Primate Conservation 2022 (36): 203-231

A Review of the Assamese Macaque *Macaca assamensis* Complex and Its Geographical Variation

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Abstract: The Assamese macaque, *Macaca assamensis* (McClelland, 1840), is a relatively large and heavy monkey that occurs in South and Southeast Asia. It shows considerable geographic variation in its facial features and the shades of its brownish coat color and is, as such, a complex of several forms. *Macaca assamensis* ranges from Uttarakhand in north India to Vietnam and southern China, through Nepal, Bhutan, Bangladesh, Myanmar, Thailand, Laos and probably also Cambodia. Its type specimen, collected in 1835–1837 "from Assam" is now unavailable. There are two recognized subspecies, based on tail length—the nominate *assamensis* with a shorter tail and *pelops* (Hodgson, 1841), with a longer tail. Two more macaques are here considered subspecies of *assamensis*: *munzala* Sinha, Datta, Madhusudan & Mishra, 2005; and *leucogeny*s Cheng Li, Chao Zao & Peng-Fei Fan, 2015—both of which were described as full species. Their lack of sufficiently unique characters and their similarity to other forms prompted this study to place them as subspecies. The recently described *Macaca selai* Ghosh, Thakur, Singh, Durra, Sharma, Chandra & Banerjee, 2022, and *munzala* were found to be inseparable morphologically, and they are not separated by any geographic or ecological barrier. Larger rivers have played a role in isolating some of the species' populations. The Brahmaputra River separates the nominate subspecies to its south from *pelops* to the north. The Siang River separates *pelops* on its west bank from *leucogenys* on the east bank. Similarly, the Lohit River separates *leucogenys* from the nominate subspecies, but it is not known if the type of *assamensis* (if from this general area) was collected from the north or the south of the Lohit River. An attempt has been made here to fix the type locality as 'eastern Assam/Arunachal Pradesh, south of the Brahmaputra and north/south of the Lohit River;' that is, within the range of *M. a. assamensis* and marginally of *M. a. leucogenys* as currently applied, to preserve nomenclatural stability. The Assamese macaque occurs in the plains of the Brahmaputra valley as well as in hilly and mountainous tracts, from 15 m elevation in the plains of Tripura to 3,500 m in the Great Himalaya. Habitat loss, poaching for the cooking pot, and development activities such as dams for hydro-electric power are the major threats.

Key words: *Macaca assamensis,* Assamese macaque, *pelops*, *munzala, leucogenys, selai,* geographic variation.

Introduction

Variation in the external morphology of the Assamese macaque, *Macaca assamensis* (McClelland, 1840), across its range is considerable and merits a thorough study. A relatively large and heavy monkey, its fur can be wavy or smooth and various shades of brown—dark brown to light brown, with the crown, neck, shoulders and arms lighter, having a yellowish/light golden hue in color. The lower back is darker. The face is somewhat similar to that of the Rhesus macaque *M. mulatta*, i.e., light pink or flesh color, but can also be grayish. The tail is pendulous and well-haired. It is distinguished at once from the Rhesus macaque by the absence of the orange-red hue on its loins and rump. On closer observation the difference of general body color is conspicuous (various shades of brown in the Assamese macaque to olive in the Rhesus macaque) as is the shape of the face. Adult Assamese macaques have a variety of facial features, and both sexes show various shades of brownish coat color, making it a complex. When juvenile, the pelage of these macaques shows less variation in both intraspecific and interspecific comparisons.

The range of the Assamese macaque is from north India to Vietnam and southern China (Zhang *et al*. 1981; Fooden 1982; Choudhury 1988, 2016; Corbet and Hill 1992; Duckworth *et al*. 1999). In India, it is confined to a small pocket in Uttarakhand but widespread in the northeast (Choudhury 2016) (Figs. 1 and 2). The type locality of the species is eastern Assam/eastern Arunachal Pradesh (originally recorded as "Assam"), India (McClelland, 1839 [1840]).

Its occurrence in the Sunderbans of both India and Bangladesh would be ecologically anomalous, and it has not been found there since the report in the 1870s (could be from elsewhere also, see below) despite substantial wildlife survey efforts since then. This occurrence should therefore be ruled out completely, though some authors such as Prater (1948), Fooden (1982), and Roonwal and Mohnot (1977) mentioned their occurrence there, which was subsequently referred to by many authors. Agrawal *et al.* (1992), however, did not mention it. The only record was a specimen at the Zoological Survey of India, Kolkata [Calcutta]. It was based on two specimens collected in 1870 for J. Anderson, then Curator of the Indian Museum. One of these (ZSI 11999, skin only) is extant. But it was not collected by Anderson himself but by another person, a 'collector' (Anderson 1872). The specimens in question were reportedly shot about 50 miles or 80 km east of Calcutta and they only reached him as skins. So, the authenticity of the collection site lies not with Anderson but the 'collector', whose details are not known. It could be that he was "assigned to bring two types of specimens" and he somehow managed! Timmins and Duckworth (2013) also surmised that the only possibility for error seems to be a dishonest collector who for some reason falsified the locality. While preparing the catalogue of the mammals in the Indian Museum, Anderson changed his mind as to the affinities of the Sunderban macaque (Hinton and Wroughton 1921). The reason for doing so was not recorded by Anderson, but no survey in the entire Sunderbans has revealed the existence of a single Assamese macaque or even any secondary evidence (Khan 1986; Siddiqi 2001; Mallick 2011; Chandra *et al*. 2017).

Despite its wide range, there are relatively few studies; it is among the most poorly-known primates in its range (Fooden 1982; Eudey 1991; Rowe 1996; Rowe and Myers

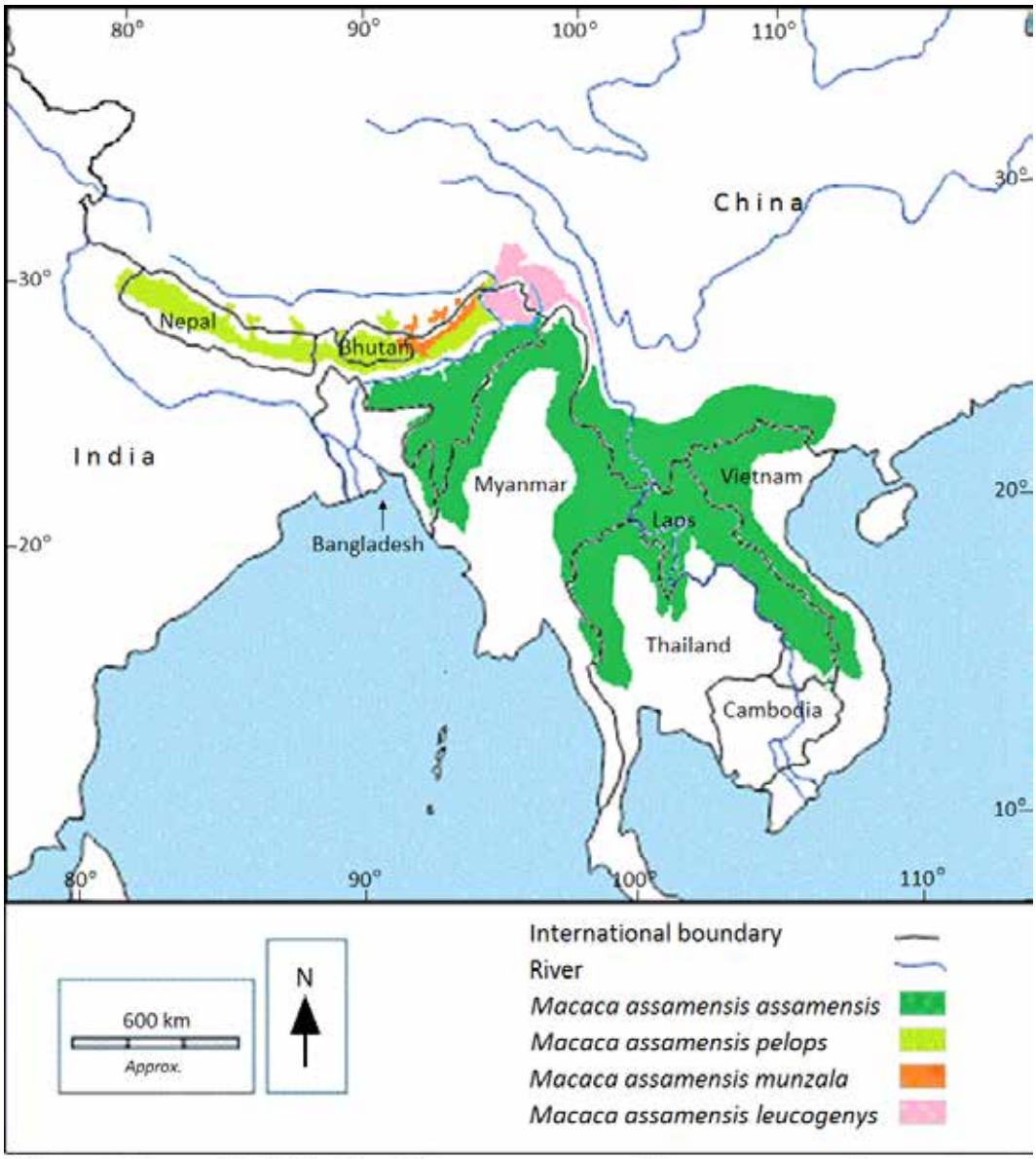


Figure 1. Geographic distribution of the Assamese macaque, *Macaca assamensis*.

2016). In fact, knowledge of the species was so scanty that even fairly recently Fooden (1982, p.34) indicated that it does not occur in present Assam and the reports from Garo Hills, Meghalaya, were erroneous. Some published information is available on the Assamese macaque: Hill and Bernstein (1969), Fooden (1982, 1988, 2003), Choudhury (1988, 1989, 1995a, 1996, 1998a, 1998b, 2001, 2002, 2008, 2018a, 2018b), Cooper and Bernstein (2000); Chalise (2003, 2013), Mitra and Alfred (2007), Timmins and Duckworth (2013), Zhou *et al*. (2014), Sarkar (2014), Sarkar and Bhattacharya (2015) and Li *et al*. (2019). Useful information can also be found in other synoptic works on primates in general or on wildlife: for example, Pocock (1939), Fooden (1976), Roonwal and Mohnot (1977), Corbet and Hill (1992), Choudhury (1995b, 1997, 2013, 2016) and Groves (2001).

In this article, I review and describe the distribution, conservation and significant intraspecific and geographic variations of the Assamese macaque and discuss various aspects of recently described 'species', which are geographically separated or with marginal sympatry.

Methods

The data were obtained during numerous field surveys carried out from October 1985 to March 2022, mainly in Northeast India as part of a broader survey of wildlife. I also visited Bhutan, Bangladesh, Nepal, Myanmar, China, Thailand, Cambodia and Vietnam. The presence of Assamese macaques was ascertained by direct sightings, as well as through finding preserved skulls in the tribal villages and by interviewing local forest staff, villagers, and hunters (using visual aids such as photos and drawings). Direct observations were carried out along trails (mostly during foot-transect), roads (by car), and rivers (by boat). Some

