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RESEARCH ARTICLE

The Enigmatic Arunachal Macaque: Its Biogeography, Biology and Taxonomy in Northeastern India

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The purpose of this study was to determine the taxonomic status of an unidentified enigmatic macaque seen by scientists since the late 1990s in Arunachal Pradesh, India. We surveyed 49 troops of enigmatic macaques in four districts of Arunachal Pradesh. The population studied is from the macaque sinica-group as defined by the reproductive organs. The main species-separating trait in the sinica-group is tail length to head and body length ratio that decreases with latitude and elevation. We gathered data on morphology, pelage descriptions, tail to head and body ratios and tail to hind foot ratios from photos and live animals (43 individuals from 36 areas) within the range of and between the two subspecies of the Assamese macaque (*Macaca assamensis*). We compared the data to six western Assamese macaques and studies of Assamese macaques and related species. We found great variability in tail length, pelage color, facial skin color, and facial and hair patterns. The tail/head–body and tail/foot ratios, although varied, supported the hypothesis that these enigmatic forms were part of a population of Assamese macaques found in the gap between the two subspecies ranges and were not a new species as described earlier. Instead, we found evidence that darker pelage, larger body size, and shorter tails occur at higher elevations and latitudes similar to the general trend in the sinica-group's adaptations to colder climates. Thus, the population may be important for its variation, throwing light on the speciation process and how the northern species of Tibetan macaques evolved from an ancestor similar to the Assamese macaques as adaptations to a colder climate. Am. J. Primatol. 73:1–16, 2011.

Key words: Arunachal macaque; Assamese macaque; *Macaca assamensis*; *Macaca thibetana*; *Macaca munzala*; Tibetan macaque

INTRODUCTION

The evolutionary history of the sinica-group of macaques is problematical [Hoelzer & Melnick, 1996]. An enigmatic macaque, seen by scientists since the 1990s in Arunachal Pradesh, India, in the unstudied geographical gap between the two subspecies of the Assamese macaque, is at the center of the controversy. Its taxonomic status has been a concern and puzzle to scientists, some of whom have recently described it to be a new species, *Macaca munzala* [Sinha et al., 2005]. This study is an attempt to clarify the status of this enigmatic primate by comparing data on *M. munzala* and that of two populations of *Macaca assamensis* in eastern and western Arunachal Pradesh. *M. munzala* was described from an area at the extreme east of the western subspecies *Macaca assamensis pelops* [Sinha et al., 2006] while this study has examined that population and another from the extreme west of the eastern subspecies *M. assamensis assamensis*. Although this study shows great morphological variability of the two populations of the enigmatic macaque, it also re-examines the data from *M. munzala* to show how data from this study and that of *M. munzala* are consistent with data on the two subspecies of the Assamese macaque rather than with a new species denomination.

Choudhury [1998, 2000] first reported an enigmatic macaque with a short tail and dark pelage from Pirila Peak in Eagle Nest Wildlife Sanctuary in West Kameng District in northwestern Arunachal Pradesh (Fig. 1 no. 1). The robust males with buffy, prominent whiskers, were initially presumed to be

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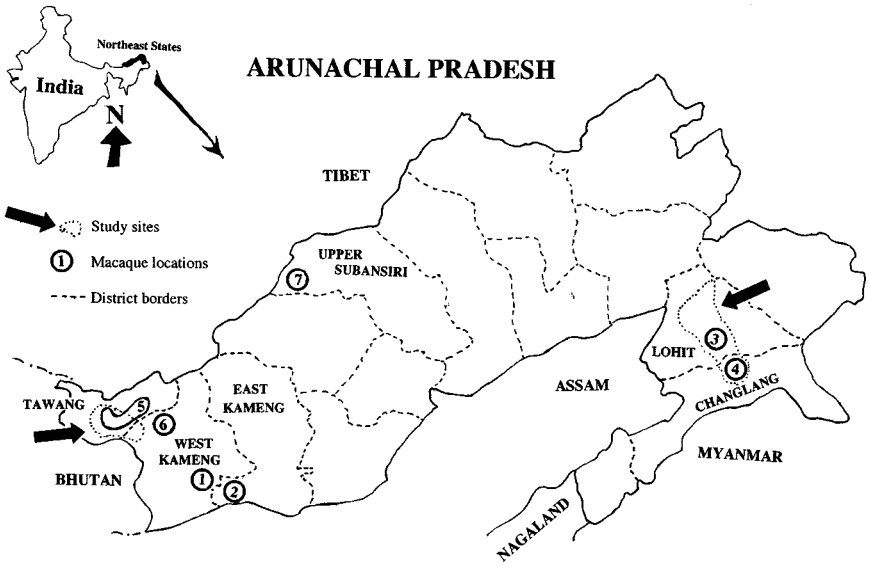

Fig. 1. Map of Arunachal Pradesh indicating historical sightings of the enigmatic macaque. No. 1—Pirila Range–Eagle's Nest Wildlife Sanctuary, between Jang and Thingbu, between Tawing and Lumla, Geshela, No. 2—Pakhui Wildlife Sanctuary, No. 3—Namdapha National Park, No. 4—adjacent to Namdapha National Park, Nos. 5 and 6—Gispu in Lower Nyamjang Chu Valley, Zemithang in Upper Nyamjang Valley, Gorsam, Mirba, Mukto, Pak Chui, Jang, Dushingthang, Nawrok in Lower Namshu Valley, Lhou, Lumpo, Shakti, Sherbang in Lower Rongchu Valley, Thingbu, No. 7—Takising.

the Tibetan (Pere David's) macaque (*Macaca thibetana*) [Choudhury, 1998, 2000]. Kumar [personal communication] also reported an Assamese macaque with a shorter tail length from Pakke Wildlife Sanctuary, East Kameng District adjacent to Eagle Nest Wildlife Sanctuary (Fig. 1 no. 2).

In 2002, Biswas et al. observed a short-tailed enigmatic macaque group in Namdapha Tiger Reserve at Bismile (27°28N, 96°24E and 450 m altitude) (Fig. 1 no. 3), Arunachal Pradesh [Chetry et al., 2003], while conducting a distributional survey of the nonhuman primates. Similar to *M. assamensis,* the males were dark bodied and robust (Fig. 2A) with buffy, prominent whiskers extending up to the cheek (Fig. 3B) and a white mark on the eyebrow similar to *Macaca leonina,* but more prominent and wider (Fig. 2C and D). The adult males produced a peculiar alarm call, which continued for half an hour and the group climbed down from the trees and hid under the bushes in the bamboo thicket. The tail was shorter than that of *M. assamensis* (Fig. 3A) but longer than that of *Macaca arctoides*. Unlike *M. assamensis*, the facial color was pale (Fig. 4A). In another instance in 2004, a dead adult male macaque that was photographed (after being killed by hunters near Kamlang Wildlife Sanctuary (Fig. 1 no. 4), adjacent to Namdapha Tiger Reserve) had physical characteristics similar to those macaques observed in Namdapha Tiger Reserve. More recently, Sinha et al. [2005, 2006] reported an unknown macaque species with a short tail and darker body pelage from different sites in West Kameng and Tawang district of Arunachal Pradesh (Fig. 1 nos. 5 and 6) at altitudes of 1,000–3,500 m which they first designated the Tawang macaque then as a new species, *M. munzal*a based on sightings of 14 troops and measurements of two adult male photos and three captive juveniles [Sinha et al., 2005]. Most recently the researchers obtained a specimen for analysis [Chakraborty et al., 2007; Mishra & Sinha, 2008].

From these varied observations, these enigmatic macaques seem to have a mixture of features resembling the Tibetan macaque (*M. thibetana*) and the eastern subspecies of Assamese macaque (*M. a. assamensis*), although the only report of the Tibetan macaque from India is from a single skin which was reported to be a Tibetan macaque despite its morphological measurements being well outside of the range of the species [Kumar et al., 2005] (Fig. 1 no. 7).

This taxonomic puzzle stimulated the present study of the morphology, demography, and biology of enigmatic macaque groups in four districts of Arunachal Pradesh. The thrust of the study was to identify the morphological characteristics and their variations from different locations and different elevations, treating them as one population. By doing so, any consistent variations representing a second species would reveal itself from the data analyzed.

