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The Tenasserim Lutung, *Trachypithecus barbei* (Blyth, 1847) (Primates: Cercopithecidae): Description of a live specimen, and a reassessment of phylogenetic affinities, taxonomic history, and distribution

Thomas Geissmann[1], Colin P. Groves[2], Christian Roos[3]
[1] *Anthropological Institute, Universität Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland, e-mail: thomas.geissmann@aim.unizh.ch;* [2]*School of Archaeology and Anthropology, Australian National University, Canberra, ACT 0200, Australia, e-mail: colin.groves@anu.edu.au;* [3]*Gene Bank of Primates, Primate Genetics, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany, e-mail: croos@dpz.gwdg.de*

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Abstract

The Tenasserim lutung *Trachypithecus barbei* was previously known from museum specimens and field observations only. We discovered a zoo specimen and present the first confirmed evidence for the continued existence of the species since 1967. We describe the cranial pelage and coloration characteristics of this species which were previously unknown. We present first molecular evidence for recognizing *T. barbei* as a distinct species and for assessing its phylogenetic affinities relative to other members of the genus *Trachypithecus*. We document the taxonomic history of *T. barbei* and present a distribution map based on a compilation of all known locality records.

Contents

Introduction

The Tenasserim Lutung, *Trachypithecus barbei* (Blyth, 1847) is the least known of all of Asia's primates. For instance, the only synthesis of colobine research (Davies and Oates, 1994) mentions *T. barbei* only once and does not provide any information on the species. Likewise, Corbet and Hill (1992) include the species as *Semnopithecus* incertae sedis, and Rowe (1996) does not mention it at all. The species is restricted to a tiny range around 14°00'-15°15'N, 98°00'-98°25'E on the Burma-Thailand border. It was described by Blyth (1847), but redescribed by him in 1863 in a way which has muddied the waters ever since.

On 21 March 2001, TG encountered a leaf monkey at the Bangkok Zoo which, to judge by facial characteristics, appeared to be a member of the *T. obscurus* group (*sensu* Groves, 2001, i.e. including *T. obscurus* and *T. phayrei*) but did not fit the description of either *T. obscurus* or *T. phayrei*. The mammal curator of the Bangkok Zoo, Dr. Yong Chai, suggested it might be a hybrid between the two species. The provenance of the animal is unknown; it was bought in an animal market. Because captive leaf monkeys have rarely bred in Asia (TG, pers. observation in numerous zoos), the study animal is unlikely to be captive bred. This leaf monkey will be referred to as simply "study animal" in the following text.

CPG examined the syntypes of *Pr(esbytis) barbei* Blyth in the Zoological Survey of India, Calcutta, in the early 1980s, and specimens of Thai and Bur

mese lutungs in the Natural History Museum, London, in the 1980s and 1990s and in October, 2003.

Materials and methods

To test the phylogenetic relationship of the study animal to other langurs, CR sequenced a fragment of the mitochondrial cytochrome *b* gene. DNA was extracted from hair samples (*T. barbei*, *T. phayrei crepusculus*, *T. auratus auratus*, *T. cristatus*, *T. germaini*, *T. francoisi francoisi*, *T. vetulus*, *T. johnii*, *P. comata comata*, *P. melalophos mitrata* and *S. entellus hector*), peripheral blood lymphocytes (*T. obscurus*, *S. entellus priam* and *C. guereza*) and museum skin (*T. phayrei phayrei*) by standard methods as outlined in Walsh et al. (1991) and Sambrook et al. (1989) and the QIAamp DNA Mini Kit, respectively. A 620 bp long fragment of the gene was PCR-amplified (Saiki et al., 1988) using the oligonucleotide primers 5'-CTCCTCATTGAAACATGAAATAT-3' and 5'-CTTTGTTGTTTGGATTTGTG-3'. The resulting PCR products were separated on 1% agarose gels and visualized by ethidium staining. The fragments were excised from the gel and the DNA extracted using the Qiagen Gel Extraction Kit. Direct sequencing reactions were performed with the same primers as indicated above with the Big Dye Terminator Cycle Sequencing Kit (Perkin-Elmer) following the manufacturer's recommendations. All sequence reactions were run on an automated ABI377 sequencer (Perkin-Elmer). Sequences were deposited at GenBank and are available under the accession numbers AY519449 – AY519463 (see also Table 1).