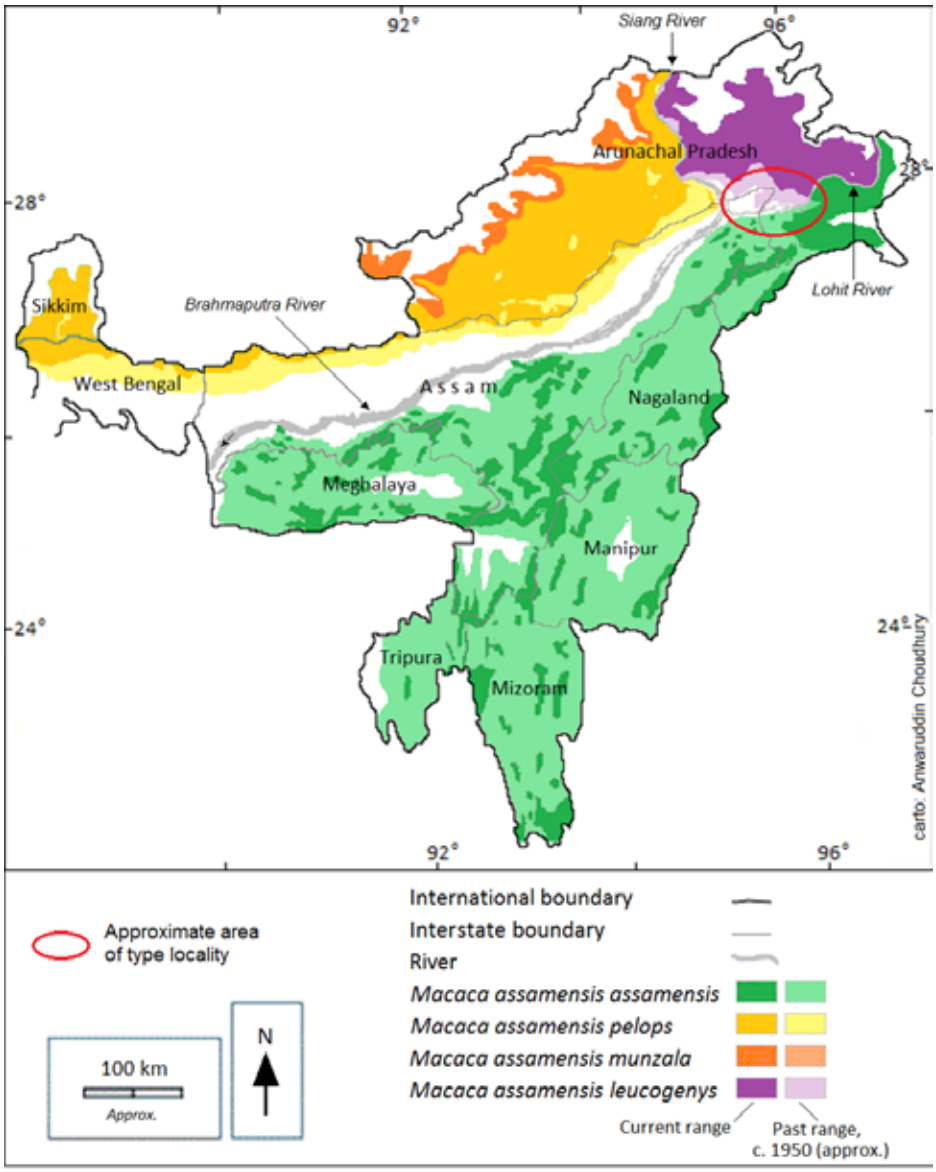


Figure 2. Northeast India where all the four taxa of *Macaca assamensis* occur showing some details of the distribution and the approximate area of the type locality of *M. a. assamensis*.

3a–f. Goalpara

3b.

3c.

3d.

3e.

3f.

3g and h. Bherjan

3h.

3i. Tripura

3j. Yunnan

3k and l. Karimganj

3l. (subadult)

3m. Goalpara

3n–q. Central Annamite

3o.

3p.

3q.

3r. Bangladesh

3s. Vietnam

3t. Namdapha

Figures 3: Close-up of facial features of male *Macaca a. assamensis*. Photographs by Anwaruddin Choudhury (**3a–e**, **g–i**, **k–m** and **t**); Narayan Sharma (**3f**); Li Xueyou (**3j**); Association Anoulak, Laos (**3n–q**); Tanvir Ahmed Shaikot (**3r**), and Tilo Nadler (**3s**).

of the photographs were taken from other field workers and agencies, who were given due credit. In addition, most of the relevant literature on the species was studied and many are listed here. The locations of field observations and photographs (Figures 3–19) are given in Figure 20.

Results and Discussion

Distribution and type locality

The Assamese macaque occurs in India (Arunachal Pradesh, Assam, Manipur, Meghalaya, Mizoram, Nagaland, northern West Bengal, Sikkim, Tripura and Uttarakhand), Nepal, Bhutan, eastern Bangladesh, Myanmar, northwestern Thailand, Lao PDR, northern Vietnam, southern China (Guangxi, Guizhou, Tibet and Yunnan) and probably extreme northeast Cambodia as its range in Lao PDR indicates (Timmins and Duckworth 2013). Two subspecies were listed by Ellerman and Morrison-Scott (1951) and subsequently by Fooden (1982) and Groves (2001). Choudhury (2013) listed three (four described here) as he found a few variants from a population previously undocumented (Choudhury 1998b, 2004). The morphological and geographic variations are listed in Table 1 and discussed below.

The type specimen of the Assamese macaque was an adult male, stuffed skin with skull, which was collected by J. McClelland, September 1835 – February 1837 (McClelland in Horsfield 1840; Griffith 1847). It was preserved in the Zoological Museum of the East India Company, London, where it was examined and characterized by Horsfield (1851, p. 64) but he was unable to find the skull. Later on, Gray (1870, p.31) and Sclater (1871, p.222) were unable to locate the specimen. The collections of the Zoological Museum of the East India Company were transferred to the British Museum (Natural History) in 1879 but there is no evidence that this type specimen was received by the British Museum, and it has not been seen since some time before 1888 (Blanford 1888, p.16; Elliot 1913, p.211; Fooden 1982). External measurements of the dry skin were recorded by Anderson (1879, p. 65), as follows: "The length of the animal along the curve of the head and back is 26.75 inches [679 mm], the tail measuring 9.25 inches [235 mm; relative tail length 0.35]."

The type locality was not precisely known; originally given as "Assam" (Horsfield, 1840, p.147), which at that time included Meghalaya, Nagaland and eastern Arunachal Pradesh. The type specimen was collected during the course of a 17-month expedition to explore for tea-producing areas in northeastern India. The expedition started from near Pabna in present Bangladesh, near the confluence of Padma and Jamuna rivers (24°N, 90°E), then after some land journey in Khasi Hills, Meghalaya, upward along the Brahmaputra River and its tributary, the Lohit from Guwahati, to as far east as the Mishmi Hills (28°N, 96°30'E) (Griffith 1847). The exact or approximate point along this route where the type specimen of *M. assamensis* was obtained was perhaps not recorded by the expedition party. Blanford (1888, p.15) speculated that the type specimen may have been collected "from Assam, possibly from the hills to the northward."—that is, in the Mishmi Hills in present Arunachal Pradesh, as the journey ended somewhere in Singpho country in eastern Arunachal Pradesh on the Lohit River and then some overland travel in areas near Parshuram (Brahma) Kund and Tidding River in Mishmi country.

To date, the macaques occurring south of the Brahmaputra River are considered as the nominate subspecies believing that the type locality was in this part of the range. From the foregoing account, however, it was not clear whether the type specimen was from the north or the south of the Lohit River. This matter was immaterial until the description of a new taxon *leucogenys* from north of the Lohit River, type locality Gangrigebu (29°28019.73N, 95°49025.00E, 2410 m above sea level), Medog County, Tibet, China (Li *et al*. 2015). If the type specimen was found to be from the north, then (based on the distributional information assembled here) the taxon named as *leucogenys* would, being distinct become the nominate subspecies and the population presently referred to as the nominate one would, if considered taxonomically distinct from *leucogenys* (as currently applied) have to be renamed, either from a name presently in the synonymy of *M. a. assamensis* (as currently defined) or if no suitable name exists, with a new name. This could lead to future confusion. With no likelihood of access to the type specimen, no available information on its characters relevant to separating the two taxa, and no apparent likelihood of clarifying its geographic origin, there seems no likelihood of evidential basis for determining precisely the locality from which the type came. Thus, the type locality is restricted here to 'eastern Assam/Arunachal Pradesh, south of the Brahmaputra and north/south of the Lohit rivers'; that is, within the range of *M. a. assamensis* and marginally of *M. a. leucogenys* as currently applied, to preserve nomenclatural stability. This restriction allows us to keep the existing arrangement in the case of the nominate subspecies.

Geographic variation and discussion

Tables 1, 2 and 3 and the photographs (Figs. 3–19; see Appendix 1 for a gazetteer of the localities) show how Assamese macaques are extremely variable, something probably not found in any other macaque species. Even within a group there can be a high level of variation. It somehow lacks clear-cut basic characteristics that, for example, the stump-tailed *M. arctoides* has, such as its unique face and tail and also those of pig-tailed *M. leonina/nemestrina* species, also having unique head and tail pattern. This is why I treat it as a complex. Fooden (1982) stated tail length while classifying subspecies *assamensis* and *pelops* and the geographic separation either side of the Brahmaputra River. However, if small numbers of individual specimens are sporadically examined it could be difficult to separate them, as the tail-length has a large range and the longest of *assamensis* (Figs. 19c and 19e) may overlap with the shortest of *pelops* (Fig. 13k). But Table 1 and the photographs (Figs. 3–6 and 11–14) show that some other features also help separate the two,

4a–e. Goalpara **4b.** **4c.** **4d.**

4e. **4f.** Karimganj **4g.** Goalpara **4h.** Bherjan

4i. Goalpara **4j–l.** Central Annamite **4k.** **4l.**

Figures 4: Close-up of facial features of female *Macaca a. assamensis*. Photographs by Anwaruddin Choudhury (**4a–i**) and Association Anoulak, Laos (**4j–l**).

such as lack of side whiskers and beard-like hairs in females of *pelops.* Even in male *pelops* such hairs are visibly less prominent than the nominate subspecies.

While there is nothing diagnostic in the tail of *leucogenys,* in *munzala* it is noteworthy although not diagnostic, from very short to 'normal' long (see Figs. 15–16). But *munzala*'s main problem is that many macaques can fit into *assamensis* or *leucogenys* (Fig. 3–19). Some *leucogenys* females have very prominent, whitish side whiskers as well as a long beard, but these are characteristic of two other forms as well, *assamensis* and *munzala* (Figs. 4h and 4j, 8a and 8b and 12g). No one form can be assigned uniqueness in this respect. Regarding the color of the penis, pinkish or flesh colored, this is variable; in this case the shape of the penis, if any consistent variation was present, could be pertinent. The claimed penis character in *leucogenys* is difficult to discern with just one image of poor quality. If collected in isolation, some females of Tukreswari, Goalpara in Assam could well be considered as being distinct with their unique style of beard and whitish hair around the cheeks, somewhat similar to the macaques from Laos (Figs. 4a, 4b, 4c, 4j, 4k and 4l). The female *pelops* in Figures 6a–6h show that that this form is unique in having short or no side-whiskers or beard. The dark *pelops* (Figs. 14c and 14f) could confuse one as *munzala*-like. Moreover, macaques living in higher elevations with snowfall may develop relatively thicker fur—adaptive modifications for survival in the colder climates.

Fooden (1982) noted that erythrism, in which dorsal fur coloration tends to bright, burnt orange, is sporadic in *M. assamensi*s. Among specimens examined, three *M. a. pelops* skins were found to be exceptionally brightly colored (BNHS 5119 9, Rongli; BNHS 5121 8, Sookia Pokhari; ZMB 91098 8, Manshitang), as were two *M. a. assamensis* skins (BNHS 5115 8, Mokokchung; ZSI 11924 8, Bhamo vicinity, captive). Similar coloration is also observed in *munzala* and *leucogenys*. General color variation even within a group can be extreme (15b, 15c,15d, 15f, 15 g, 16b, 16f, 16g and 19g).

5a. Kathmandu Zoo **5b-c.** South Sikkim **5c.** **5d-g.** Darjeeling

5e. **5f.** **5g.** **5h.** Chirang RF

5i and j. Itanagar Zoo **5j.** **5k.** Royal Manas **5l.** Manas

5m and n. Nepal **5n.** **5o.** Pakke

Figures 5: Close-up of facial features of male *Macaca a. pelops*. Photographs by Anwaruddin Choudhury (**5a–f** and **h–j**); Ayan Banerjee (**5g**); Rustom Basumatary (**5k–l**); Mukesh Kr. Chalise (**5m–n**), and Aftab Ahmed (**5o**).