METHODS

This research adheres to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates. The study was in compliance with national laws of India.

Fig. 2. (**A**) Adult male and female enigmatic macaque with dark chocolate pelage, stocky size, and side whisker at Zimithang, Tawang district, (**B**) Juvenile male with yellow whorl patches on his crown, (**C**) Adult male with distinct ''cap'' on the head and white eyebrow patches at Tawang, (**D**) Adult without central whorl at the crown and with white patches on its eye(s) and prominent beard (left Kamlang WLS, right Lhou, Tawang).

We conducted extensive field surveys to determine the distribution and status of nonhuman primates between February 2005 and May 2006 in Tawang, West Kameng, Lohit, and Changlang districts of Arunachal Pradesh, India (Fig. 1) using a modified line transect method [Burnham et al., 1980; Mohnot et al., 1998; National Research Council, 1981]. We made additional driving transects along roads and ad lib observations. We laid transects in the existing forest trails in a stratified random manner to cover all representative areas [Mueller-Dombois & Ellenberg, 1974]. When a macaque group was encountered during the transect walk, driving transect, or ad lib observations, we monitored individuals for as long as possible to record their characteristics and subspecific status and to photograph individuals. We determined population and demographic structure by carefully recording age and sex classes and total group sizes. We also recorded the characteristics of each individual's morphology and behavior. We feel confident of our data on these un-habituated groups since the senior author has been employing transect and direct count census methods on northeast India primates for well over 10 years.

The data analyzed in this article and compared with *M. munzala* were collected from photographs of wild individuals and eight captive individuals. Measurements were made from all photographs that displayed a clear full head and body, tail, and hind foot view. From measurements taken by the same scale, the tail measure was then divided by the head–body measure and by the hind foot to get the T/HB or T/HF ratios. The same measurements were performed with the captives recording the measurements in mm and similarly dividing them to get the T/HB and T/HF ratios.

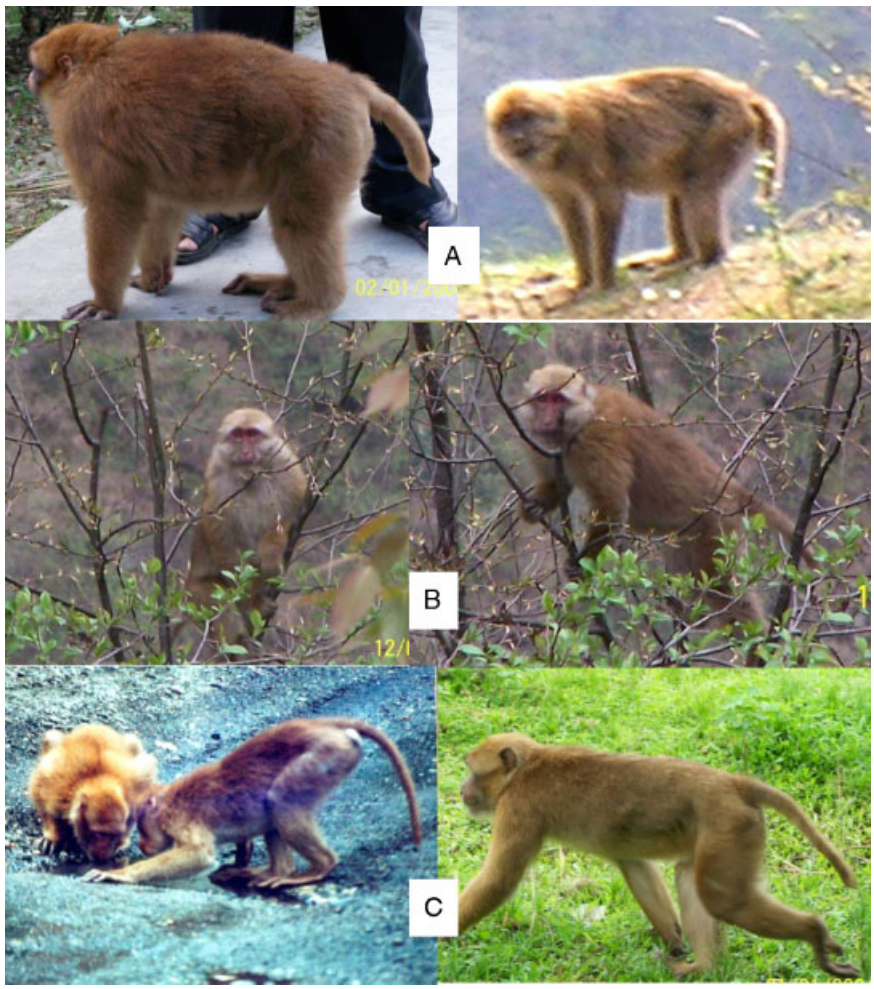

Fig. 3. (**A**) Adult captive male from Tezu (Lohit district) (left) and male from BTK Forest, Tawang (right) with short tails, (**B**) Individual macaque with pale collar and chest hair and prominent check and chin whisker, red facial skin from near Zimithang, (**C**) Individuals of Assamese macaque with long tail (left *Macaca assamensis pelops* from Darjeeling and right from Tukreswari temple, Goalpara).

Statistical Methods Used

Simple descriptive statistical analysis of means and size/ratio ranges were used since we were dealing with simple diagnostic taxonomic characteristics of body ratios based on Fooden's works. Therefore, ranges and means were sufficient to compare the populations to each other and to data from Fooden's works. Since there was so much variability in the population we studied and since the individual numbers studied by Sinha et al. [2005] were small, it was important to use ranges to show how individuals from our and their populations fit within the *M. assamensis* species range in contrast to the means used by Sinha et al. [2005].

Group numbers for the Tawang/West Kameng (Table I) and the Changlang/Lohit (Table II) populations were totaled and divided by the number of troops to obtain average group sizes. The numbers of adult males and adult females for the Tawang/West Kameng (Table I) and Changlang/Lohit (Table II) populations were totaled and the number of females was divided by males to determine the sex ratios.

Data in Table III of the tail to head–body ratios for all age and sex categories were totaled and divided by the number of each age/gender class to obtain the average ratios for the Golpara, Tawang/West Kameng, and Changlang/Lohit populations. Since we felt the Tawang/West Kameng and Changlang/Lohit populations were the same, we lumped them for a general average ratio (Table IV).

RESULTS

Group Population Censuses

We observed a total of 422 individuals of enigmatic macaques in 20 groups in Tawang and West Kameng districts of Arunachal Pradesh (Table I). The average group size was 21.1 ranging from 5 to 43 individuals. The adult sex ratio was 1:1.55. We observed 427 individuals of enigmatic macaques in 16 groups from

