical treatments of animals involved, and research stipulations of Malaysia as well as the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

REFERENCES

Anderson MJ. 2000. Penile morphology and classification of bush babies (subfamily Galagoninae). Int J Primatol 21:815–835.

Bearder SK. 1999. Physical and social diversity among nocturnal primates: a new view based on long term research. Primates 40:267–282.

Bearder SK, Nekaris KAI, Curtis DJ. 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. Folia Primatol 77:50–71.

Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I. 2006. Cryptic species as a window on diversity and conservation. Trends Ecol Evol 22:148–155.

- Bradley BJ, Mundy NI. 2008. The primate palette: the evolution of primate coloration. Evol Anthropol 17:97–111.
- Brockelman WY. 2004. Inheritance and selective effects of color phase in white-handed gibbons (*Hylobates lar*) in central Thailand. Mammal Biol 69:73–80.
- Cabrera A. 1908. Sobre los loris, y en especial sobre la forma Filipina. Boletín de la Real Sociedad Española de Historia Natural. Madrid 8:135–139.
- Carraway LN, Verts BJ. 2002. Geographic variation in pelage color of Pinon mice (*Peromyscus truei*) in the northern great basin and environs. West N Am Naturalist 62:458–465.
- Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E, Pariente GS, Petter-Rousseaux A, Petter JJ, Schilling A. 1980. Nocturnal malagasy primates: ecology, physiology and behavior. New York: Academic Press.
- Chen JH, Pan D, Groves CP, Wang YX, Narushima E, Fitch-Snyder H, Crow P, Thanh VN, Ryder O, Zhang HW, Fu YX, Zhang YP. 2006. Molecular phylogeny of *Nycticebus* inferred from mitochondrial genes. Int J Primatol 27:1187–1200.
- Ford SM. 1994. Taxonomy and distribution of the owl monkey. In: Baer JF, Weller RE, Kakoma I, editors. Actus: the owl monkey. New York: Academic Press. p 1–57.
- Groves CP. 1971. Systematics of the genus *Nycticebus*. In: Biegert J, Leutenegger W, editors. Taxonomy, anatomy, reproduction. Proceedings of the 3rd International Congress of Primatology 1:p. 44–53.
- Groves CP. 1998. Systematics of tarsiers and lorises. Primates 39:13–27.
- Groves CP, Maryanto I. 2008. Craniometry of slow lorises (genus *Nycticebus*) of insular Southeast Asia. In: Shekelle MI, Maryanto C, Groves C, Schulze, H, Fitch-Snyder H, editors. Primates of the oriental night. Jakarta: LIPI. p 115–122.
- Isaac NJB. Mallet J, Mace GM. 2004. Taxonomic inflation: its influence on macroecology and conservation. Trends Ecol Evol 19:464–469.
- IUCN. 2010. IUCN red list of threatened species. Available online at: http://www.iucnredlist.org.
- Jacobs DS, Eick GN, Schoeman MC, Matthee CA. 2006. Cryptic species in an insectivorous bat, Scotophilus dinganii. J Mammal 87:161–170.
- Lydekker R. 1893. Mammalia. Zool Record 29:24-25.
- Lyon MW. 1906. Notes on the slow lemurs. Proc United States Nat Mus 31:527–538.
- Masters JC, Bragg NP. 2000. Morphological correlates of speciation in bush babies. Int J Primatol. 21:793–813.
- Merker S, Driller C, Dahruddin H, Wirdateti, Sinaga W, Perwitasari-Farajallah D, Shekelle M. 2010. *Tarsius wallacei*: a new tarsier species from Central Sulawesi occupies a discontinuous range. Int J Primatol 31:1107–1122.
- Munshi-South, J. 2006. Asocial monogamy, extra-pair paternity, and dispersal in the large treeshrew (tupaia tana) [Ph.D. dissertation]. College Park (MD): University of Maryland.
- Nekaris KAI, Jaffe S. 2007. Unexpected diversity of slow lorises (*Nycticebus* sp.) within the Javan pet trade: implications for loris taxonomy. Contrib Zool 76:187–196.
- Nekaris KAI, Nijman V. 2007. CITES proposal highlights rarity of Asian nocturnal primates (Lorisidae: *Nycticebus*). Folia Primatol 78:211–214.
- Nekaris KAI, Blackham G, Nijman V. 2008. Conservation implications of low encounter rates of five nocturnal primate species (*Nycticebus* sp.) in Southeast Asia. Biodivers Conserv 17:733–747.
- Nekaris KAI, Munds R. 2010. Using facial markings to unmask diversity: the slow lorises (Primates: Lorisidae: Nycticebus) of Indonesia. In: Gursky S, Supriatna J, editors. The primates of Indonesia. New York: Springer. p 383– 396.
- Niemitz C. 1984. The biology of tarsiers. New York: Gustav Fischer Verlag.