The diagnostic characteristics of *munzala* Sinha *et al.*, 2005, were that it can be distinguished from *M. a. assamensis* by distinctive facial features and external morphology. Table 1 and figures 3–19 show that these are not unique to it. This issue has also been discussed at length by Biswas *et al*. (2011), who showed clearly that *munzala* is a variant of *assamensis*; hence, I am not repeating it here in detail. The prominently dark crown patch, characteristic facial marks on the temple and forehead, pale collar of hair around the neck and distinctive relative tail length are not unique. They are seen in *assamensis* and *leucogenys* but rarely in *pelops*. Generally large and heavyset individuals with a short tail

Table 1. Key differences between different subspecies of *Macaca assamensis.*

	assamensis	***pelops***	***munzala***	***leucogenys***	**Reference to photos (Figures)**
Tail (% of head & body)	25–59	50–70	25–61	33–54	
Tail length variable	+	+	+	+	11a, d, f, g, h, 12d, h, 13a, e, i, j, k, m, n, o, p, 14b, c, d, e, g, h,15a, b, h–m, 16b, d, g–l, 17b, f, 18b, d, e, i, j,19a–h
Crown, neck, shoulders and arms lighter with yellowish or golden hue (conspicuous in some, seen in close-up view in others)	+	+	+	+	11b,12b, g,13a, i, 14b, h,15b, h–j, 16a, j, k, 17a, c, e, f, 18b, 19a
Dorsum	Variable brownish shades. Light to darker brown often with yellowish or chocolate-brown hue.	Variable brownish shades. Light to darker brown often with yellowish or chocolate-brown hue.	Variable brownish shades. Dark brown to lighter brown often with yellowish or chocolate-brown hue. Some animals not separable from *assamensis, pelops* and *leucogenys.*	Variable brownish shades. Dark brown to lighter brown often with yellowish hue. Many animals not separable from *assamensis* and *munzala,* and some from *pelops.*	11 to 18
Ventrum: whitish	+	+	+	+	11e, i, 12a, 13f, h, k, 14a, e, i, 15c, d, 17d, 18f
Ventrum: some light gray and some may be variable light colors	+	+	+	+	11c, d, 13c, d, 15b, e, g, 16c, e, h, 17c, e, 18c
No contrasting side-whiskers	+	+	+	+	3a, h, i, n, 5b, c, j–n, 6f, 7c, g, 8d, i, 9a
Often with whitish hairs near cheeks	+	+	+	+	3c, o, q, s, 5a, d, e, 6b, g, 7k, 9b–e, 10b, d
Side whiskers, often whitish, present in some adult males	+	–/+	+	+	3c–g, j, l, o–s, 5a, d, g, h, i, 7a, b, e, f, h, j, k, l, 9a–e
Side whiskers, often whitish, prominent in some adult females	+	–	+	+	4a, b, c, j, k, l, 8a, b, c, f, 10b–e, g,
Chin whiskers in males – prominent	+	–	–	–	3b–d, i, q–s
Chin whiskers in males – not prominent or nearly absent	+	+	+	+	3a, e–g, n, p,5a–o, 7a, b, e–g, i–k, 9a, c, d
Chin whiskers in females – prominent	+	–	+	+	4a-e, g, h, j–l, 6g, 8a–c, e, 10b–g
Chin whiskers in females – not prominent or nearly absent	–/+	+	–/+	–/+	4i, 6a, b, d, f, h, 8, d, f, 10a
Overall beard-like hairs present in many males	+	–/+	+	+	3a–f, i, o, q, s, 5e, 7h, 9b, c
Overall beard-like hairs prominently present in some females	+	–	+	+	4a–e, g, h, j–l, 8a, b, f, 10b–e, g
A contrasting small patch (dark or light), may or may not be present on the crown	+	+	+	+	Present in 3l, m, 4d, e, 5b, e, k, m, 6g, 7a, h, k, 8d, 9d, e
Hair pattern on the crown variable: parted on the middle (clear in some animals)/have whorls/have small tuft	+	+	+	+	3a–i, m–s, 4a–d, g–l, 5b–n, 6a, c–h, 7a–l, 8a–j, 9a, b, d, 10a–g,

Table 1. Cont'd.

	assamensis	*pelops*	*munzala*	*leucogenys*	**Reference to photos (Figures)**
Bare face light pink or flesh color	+	+	+	+	3d, f, g, i, o–r, 4g, 5a, b, e, f, k, m, n, 6a, f, h,7c, d, e, k, 8f–h, j, 9b, d,10f
Bare face grayish in some males	+	+	+	+	3a, c, n, 5c, j, l, 7a, f, g, h, i, 9a, c
Bare face, wholly or in part deeper pinkish or reddish in many females	+	+	–	+	4a, b, c, e, f, h, i, j, l, 6b, c, e, g, 10b, c, g
Bare face, wholly or in part purplish in a few females	–	–	+	–	8b, c, i
Color of bare skin on muzzle	Light pink or flesh color, light brown, darker brown, gray-brown; reddish in some females	Light pink or flesh color, light brown, darker brown, gray-brown; reddish in some females	Light pink or flesh color, darker brown, gray-brown, light brown; purplish in some females.	Light pink or flesh color, darker brown, gray-brown, light brown; reddish in some females	
Color of areas around eyes in some adults is pale	+	+	+	+	3f, h, i, r, 5c, i, j, k, 7a, b, g–k, 9a, b, 10a, f
End of tail bends toward the ground or upwards in some individuals	+	–/+	+	+	11d, f, h, 13k, p, 14c, f, h, 15a, j, l, 16b, d, g, h, 18e, i, j
Tail not hairless	+	+	+	+	11a, c, d, f–h, 12d, h, 13a, c, e, i–k, m, n, o, p, 14b–f, h, 15a, b, f–m, 16a, b, d, g–l, 17b, f, 18b, d, e, g, i, j, 19b–h
Occurs N of Brahmaputra River	–	+	+	–	
Occurs S of Brahmaputra River	+	–	–	–	
Occurs E of Siang River	–	–	–	+	
Occurs N of Lohit River	–	–	–	+	
Elevation range (m)	15–3200	60–3000	1800–3500	130–3041	

Macaca thibetana **and** *M. mulatta* have not been compared as they are distinct and there is no identification confusion with any form of *assamensis*. + present or yes; – absent or no.

Table 2. The tail length of *assamensis* and *pelops* in Fooden (1982) and this study.

	Fooden (1982)		This study	
	assamensis (n=25)	*pelops* (n=13)	*assamensis* (n=16)	*pelops* (n=17)
Tail (% of head & body)	26–47	44–69	33–59	46–70

Table 3. The tail length of *munzala* in Biswas *et al*. (2011), *leucogenys* in Li *et al*. (2015) and this study.

	munzala		*leucogenys*	
	Biswas *et al*. (2011) (n=37)	This study (n=14)	Li *et al*. (2015) (n=4)	This study (n=13)
Tail (% of head & body)	33–68	25–61	35–45	33–54




6a–b. South Sikkim **6b.** **6c–e.** Darjeeling **6d.**




6e. **6f.** Chirang RF **6g and h.** Nepal **6h.**

Figures 6: Close-up of facial features of female *Macaca a. pelops*. Photographs by Anwaruddin Choudhury (**6a–d** and **f**), Mukesh Kr. Chalise (**6h**); Ayan Banerjee (**6e**), and Bishnu Prasad Pandey (**6g**).

are also not unique. Neither is the body color of *munzala* adults, as is evident in Table 1 and photographs (Figs. 11–14, 17–18).

The facial skin in *munzala* is also not, as a rule, unique, and Sinha *et al*. (2005) also mentioned "in several of the adult males" but not "all or many", which clearly shows that this feature is not valid for species identification (Figs. 3–10 show the same). A purplish color of the facial skin in a few females and the lack of prominent deep pinkish or reddish on a bare face are, however, features so far unique to *munzala*, although not found in all females. There is a prominent dark patch on either temple, occasionally extending as a stripe from the outer corner of the eye (canthus) or the upper cheek to the ear, which has been claimed to be present in virtually every individual, and it appears to be a distinctive species-specific morphological trait. Figures 3–6 and 9–10 show that it may be present in some individuals of other forms and may not be present in all *munzala* (Figs. 7–8). The skin around the eyes is usually pale in some individuals, producing a faintly spectacled appearance but it is present in all other forms (see figures).

The diagnostic characteristics of *leucogenys* Li *et al.*, 2015, were that it is robust, heavyset with a relatively short tail, features that were also mentioned in the description of *munzala*, and they are not unique. The analysis made at length by Biswas *et al*. (2011) is also applicable in the case of *leucogenys*, clearly showing that both *munzala* and *leucogenys* are variants of *M. a. assamensis*. This is evident from the characteristics listed in Table 1 and also described in Biswas *et al*. (2011). The description further said "The species can be morphologically distinguished from all other known *Macaca* species, especially potential sympatric species by a suite of characteristics including relatively uniform dorsal pelage, hairy ventral pelage, relatively hairless short tail, prominent pale to white side- and chin-whiskers creating a white cheek, and round facial appearance, dark facial skin on the muzzle, and long and thick hairs on neck" (Table 2 in Li *et al*. 2015). None of these features, however, seem to be unique to *leucogenys*—they are also found in *assamensis* and *munzala,* and, uncommonly, in *pelops*. Some subadults may resemble *munzala* and even the nominate subspecies (Figs. 3l in this work and 3A in Li *et al*. 2015). Descriptions of the trunk and the variability of the dorsal pelage color are the same in all the four forms. Adult males being larger than adult females is common to all forms, in fact to most macaques.

In the description of *munzala*, it was noted that the front of the crown of every individual is very characteristic in having a prominent pale-yellow patch with a central group of dark hairs. In one adult male, it formed an erect tuft, though in all other individuals it was more reminiscent of a whorl of hairs (Sinha *et al*. 2005). Figures 4d, 4e, 5b, 5k, 6a, and 6g, however, have dark or pale patches, and 6a has an erect tuft indicating these are not unique to *munzala*. Neither is there anything unique in the head pattern. In fact, Fooden (1982) noted that hair arrangement on the crown of *M. assamensis* is highly variable, also previously indicated by Pocock (1939, p.52 and 1941, p.470).

In adults, facial skin on the muzzle can be variable, as seen in the figures. Adults and large juveniles/subadults have prominent white side-whiskers, which extend from cheek to ears, creating a white cheek and white ear


7a–d. Jang


7b.


7c.


7d. (subadult)


7e. Jang


7f and g. Gorsam Gompha


7g.


7h. Brokser


7i. Tawang


7j. Mandla-Phudung


7k. Eagle's Nest


7l. Northeast Bhutan

Figures 7: Close-up of facial features of male *Macaca a. munzala*. Photographs by Anwaruddin Choudhury (**7a–d** and **f–g**), Ayan Banerjee (**7e** and **i–k**), Rupin Dang (**7h**) and Phuntsho Thinley (**7l**).

appearance in *leucogenys*. This is also conspicuous in many *munzala* and some *assamensis* but can be inconspicuous or absent in *pelops*. The white to pale side-whiskers also grow longer with age and cover the ears in adults, a fact present in other forms as well. Long side-whiskers create a round facial appearance in adults (Fig. 4 in Li *et al*. 2015) but see the images of *munzala*.

The tail is not hairless and is not diagnostic. For *leucogenys*, the authors (Li *et al*. 2015, Table III) also mentioned that there is no obvious difference in relative tail length between *leucogenys* and *assamensis* and *munzala*. Only one case of a hairless tail has been found (Fig. 19a) but its length (too short) and shape, and comparison with the tails of other individuals in the same group (Fig. 19b) indicate that it was a disease or was injured by a predator. The relative tail lengths of the four subspecies are listed in Tables 2 and 3.

The Assamese macaque's two, long-recognized subspecies or races are based on tail morphology and isolation by a river barrier. The white-cheeked macaque is also mostly isolated by rivers, hence, there is no overlapping range with any other form. The Arunachal macaque, *munzala,* however, may be partially sympatric with *pelops*, as there is no zoogeographic barrier but *munzala* occurs at higher elevations, *pelops* generally tend to remain at slightly lower elevations (Choudhury 2013; per. obs. for post-2013 data). The closest observation points are near Lamacamp, outside Eagle's Nest Wildlife Sanctuary and Sessa Orchid Sanctuary. A group of *pelops* was observed about 50 m away from where *munzala* had been seen previously, in 1998. In addition to relative tail length, there is one more diagnostic feature for *pelops*, the lack of long, whitish side-whiskers and beards (including chin-whiskers) that are present in various degrees in males and females and very prominently in some females of *assamensis*, *munzala* and *leucogenys* (Figs. 4h, 4j, 8a, 8b, 10b, 10d, 10e and 10g in this work and 4B, and 4C in Li *et al*. 2015). Table 1 shows that *munzala* is more similar to *assamensis* than *pelops*, but *assamensis* does not occur north of the Brahmaputra where *munzala* occurs. The purplish face in some *munzala* females is somewhat unique. These, along with some other features listed in Table 1, are the key considerations for treating *munzala* a separate taxon.

8a–c. Jang **8b.** **8c.** **8d.** Northeast Bhutan

8e–f. Tawang **8f.**

8g–h. Jang (subadult) **8h.** **8i.** Jang **8j.** Zemithang

Figures 8: Close-up of facial features of *Macaca a. munzala,* females in 8a–f and indeterminate sex in 8g–j. Photographs by Anwaruddin Choudhury (**8a–d** and **g–i**) and Ayan Banerjee (**8e**, **f** and **j**).