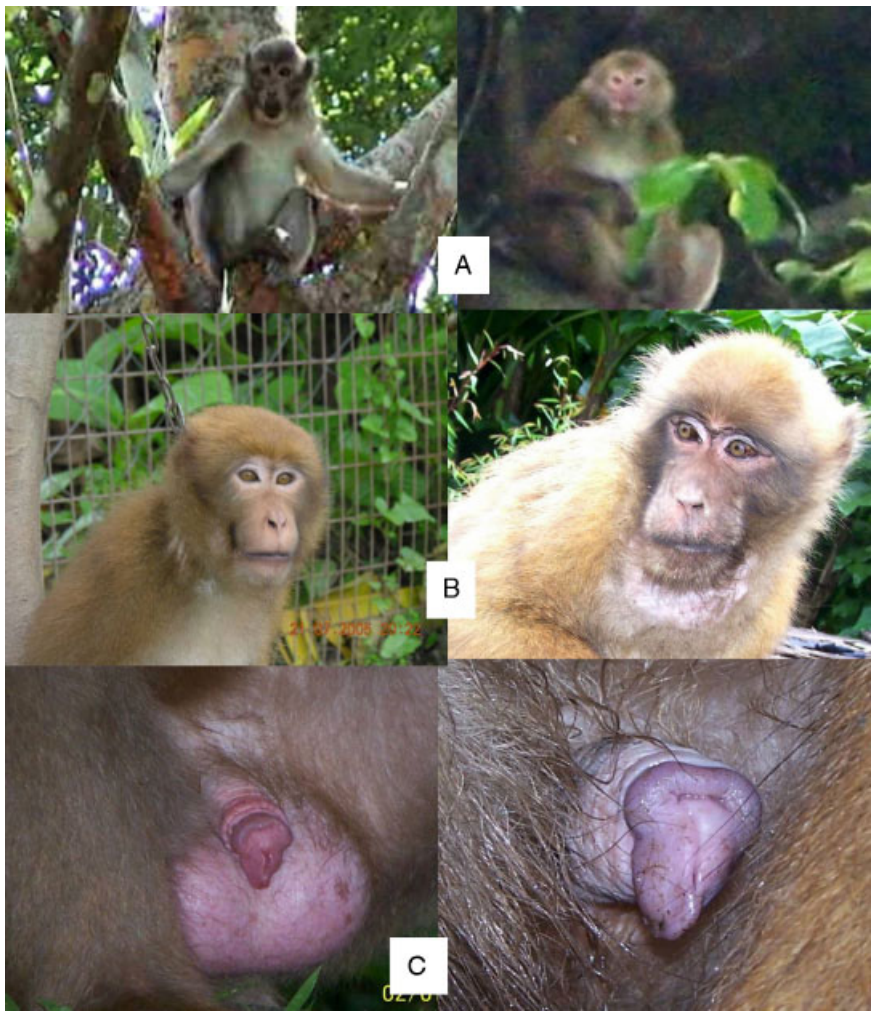

Fig. 4. (**A**) Individuals with variable facial and pelage color from Lohit district, (**B**) Sub adult male macaque from Tezu, Lohit (left) and New Lumla, Tawang district (right) showing prognathous head with elongated muzzle, (**C**) Glans penis of Assamese macaque (left) from Goalpara and the enigmatic macaque (right) from New Lumla, Tawang district, Arunachal Pradesh.

Lohit and Changlang districts (Table II). The average group size was 26.7 individuals ranging from 6 to 63 individuals. The adult sex ratio was 1:1.44.

General Morphology

As in other species of the sinica-group, the genitalia of male enigmatic macaques, i.e. glans penis, is visible in adult males and is pink in color, whereas in subadults and juveniles, it is sometimes concealed inside the shaft. The adult male glans penis is inflected relative to the shaft of penis (Fig. 4C). The scrotal sac is pendulous and heavy in adult males and pinkish white in color but in juveniles and subadults it sometimes cannot be seen.

Pelage Color

Tawang and West Kameng

This population is typified by a great variability even within the same troops. Individual macaques, particularly males, in high altitudes of Tawang and West Kameng districts are larger in size and stocky in structure (Fig. 2A). They have a distinctly short tail (Figs. 2A and 3A) compared with other sinica-groups except for the Tibetan macaque. The dorsal pelage of the adult male varies between dark brown tints with black hair in the upper portion to chocolate in the lower part, similar to the Tibetan macaque, to a reddish brown with a blackish tint (Fig. 2A). Coloration varies among individuals; in some individuals, the dorsal pelage color is brown tinted with red with a paler ventrum and fore legs. The upper body and limbs are lighter than the lower and in some individuals the dorsal pelage color distinctly divides the body laterally. In certain individuals, the upper trunk has pale buff hairs extending from the ventral surface of the lower torso. Juvenile pelage also varies between dark to light brown intermingled with black hairs. The ventrum is paler with a whitish to gray tint in the chest (Figs. 3B

TABLE I. Age Sex Classification of Assamese Macaque Groups in Tawang and W. Kameng Districts

			Age–sex composition									
#	District	Forest	AM	AF	SAM	SAF	A?	JM	JF	J?	In	Total
1	Tawang	Mukto	2	2		1	2			3	1	11
2	Tawang	Near Jang	2	3	2	1	3	1	1	5	3	21
3	Tawang	Louh	3	4	2	2	2	2	2	6	4	27
4	Tawang	4 Bridge	2	5	2	1	3	1	1	6	4	25
5	Tawang	Near Gorsam	2	3	2	1	2	2	1	3	3	19
6	Tawang	BTK	3	4	1	2	2	1	1	6	5	25
7	Tawang	Near Ramasaper	3	5	2	2	2	2	2	7	5	30
8	Tawang	Sherbhan	2	3		1	1	1	1	2	1	12
9	Tawang	Keleng	3	3	2	1	2	1	2	4	4	22
10	Tawang	Thonglen	2	3	1	1		1	1	3	2	14
11	Tawang	Near Lumla	2	4	1	1			2	4	3	17
12	Tawang	Near Mukto	1	2		1				1		5
13	Tawang	Zimithang	3	5	3	3	2	1	2	7	5	31
14	Tawang	Near Mirba	2	3	1	1		1	2	3	2	15
15	W. Kameng	Lubrang	1	3	1				2	2	1	10
16	W. Kameng	Namgproang	2	3	1	2	2	1	2	5	3	21
17	W. Kameng	Near Dirrang	2	4	1	1		1	2	2	1	14
18	W. Kameng	Sessa WLS	7	9	2	1	5	1	2	9	7	43
19	W. Kameng	Eagle nest WLS	5	8	2	2	3	1	3	9	6	39
20	W. Kameng	NearLama Camp	2	3	1	1	2		1	6	5	21

TABLE II. Age Sex Classification of Assamese Macaque Groups in Changlang and Lohit Districts

			Age–sex composition									
#	District	Forest name	AM	AF	SAM	SAF	A?	JM	JF	J?	In	Total
1	Changlang	Namdapha NP	5	7	1	1	3	2	3	9	5	36
2	Changlang	Pangsu	2	3	1		2	1	1	3	2	15
3	Changlang	Honkap RF	3	4		1	2	1	2	5	3	21
4	Changlang	Rima RF	3	5	1	1	2	1	2	4	3	22
5	Changlang	Diyun RF	2	4	1		2	1	3	4	3	20
6	Changlang	Namchick RF	3	3	1	1	3	1	1	7	4	24
7	Changlang	Miao RF	2	3	2	1	1	2	3	5	3	22
8	Lohit	Kamlang WLS	5	9	2	1	3	3	4	7	7	41
9	Lohit	Turung RF	7	9	2	2	2	2	4	10	6	44
10	Lohit	Kamlang RF	12	15	3	2	3	2	4	12	10	63
11	Lohit	Kamphai ARF	7	11	3	2	3	3	5	10	8	52
12	Lohit	Madhuban RF	2	3	2	1	1	1	2	4	3	19
13	Lohit	Paya RF	2	2			3		1	5	2	15
14	Lohit	Tebang RF	2	2		1	3		1	6	3	18
15	Lohit	Lai ARF	1	2					1	1	1	6
16	Lohit	Dening RF	1	3		1		1		2	1	9

and 4A), abdomen, and lower portion of the legs but in certain individuals it varies from pale brown to buffy white. The hands and feet are pale brown in color and in some juveniles turns darker. The upper body pelage is generally long but short and smooth in the lower body. Some adults and subadults have light-colored hair between the head and trunk forming a ring-like collar (Fig. 3B). The tail is also dark, with white hair at the tip in most individuals. The tail is almost hairless in young juveniles and infants tapering at the end.