To get a more complete overview on *Trachypithecus* evolution, the data set was expanded with homologous sequences from *T. pileatus* and *T. geei*, both deposited at GenBank. Sequence differences and distances in the 573 bp long alignment were estimated by two measures of sequence divergence. First, the observed proportion of base differences between taxa was calculated by PAUP 4.0b10 (Swofford, 1999). Second, a maximum-likelihood (ML) estimate was obtained with the PUZZLE software, version 5.0 (Strimmer and Von Haeseler, 1996) with base frequencies (28.9% A, 30.2% C, 11.7% G, 29.1% T) and a transition:transversion ratio (9.11) estimated from the data set.

Phylogenetic tree reconstructions were carried out using three algorithms: maximum-parsimony (MP) (Fitch, 1971) and neighbor-joining (NJ) (Saitou and Nei, 1987) as implemented in PAUP and maximum-likelihood, included in PUZZLE. Support of

Table 1. Origin of samples for the genetic study

Species	Origin	Institution/Sponsor [a]	Accession-Nr.
Trachypithecus barbei	-	Bangkok Zoo, Thailand	AY519462
T. obscurus	-	Wuppertal Zoo, Germany	AY519459
T. phayrei phayrei	SW-Burma	ZMB, Germany	AY519460
T. p. crepusculus	Vietnam	EPRC, Vietnam	AY519461
T. francoisi francoisi	-	Bristol Zoo, Great Britain	AY519458
T. cristatus	-	Singapore Zoo, Singapore	AY519456
T. germaini	-	Bangkok Zoo, Thailand	AY519457
T. auratus auratus	-	Bristol Zoo, Great Britain	AY519455
T. pileatus	-	GenBank	AF294626
T. geei	-	GenBank	AF294618
T. johnii	-	Erfurt Zoo, Germany	AY519453
T. vetulus	-	Bristol Zoo, Great Britain	AY519454
Semnopithecus entellus priam	-	Krefeld Zoo, Germany	AY519452
S. entellus hector	Nepal	DPZ, Germany	AY519451
Presbytis comata comata	-	Howletts Zoo, Great Britain	AY519449
P. melalophos mitrata	-	Howletts Zoo, Great Britain	AY519450
Colobus guereza	-	Munich Zoo, Germany	AY519463

[a] Abbreviations: ZMB: Zoologisches Museum der Humboldt Universität Berlin; EPRC: Endangered Primate Rescue Center, Cuc Phuong National Park; DPZ: Deutsches Primatenzentrum.