The penile morphology of *assamensis, pelops* and *munzala* is similar to that of the *sinica* group of macaques (Fooden 1976, 1980). In *leucogenys*, the characteristics given for the glans penis and shaft base are not convincing because it was from a low-quality camara-trap photograph of just one adult male and it is premature to draw any conclusions. Minor skin color or anatomical differences might exist but not the basic characteristics. This feature, i.e., penile morphology, remains unconvincing and needs further work.

Khanal *et al*. (2021, p.11) also argued that there is taxonomic ambiguity concerning *munzala* and *leucogeny*s. They suggested that it "needs to be resolved by detailed phylogenetic assessment using multiple mitochondrial and nuclear DNA loci together with morphological, behavioral, and distribution data, and should include samples from the type localities of *assamensis* and *pelops*."

The Chinese animals, especially those in Yunnan Province, were described as a subspecies, *M. a. coolidgei* Osgood, 1932 (see Jiang *et al*., 1993). The type locality of *coolidgei* is Hoi Xuan, Annam (= Vietnam). The distinction was unconvincing, however, and *coolidgei* was treated as a synonym by Ellerman and Morrison-Scott (1951; see also Fooden, 1982; Groves, 2001). Khanal *et al*. (2021) surmised that the Nepal population could be a new species but did not discuss *pelops*, indicating that its type locality was in western Arunachal (p.11) when in fact it is in Nepal (Hodgson, 1841, p. 1213). Any other name would be a junior synonym.

Ghosh *et al.* (2022) split *munzala* into two, with a new species they named *M. selai*, type locality "Nyukmadung (27.4057°N, 92.1332°E), West Kameng district of Arunachal Pradesh, altitude 2016 [m] above sea level" on the southern and eastern side of the Sela mountain pass, at elevations of 1133 to 2794 m, possibly extending into Tibet

9a. Walong, Mishmi Hills

9b and c. Dibang Valley, Mishmi Hills

9c.

9d and e. Lohit, Mishmi Hills

9e.

9f. Dibang Valley, Mishmi Hills

Figures 9: Close-up of facial features of male *Macaca a. leucogenys*. Photographs by Udayan Borthakur (**9a**); GV Gopi/WII (**9b, c** and **f**), and Anwaruddin Choudhury (**9d** and **e**).

10a and b. Walong, Mishmi Hills

10b.

10c. Hayuliang, Mishmi Hills

10d–h. Dibang Valley, Mishmi Hills

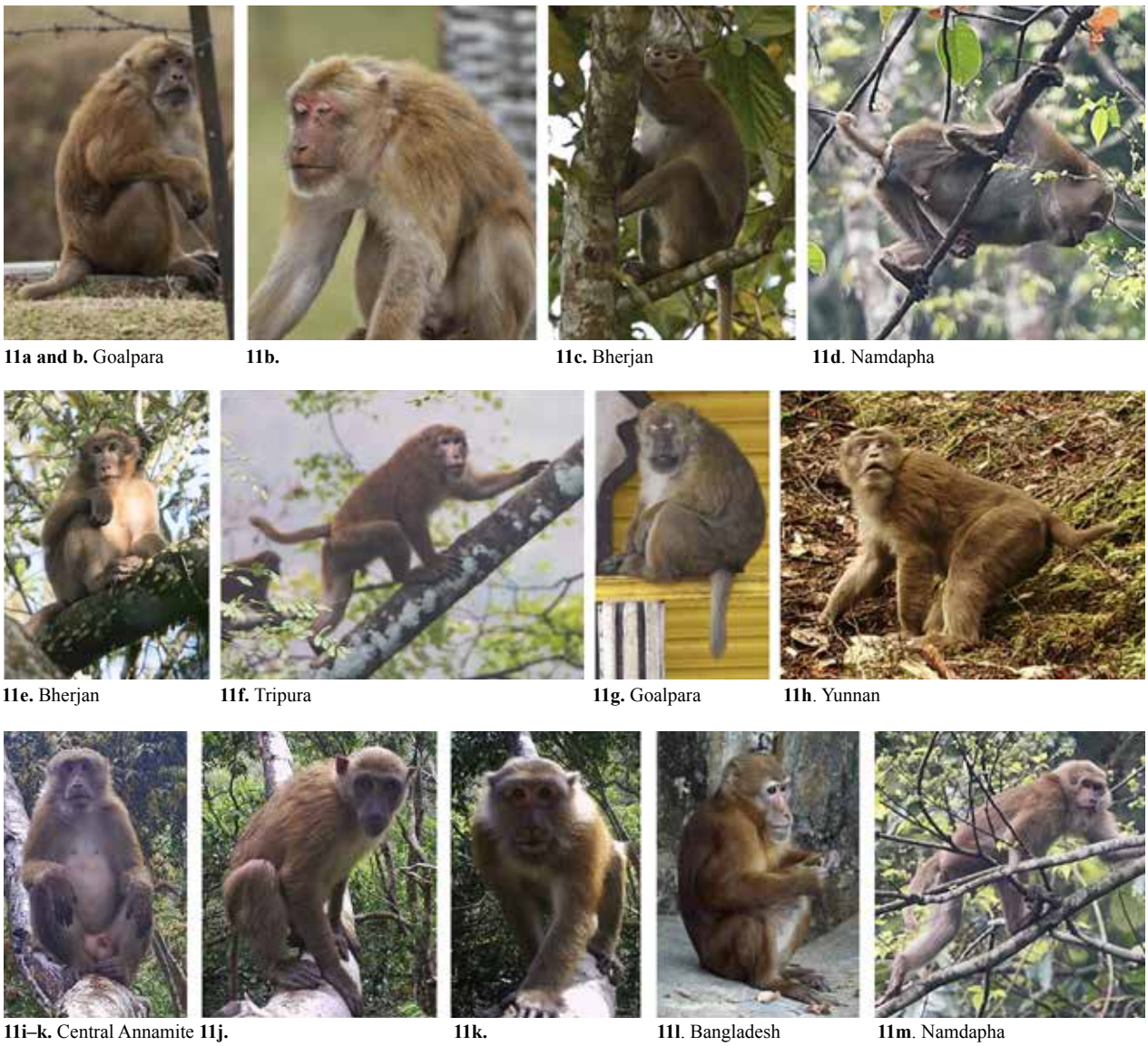
10e. Dibang Valley, Mishmi Hills

10f.

10g.

10h. (subadult)

Figures 10: Close-up of facial features *Macaca a. leucogenys*, females in 10a–g and indeterminate sex in 10h. Photographs by Udayan Borthakur (**10a**); Binanda Hatiboruah (**10b**); Ranjan Kr. Das (**10c**), and GV Gopi/WII (**10d–h**).



11a and b. Goalpara **11b.** **11c.** Bherjan **11d**. Namdapha

11e. Bherjan **11f.** Tripura **11g.** Goalpara **11h**. Yunnan

11i–k. Central Annamite **11j.** **11k.** **11l**. Bangladesh **11m**. Namdapha

Figures 11: Head, body and tail features of male *Macaca a. assamensis*. Photographs by Anwaruddin Choudhury (**11a–g** and **m**); Li Xueyou (**11h**); Assoc. Anoulak, Laos (**11i–k**), and Tanvir A. Shaikot (**11l**).

and Bhutan. They suggested that *munzala* evolved into two phylogenetic species about 1.96 mya, following allopatric speciation either side of the Sela pass in Arunachal Pradesh, India. They found that *selai* interestingly exhibited high intra-specific genetic variation and also harbors at least two conservation units. Further, they report the past demographic trajectories and quantify genetic variation required for taxonomic clarification. The photographs of the holotype, an adult male, were of poor quality and are inseparable from *munzala* (Tables 1,2,3). As claimed, *munzala* and *selai* are not allopatric. The Sela ridge is short and may have separated the groups immediately north-west and south-east to the pass but not for any great distance.

In the diagnosis, they mentioned phylogenetic analysis and penile morphology. But how unique is the penile morphology was not spelled out, and there was no mention of sample size and no accompanying photos. The relative tail length was compared with some other species based upon just three samples but it is not clear whether the measurements were on skins, live animals or photographs. The tail features are not clearly visible in the photographs. There is nothing unique, however, in the tail length. They mentioned that dorsal pelage color varies from brown to dark brown and the color of collar and muzzle are brown, neither features of which can be considered unique in view of the variation seen in figures 3–19. In their diagnosis, Ghosh *et al.* (2022) further stated that "It can be differentiated from all the species of the *sinica* group by a suite of traits including brown to dark brown dorsal pelage, brown colored collar hair and muzzle, pale brown side whiskers, pale facial skin, thick brown hair around the neck and absence of chin whiskers". From figures 3–19, however, it is evident that all these features are similar to *munzala*, also many to *leucogenys* and none is unique to *selai*. Table 3 in Ghosh *et al.* (2022) compared 16 features with *munzala*, of which seven were identical. Of the rest, the differences are "pink vs. dark

12a–c. Goalpara

12b.

12c.

12d. Karimganj

12e and f. Central Annamite

12f.

12g. Vietnam

12h. Dum Duma RF

Figures 12: Head, body and tail features of *Macaca a. assamensis*, females in 12a–g and indeterminate sex in 12h. Photographs by Anwaruddin Choudhury (**12a–d** and **h**); Assoc. Anoulak, Laos (**12e** and **f**), and Tilo Nadler (**12g**).

pink" (regarding the penis the number of samples examined was not mentioned and there were no photographs), "brown vs dark brown," which, in an otherwise variable taxon with different color shades present even within a single group, are certainly not strong distinguishing features. The male in photographs c and d in Figure 3 in Ghosh *et al.* (2022) appear not to be full-grown males but subadults. By comparison, some full-grown adult males (from the range of *selai*) can be seen in Figure 15a, 15h, and 15i, which were taken in West Kameng. In fact, macaques in figures 3–19 here show all sorts of oddities in these pelage characters which unless unique are of little use in diagnosing a full species.

Subspecies Accounts

Macaca assamensis assamensis

This subspecies occurs in India (Assam, south of the Brahmaputra and Lohit rivers; in Arunachal Pradesh, south and east of the Lohit River; Nagaland; hills of Manipur; Mizoram; Tripura and Garo-Khasi-Jaintia hills in Meghalaya); eastern and south-eastern Bangladesh; north-western, northern and eastern Myanmar; north-western Thailand; Lao PDR; northern Vietnam; southern China (Guangxi, Guizhou and Yunnan) and probably extreme northeast Cambodia as the range in Lao PDR indicates (Timmins and Duckworth 2013). This subspecies has the largest range and occurs at elevations as low as 15 m in the Tripura plains to above 3200 m in Saramati on the Nagaland-Myanmar border. It used to occur widely in the floodplain and other plains areas of the Brahmaputra valley in Assam until their habitats came under paddy cultivation and tea plantations. Populations in lowland plains areas still exist in fragments in Assam (Choudhury 1995b, 2013; Sarkar 2014). In the hilly and mountainous tracts, it is rather more abundant than the Rhesus macaque. The Garo Hills in Meghalaya mark its westernmost range (89º51'), and the Mishmi Hills (east of the Lohit River) in Arunachal Pradesh the northernmost (28º21') (author's own observations).

Macaca assamensis pelops

The macaques occurring north of the Brahmaputra River are considered a subspecies, with the type locality in Nepal. However, the extent of its range in the east is debated. Boonratana *et al*. (2020a) mentioned the Manas River as its eastern limit. Several other authors do not mention any river but show a somewhat similar range. So, which subspecies occurs in the eastern areas north of the Brahmaputra and west of the Siang River is still in doubt. My observations of macaques in the Doimara Reserved Forest, the Sessa Orchid Sanctuary, the Pakke Tiger Reserve, the Tâle Valley Wildlife Sanctuary, and elsewhere in Lower Subansiri district in Arunachal Pradesh indicate that they are also *pelops*. Fooden (1982) rightly noted "probably, Arunachal Pradesh (India) as far east as the great bend of the Brahmaputra River" but apparently without any specific record.


13a. Kathmandu Zoo


13b and c. South Sikkim


13c.


13d–f. Darjeeling


13e.


13f.


13g. Chirang RF


13h. Itanagar Zoo


13i. Talle Valley WS


13j and k. Royal Manas


13k.


13l. Manas


13m and n. Nepal


13n.


13o and p. Pakke


13p.

Figures 13: Head, body and tail features of male *Macaca a. pelops*. Photographs by Anwaruddin Choudhury (**13a–e**, **g** and **h**); Ayan Banerjee (**13f**); Ngunu Ziro (**13i**); Rustom Basumatary (**13j–l**); Mukesh Kr. Chalise (**13m** and **n**), and Aftab Ahmed (**13o** and **p**).