The forehead is much paler compared with the dorsal body. In adults, it is almost whitish to buff; long whisker hairs project laterally from the cheek and extend behind the ears and are more prominent in adult males but absent in juveniles (Fig. 3B). A beard, pale to white in color, is common in adults, but is not so prominent in some individuals. Certain

TABLE III. Relative Tail Length to Head and Body of the Enigmatic Macaque From Different Localities of Arunachal Pradesh Along With the Assamese Macaque From the Tukresari Temple Population, Goalpara, Assam

No.	District	Localities	Age/sex	Latitude	Longitude	Tail to head and body length
1	Goalpara	Tukresari	Juvenile M	26°00′02″	90°35′02″	0.68
2	Goalpara	Tukresari	Adult M	26°00′02″	90°35′02″	0.44
3	Goalpara	Tukresari	Juvenile M	26°00′02″	90°35′02″	0.57
4	Goalpara	Tukresari	Adult F	26°00′02″	90°35′02″	0.61
5	Goalpara	Tukresari	Adult M	26°00′02″	90°35′02″	0.67
6	Goalpara	Tukresari	Sub adult M	26°00′02″	90°35′02″	0.52
7	Tawang	Near Jang	Adult M	27°34′51″	91°58′16″	0.43
8	Tawang	Mirba	Adult M	27°33′27″	91°47′36″	0.46
9	Tawang	Four Bridge	Adult M	27°34′54″	91°58′20″	0.46
10	Tawang	Four Bridge	Adult M	27°34′54″	91°58′20″	0.45
11	Tawang	Four Bridge	Adult M	27°34′54″	91°58′20″	0.46
12	Tawang	Near Ramasapar	Sub adult M	27°35′50″	91°59′37″	0.36
13	Tawang	Near Ramasapar	Sub adult M	27°35′50″	91°59′37″	0.41
14	Tawang	Near Ramasapar	Adult M	27°35′50″	91°59′37″	0.39
15	Tawang	Zimithang	Sub adult M	27°42′29″	91°43′41″	0.38
16	Tawang	Zimithang	Sub adult M	27°42′29″	91°43′41″	0.40
17	Tawang	Zimithang	Sub adult M	27°42′29″	91°43′41″	0.41
18	Tawang	Zimithang	Adult F	27°42′29″	91°43′41″	0.40
19	Tawang	Zimithang	Adult F	27°42′29″	91°43′41″	0.40
20	Tawang	Zimithang	Sub adult F	27°42′29″	91°43′41″	0.38
21	Tawang	Zimithang	Adult M	27°42′29″	91°43′41″	0.43
22	Tawang	Zimithang	Sub adult M	27°42′29″	91°43′41″	0.38
23	Tawang	Zimithang	Adult F	27°42′29″	91°43′41″	0.42
24	Tawang	BTK	Adult F	27°40′10″	91°42′571″	0.35
25	Tawang	Zimithang	Adult M	27°42′37″	91°43′521″	0.43
26	Tawang	Zimithang	Adult M	27°42′37″	91°43′521″	0.45
27	Tawang	Zimithang	Adult M	27°42′37″	91°43′521″	0.33
28	Tawang	Zimithang	Adult F	27°42′37″	91°43′521″	0.38
29	Tawang	Zimithang	Adult F	27°42′37″	91°43′521″	0.39
30	Tawang	Lhou	Sub adult M	27°34′28″	91°56′21″	0.46
31	Tawang	Lhou	Adult M	27°34′28″	91°56′21″	0.42
32	Tawang	Lhou	Adult M	27°34′28″	91°56′21″	0.51
33	Tawang	Lhou	Adult F	27°34′28″	91°56′21″	0.43
34	Tawang	Lhou	Sub adult M	27°34′28″	91°56′21″	0.5
35	Tawang	Lhou	Adult F	27°34′28″	91°56′21″	0.49
36	W. Kameng	Two Bridge	Adult M	27°26′11″	92°06′58″	0.48
37	W. Kameng	Two Bridge	Adult M	27°26′11″	92°06′58″	0.39
38	Changlang	Namdapha NP	Adult M	27°29′42″	96°24′22″	0.44
39	Changlang	Namdapha NP	Adult M	27°29′42″	96°24′22″	0.43
40	Lohit	Kamlang RF	Adult M	27°46′13″	96°20′19″	0.36
41	Lohit	Kamlang RF	Adult M	27°46′10″	96°20′11″	0.37
42	Lohit	Turung RF	Adult F	27°45′42″	96°20′06″	0.58
43	Lohit	Turung RF	Adult M	27°45′42″	96°20′06″	0.51
44	Lohit	Kamphai ARF	Adult M	27°45′52″	96°20′49″	0.51
45	Lohit	Tezu	Adult M	27°52′19″	96°16′18″	0.35
46	Lohit	Hyuliang	Infant M	28°04′56″	96°31′33″	0.53
47	Lohit	Tezu	Adult M	27°52′19″	96°16′18″	0.41
48	Lohit	Tezu	Adult M	27°52′19″	96°16′18″	0.36
49	Lohit	Tebang RF	Adult F	27°56′00″	96°13′44″	0.40

adults have slightly elongated crown hairs that radiate from a central whorl of yellowish brown hairs to form an oval shaped ''cap'' at the top of the head (Fig. 2B–D). This oval crown is encircled by paler short hair extending laterally from both eyes to form wide contrasting stripes at the crown. In other individuals (both adults and juveniles), a prominent pale yellowish patch with a central group of dark brown hairs forms a groove in the front of the crown. Near Ramasapar (27°36N, 91°59E 2,547 m), adult individuals had brown hair with a golden tint that radiates in all directions forming a distinct ''cap'' with a well-defined anterior edge on the crown resembling *Macaca leonina* [Pocock, 1939] (Fig. 2C and D). This

TABLE IV. Tail to Head–Body Ratio Ranges and Means for Enigmatic Macaques and Western Subspecies *Macaca assamensispelops* (Data Based on Table III of This Study)

	Ad male	Ad female	SubAd Male	SubAd Female	Jv Male	Inf Male
Range	0.33–0.51 (21)	0.35–0.58 (10)	0.36–0.50 (8)	0.38 (1)	–	0.53 (1)
4 Districts						
Mean	0.42	0.42	0.41	0.38	–	0.53
4 Districts						
Range	0.33–0.51 (14)	0.35–0.48 (8)	0.36–0.50 (8)	0.38 (1)	–	–
Mean	0.44	0.41	0.41			
Tawang						
W. Kameng						
Range	0.35–0.51 (9)	0.40–0.58 (2)	–	–	–	–
Mean Changlang Lohit	0.42	0.49				
M. a. pelops						
Goalpara						
Range	0.44–0.67 (2)	0.61 (1)	0.52 (1)	–	57–0.68 (2)	0.53 (1)
Mean	0.56	0.61	0.52		0.63	

characteristic is not visible in all individuals even within the same group and in some individuals, just a central whorl in the crown is visible. There is a prominent dark patch of hair on either side of the face extending from the upper part of the cheek or from the lateral side of the eyes to the ear forming a dark line (Fig. 2C). A white eyelid patch as in *Macaca leonina* is present, but it is more prominent and wider, encircling the eyes in adults forming spectacles. Some adults have a white patch resembling an eyebrow (Fig. 2C and D). The face is hairless and darker but a few individuals have red to pale red facial skin (Fig. 3B).

The head is more prognathous and the muzzle is more elongated compared with what is commonly seen in *M. assamensis* while the upper portion of the face is broader than the muzzle (Fig. 4B). The nostril is slightly blunt and protruding outside.

Lohit and Changlang

Color varies among individuals and age groups in Lohit and Changlang districts. Dorsally, color varies from dark brown to chocolate to light brown with white to pale brown ventrally. The chest and trunk region is much paler than the belly. Pale to white prominent side whiskers extend from the cheek in certain adults. Unlike individuals of Tawang and West Kameng, there is no crown whorl, but instead either a rudimentary centered cap, an irregular tuft of hair or smooth, posteriorly directed, dark crown hair. A black patch extending between the upper cheek and the eye projecting laterally toward the ear is common which is absent in the eastern subspecies of the Assamese macaque. The upper portion of the eyelids has a white patch encircling the eyes. The face is pale to pink in color while in some individuals it turns dark.

In Kamlang Wildlife Sanctuary in Lohit district, we found two individuals from different sites with paler to pinkish facial skin with a dark-colored patch on the mouth. The crown had a prominent dark patch surrounded by a buff to pale-colored ring giving the appearance of a cap. The eyes are encircled by white spectacles (Fig. 4A). In certain adults, the eyebrow has a white patch. In adults, the large, prominent side whiskers are white with a white beard. General body pelage color is dark brown to chocolate. The ventrum including the chest, belly, and inner thighs are white.

The tail is hairy unlike Tawang individuals; all juveniles had a hairy tail except for one captive juvenile whose hairless tail tapered at the tip. Infants are off white to pale pink with the anterior forehead hairless and pinkish facial skin.