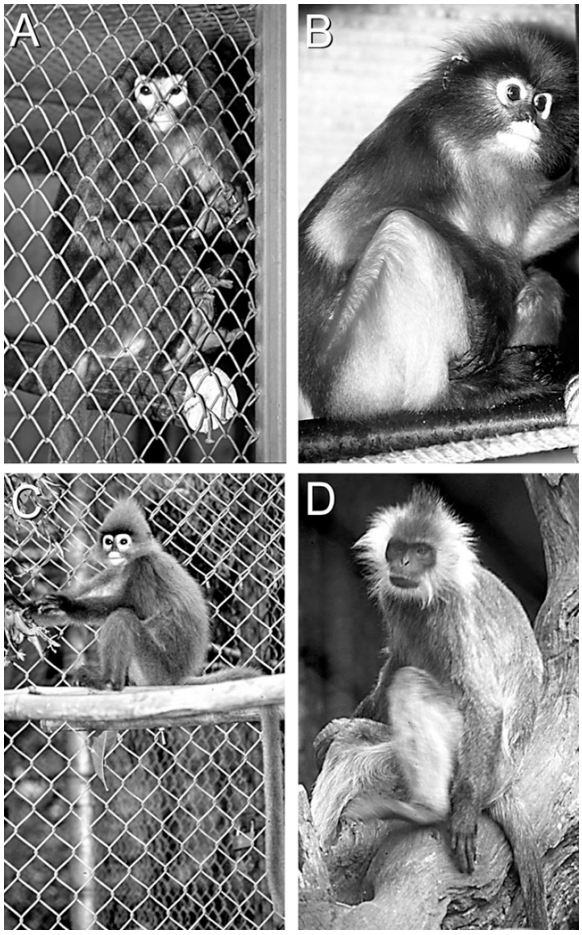

Fig. 1. Photographs showing pelage characteristics of (A) the study animal, i.e. *Trachypithecus barbei* (Bangkok Zoo, Thailand); (B) *T. obscurus* (Zürich Zoo, Switzerland); (C) *T. phayrei crepusculus* (Endangered Primate Rescue Center, Cuc Phuong, Vietnam) and (D) *T. germaini* (Bangkok Zoo). Photographs by TG.

internal branch lengths was either determined by bootstrap analyses (MP and NJ) performed with 1000 replications or indicated by the ML quartet puzzling support values (1000 puzzling steps).

Results

Pelage characteristics

Figure 1 shows pelage characteristics of the study animal and of other species of the genus *Trachypithecus*.

The general color of the study animal is grayish black with no silvering, and only slightly lighter ventrally (Fig. 1a). The tail is dark gray, slightly paler than the body. The root of the tail and the area around the ischial callosities are whitish. The long, upright crown hair forms a distinct crest. The face is gray with a violet tinge. The animal has the whitish eye-rings fully encircling the eyes and a depigmented area on the mouth typical of leaf monkeys of the *T. obscurus* group.

With the possible exception of some aspects of facial pigmentation, the study animal closely fits the original description of *T. barbei* (Blyth, 1847) and the coloration of the syntypes of *T. barbei* (as summarized in Groves, 2001). It differs from *T. obscurus* (Fig. 1b) in that the legs and the crown are not contrastingly paler than the body. It differs from *T. phayrei* in the absence of any brownish or buffy pelage. It further differs from *T. p. phayrei* in the absence of contrastingly light underparts, from *T. p. crepusculus* (Fig. 1c) in the presence of large white eyerings, and from both *T. p. crepusculus* and *T. p. shanicus* in its much darker overall coloration.

It differs from members of the *T. cristatus* group in exhibiting light face markings (although there can be a lighter gray area round the mouth and eyes in one species, *T. germaini*), and from *T. germaini* (Fig. 1d), the only species of the group occurring in Thailand, in the much darker overall coloration and the absence of long, light circumfacial hair.

DNA sequences

In order to elucidate the phylogenetic position of the study animal, a 573 bp long fragment of the mitochondrial cytochrome *b* gene was sequenced from a number of langur species and phylogenetically analyzed.

Pairwise difference analyses within *Trachypithecus* revealed that *T. barbei* is different in 4.4-16.4% to other species of the genus (Table 2). The lowest differences of the study animal to other *Trachypithecus* species were detected to *T. obscurus* and *T. p. phayrei* (4.4 - 4.5%) and so even higher than those observed between the three members of the *T. cristatus* group (*T. cristatus*, *T. germaini* and *T.*

Table 2. Distances among analysed leaf monkey taxa.[a]