In India, the subspecies *pelops* occurs in Assam, north of the Brahmaputra River, now mostly confined to the Himalayan foothills and adjacent plains; Arunachal Pradesh, west of the Siang River; eastern Uttarakhand; northern West Bengal and Sikkim; Nepal; Bhutan, and small areas of China (Tibet, west of the Tsangpo bend and along the trans-Himalayan river valleys of Trishuli, Bhote Koshi or Poiqu, Arun or Bum Chu [all in Nepal], Kurichu [in Bhutan], Subansiri (?) and

14a and b. South Sikkim

14b.

14c and d. Darjeeling

14d.

14e. Nepal

14f and g. Darjeeling

14g.

14h. Chirang RF

14i. Nepal

Figures 14: Head, body and tail features of female *Macaca a. pelops*. Photographs by Anwaruddin Choudhury (**14a**, **b**, **d**, **g** and **h**); Ayan Banerjee (**14c** and **f**); Mukesh Kr. Chalise (**14e**), and Bishnu Prasad Pandey (**14i**).

Siang/Tsangpo [both in Arunachal Pradesh, India]). This subspecies has the second largest range and occurs down to 60 m above sea level in the northwest Assam plains to above 3,000 m in the Great Himalaya. It also used to occur widely in the plains areas of the Brahmaputra valley and northern West Bengal till their habitats came under paddy cultivation and tea plantations. Populations in lowland plains areas still exist but with a reduced range (several observations by the author and a photograph from the Chirang Reserved Forest at 60 m elevation in Choudhury 2019). In the Himalaya, it is rather more abundant than the Rhesus macaque. Pithoragarh district in Uttarakhand is its (and also of the species) westernmost location (80º18') (Verma and Verma 2013), and the Siang River in Arunachal Pradesh the easternmost (95º20').

Macaca assamensis munzala

An enigmatic population of macaques was first documented and photographed in West Kameng district, Arunachal Pradesh in 1997 (Choudhury 1998b). Subsequently similar macaques were seen in other high elevation areas of West and East Kameng, Tawang and West Siang districts, normally above 2000 m (Choudhury 2004, 2013). These macaques were initially considered Tibetan macaques *Macaca thibetana* (see Choudhury 1998b) but were later described as a new species *M. munzala*, with Zemithang (27º42'N, 91º43'E; altitude 2180 m above sea level), Tawang District, Arunachal Pradesh as the type locality (Sinha *et al*. 2005). A detailed analysis by Biswas *et al*. (2011) confirmed, however, that it is not a species but a variant. Biswas *et al.* failed to find any support for species-level treatment of this population, even questioning whether it represented a distinct taxon at all. In the original description, comparison of intraspecific variation, more particularly with other forms of *assamensis* was not comprehensive. It has probably more relative variability, including in tail length and coat color, than is found among the two long-accepted subspecies of Assamese macaques and one of the variants was taken for the type, which somehow could not represent the entire population. Although Biswas *et al*. (2011) questioned whether it was apt, given this variability, to treat the population as a taxon, it was subsequently treated as a subspecies in Choudhury (2013).

Chakraborty *et al*. (2007)'s, and Mishra and Sinha (2008)'s reasons for species treatment were satisfactorily refuted by Biswas *et al*. (2011). Post-Biswas *et al*. (2011) studies include Sinha *et al.* (2013) and Sarania *et al*. (2021). Sinha *et al*. (2013) continued to support the consideration of this macaque as a species but did not refute Biswas *et al.* (2011). Sarania *et al*. (2021), however, corroborated Biswas *et al*. (2011), and questioned all the claimed differences from *M. assamensis*. In their assessment of the IUCN Red List status of *munzala*, Kumar *et al.* (2020) did not cite Biswas *et al*. (2011) and listed it as a species, while mentioning that "Morphology, genetics and taxonomic variation in northeastern Indian macaques, including this taxon, is very poorly known […]. Further taxonomic research is required."

15a. Lamacamp

15b–d. Jang

15c.

15d. Jang

15e. Brokser

15f and g. Gorsam Gompha

15g.

15h. Mandla Phudung

15i. Eagle's Nest

15j. Jang

15k and l. Gorsam Gompha

15l.

15m and n. Northeast Bhutan

15n.

Figures 15: Head, body and tail features of male *Macaca a. munzala*. Photographs by Anwaruddin Choudhury (**15a–d**, **f**, **g**, and **j–l**); Rupin Dang (**15e**); Ayan Banerjee (**15h** and **i**), and Phuntsho Thinley (**15m** and **n**).

The evidence to date provides no basis for recognition of it as a species under any credible species concept.

The subspecies *munzala* occurs in India (Arunachal Pradesh, upper areas west of the Siang River); Bhutan (northeast in Trashi Yangse and Trashigang dzongkhags) and in China (small areas in southeast Tibet) (Choudhury 2009, Chang *et al.* 2018), west of the Tsangpo bend, chiefly along the trans-Himalayan river valleys of Kurichu (in Bhutan) (?),


16a and b. Jang


16b.


16c. Tawang


16d. Northeast Bhutan


16e. Tawang


16f and g. Jang


16g.


16h. Zemithang


16i. Mandla Phudung


16j–l. Jang


16k.


16l.

Figures 16: Head, body and tail features of *Macaca a. munzala*, females in 16a–h, indeterminate sex in 16i-l. Photographs by Anwaruddin Choudhury (**16a, b**, **d**, **f–h,** and **j–l**) and Ayan Banerjee (**16c, e** and **i**).

Manas (Nyamjang Chu), Subansiri (?) and Siang/Tsangpo (?) (all in Arunachal Pradesh, India). This subspecies has a relatively small range and occurs from 2000 m (sometimes down to 1800 m in middle Himalaya to 3100 m (occasionally up to 3,500 m) in the Great Himalaya.

Macaca asssamensis leucogenys

These enigmatic macaques were also first observed in 1993 in the Lower Dibang Valley district in Arunachal Pradesh, more specifically, where the Sesseri River spreads out on to the plains. They were subsequently observed elsewhere in Mishmi Hills and recorded as typical *assamensis*. In 2015, a population of these macaques was described as a new species *M. leucogenys* by Li *et al*., with the type locality Gangrigebu (29°17'N, 95°29'E; elevation 2410 m above sea level), Modog [=Medog] county, Tibet, China. As in *munzala*, the comparison with other forms of *assamensis* was insufficient. The camera trap photos of the holotype were not properly exposed, rather over-exposed above with an under-exposed frontal view. The full features were indistinct. The figures in the present article show how important is such an exercise. Sarania *et al*. (2021) mentioned that the external morphological traits that are being used to distinguish these macaque species (*munzala* and *leucogenys* vis à vis *assamensis*) are highly variable even within the same species, and there is an urgent need to identify more precise species-specific morphological traits. Fan *et al*. (2017), while confirming full species status to *leucogenys*, stated that "The mitochondrial gene tree showed that *M. leucogenys* is phylogenetically close to *M. munzala* and *M. radiata* within the *sinica* group; however, their relationships were unresolved by Y chromosomal phylogenies, which indicates a possible historical episode of male introgression. Further studies using an integrative approach that combines morphological and ecological characterizations and population-based genome-wide analysis are needed to investigate divergence and reproductive isolation […]".

17a. Lohit, Mishmi Hills

17b and c. Dibang Valley, Mishmi Hills

17c.

17d. Walong, Mishmi Hills

17e–g. Dibang Valley, Mishmi Hills

17f.

17g.

Figures 17: Head, body and tail features of the male *Macaca a. leucogenys*. Photographs by Anwaruddin Choudhury (**17a**); GV Gopi/WII (**17b**, **c**, and **e–g**), and Udayan Borthakur (**17d**).

Pending further investigation, especially the claimed diagnostic differences in penis morphology based on larger samples, I treat *leucogenys* as a subspecies mainly for its geographic isolation and features similar to *munzala* but with which it is separated by the zoogeographic barrier of the Siang River. The subspecies *leucogenys* occurs in India (Arunachal Pradesh, east of the Siang and north of the Lohit rivers in Mishmi Hills, and Assam in Sadiya area, north of the Lohit) and in China (Modog or Medog county and apparently Zayu county in southeastern Tibet and a small area in northwest Yunnan; Anon. 2021). This subspecies also has a relatively small range and occurs from 130 m in Sadiya, Assam (probably extirpated) to 3041 (Anon. 2021).

Low-Altitude Records

The comprehensive reviews by Fooden (1982, 1986) found most records to be from 150–1900 m above sea level, with some up to 3100 m, excluding the doubtful disjunct, record from sea level at Sunderbans. There are now multiple records from well below 150 m, as detailed below. Those without published citations are the author's own observations.

Macaca a. assamensis. In the town of Goalpara, Assam, recorded at 35 m. In nearby Tukreswari, it occurs at 40 m when they come down from the hillocks (Sarkar and Bhattacharya 2015). In the scattered forest pockets of Goalpara district this macaque occurs from 35 m above sea level. In the floodplain of Dibru-Saikhowa National Park and nearby Bherjan-Borajan-Podumoni Wildlife Sanctuary (Choudhury 1995b) it occurs at 110–130 m. In Tripura, photographed at 100 m (Fig. 11f) (Choudhury 2018a) and formerly spread over adjacent plains at 20 m and near the Bangladesh border at 15 m. In Karimganj district, Assam, photographed in Patharia Hill Reserved Forest at about 100 m (Figs. 3k and 4f) but they move to the base of the low hills at 15 m. Near Baghmara in Garo Hills, Meghalaya observed at 50 m. It probably occurred farther down to 10 m in Bangladesh but not specifically reported.

Macaca a. pelops. In northern West Bengal, the lowest area of sighting was near Damdim in 1995 at 140 m. In the past, it occurred further down, to 110 m. A recent survey in Bhutan found Assamese macaques down only to 600 m (Kawamoto *et al*. 2006) but they probably did not survey the areas along the Indian border. Choudhury (2008) noted occurrences as low as 100 m (along riverbeds on the Indian border). Further down from the India-Bhutan border a group was photographed in the flat terrain of the Chirang Reserved Forest, Assam, at 60 m near the Assam – Bhutan road through Ultapani (Figs. 6f and 14h). The macaques used to occur farther down to 45 m near Bismuri on the same road and south of it till their habitat was destroyed in the 1990s.

Macaca a. leucogenys. In Sadiya, Assam, it used to occur as low as 130 m in the Kundil Kaliya Reserved Forest but has been extirpated by habitat loss and poaching. In the adjacent areas of Arunachal Pradesh it also occurred from 135 m upwards, but most of the low elevation macaques vanished for the same reasons. It now occurs mostly above to 250 m in eastern Arunachal Pradesh.

18a. Walong, Mishmi Hills

18b. Hayuliang, Mishmi Hills

18c–j. Dibang Valley, Mishmi Hills

18d.

18e.

18f.

18g.

18h.

18i.

18j.*

Figures 18: Head, body and tail features of *Macaca a. leucogenys*, female in 18a–i, indeterminate sex in 18j. Photographs by Binanda Hatiboruah (**18a**); Ranjan Kr. Das (**18b**); GV Gopi/WII (**18c–j**). * Note the similarity between individuals of 16l (*munzala*) and 18j (*leucogenys*).

Conservation

Habitat destruction

Destruction of forests by tree felling, encroachment, *jhum* or slash-and-burn shifting cultivation (of the hill tribes), and monoculture tree plantations is a major threat to the survival of the Assamese macaque, which it shares in general with all other forest-dwelling primates. The destruction of their forests is also resulting in fragmentation. Since the Assamese macaque is a forest-dweller, its survival depends upon the continued existence of the forest cover. Depredation of plantations and orchards by crop-raiding Assamese macaques worsens when forests are destroyed and fragmented. Overall, it is uncommon but can have a high impact locally, especially in patches of *jhum* cultivations, where the macaques can find maize and other crops.

Poaching

Like most other primates, the Assamese macaque is also killed for the cooking pot by many people in Northeast India, Myanmar, and elsewhere in Southeast Asia. In the past, traditional weapons including snares and self-made muzzle-loaders were used but with the easy availability of automatic firearms the situation has worsened over the last three decades.

Trade

There is no significant trade in India, however, any young animal within easy reach is usually captured for sale as a pet. In parts of Southeast Asia some are sold for meat in markets (also to some extent in Nagaland and the hilly tracts of Manipur in India).