Tail Length Variation

We estimated the ratio of the tail length to head and body length of the enigmatic macaque from photographs and captive individuals (Table III). This ratio of the enigmatic macaque found in the four districts of Arunachal Pradesh was compared with *M. assamensis* population from Goalpara, Assam (Fig. 5, Table IV). The average photo estimated values of tail length to head and body length at Tawang and West Kameng district is 0.42 ± 0.09 ($n = 29$) while that of Lohit and Changlang district is 0.43 ± 0.08 ($n = 10$). Ratios from captive individuals (Tawang 0.41 ($n = 4$) [−0.44, −0.39]; Lohit 0.42 ($n = 4$) [−0.42, −0.42]) was similar. One individual male of Lohit district had a tail to head and body ratio much lower (0.33) than the average of the others (0.42, $n = 4$) (Fig. 6).

We also measured the tail length to hind foot length ratio of eight captive individuals as well as photographs from different localities in Tawang district and Lohit district (Table V). The average ratio of tail to hind foot length of macaques of

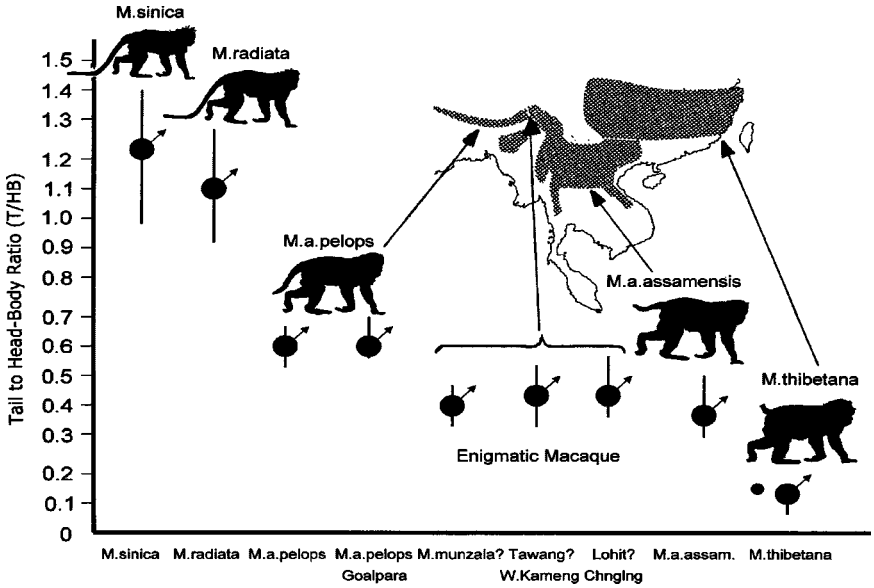

Fig. 5. Comparative accounts of male tail length to head and body length ratio of the present study (photographs and captive individuals) [General figure format transformed from Fooden, 1988]. *N* values are for the following adult males: *Macaca sinica* (21), *Macaca radiata* (12), *Macaca assamensis pelops* (8), *Macaca assamensis assamensis* (21), *Macaca thibetana* (4) [Fooden, 1988]; *A. assamensis pelops* Golpara (2), enigmatic macaque of Tawang-west Kameng (14), Changlang-Lohit (9) (this study); *Macaca munzala* (2) [Sinha et al., 2005].

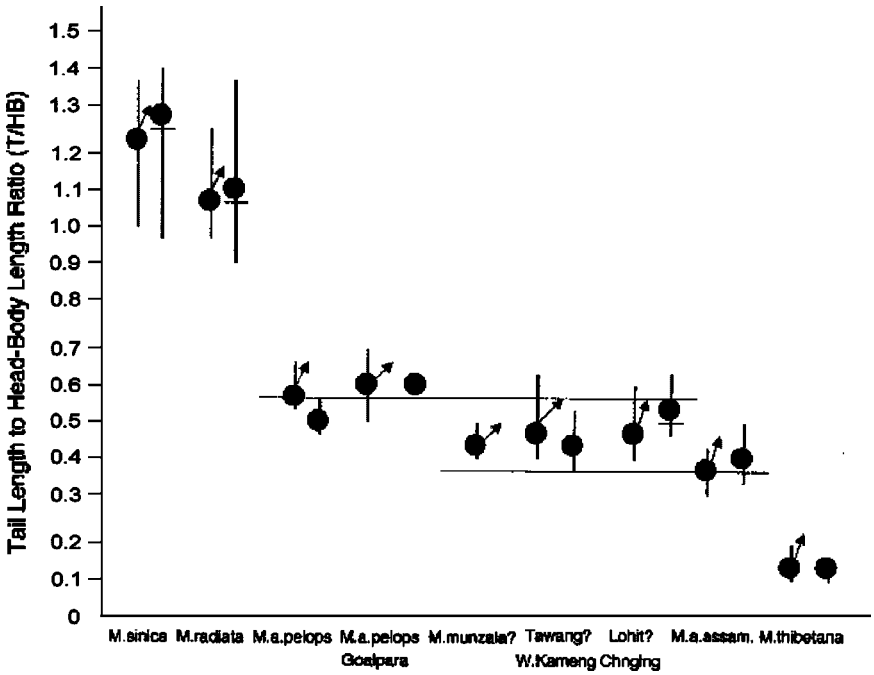

Fig. 6. Tail to head–body ratio means and ranges for males and females of the sinica group [all data from Fooden, 1988 except *Macaca munzala* from Sinha et al., 2005]. Horizontal lines indicate *Macaca assamensis pelops* (upper left) and *Macaca assamensis assamensis* (Lower right) male means. *n* = : *Macaca sinica* male (21), female (12), *Macaca radiata* male (12), female (10), *M. a. pelops* male (8), female (5), *M. a. assamensis* male (21) female (16), *Macaca thibetana* male (4) female (4); *M. a. pelops* Goalpara male (2) female (1) enigmatic macaque this study male (21) female (10); *Macaca munzala* male (2).

Tawang district is 1.37 ($n = 6$) and that of Lohit district is 1.35 ($n = 4$) (Fig. 7). We recorded similar data from the Tukresari temple population in Goalpara, Assam (Fig. 3C) (1.77, $n = 4$) and used a comparative account of the relative tail length to hind foot by Fooden [1988, 2003] (Fig. 7). Individual macaques in both the Tawang and Lohit have a similar value as the eastern subspecies of the

TABLE V. Relative Tail Length to Hind Foot of Enigmatic Macaques From Different Localities of Arunachal Pradesh Along With Assamese Macaques From the Tukresari Temple Population, Goalpara, Assam

No.	District	Localities	Age/sex	Tail/hind foot length ratio
1	Tawang	Zimithang (Photo)	Adult M	1.29
2	Tawang	Zimithang (Photo)	Adult M	1.21
3	Tawang	Zimithang	Adult F	1.56
4	Tawang	BTK	Sub adult F	1.41
5	Tawang	New Lumla	Sub adult M	1.27
6	Tawang	New Lumla	Infant F	1.5
7	Lohit	Tezu	Adult M	1.48
8	Lohit	Tezu	Adult M	1.15
9	Lohit	Tebang	Adult F	1.41
10	Lohit	Hyuliang	Infant F	1.38
11	Goalpara	Tukresari Tample	Juvenile M	1.81
12	Goalpara	Tukresari Tample	Adult F	1.83
13	Goalpara	Tukresari Tample	Adult M	2.62
14	Goalpara	Tukresari Tample	Sub adult M	1.33