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
T. barbei (1)	-	0.047	0.045	0.114	0.114	0.071	0.079	0.083	0.182	0.183	0.200	0.201	0.192	0.210	0.225	0.227	0.237
T. obscurus (2)	0.045	-	0.038	0.106	0.106	0.077	0.087	0.077	0.189	0.185	0.194	0.198	0.184	0.199	0.225	0.216	0.241
T. phayrei phayrei (3)	0.044	0.037	-	0.097	0.097	0.079	0.083	0.087	0.182	0.183	0.202	0.196	0.192	0.203	0.231	0.217	0.245
T. phayrei crepusculus (4)	0.103	0.096	0.089	-	0.089	0.106	0.110	0.106	0.230	0.231	0.230	0.216	0.230	0.209	0.234	0.230	0.235
T. francoisi francoisi (5)	0.103	0.096	0.089	0.082		0.101	0.101	0.097	0.216	0.217	0.235	0.220	0.235	0.227	0.250	0.235	0.233
T. cristatus (6)	0.066	0.072	0.073	0.096	0.093	-	0.036	0.032	0.182	0.182	0.205	0.203	0.202	0.197	0.210	0.196	0.220
T. germaini (7)	0.073	0.080	0.077	0.099	0.093	0.035	-	0.044	0.187	0.187	0.220	0.208	0.204	0.202	0.226	0.211	0.220
T. auratus auratus (8)	0.077	0.072	0.080	0.096	0.089	0.031	0.042	-	0.177	0.183	0.200	0.206	0.194	0.198	0.221	0.207	0.226
T. pileatus (9)	0.152	0.157	0.152	0.185	0.176	0.152	0.155	0.148	-	0.007	0.065	0.075	0.071	0.089	0.240	0.225	0.243
T. geei (10)	0.152	0.154	0.152	0.185	0.176	0.152	0.155	0.152	0.007	-	0.065	0.071	0.067	0.089	0.235	0.220	0.239
T. johnii (11)	0.164	0.161	0.166	0.185	0.188	0.167	0.178	0.164	0.061	0.061	-	0.102	0.098	0.087	0.235	0.220	0.255
T. vetulus (12)	0.164	0.162	0.161	0.175	0.178	0.166	0.169	0.168	0.070	0.066	0.093	-	0.033	0.108	0.222	0.218	0.235
S. entellus priam (13)	0.157	0.152	0.157	0.183	0.187	0.164	0.166	0.159	0.066	0.063	0.089	0.031	-	0.108	0.232	0.222	0.249
S. entellus hector (14)	0.171	0.164	0.163	0.171	0.183	0.162	0.166	0.162	0.082	0.082	0.080	0.098	0.098	-	0.237	0.222	0.260
P. comata comata (15)	0.182	0.182	0.185	0.187	0.197	0.171	0.182	0.178	0.190	0.187	0.187	0.178	0.183	0.188	-	0.033	0.241
P. melalophos mitrata (16)	0.182	0.175	0.175	0.183	0.187	0.161	0.171	0.168	0.180	0.176	0.176	0.175	0.176	0.178	0.031	-	0.242
C. guereza (17)	0.187	0.190	0.192	0.187	0.185	0.176	0.176	0.180	0.192	0.188	0.199	0.185	0.194	0.202	0.188	0.188	-

[a] Values represent substitutions per position. Below the diagonal are observed differences, above the diagonal are ML distances corrected with the HKY model and an estimated transition:transversion ratio of 9.11.

a. auratus) (3.1 - 4.2%). The two analyzed subspecies of *T. phayrei* (*T. p. phayrei* and *T. p. crepusculus*) differ in 8.9% which is as unexpected as the extremely high difference detected between four species of *Trachypithecus* (*T. geei*, *T. pileatus*, *T. johnii* and *T. vetulus*) and all the other species of the group (14.8 - 18.8%). Interestingly, the latter four species differ only in 3.1 - 9.8% from the two members of the genus *Semnopithecus* (*S. e. hector* and *S. e. priam*). The two analyzed species of *Presbytis* (*P. c. comata* and *P. m. mitrata*) differ in 3.1%.

All three tree reconstruction methods revealed the same topology and differed only by bootstrap or puzzling support values (Figure 2). The analyzed langur species are divided in three significantly supported clades with one containing the two *Presbytis* species, one the two representatives of *Semnopithecus* as well as *T. geei*, *T. pileatus*, *T. johnii* and *T. vetulus* (in the following named Indian clade) and finally, a clade with all the remaining *Trachypithecus* species including the study animal. The relationships among the three clades however are not significantly supported (57 - 89%), although a *Trachypithecus*/Indian clade grouping is indicated. Within the Indian clade, the relationships among the species are not well resolved. There is strong support, however, for a *S. e. priam*/*T. vetulus* and a *T. geei*/*T. pileatus* clade. The *Trachypithecus* clade consists for three significantly supported major groups with unresolved relationships among them. One comprises all members of the *T. cristatus* group (*T. cristatus*, *T. germaini* and *T. a. auratus*), a second one *T. p. crepusculus* and *T. f. francoisi*, and a third one including *T. obscurus*, *T. p. phayrei* and *T. barbei*. The reconstructed trees allow no clear resolution of the relationships among the latter three species, however, although NJ and ML algorithms indicate a sister grouping of *T. obscurus* and *T. p. phayrei*.