Other problems

Unsustainable harvesting of bamboo for large paper mills, oil mining and exploration, and open-cast coal mining are some of the other conservation issues that are destroying the habitat and besides causing pollution and disturbance. Feeding Assamese macaques is relatively uncommon but occurs at a few places. This habit encourages congregations

19a and b. Mishmi Hills

19b.

19c. Tripura

19d. Bherjan

19e. Karimganj

19f. Lamacamp

19g. Nepal

19h. Pakke

Figures 19: Other features of *Macaca a. leucogenys* (**19a** and **b**), *Macaca a. assamensis* (**19c–e**), *Macaca a. munzala* (**19f**), and *Macaca a. pelops* (**19g** and **h**). Photographs by GV Gopi/WII (**19a** and **b**); Anwaruddin Choudhury (**19c–f**), Mukesh Kr. Chalise (**19g**), and Aftab Ahmed (**19h**).

of more than one group, some are runover by vehicles, and they also spread disease. The Sevoke bridge area, and along Siliguri-Darjeeling and Sevoke-Gangtok roads in northern West Bengal and Sikkim (all *pelops*) and Tukreswari temple in Assam's Goalpara district (*assamensis*) are some areas where such macaques are found.

A major threat that has emerged in recent decades, however, is the construction of dams for hydro-electric power on most of the rivers in and around the habitat of Assamese macaques. An example in Northeast India is the Dibang dam, among the largest in India. At 288 m, this dam will be the tallest concrete dam in the world! The submergence areas of all the dams once completed will flood good primate habitat. The accompanying infrastructure that accompanies the construction and maintenance of these dams also cause damage to the habitat and (at least in Northeast India and Southeast Asia) increase access for hunter and traders and so therefore often result in greatly increased illegal offtake of middle and low commercial value species such as macaques, that formerly had not been worth carrying out of

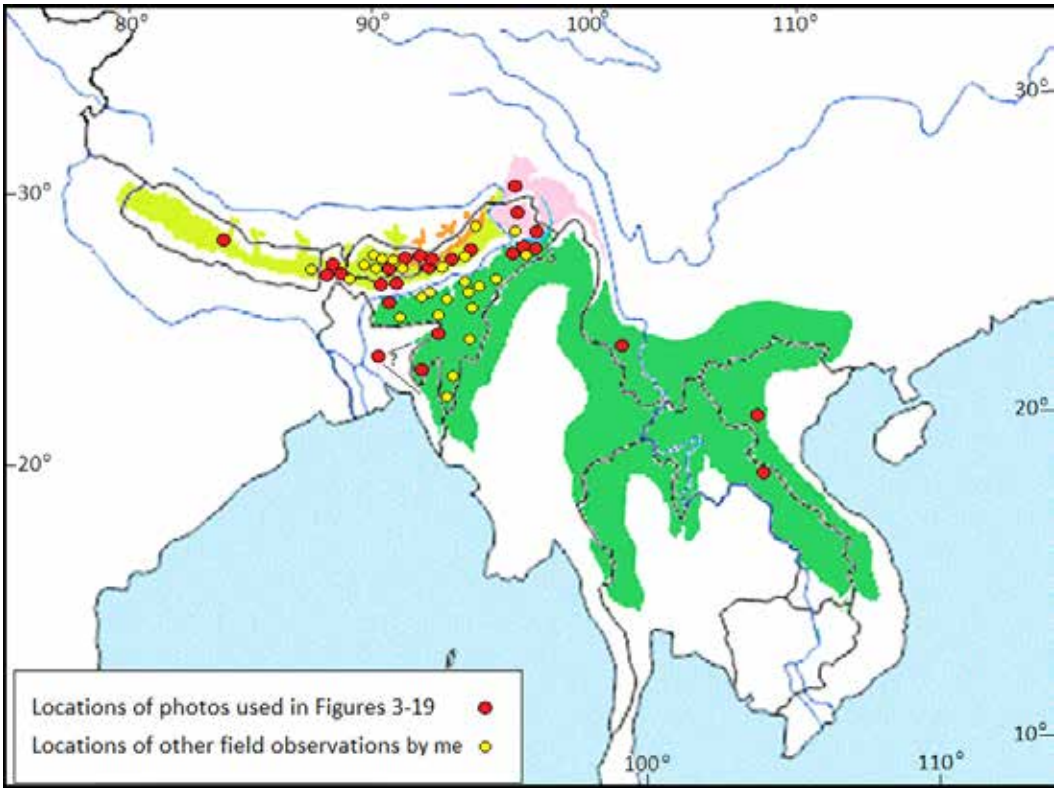


Figure 20. Locations of the photographs used in figures 3–19 and locations of field observations by the author. See Appendix 1.

remote forest. The huge work force of several thousands of construction workers also impacts the surroundings increasing biotic pressure on the habitat manifold.

Legal protection

The Assamese macaque is protected under Schedule-I (part A) of the Wild Life (Protection) Act in India, which is the highest level of protection in the Act. It is listed in Schedule III in the Bangladesh Wildlife (Preservation) (Amendment) Act, 1974. In Myanmar, it is protected according to the 1994 Wildlife Protection Law. In Thailand, the species is protected by the Wildlife Protection Act, 1960. In Nepal, it is listed as nationally endangered and protected under the National Park and Wildlife Protection Act 1973. In China, it is protected under the Wildlife Protection Law as first class which strictly forbids killing. Enforcement in the field, however, is inadequate except in some protected areas. Most locals are also unaware of such legal status. IUCN has listed it as "Near Threatened" (Boonratana *et al.* 2020b).

Habitat protection

The Assamese macaque is found in many protected areas in its range (see Appendix 2).

Recommendations

1. The existing protected areas should be provided with adequate protection.

2. Measures should be taken to control *jhum* cultivation as well as poaching for meat.

3. Development projects, especially major dams for generating hydro-electric power need to be reviewed and modified, incorporating appropriate measures for the conservation of the wildlife and the natural landscapes or shelved.

4. Further research, including genetics, with strong data sets should be taken up, focusing on diagnostic differences in these identified variants, including especially penis morphology for *leucogenys, munzala* and *selai.*

Acknowledgments

During my field studies, I received invaluable support and assistance from many civil and forest officials, NGO activists, conservationists, and members of civil society in India, Bhutan, Nepal, and for short tours in Bangladesh, Myanmar, Thailand, Cambodia, Vietnam and China, and I thank them all collectively. For providing photographs I thank Ayan Banerjee, Will Duckworth, Udayan Borthakur, Ranjan Kr. Das, Binanda Hatiboruah, Rupin Dang, Phuntsho Thinley, Rustom Basumatary, Chenchen Ding of Beijing Normal University, Li Xueyou, Arjun Thapa, Bishnu Prasad Pandey, Camille Coudrat (Association Anoulak, Laos), Ngunu Ziro (NGO, Arunachal Pradesh), G.V. Gopi/Wildlife Institute of India, Tanvir Ahmed Saikot, Mukesh Kumar Chalise, Aftab Ahmed and Tilo Nadler.

I am grateful to Anil Kr. Goswami, M. I. Bora, R. P. Neog, Thomas Kent, K. Shohe, R. K. Ranjan Singh (now a

minister of India), T. K. Barman, Akato Sema, T. Deb Roy, Lima Ao, K. Muivah, N. Pradhan, K. Hramzama, S. Saikia, Muankima, Rinsanga, T. Zakiau, P. Rahlo, J. Mazumdar, Nur Husain, Sarsing Rongphar, Siddartha Deb Barman, Heerak Nandy, S. S. Saha, S. Tana Hmar, B. Suchiang, Havildar K. Das, Sakul, Dilip, Babul, B. Chakravarty, Assam Science Tech. & Environ. Council, American Society of Primatologists, H. Lhato, S. N. Kalita, S. Ahmed, Radhe Appa, D. R. Ram, Amonge Mili, Maila Lama, Anoko Mega, Maya Tamang and her in-laws, S. K. Raha, P. Ringu, D. Deka, T. R. Taku, Empi Meya, K. Taku, Narayan Das, Sanjay Kr. Singh, K. P. Gupta, Suresh Melo, T. Rahman, L. Miso, K. N. Bhar, Sal B. Chetry (Chotu), Deben Sharma, Kundan S. Raut, Cheena Miso and his father the Gaon Burha of Hunli, Badio Tega, V. Sonar, Y. Tega, Sajalu Tega, S. Biswakarma, Jerow Mipi, Baputi Mipi, Kanari Mipi, Hati Mipi, A. Mili, Ahomu Mihu, A. Miyu, A. Mihu, M. Mili, Chhoje Lama, Gopal, M. Milo, D. Mihu, Akuto, Suleman Ansari and others of Border Road Organisation's camp at 29th km on Hunli-Aini road, and staff of The Rhino Foundation for nature in North East India (Mrs Anne Wright, Ratul Talukdar, Hakim and Hashim Choudhury), my parents and wife besides a large number of other villagers, hunters and porters for their help during field work.

Literature Cited

Agrawal, V. C., P. K. Das, S. Chakraborty, R. K. Ghose, A. K. Mandal, T. K. Chakraborty, A. K. Poddar, J. P. Lal, T. P. Bhattacharya and A. K. Ghosh. 1992. Mammalia. *State Fauna Series 3: Fauna of West Bengal.* Part 1: 27–169, Zoological Survey of India, Calcutta.

Anderson, J. 1872. On a supposed new monkey from the Sunderbunds to the east of Calcutta. *Proc. Zool. Soc. Lond*. 1872: 529–533.

Anderson, J. 1879. Anatomical and zoological researches: comprising an account of the zoological results of the two expeditions to Western Yunnan in 1868 and 1875. Vol. 1. Bernard Quaritch, London. For date of publication, see Corrigenda, xii-xiii

Anon. 2021. A new population of white cheek macaques found in Gaoligong Mountain. *DayDayNews*. 23 April 2021. https://daydaynews.cc/en/housepet/a-new-population-of-white-cheek-macaques-found-in-gaoligong-mountain.html 1/2

Biswas, J., D. K. Borah, A. Das, J. Das, P. C. Bhattacharjee, S. M. Mohnot and R. H. Horwich. 2011. The enigmatic Arunachal macaque: its biogeography, biology and taxonomy in Northeastern India. *Am. J. Primatol.* 73: 1–16.

Blanford, W. T. 1888. *The Fauna of British India, Including Ceylon and Burma*. *Mammalia (Introduction, Primates, Carnivora, Insectivora)*. Taylor and Francis Ltd., London.

Boonratana, R., M. Chalise, D. Chetry, S. Htun, and R. J. Timmins. 2020a. *Macaca assamensis* ssp. *pelops*. The IUCN Red List of Threatened Species 2020: e.T39767A17985727.

Boonratana, R., M. Chalise, S., Htun and R. J. Timmins. 2020b. *Macaca assamensis*. The IUCN Red List of Threatened Species 2020: e.T12549A17950189.

Chakraborty, D., U. Ramakrishnan, J. Panor, C. Mishra and A. Sinha. 2007. Phylogenetic relationships and morphometric affinities of the Arunachal macaque, *Macaca munzala*, a newly described primate from Arunachal Pradesh, northeastern India. *Mol. Phylogenet. Evol*. 44: 838–849.

Chalise, M. K. 2003. Assamese monkeys (*Macaca assamensis*) in Nepal. *Primate Conserv.* (19): 99–107.

Chalise, M. K. 2013. Fragmented primate populations of Nepal. In: *Primates in Fragments: Complexity and Resilience*, L. K. Marsh and C. A. Chapman (eds.), pp. 329–356. Springer, New York.

Chandra, K., J. R. B. Alfred and B. Mitra. 2017. *Fauna of Sundarban Biosphere Reserve*. Zoological Survey of India, Kolkata, India.

Chang, Y.-B, C.-X. Jia, G. Song and F.-M. Lei. 2018. Discovery of *Macaca munzala* in Cona, Tibet. *Chinese J. Zool*. 53(2): 243–248.

Choudhury, A. U. 1988. Priority ratings for conservation of Indian primates. *Oryx* 22: 89–94.

Choudhury, A. U. 1989. Primates of Assam: Their Distribution, Habitat and Status. Ph.D. thesis, Gauhati University, Guwahati. 300pp.

Choudhury, A. U. 1995a. The primates of Namdapha National Park. *IPPL News* 22(2): 23–24.

Choudhury, A. U. 1995b. *Wildlife Survey in Bherjan, Borajan and Podumoni RFs of Tinsukia District, Assam, with a Proposal for a Wildlife Sanctuary.* The Rhino Foundation for Nature in NE India, Guwahati. 18pp.