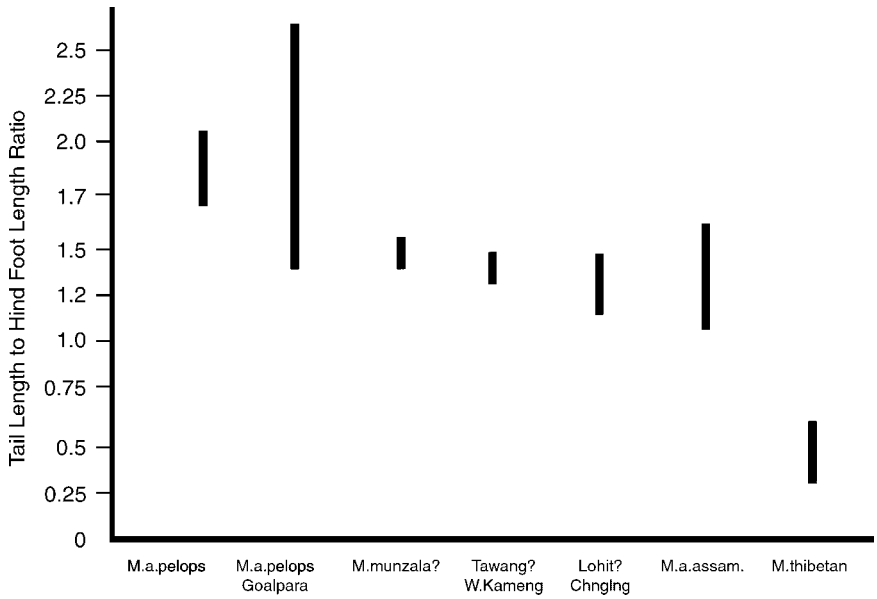

Fig. 7. Ranges of tail to hind leg ratio [data from Sinha et al., 2005; Fooden, 2003 and this study] $n =$: *Macaca assamensis pelops* (8), *Macaca pelops* Goalapara (4), *Macaca munzala* (2) *Macaca assamensis assamensis* (21), enigmatic macaque Tawang-w. Kameng (6), Lohit-Changlang (4) *Macaca thibetana* (7).

Assamese macaque (*M. a. assamensis*) whereas values of the Goalpara population are identical to the western subspecies (*M. a. pelops*).

We calculated ratios using the full population because tail length variation in *M. assamensis* is generally similar to that in adult males [Fooden, 1988, 2003]. However, Table IV shows the age and sex classes for the tail to head-body ratio in the enigmatic macaques from the two populations in Arunachal Pradesh. It shows the ranges and means in adult males in all four Districts and the two west and east districts compared with the western *M. assamensis* subspecies (i.e. Golpara, Assam population). Although the ranges and means are fairly similar between the western and eastern populations of the enigmatic macaques, there is perhaps a slight shortening of the ratio in the eastern population.

DISCUSSION

Individual enigmatic macaques showed a wide range of morphological variation even within the same region and same group, in different altitudinal gradients and in different vegetation. In Tawang district, the macaques showed incredible adaptation to their local environment inhabiting areas commensally with humans, in crop fields, in broadleaf forest

as well as the edges of conifer forest up to an altitude of 3,000 m next to the snow line.

This study indicates that the enigmatic macaque population in Arunachal Pradesh is a very variable population of Assamese macaques, *M. assamensis* that inhabits a previously unstudied gap between the two subspecies [Fooden, 1982; see Sinha et al., 2005]. The following points support this:

1. Penile morphology noted (Fig. 4C) is similar to sinica macaques [Fooden, 1976, 1980] and confirms that the enigmatic macaques are in the sinica-group comprised of four species and six subspecies [Fooden, 1988] of which only one species, the Assamese macaque, *M. assamensis* occurs in Northeast India [Fooden, 1988, 2003].
2. The most definitive trait used to separate species of the sinica-group is the tail length or tail to head–body length ratio (T/HB) [Fooden, 1982, 1988]. The Assamese macaque has two recognized subspecies or races based on tail morphology. The eastern subspecies, *M. assamensis assamensis,* has a short tail, sometimes less than a third but always much less than half the length of head and body, and only a little longer than the foot [Pocock, 1939]. The western subspecies, *M. a. pelops,* has a relatively longer tail, typically considerably more than half the length of the head and body and about twice the length of the hind foot or possibly slightly smaller [Pocock, 1939] (Fig. 3C). Figures 5 and 6 show how the T/HB ratio data from the enigmatic macaques fits intermediately between the two subspecies. The three central data points, which include the population named *M. munzala*, are very close and fall below the western subspecies (*M. a. pelops*) and are slightly higher than the eastern subspecies (*M. a. assamensis*). Sinha et al. [2005] note that ''surprisingly, the relative tail lengths of Arunachal macaque males overlap those of eastern Assamese macaques though, in its distribution, it is sympatric only with the Western Assamese macaque, the adult males of which have significantly longer relative tail lengths.''
3. Table VI compares the characters of two individuals of *M. munzala* measured by Sinha et al. [2005] and Mishra and Sinha [2008] and our data on 22 enigmatic macaques with data from Fooden [1988, 2003] on the two subspecies of Assamese macaques. Although the papers by Sinha et al. [2005] and Mishra and Sinha [2008] compare *M. munzala* with character means of the Assamese macaque two subspecies, Table VI relates the *M. munzala* data and our data to the range of the various measurements of the two subspecies. The last two columns place the character as within the range of one or the other subspecies or between the subspecies and thus within the range of the species. Table VI shows conclusively that all the characters for which there is comparative data of *M. munzala* and the enigmatic macaque population, fall within the range of *M. assamensis*. Table VI additionally shows that the enigmatic macaques and *M. munzala* show a greater relationship to the eastern subspecies, *M. a. assamensis,* yet show a mitochondrial genetic relationship to the western subspecies (*M. a. pelops*). Given this data, the only conclusion is that the enigmatic macaque, alias *M.munzala,* is a variable and distinct population of Assamese macaques.

Macaque Genetics

The genetic information presented by Chakraborty et al. [2007] in light of other studies of macaque genetics, also support placing the enigmatic macaque population as Assamese macaques. The interspecific mitochondrial and nuclear DNA distances for all species of the sinica-group measured were greater than the intraspecific distances. ''The only exception is the interspecific distance for the TSPY sequence between *M. munzala* and *M. assamensis*'' [Chakraborty et al., 2007, p 843]. This places them together as the same species. Although the low nuclear genetic variability of the three specimens tested might suggest specific designation, these three animals are better explained by the fact that they are from the same geographic location and thus probably from a genetically related population [Gachot-Neveu & Ménard, 2004]. None of the studies of *M. munzala* have looked at the population in the eastern districts of Lohit and Changlang.

Additionally, the other findings of the Chakraborty et al. study [2007] are in agreement with other macaque genetic studies placing the *M. munzala* population in the same relationships to other sinica-group macaques as *M. assamensis*, indicating that they are the same. Additionally, the analysis of Chakraborty et al. [2007] seems to lack any *M. assamensis* specimens from the broad region of northeastern India where these populations occur and thus the relationships in their Figure 1 might be problematic due to geographic considerations.

The mitochondrial data indicated *M. munzala* (which is sympatric to *M. a. pelops*) to be closer to *M. radiata* than to *M. a. assamensis* or *M. thibetana*. Hoelzer et al. [1992] found *M. a. pelops* and *M. a. assamensis* widely separated from each other and found *M. a. pelops* similarly allied with *M. radiata* while *M. a. assamensis* was linked first with *M. thibetana* and next with *M. sinica*. Data and phylogenetic trees by Morales and Melnick [1998] and Hoelzer and Melnick [1996] indicated similar relationships.