Discussion

Taxonomic history

Blyth (1847:34) described "*Pr. Barbei (?)* nobis, *n.s.?*" from an adult male and female presented by the Rev. J. Barbe, from "the Tenasserim Province of Ye", in the collection of the Asiatic Society of Bengal, Calcutta. He compared it to "*Pr. Phayrei*" and "*Pr. obscurus*", distinguishing it by having

"no vertical crest, as in the former; nor is the occipital hair lengthened and conspicuously paler, as invariably in the latter species: the shoulders and outside of the arm are silvered in both specimens; and underparts resemble those of *Pr. obscurus*. The tail is very slightly paler than the body; whereas in twelve adults of *Pr. obscurus*… the tail is in every one much paler than the body. The size of the full grown animal is also considerably inferior to that of *Pr. obscurus*, and perhaps a little exceeds that of *Pr. Phayrei*. In the female specimen, there is a white space at the interior base of the thigh, more developed on one side than on the other. The pale markings of the face resemble those of *Pr. obscurus*…."

Yet all was not quite clear, because in a footnote he added that the taxidermist who prepared the skins was positive that they had "a thin raised crest" when fresh. Then sixteen years later he (Blyth, 1863) changed the type locality to the interior of Tippera Hills (now Tripura, northeastern India), and altered the description, stating that the face is totally black. Thus began a century and a half of confusion.

Apart from brief descriptions by Anderson (1881) and Blanford (1888), both of whom accepted Blyth's (1863) altered account, the next important mention was by Wroughton (1917), who figured the head of "the type", and stated that "the evidence seems to me conclusive that *barbei* belongs to the section of langurs which have the hair laid straight back from the forehead over the crown" (p.47). The photograph (which is of the male syntype, as verified by CPG, who examined lutung types in the Zoological Survey of India in 1978) shows an animal with a totally black face.

Pocock (1928) accepted Blyth's alterations of 1863, apparently mainly because "the Rev. J. Barbe… is known to have collected in Chittagong and the Tipperah Hills" (p.668), and consequently used the name *barbei* as a senior synonym for *melamerus*, the northernmost subspecies of what he called *Pithecus pyrrhus*, a species in which he placed almost all mainland Southeast Asian lutungs