Choudhury, A. U. 1996. Survey of Primates in Some Parts of Eastern and Central Assam. Final report to ASTEC (Assam Science, Technology & Environment Council), Guwahati. 32pp.

Choudhury, A. U. 1997. *Checklist of the Mammals of Assam.* Revised 2nd edition. Gibbon Books & ASTEC, Guwahati.

Choudhury, A. U. 1998a. A survey of primates in the Jaintia Hills. *ASP Bull*. 22(3): 8–9.

Choudhury, A. U. 1998b. Père David's macaque discovered in India. *Newsl. Rhino Found. Nat. NE India.* 2(1): 7.

Choudhury, A. U. 2001. Primates in NE India: an overview of their distribution and conservation status. *ENVIS Bull.: Wildlife and Protected Areas* 1(1): 92–101.

Choudhury, A. U. 2002. Survey of primates in West Kameng District, Arunachal Pradesh, India. *ASP Bull.* 26(1): 12.

Choudhury, A. U. 2004. The mystery macaques of Arunachal Pradesh. *Newsl. J. Rhino Found. Nat. NE India* 6: 21–25.

Choudhury, A. U. 2008. Primates of Bhutan and observations of hybrid langurs. *Primate Conserv.* (23): 65–73.

Choudhury, A. U. 2009. Five possible additions to the mammals of China. *Newsl. J. Rhino Found. Nat. NE India* 8: 41–45.

Choudhury, A. U. 2013. *The Mammals of North East India.* Gibbon Books, and The Rhino Foundation for Nature in NE India, with support from Forestry Bureau (COA), Taiwan. Guwahati, India. Pp. 432.

Choudhury, A. U. 2016. *The Mammals of India: A Systematic and Cartographic Review.* Gibbon Books, and The Rhino Foundation for Nature in NE India, with support from the Forestry Bureau (COA), Taiwan. Guwahati, India.

Choudhury, A. U. 2018a. Photographic record of the Assamese macaque *Macaca assamensis* in Tripura, northeastern India. *Asian Primates J.* 7(1): 2–5.

Choudhury, A. U. 2018b. Assamese macaque. In: *Natural History of North East India. Vol. 1*: *Mammals*, A. U. Choudhury (ed.), pp. 66–69. Rashmi Prakash, Guwahati, India.

Choudhury, A. U. 2019. *Manas: India's Threatened World Heritage*. Gibbon Books and The Rhino Foundation, Guwahati, India.

Choudhury, A. U. 2021. Dihing-Patkai and Raimona, Assam's new National Parks. *Oryx* 55(6): 813–814.

Choudhury, A. U. and M. K. Palit. 2004. Yardi-Rabe Supse Wildlife Sanctuary. In*:Important Bird Areas in India: Priority Sites for Conservation*, M. Z. Islam and A. R. Rahmani (eds.), p.228. Bombay Natural History Society, Mumbai and BirdLife International (UK).

Cooper, M. A. and I. S. Bernstein. 2000. Social grooming in Assamese macaques (*Macaca assamensis*). *Am. J. Primatol.* 50: 77–85.

Corbet, G. B. and J. E. Hill. 1992. *The Mammals of the Indomalayan Region: A Systematic Review*. Oxford University Press, Oxford, UK.

Duckworth, J. W., R. E. Salter and K. Khounboline (comp.). 1999. *Wildlife in Lao PDR: 1999 Status report*. IUCN The World Conservation Union/The Wildlife Conservation Society/Centre for Protected Areas & Watershed Management, Vientiane.

Ellerman, J. R. and T. C. S. Morrison-Scott. 1951. *Checklist of Palaearctic and Indian Mammals, 1758 to 1946.* British Museum (Natural History), London.

Elliot, D. G. 1913. *A Review of the Primates*. Volume 2. American Museum of Natural History, New York. For date of publication, see *Zool. Rec.: Mammalia* 1913: 9.

Eudey, A. A. 1991. Macaque habitat preference in west-central Thailand and Quaternary glacial events. In: *Primatology Today*, A. Ehara, T. Kimura, O. Takenaka and M. Iwamoto (eds.), pp. 21–24. Elsevier, Amsterdam, Netherlands.

Fan, P, Y. Liu, Z. Zhang, C. Zhao, C. Li, W. Liu, Z. Liu and M. Li. 2017. Phylogenetic position of the white-cheeked macaque (*Macaca leucogenys*), a newly described primate from southeastern Tibet. *Mol. Phylogenet. Evol.* 107: 80–89.

Fooden, J. 1976. Primates obtained in peninsular Thailand, June–July 1973, with notes on the distribution of continental Southeast Asian leaf-monkeys (*Presbytis*). *Primates* 17(1): 95–118.

Fooden, J. 1980. Classification and distribution of living macaques (*Macaca* Lacépède, 1799). In: *The Macaques: Studies in Ecology, Behavior and Evolution*, D. G. Lindburg (ed.), pp. 1–9. Van Nostrand Reinhold Co., New York.

Fooden, J. 1982. Taxonomy and evolution of the *sinica* group of macaques: 3. Species and subspecies accounts of *Macaca assamensis*. *Fieldiana Zool., n. s*. 10: 1–52.

Fooden, J. 1986. Taxonomy and evolution of the sinica group of macaques: 5. Overview of natural history. *Fieldiana Zool*., n.s. 29: 1–22.

Fooden, J. 1988. Taxonomy and evolution of the sinica group of macaques: 6. Interspecific comparisons and synthesis. *Fieldiana Zool., n. s*. 45: 1–44.

Fooden, J. 2003. Tail length in enigmatic North-east Indian macaques and probable relatives. *J. Bombay Nat. Hist. Soc*. 100: 285–290.

Ghosh, A., M. Thakur, S.K. Singha, R. Dutta, L.K. Sharma, K. Chandra and D. Banerjee. 2022. The Sela macaque (*Macaca selai*) is a distinct phylogenetic species that evolved from the Arunachal macaque following allopatric speciation. *Mol. Phylogenet. Evol.* doi.org/10.1016/j.ympev.2022.107513

Gray, J. E. 1870. *Catalogue of Monkeys, Lemurs, and Fruit-eating Bats in the Collection of the British Museum*. British Museum, London.

Griffith, W. 1847. *Journal of Travels in Assam, Burma, Bootan, Afghanistan and the Neighboring Countries; Arranged by J. M'Clelland.* Government of Bengal, Calcutta.

Groves, C. P. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.

Hill, W. C. O. and I. S. Bernstein. 1969. On the morphology, behaviour and systematic status of the Assam macaque (*Macaca assamensis* McClelland, 1839). *Primates* 10(1): 1–17.

Hinton, M. A. C. and R. C. Wroughton. 1921. The synonymies, characters and distribution of the macaques included under the names rhesus and *assamensis* in Blanford's Mammals. *J. Bombay Nat. Hist. Soc.* 27: 665–72.

Hodgson, B. H. 1841. Three new species of monkey; with remarks on the genera *Semnopithecus et Macacus*. *J. Asiatic Soc. Bengal*, Calcutta, pt. 2, 9: 1211–1213. For date of publication, see p. 1213.

Horsfield, T. 1840. List of Mammalia and birds collected in Assam by John McClelland. *Proc. Zool. Soc. Lond*. 1839: 146–67. For date of publication, see *Proc. Zool. Soc. London*, 107(Ser. A): 79 (1937).

Horsfield, T. 1851. *A Catalogue of the Mammalia in the Museum of the Hon. East-India Company*. East India Co., London.

Jiang, X., Wang, Y. and Ma, S. 1993. Taxonomic revision of *Macaca assamensis*. *Zool. Res.* 14: 110–117.

Karim, R. and F. Ahsan. 2016. Mammalian fauna and conservational issues of the Baraiyadhala NP in Chittagong, Bangladesh. *Open J. Forestry* 6: 123–134.

Kawamoto, Y., A. Mitsuru, T. Wangchuk and S. Sherub. 2006. Distribution of Assamese macaques (*Macaca assamensis*) in the Inner Himalayan region of Bhutan and their mtDNA diversity. *Primates* 47(4): 388–392.

Khan, M. A. R. 1986. Wildlife in Bangladesh mangrove ecosystem. *J. Bombay Nat. Hist. Soc.* 83: 32–48.

Khan, M. M. H. 2008. *Protected Areas of Bangladesh: A Guide to Wildlife*. Nishorgo Program, Forest Department, Dhaka, Bangladesh.

Khanal, L., M. Chalise, P.-F. Fan, R. Kyes and X.-L. Jiang. 2021. Multilocus phylogeny suggests a distinct species status for the Nepal population of Assam macaques (*Macaca assamensis*): implications for evolution and conservation. *Zool. Res*. 42(1): 3−13.

Kumar, A., A. Sinha and S. Kumar. 2020. *Macaca munzala*. *The IUCN Red List of Threatened Species* 2020: e.T136569A17948833.

Li, C., C. Zao and P.F. Fan. 2015. White-cheeked macaque (*Macaca leucogenys*): a new macaque species from Modog, southeastern Tibet. *Am. J. Primatol*. 77(7): 753–766.

Li, Y., Z. Huang, Q. Zhou, G. Ma and C. Huang. 2019. Daily activity pattern in Assamese macaques inhabiting limestone forest, southwest Guangxi, China. *Global Ecol. Conserv.* 20: 1–9. doi.org/10.1016/j.gecco.2019.e00709

Mallick, J. 2011. Status of the mammal fauna of Sundarban Tiger Reserve, West Bengal – India. *Taprobanica*. DOI:10.4038/tapro.v3i2.3961

McClelland [M'Clelland], J. 1839 [1840]. List of Mammalia and birds collected in Assam. *Proc. Zool. Soc. Lond.* 7: 146–167.

Mishra, C. and A. Sinha. 2008. A voucher specimen for *Macaca munzala*: interspecific affinities, evolution, and conservation of a newly discovered primate. *Int. J. Primatol*. 29: 743–756.

Mitra, S. and J. R. B. Alfred. 2007. Reproductive behaviour of the Assamese macaque (*Macaca assamensis*) in Darjeeling district, India. *Rec. Zool. Survey India* 107(pt.4): 33–42.

Pocock, R. I. 1939. *The Fauna of British India, Including Ceylon and Burma: Mammalia. Vol. I. Primates and Carnivora* (in part). Taylor & Francis, London.

Pocock, R. I. 1941. *The Fauna of British India, including Ceylon and Burma: Mammalia. Vol. II. Carnivora* (in part). Taylor & Francis, London.

Prater, S. H. 1948. *The Book of Indian Animals.* Bombay Natural History Society, Bombay (Mumbai). (Now in its 4th edition).

Roonwal, M. L. and S. M. Mohnot. 1977. *Primates of South Asia: Ecology, Sociobiology and Behaviour.* Harvard University Press, Cambridge, MA.

Rowe, N. 1996. *The Pictorial Guide to the Living Primates*. Pogonias Press, East Hampton, NY.

Rowe, N. and Myers, M. 2016. *All the World's Primates*. Pogonias Press, East Hampton, NY.

Sarania, B., A. Kumar, K. Sarma, B. S. Brahma, H. Basumatary and A. Devi. 2021. A comparative assessment of external morphological traits between *Macaca munzala*, Tawang and *Macaca assamensis*, Goalpara population in Northeast India. *Primates* 62(2): 343–360.

Sarkar, P. 2014. *Assamese Macaque: Ecology and Social Dynamics*. LAP Lambert Academic Publishing, Saarbrüken, Germany.

Sarkar, P. and A. Bhattacharya. 2015. Who grooms more – male or female? Study on a provisioned group of Assamese macaques. *Int. J. Adv. Res. Biol. Sci*. 2(12): 228–233.

Sclater, P. L. 1871. Notes on rare or little-known animals now or lately living in the Society's Gardens. *Proc. Zool. Soc. Lond*. 1871: 221–240.

Siddiqi, N. A. 2001. *Mangrove Forest in Bangladesh*. Institute of Forestry and Environmental Science, University of Chittagong, Bangladesh.

Sinha, A., A. Datta, M. S. Madhusudan, and C. Mishra. 2005. The Arunachal macaque *Macaca munzala*: a new species from Western Arunachal Pradesh, Northeast India. *Int. J. Primatol.* 26: 977–989.

Sinha, A., D. Chakraborty, A. Datta, N. Gama, R Suresh, M.D. Kumar, U. Mendiratta, U. Ramakrishnan, and C. Mishra. 2013. Arunachal macaque *Macaca munzala*. In: *Mammals of South Asia*, A. J. T. Johnsingh and N Manjrekar (eds.), pp. 198–210. Universities Press, Hyderabad.