Although mitochondrial DNA studies have generated conflicting conclusions or suggested phylogenetic relationships that were either unsuspected or poorly supported by other data [Deinard & Smith,

TABLE VI. Comparing Characteristics of Adult Male *Macaca munzala*, the Enigmatic Macaque of This Study and Data of the Assamese Macaque Subspecies Ranges From Fooden

Characters	*Macaca assamensis pelops*	*Macaca assamensis assamensis*	*Macaca munzala*	Enigmatic macaque	Assamese macaque	New species
Head–body (mm)	550–635 (8) ♯1	532–730 (24) ♯1, ♯8	575 (1) ♯4		+ a.assam + a.pelops	–
Tail (mm)	283–360 (8) ♯1	190–250 (22) ♯1	264 (1) ♯4			+?
Ear (mm)	38–42 (8) ♯1	30–41 (20) ♯1	36 (1) ♯4		+ a.assam	–
Tail/head–body (T/HB)	0.50–0.63 (8) ♯1	0.29–0.44 (21) ♯1	0.39–0.45, 0.46 (2), (1) ♯2, ♯4	0.33–0.51 (22)	+ a.assam	? –
Ear/head–body (E/HB) × 100	6.0–7.3 (8) ♯1	4.6–7.7 (20) ♯1	6.3 (1) ♯4		+ a.assam + pelops	–
Tail/hindfoot T/HF	1.73–2.07 (8) ♯6	1.11–1.56 (21) ♯6	1.52 ♯2	0.8–1.21 (2) ♯6 1.15–1.48 (5) ♯7	+ a.assam	–
Weight (kg)	10.4–12.7 (5) ♯1	7.9–16.5 (16) ♯1	15.0 (1) ♯4		+ a.assam	–
Cranium greatest length (GL) (mm)	131.9–154.1 (11) ♯1	138.1–160.3 (28) ♯1	155.0 (1) ♯2		+ a.assam	–
Cranium ZB/GL	0.63–.70 (11) ♯1	0.62–70 (28) ♯1	106.0 (1) ♯2		+ assam	–
Rostrum			62.0 (1)			
Cranial postrostral (mm)	89.9–101.1 (10) ♯1	93.9–107.8 (26) ♯1	107.8 (1) ♯4		+ a.assam	–
RL/PL	0.51–0.62 (10) ♯1	0.50–0.65 (25) ♯1	0.55 (1) ♯2		+ assam	–
Cranium rostrum/GL			0.402 (1) ♯4			
Baculum		17.6–26.9 ♯1	30.4(1) ♯4			+?
MtDNA	*Macaca radiata*	*Macaca thibetana*	*Macaca radiata* ♯5		+ a.pelops	–
NucDNA			♯5		+ assam	–
TSPY			♯5		+ assam	–

ZB/GL, relative zygomatic breadth; RL/PL, rostral/postrostral ratio; mt, mitochondrial; nuc, nuclear; TSPY, testis-specific protein Y-encoded; + assam, same as Assamese macaque; + a.assam, same as eastern subspecies; + a.pelops, same as western subspecies. (♯ refers to the reference for the data point; +, –, ? indicates whether the character indicates a new species (+), no new species (–), or the data are not clear (?). The mtDNA row indicates the speciies affinity shown by Assamese subspecies and populations to what other sinica species. (1) Fooden [1988], (2) Sinha et al. [2005], (3) Sinha et al. [2006], (4) Mishra and Sinha [2008], 200, (5) Chakraborty et al. [2007], (6) Fooden [2003], (7) this study, (8) Fooden [1982].

2001], the nuclear DNA data from Chakraborty et al. [2007] and that from Deinard and Smith [2001] similarly confirm the morphological data of Delson [1980] and Fooden [1988].

Table VI was compiled to compare all the characters measured on *M. munzala* [Mishra & Sinha, 2008; Sinha et al., 2005], those from this study and one noted by Fooden [2003] with the two subspecies on either side [Fooden, 1988]. It is most important to look at how the variations of the enigmatic-munzala population fit within the ranges of the characters of the two subspecies.

Biogeography

M. a. assamensis is distributed in eastern Arunachal Pradesh, Assam, Nagaland, Manipur, Mizoram eastward through northern and eastern Myanmar to Thailand, Laos, Vietnam, and the Yunan and Guangxi provinces of China [Fooden, 1988; Pocock, 1939] (Fig. 5). *M. a. pelops* is distributed in central Nepal eastward through the Indian states of Sikkim, northern West Bengal, Bhutan, and northeastern Assam [Choudhury, 1998; Fooden, 1982] (Fig. 5). The last record of the eastern subspecies (*M. a. assamensis*) in the northwest section of its distribution was reported from two specimens collected at River Tebang (2,000 ft), Mishmi Hills, Assam, now in eastern Arunachal Pradesh, India [Hinton and Lindsay, 1926] and at Beibeng (29°15N, 95°30E and 900 m), Yigong (30°08N, 95°02E and 2,250 m) of Xizang province of China [Fooden, 1982]. It was thought to be limited to eastern Arunachal Pradesh, India, and eastern Xizang province of China. The last distribution record of the western subspecies, *M. a. pelops*, was reported at Chuntung (27°38N, 88°35E and 5,350 ft), Sikkim [Wroughton, 1916] and Dalmacote (approx. 27°N, 88°E), West Bengal [Gray, 1870], India and at Zhangmu (28°02N, 85°55E) of Xizang province, China [Fooden, 1988].

There was thus a 400-km gap in the distribution of the two subspecies in northeast Arunachal Pradesh noted [Fooden, 2003] before Choudhury's [1998] findings of the Pirila macaque, which Fooden [2003] broadly categorized as the eastern subspecies of Assamese macaque. Thus, *M. a. pelops* is narrowly restricted to the outer and lesser Himalayas while *M. a. assamensis* is extensively distributed in lower and mountain ranges of continental Southeast Asia [Fooden, 1982, 2003]. Based on these records, Fooden [1988] suggested that the western subspecies might be present in western Arunachal Pradesh and central Bhutan [see Chalise, 2003], although there were no sighting records and that the eastern subspecies was limited to eastern Arunachal Pradesh and eastern Xizang province of China. But Choudhury's [1998, 2000] findings of the Pirila macaque at Eagle nest Sanctuary (27°07′N, 92°26′E and 2,700 m), West Kameng district of western Arunachal Pradesh (Fig. 1), fits with the physiognomy of the eastern subspecies, *M. a. assamensis*. From Choudhury's observation, Fooden [2003] felt that the eastern subspecies, previously thought to be in eastern Arunachal Pradesh, might extend to West Kameng district and adjacent areas, a 400 km range extension west which he illustrated. Our findings of the enigmatic macaque also fit with the animals described by Choudhury [1998, 2000]. Fooden [2003] using data from Choudhury [2004] concluded that they were the eastern subspecies of Assamese macaque.

It should be noted that a study of Assamese macaques in China [Jiang et al., 1993] (from an English abstract) noted a third subspecies (*M. a. coolidgei*) in Yunan Province based on greater genetic deviation of mtDNA in intraspecies of Assamese macaques than interspecific between Assamese and Tibetan macaques. The authors diagnoses included the subspecies to have a smaller body size, short scapular hair, less dorsal hair annulation, and grayer hair on the hind parts [Jiang et al., 1993]. The same scientists described four subspecies of Tibetan macaques [Jiang et al., 1996] (1) *M. thibetana thibetana* in northwest Sichuan and southwest Shaanxi Provinces, (2) *M. t. pullus* in Fujian, southwest Zhejiang, and north Guangdong Provinces, (3) *M. t. huangshanensis* in Anhui Province, and (4) *M. t. guiahouensis* in Guiahou Province).

The species-specific trait of tail length in sinica groups of macaques, which declines with the change in latitudinal gradients, and clearly progressively declines in the two subspecies of Assamese macaque, is one of the major considerations of subspecific status. Our data of tail to head and body and tail to hind foot ratios from Tawang (1.37) and Lohit/Changlang is close to the mean value of the eastern subspecies of Assamese macaque (1.26) (Figs. 5 and 6). This study supports that the enigmatic macaque is the eastern subspecies of the Assamese macaque (*M. a. assamensis)* whose distribution extends 400–450 km west into western Arunachal Pradesh and north eastern Bhutan (Trashyangtse and Trashigang Districts) [Choudhury, 2008].

The tail to head and body (0.58, $n = 6$) and tail to hind foot ratios (1.9, $n = 4$) of the Goalpara, Assam population match the western subspecies of Assamese macaque (Figs. 6 and 7). The rough pelage with light brown to golden brown color, absence of dark stripe at the temple and circular whorl at the crown and small body compared with Tawang shows its close affinity with the western subspecies *M. a. pelops*. Although Goalpara is situated at the same latitude to that of other distribution sites of *M. a. pelops* in the Indian peninsula, the river Brahmaputra is a major barrier. Thus, with the present findings through an assessment of relative tail length to head and body and hind foot length at

Goalpara, Assam that seems to be western subspecies, the entire subspecific distribution status of the Assamese macaque should be revisited.