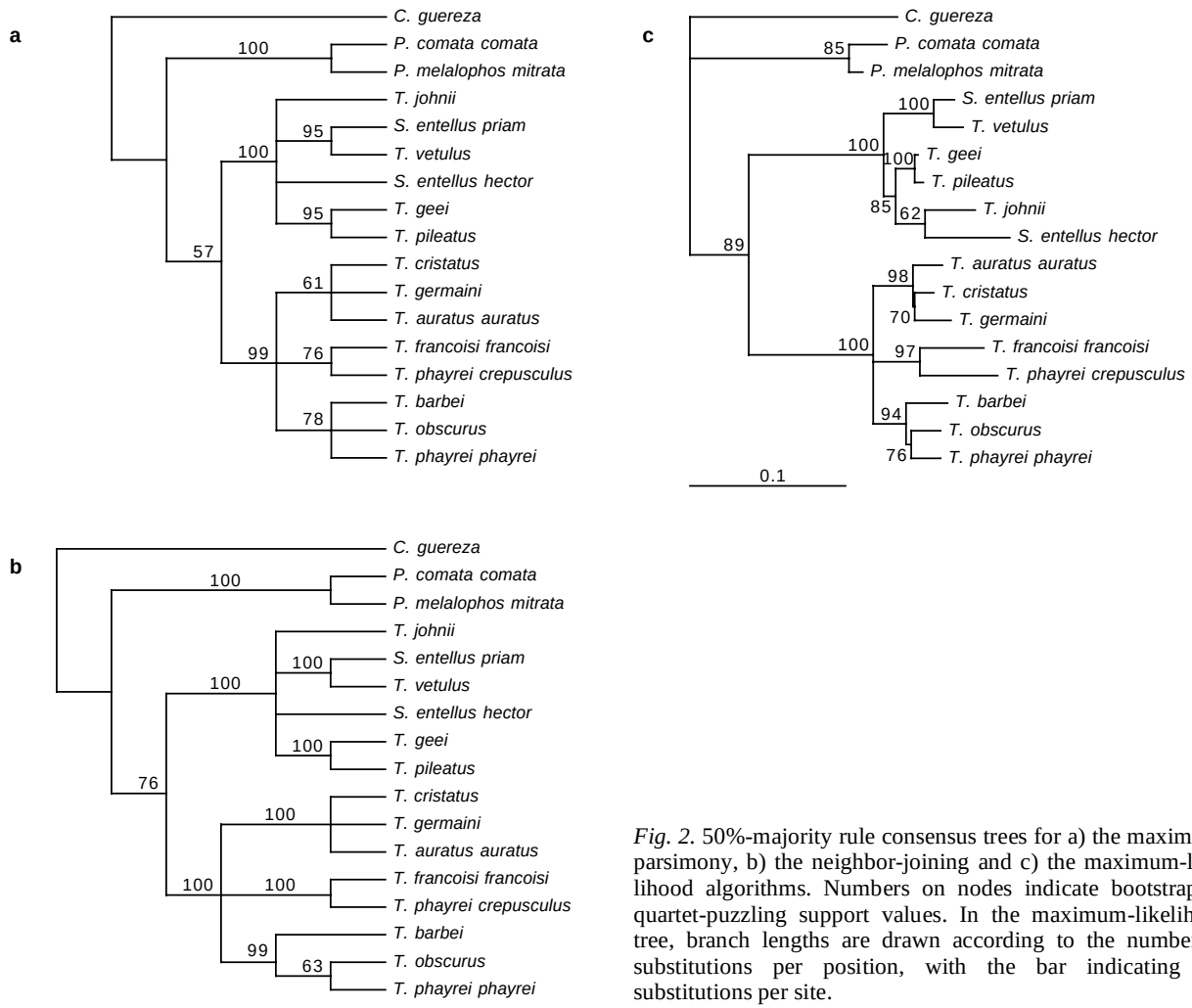

Fig. 2. 50%-majority rule consensus trees for a) the maximum-parsimony, b) the neighbor-joining and c) the maximum-likelihood algorithms. Numbers on nodes indicate bootstrap or quartet-puzzling support values. In the maximum-likelihood tree, branch lengths are drawn according to the number of substitutions per position, with the bar indicating 0.1 substitutions per site.

(including *cristatus*, *germaini*, *obscurus* and *phayrei*). At the same time, he described a new subspecies, *atrior*, with type locality Ye Forest, "in the island of Moulmein in the Ataran Division of Tenasserim", as follows (p.673):

"A very dark form nearly uniformly coloured deep, dusky brown all over the upper parts and the outside of the legs, with less sheen on the hairs; but the outer side of the arms, especially about the elbows, is paler than the shoulders and back. The under side is dark, dusky grayish brown. The tail is at most only slightly paler than the body."

He specified that the skin of the lips and chin is black. Four other specimens were identified with the new subspecies: one from the foot of Mt. Nwalabo, Tavoy (a little grayer on the tail and underside than the type), one from 14°25'N, 98°45'E, east of Tavoy but in Thailand (slightly grizzled on the head, tail and elsewhere), one from "Maw to Maw Lai" (sic), Thailand, and one of unknown locality.

A few years later, the same author reconsidered some of his taxonomic lumping, dividing Southeast Asian langurs into *Presbytis* and *Trachypithecus* and, within the latter, recognizing *obscurus* and

phayrei as species distinct from *pyrrhus* (Pocock, 1935). He referred *atrior* to *T. pyrrhus* as a subspecies, and corrected its type locality from "the island of Moulmein" to "100 miles S. of Moulmein" (making it apparently the exact same locality as *barbei*). Some of the other localities were also given in slightly different form; according to Napier (1985), the correct localities, with approximate coordinates, are as follows: foot of Mt. Nwalabo, ca.14°01'N, 98°25'E; H. Maw Tee Maw (= Huai Mothimo), 14°31'N, 98°38'E; Menam Noi, 14°25'N, 98°51'E; and 14°25'N, 98°45'E (in the Sai Yoke area). The coordinates of Ye are approx. 15°15'N, 98°E. Ye and Mt. Nwalabo are in Burma, the other three are in Thailand.