- Nijman V, Nekaris KAI. 2010. Checkerboard patterns, interspecific competition, and extinction: lessons from distribution patterns of tarsiers (*Tarsius*) and slow lorises (*Nyctice-bus*) in insular Southeast Asia. Int J Primatol 31: 1147–1160
- Osman Hill WC. 1953. Primates, comparative anatomy and taxonomy. I. Strepsirhini. Edinburgh: Edingburgh University Press.
- Rautner M, Hardiono M. 2005. Borneo: treasure island at risk. Frankfurt am Main: WWF Germany.
- Ravosa MJ. 1998. Cranial allometry and geographic variation in slow lorises (*Nycticebus*). Am J Primatol 45:225–243. Roos C. 2003. Molekulare Phylogenie der Halbaffen,
- Roos C. 2003. Molekulare Phylogenie der Halbaffen, Schlankaffen, und Gibbons [dissertation] München (Germany): Technischen Universität.
- Surridge AK, Osorio D, Mundy NI. 2003. Evolution and selection of trichromatic vision in primates. Trends Ecol Evol 18:198–205.
- Tattersall I. 2007. Madagascar's lemurs: cryptic diversity or taxonomic inflation? Evol Anthropol 16:12–23.
- Thorn JS, Nijman V, Smith D, Nekaris KAI. 2008. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (primates: *Nycticebus*). Divers Distribut 15:289–298.
- Timm RM, Birney EC. 1992. Systematic notes on the Philippine slow loris, Nycticebus coucang menagensis (Lydekker, 1893) (Primates: Lorisidae). Int J Primatol 13:679–686.
- Wells K, Linsenmair KE, Pfeiffer M, Lakim MB. 2004. Use of arboreal and terrestrial space by a small mammal community in a tropical rain forest in Borneo, Malaysia. J Biogeogr 31:641–652.
- Wiens F, Zitzmann A. 2003. Social structure of the solitary slow loris *Nycticebus coucang* (lorisidae). J Zool 261:35–46.
- Yoder AD, Rasoloarison RM, Goodman SM, Irwin JA, Atsalis S, Ravosa MJ, Ganzhorn JU. 2000. Remarkable species diversity in Malagasy mouse lemurs (primates, *Microcebus*). Proc Nat Acad Sci 97:11325–11330.

APPENDIX A FACIAL MASK GUIDE FOR BORNEAN LORISES

CIRCUMOCULAR EYE PATCH: A distinct dark furred area circling the eyes creating a mask. They are divided by lighter patches.



PATCH TOP: The part of eye patch nearest the top of the head, right before patches connect.

Pointed: Narrow to absent in width, similar to the tip of a triangle.

Round: Medium width, rectangular in shape, distinct from the crown patch.

Diffused: Wide, no distinct shape, and blends with crown

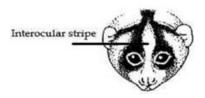
PATCH BOTTOM: The part of the eye patch found below eye.

Under eye: Patch ends immediately below the eye.

Above/on zygomatic arch: Patch ends right above or directly on top of the cheekbone.

Below zygomatic arch: Patch ends below the arch, sometimes to the chin.

INTEROCULAR STRIPE: The light stripe that runs down the center of the face and separates the eye patches. Starts from the nose and ends where the eye patch tops connect.



INTEROCULAR WIDTH: Measured between the eyes (middle eye patch section).

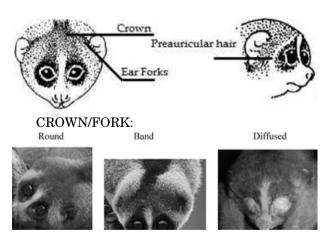
Narrow: The eye patch tops lean toward each before reaching the crown.

Wide: The patches lean away from each other; never connect or connect after crown.

INTEROCULAR SHAPE: Rectangle: A straight bar that runs between all sections of the eye patches. The bar remains almost the same size from top to bottom.

Bulb: A round top between where the eye patch tops meet, and part between the middle is a straight bar running to the nose.

CROWN: Area on the top of the head, beyond the circumocular patch. The crown features also include the auricular area.



Round: The crown is circular and only in the center of head. Ear forks are present, but often blend into fur or the majority of head is covered with crown. Ear forks are not visible.

Band: Rectangular strip spans from ear to ear.

Diffused (the "other" category): No shape is noticeable, it blends with the body fur.

EAR COVERAGE: The presence or absence of tufts of fur on the tip of ear. The ear is also considered covered if it is hidden from view (difficult to note on museums specimens).

Present: Small hair tufts are on the tip of the ear. Often ears are easily seen beyond the body fur. Or the ears are covered by fur.

Absent: Ears are naked and typically hidden by the body fur.

PREAURICULAR HAIR: The lighter patch of fur that runs between the ear forks and circumocular patches.

Wide: A broad gap between darker furs of the ear forks and circumocular patch.

Medium: A small, but distinctive stripe between the ear forks and circumocular patch.

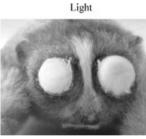
Narrow/absent: A barely visible, to no stripe separating the ear forks and circumocular patch.

BLACK AND WHITE MASK SHADE: Image set to black and white saturation, then examined to determine how distinct the facemask stands out from the rest of the facial patterns.

Dark: Facemask stands out distinctively from the rest of the face

Light: Facemask blends with the rest of the facial patterns, hart to notice.





*Loris drawings from: Schulze H. 2009. Conservation database for lorises (*Loris, Nycticebus*) and pottos (*Arctocebus, Perodicticus*), prosimian primates. Available online at: http://www.loris-conservation.org/database/

APPENDIX B

List of Specimens Examined

Museum	Museum abbreviation	Examined Nycticebus specimens
American Museum of Natural History	AMNH	$32649;106011^{\mathrm{b}}106012^{\mathrm{a}}106013;17113^{\mathrm{b}}17411^{\mathrm{b}}$ $288/417^{\mathrm{b}}$
Field Museum of Natural History	FMNH	$17619^{\rm b}\ 85926^{\rm b}\ 88277; 89464; 89465; 89466; 108856^{\rm b}$
United States National Museum (The Smithsonian)	USNM	$142232;142233;142236;142237;142238;142239;\\198267;198857;292553;292554;317185;317186^{\rm b}\\317187;317188^{\rm b}488077;124907^{\rm a}142234^{\rm a}$
British Museum of Natural History	BMNH	166; 2 047
Naturalis National Museum of Natural History Leiden	RMNH	33 670; 33 671; 33 672

^aType specimens.

^bDid not include certain specimens because damage had been done to specimen during original preparation, or pelage had been damaged over time, or location where loris was collected was not specified.