Timmins, R. J. and J. W. Duckworth. 2013. Distribution and habitat of Assamese macaque *Macaca assamensis* in Lao PDR, including its use of low-altitude karsts. *Primate Conserv.* (26): 103–114.

Tobgay, S., K. Dorji and N. Yangdon. 2019. Sighting of Arunachal macaque *Macaca munzala* Sinha *et al*., 2005 (Mammalia: Primates: Cercopithecidae) in Sakteng Wildlife Sanctuary, Bhutan. *J. Threat. Taxa* 11(6): 13805–13807.

Verma, N. and A. Verma. 2013. Field Observations of newly reported macaque from Askot Wildlife Sanctuary, Uttarakhand. *Indian Forester* 139(10): 947–949.

Zhang, Y.-Z., S. Wang, and G.-Q. Quan. 1981. On the geographical distribution of primates in China. *J. Hum. Evol*. 10: 215–226.

Zhou, Q., H. Wei., Z. Huang, A. Krzton and C. Huang. 2014. Ranging behavior and habitat of the Assamese macaques (*Macaca assamensis*) in limestone habitats of Nonggang, China. *Mammalia* 78: 171–176.

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Submitted for publication: 20 September 2021
Revised: 3 July 2022

Appendix 1

Gazetteer of Sites Mentioned in the Photographs

INDIA: **Bherjan**. Part of Bherjan-Borajan-Podumoni Wildlife Sanctuary, Tinsukia district in Assam. **Brokser**. A locality in Great Himalaya in Tawang district, Arunachal Pradesh. **Chirang Reserved Forest**. A reserved forest in Kokrajhar district, Assam. **Darjeeling**. A district in northern West Bengal. **Dibang Valley**. A district in Mishmi Hills. **Dum Duma Reserved Forest**. A reserved forest in Tinsukia district, Assam. **Eagle's Nest** or **Eaglenest**. A wildlife sanctuary in Arunachal Pradesh. **Goalpara**. All Goalpara photos are from Tukreswari Hills and temple, Goalpara district in Assam. **Gorsam Gompha**. Near Zemithang in Tawang district, Arunachal Pradesh. **Hayuliang**. In Mishmi Hills, Anjaw district, Arunachal Pradesh. **Itanagar**. Capital of the state of Arunachal Pradesh. **Jang**. In Tawang district, Arunachal Pradesh. **Karimganj**. A district in southern Assam. The photos were from Patharia Hill reserved forest. **Lamacamp**. Near Eagle's Nest Wildlife Sanctuary in Arunachal Pradesh. **Lohit**. A district in Mishmi Hills. **Manas**. A national park and world heritage site in Assam. **Mandla Phudung**. In West Kameng district, Arunachal Pradesh. **Mishmi Hills**. The mountains east of the Himalaya in Arunachal Pradesh. Includes **Namdapha**. A national park in Arunachal Pradesh. **Sela.** It is a ridge or range of the Great Himalaya and where it is cut by a highway is called 'Sela pass'. **Pakke**. A wildlife sanctuary and a tiger reserve in Arunachal Pradesh. **South Sikkim**. A district in Sikkim. **Talé Valley WS**. A wildlife sanctuary in Arunachal Pradesh. **Tawang**. A township and also a district in Arunachal Pradesh. **Tripura**. An Indian state. **Walong**. In Mishmi Hills, Anjaw district, Arunachal Pradesh. **Zemithang**. In Tawang district, Arunachal Pradesh. CHINA: **Yunnan**. Photos were from Nangunhe Nature Reserve. **Southeast Tibet**. Photos in Li et al. 2015 were from Modog (Medog) county. NEPAL: **Kathmandu**. Country's capital. BHUTAN: **Royal Manas**. A national park. **Northeast Bhutan**. Trashigang and Trashi Yangshi districts.

Appendix 2

List of protected areas having Assamese macaque populations in South Asia (South-east Asian countries were not listed owing to the lack of precise information for several protected areas).

Name of the Reserve	State/Country	Area (km²)	Subspecies	Remarks
1. Dibang WS	Arunachal Pradesh, India	4,149	*leucogenys*	Choudhury (2001)
2. Eagle's Nest WS	"	217	*munzala, pelops*	Contiguous with Sessa Orchid Sactuary. Choudhury (2001)
3. Itanagar WS	"	140	*pelops*	Choudhury (2001)
4. Kamlang WS	"	730	*assamensis*	Contiguous with Namdapha NP. Choudhury (2001)
5. Kane WS	"	55	*pelops*	Choudhury (2001)
6. Mehao WS	"	281	*leucogenys*	Choudhury (2001)
7. Mouling NP	"	483	*pelops*	Choudhury (2001)
8. Namdapha NP & TR	"	1,985	*assamensis*	Core area: 1,808 km². Choudhury (1995a)
9. Pakke WS & TR	"	862	*pelops*	Choudhury (2001)
10. Sessa Orchid Sactuary	"	100	*munzala, pelops*	Contiguous with Eaglenest WS. Choudhury (2001)
11. Tāle Valley WS	"	337	*pelops*	Choudhury (2001)
12. Yordi-Rabe Supse WS	"	397	*pelops*	Choudhury and Palit (2004)
13. Amchang WS	Assam, India	78.6	*assamensis*	Choudhury (2013)
14. Barail WS	"	326	*assamensis*	Choudhury (2013)
15. Barak-Bhuban WS	"	320	*assamensis*	Personal observation.
16. Barnadi WS	"	26	*pelops*	Choudhury (2001)
17. Behali WS	"	157	*pelops*	Personal observation.
18. Bherjan-Borajan-Podumoni WS	"	7.2	*assamensis*	Choudhury (1995b)
19. Dibru-Saikhowa NP	"	340	*assamensis*	Choudhury (2001)
20. Dihing-Patkai NP	"	234	*assamensis*	Choudhury (2021)
21. East Karbi Anglong WS	"	222	*assamensis*	Contiguous with North Karbi Anglong WS. Choudhury (2001)
22. Garampani WS	"	6	*assamensis*	Choudhury (2001)
23. Garbhanga WS	"	117	*assamensis*	Personal observation.
24. Hollongapar Gibbon Sanctuary	"	21	*assamensis*	Choudhury (2001)
25. Kaziranga NP	"	914	*assamensis*	Choudhury (2001)
26. Manas NP	"	850	*pelops*	Choudhury (2001)
27. Marat Longri WS	"	451	*assamensis*	Choudhury (2013)
28. Nambor WS	"	37	*assamensis*	Choudhury (2001)
29. Nambor-Doigrung WS	"	97	*assamensis*	Choudhury (2013)
30. Nameri NP	"	200	*pelops*	Choudhury (2001)
31. North Karbi Anglong WS	"	97	*assamensis*	Contiguous with East Karbi Anglong WS. Choudhury (2001)
32. Raimona NP	"	422	*pelops*	Contiguous with Phibsoo WS in Bhutan. Choudhury (2021)
33. Sonai-Rupai WS	"	220	*pelops*	Choudhury (2001)
34. Bunning WS	Manipur, India	115	*assamensis*	Choudhury (2001)
35. Jiri-Makru WS	"	99	*assamensis*	Choudhury (2001)
36. Kailam Hill WS	"	158	*assamensis*	Choudhury (2001)
37. Yangoupokpi Lokchao WS	"	185	*assamensis*	Choudhury (2001)
38. Balpakram NP	Meghalaya, India	312	*assamensis*	Choudhury (2001)
39. Narpuh WS	"	60	*assamensis*	Choudhury (1998a)
40. Nokrek NP	"	68	*assamensis*	Choudhury (2001)
41. Nongkhyllem WS	"	35	*assamensis*	Choudhury (2001)
42. Siju WS	"	5	*assamensis*	Choudhury (2001)
43. Dampa WS	Mizoram, India	500	*assamensis*	Choudhury (2001)
44. Lengteng WS	"	60	*assamensis*	Choudhury (2001)
45. Murlen NP	"	100	*assamensis*	Choudhury (2001)
46. Ngengpui WS	"	110	*assamensis*	Choudhury (2001)

47. Phawgpui NP	"	50	*assamensis*	Choudhury (2001)
48. Pualreng WS	"	50	*assamensis*	Choudhury (2013)
49. Thorangtlang WS	"	180	*assamensis*	Photo seen.
50. Tokalo WS	"	250	*assamensis*	Choudhury (2013)
51. Fakim WS	Nagaland, India	6.4	*assamensis*	Choudhury (2001)
52. Intanki NP	"	202	*assamensis*	Choudhury (2001)
53. Gumti WS	Tripura, India	389	*assamensis*	S. Debbarma, pers. comm. on the basis of Choudhury (2018a)
54. Buxa TR	West Bengal, India	759	*pelops*	Core area: 315 km². Personal observation.
55. Jaldapara NP	"	216	*pelops*	Personal observation.
56. Mahananda WS	"	144	*pelops*	Personal observation.
57. Neora Valley NP	"	87	*pelops*	Photo seen.
58. Senchal WS	"	38.6	*pelops*	Photo seen.
59. Singalila NP	"	78.6	*pelops*	Personal observation.
60. Barsey Rhododendron Sanctuary	Sikkim, India	104	*pelops*	Personal observation.
61. Fambong Lho WS	"	52	*pelops*	Personal observation.
62. Kangchendzonga NP	"	1,784	*pelops*	Contiguous with Kanchenjunga CA of Nepal. Personal observation.
63. Kitam Bird Sanctuary	"	6	*pelops*	Personal observation.
64. Maenam WS	"	35	*pelops*	Personal observation.
65. Pangolakha WS	"	128	*pelops*	Photo seen.
66. Askot WS	Uttarakhand, India	600	*pelops*	Verma and Verma (2013)
67. Bumdeling WS	Bhutan	1,521	*munzala*	Choudhury (2008)
68. Jigme Dorji NP	"	4,316	*pelops*	Choudhury (2008)
69. Jigme Khesar Strict NR	"	609	*pelops*	Choudhury (2008)
70. Jigme Singye Wangchuk NP	"	1,730	*pelops*	Choudhury (2008)
71. Jomotsangkha WS	"	335	*pelops*	Choudhury (2008)
72. Phibsoo WS	"	269	*pelops*	Choudhury (2008)
73. Phrumsengla NP	"	905	*pelops*	Choudhury (2008)
74. Royal Manas NP	"	1,023	*pelops*	Contiguous with Manas NP, Assam. Choudhury (2008)
75. Sakteng WS	"	741	*munzala*	Choudhury (2008), Tobgay *et al*. (2019).
76. Wangchuk Centennial NP	"	4,914	*pelops*	Photo seen.
77. Annapurna CA	Nepal	7,629	*pelops*	M.K. Chalise, pers. comm.
78. Api Nampa CA	"	1,903	*pelops*	M.K. Chalise, pers. comm.
79. Dhorpatan Hunting Reserve	"	1,325	*pelops*	M.K. Chalise, pers. comm.
80. Gaurishankar CA	"	2,179	*pelops*	M.K. Chalise, pers. comm.
81. Kanchenjunga CA	"	2,035	*pelops*	Contiguous with Kangchendzonga NP of Sikkim, India. M.K. Chalise, pers. comm.
82. Khaptad NP	"	225	*pelops*	M.K. Chalise, pers. comm.
83. Langtang NP	"	1,710	*pelops*	Chalise (2003)
84. Makalu Barun NP	"	580	*pelops*	Chalise (2003)
85. Manaslu CA	"	1,663	*pelops*	M.K. Chalise, pers. comm.
86. Rara NP	"	106	*pelops*	M.K. Chalise, pers. comm.
87. Sagarmatha NP	"	1,148	*pelops*	M.K. Chalise, pers. comm.
88. Shey-Phoksundo NP	"	3,555	*pelops*	M.K. Chalise, pers. comm.
89. Shivapuri Nagarjun NP	"	159	*pelops*	Personal observation.
90. Baraiyadhala NP	Bangladesh	29.34	*assamensis*	Karim and Ahsan (2016)
91. Kaptai NP	"	54.64	*assamensis*	Tanveer A. Shaikot, pers. Comm.
92. Pablakhali WS	"	421	*assamensis*	Khan (2008)
93. Rema-Kalenga WS	"	18	*assamensis*	Khan (2008)
94. Satchari NP	"	2.4	*assamensis*	Tanveer A. Shaikot, pers. Comm.

CA = Conservation Area; NP = National Park; NPA = National Protected Area; NR = Nature Reserve; NNR = National Nature Reserve; PPA = Provincial Protected Area; TR = Tiger Reserve; WS = Wildlife Sanctuary.