An Examination of *Macaca munzala*

The recent description of the Arunachal macaque as a new species [Sinha et al., 2005] must be questioned in light of our findings. Sinha et al. [2005; p 981–982] diagnosed *M. munzala* as follows: ''A species within the *sinica* species-group of *Macaca* [Fooden, 1980], as evidenced by penile morphology. The taxon can be distinguished from *Macaca sinica*, *M. radiata*, *M. a. pelops*, and *M. thibetana* by relative tail length and external morphology and from *M. a. assamensis* by distinctive facial features and external morphology. More uniquely, it can be differentiated from all the species of the *sinica* species-group by a suite of traits including a prominently dark crown patch, characteristic facial marks on the temple and forehead, pale collar of hair around the neck, and distinctive tail length'' [Sinha et al., 2005; p 981–982]. Their own data were not conclusive, with relative tail lengths of *M. munzala* males overlapping those of the eastern Assamese macaques [Sinha et al., 2005] and are further refuted here. They also indicated that the characteristic crown hair had changed seasonally [Sinha et al., 2005]. The physiognomy of *M. munzala* [Sinha et al., 2005] as well as the enigmatic macaque in this study in Tawang and West Kameng districts revealed that these macaques share most of the morphological characters common to eastern subspecies of Assamese macaque (see Table VI) particularly the tail length (155–210 mm), the relative tail length to head and body (Figs. 5 and 6), relative tail length to hind foot length (Fig. 7) and external morphology. Species-specific traits of *M. munzala*, like the prominent pale-yellow patch with a central group of dark hair at the front of the crown as described by Sinha et al. [2005], which change seasonally, are also recorded in a *M. a. pelops* population at Kalingpong and Sikkim [Biswas, personal communication; Mitra, personal communication]. On the other hand, traits, such as dark pelage, large stocky body size, short tails, dark brown facial skin, cheek whiskers, and a terrestrial lifestyle show an affinity to the Tibetan macaque, which has the same ancestry as the western race of the Assamese macaque [Fooden, 1988]. The traits that differ from both the Assamese and Tibetan macaques is a prognathous head, wider fore face, and elongated muzzle. Mishra and Sinha [2008] found this in their voucher specimen which fit a similar description of large males we described with a dark dorsum, large size at the maximum range of *M. a. assamensis*, a relative and absolute tail length between the two subspecies [Mishra & Sinha, 2008].

The morphological variability found in this study is supported by genetic diversity studies [Hoelzer & Melnick, 1996; Kawamoto et al., 2006]. Where Sinha et al. [2005] noted only dark brown facial skin, we noted great variation in facial color (Figs. 3B and 4A) from the same localities and even within the same group at Zimithang (27°41N, 91°43E) and other localities. This cannot be a species-specific trait. Indeed, Sinha et al. [2005] remark that the new species they describe and Assamese macaques ''are otherwise remarkably similar to each other''.

Cheek whiskers, dark-colored body pelage, and relatively stocky appearances might be attributed to altitudinal or latitudinal gradients since most other species of macaques distributed in this latitude are bulkier and stockier. On the other hand, since the eastern subspecies of Assamese macaque and the Tibetan macaque occur where the Tibetan macaque diverged from the former, it is likely that both species share certain morphological traits [Fooden, 1988] in this part of their distributional range. This is supported by the skin from Taksing (28°35N, 93°13E and 2,200 m), Upper Sunbansiri District which apparently looks like Tibetan macaques due to its dark chocolate brown body pelage and short relative tail length to head and body (0.135) and was assumed to be a Tibetan macaque [Kumar et al., 2005] despite the tail, head and body lengths which were out of the Tibetan macaque measurement range. This skin's measurements approximated Choudhury's Pirila macaque, strengthening the supposition that in upper altitudes and longitudes the tail length of the eastern subspecies of Assamese macaque becomes shortened or decreased to about 160 to 100 mm adapted to cooler and higher terrain conditions along with a stout and heavy body as suggested by Fooden [1988]. Fooden [1988] hypothesized that the offshoot of this stock might have dispersed around the southern end of Hengduan Shan and became isolated in the region of upper Chang Jiang (Yangtze River) of China to become the Tibetan macaque. A short tail length with bulky body size in high altitudes may represent a transition or intermediate form and should be studied for its relationship to the two species.

What also questions the veracity of a separate species denomination [Sinha et al., 2005] is the occurrence of three sympatric sinica-group species [Fooden, 1980]. Although not impossible, the occurrence of three closely related species (*M. assamensis, M. thibetana, and M. munzala*) [Kumar et al., 2005; Sinha et al., 2005] in the same area seems highly unlikely [Scheffrahn et al., 1996].

SUMMARY AND CONCLUSIONS

Subspecies Differences

Fooden [1982] separates the two subspecies of Assamese macaques by the relative tail length in

adult males with the longer tail of *M. a. pelops* as a presumed more primitive character. Table VI supports the tail as the major subspecific difference. Using Table VI to summarize the subspecific differences, we see that subspecies *assamensis* had a slightly longer head and body length but with a great deal of overlap. Subspecies *pelops* had much longer tails with no subspecific overlap. The tail to head–body ratio similarly showed no overlap. Tail to hind foot ratio also showed no overlap confirming Fooden [1982]. *M. a. pelops* seemed to have longer ears but with overlap between the subspecies. However, there was total overlap in the ear to head–body ratio. Subspecies *assamensis* showed a slight propensity for being heavier with much overlap between the subspecies. Most significant subspecies *pelops* showed a genetic relationship with *M. radiata* while subspecies *assamensis* showed a genetic affiliation with *M. thibetana*.

The Enigmatic Macaque and *Macaca munzala*

A comparison of the mean and range of the T/HB ration shows that the Tamang/W.Kameng and the Lohit/Changlang populations of the enigmatic macaque are the same population and different from the subspecies *pelops* (Table IV). Similarly, data of the T/HB ratio of *M. munzala* fits directly within the range of the enigmatic macaques in this study and are the same population (Table VI). In all characters where there is data, the individuals designated as *M. munzala* and the enigmatic macaque fall within the range of *M. assamensis* with a greater similarity of characters with subspecies *assamensis*. The only overlap by *M. munzala* with *M. a. pelops* is the large body size and the ear/head–body ratio of the one male measured. In these characters, the two subspecies overlap. Only in genetics did the single *M. munzala* male show a relationship with *M. a. pelops* by showing genetic affinity to *M. radiata*.

That data shows that this enigmatic macaque population (including those called *M. munzala*) is not a new species but its highly variable taxonomic characters are still a mystery, which deserves more study. A number of the characters noted in the enigmatic macaques were noted in other populations such as dark pelage caps, cheek tufts, and chin whiskers [Fooden, 1982]. So where does its taxonomy fit? There are two puzzling aspects of this population inhabiting the gap between the two subspecies (1) the genetic affinity to *M. radiata* that it shares with *M. a. pelops* and (2) the high variability of characters even within the same region and group. Presumably, this speaks to some intergrade between the two subspecies and the high degree of variability probably excludes this population as a new subspecies.

However, a number of the characters that the enigmatic macaque share with *M. thibetana* seem to be related to adaptation to cold, changing in relation to higher altitudes and latitudes as noted in the skin described by Kumar et al. [2005]. Most of the enigmatic macaques, including the described skin, were living between 2,000 and 3,500 m [Fooden, 2003; Kumar et al., 2005; Sinha et al., 2005, 2006; this study]. Since this is within the range of where the Tibetan macaque was thought to diverge from the Assamese macaque, the two species share similar morphological traits [Fooden, 1988] of larger, bulkier bodies, darker pelage, facial whiskers, and shorter tails. These features invite the hypothesis that perhaps this population may be in the process of speciation, somewhat duplicating what may have occurred earlier in the evolution of the Tibetan macaque. Future studies might throw light on this population: (1) the Tawang/West Kameng and Lohit/Changalang populations are widely separated by the Brahmaputra Valley; are these seemingly similar populations continuous across northern Arunachal Pradesh as the skin may indicate? (Fig. 1, No. 7) [Kumar et al., 2005]. (2) This area needs to be surveyed and additional data collected on the location of troops and specific characters in those groups in relation to altitude and latitude.

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