Hill (1936) described the types of *barbei* in detail. The body hairs are buff at the base and black in the distal half; the shoulders and arms are lighter, "probably grey originally" (p.107), and the forearms darken again; the legs, especially the shanks, are also paler. The hands and feet are black. A few white hairs were present near the lips and round the nares, but he was unable to confirm whether there were pale areas on the facial skin: "It is impossible in these old skins to find the exact amount of skin pigmentation present. As far as the face is concerned, however, there is no indication that the area round the eyes or mouth was any paler than the rest of the face" (Hill, 1936:108). He recommended keeping *barbei* as a distinct species within the genus *Trachypithecus*, probably restricted to the type locality which he seemed to accept as being the Tippera Hills.

The matter was considered a third time by Pocock (1939), who now relegated both *barbei* Blyth, 1847 (with type locality Tipperah) and *melamerus* to the synonym of *Trachypithecus phayrei phayrei*, and continued to use the name *T. pyrrhus atrior* (synonym probably *barbei* Blyth, 1863) for the Tenasserim lutung. This time, he specified that in the type of *atrior* the eyelids are cut away, but in the other BM(NH) specimens they "have a livid, yellowish hue" (p.143).

Khajuria (1955) considered the matter in detail. He examined Blyth's syntypes, now in the Indian Museum, Calcutta, and noted that they agree with Blyth's 1847 description except that the faces are black, and thus concur with his 1863 description. He noted that the eyelids are in fact pale in the female skin, but that dirt and exposure may have altered their color in the male; and suggested that white hairs may have fallen off the lips of both skins. He also revealed that the skulls of both specimens were present in the collection, though unmentioned by Blyth. Relegating *barbei* to the status of subspecies under *Presbytis cristatus*, he diagnosed it as follows:

"… distinguished from all other races … by the general absence of silvering of the pelage which at the most is very faintly visible towards the foreparts of the dorsal surface in some skins, by the tail (especially towards the tip) being appreciably paler than the dorsal surface, and also by the general colour being somewhat paler."

He placed Pocock's *atrior* as a junior synonym, and gave it a range "from Tippera, East Pakistan, to Tenasserim and adjoining parts of Siam" (Khajuria, 1955:98).

In 1967, Fooden (1971) collected what he called *Presbytis cristatus* at three localities in Kanchanaburi, including Pocock's locality of Menam Noi (correctly Ban Huai Maenam Noi), describing them as "dark brownish-gray to blackish" (p.41), lacking the "large sharply defined whitish mouth patch" of both *P. phayrei* and *P. obscurus* (but, by implication, having the white eye-rings?).

In 1974 and 1977 Eudey (1979) observed two different species of lutung in Huay Kha Khaeng Game Sanctuary, about 15°27'-30'N, 99°15'-19'E. One, with "brown, reddish-brown, gray or black" dorsal pelage and lacking facial patches, she identified as *Presbytis cristata*. The other, more common, had "pale gray, olivaceous gray or grayish-black" color, with "gray faces with distinctive white mouth patches, although the mouth patch appeared to be pale (gray) in one group"; the degree of expression of white eye patches was variable, mainly between groups, as was the presence of a crown crest. She provisionally identified this langur as *Presbytis phayrei*.

Agrawal (1974) was the first to notice that Blyth's 1863 corrections were based on information not from the Rev. J. Barbe but from a Mr. M. Barbe, but he made nothing of this fact. Instead, he

traveled to Tripura and collected four specimens of what he correctly identified as *P. phayrei*, apparently the only lutung which he found there. He argued that his new specimens agreed with Blyth's original (1847) description, but not with the specimens labeled as syntypes (now in the Zoological Survey of India), so that these latter must be wrongly labeled and that, being from Tenasserim, they represent *P. cristatus atrior* Pocock, while *P. barbei* is a synonym of *P. phayrei*.

Given their disagreement, Khajuria and Agrawal combined forces and reexamined the presumed syntypes together in the presence of three colleagues (Khajuria and Agrawal, 1979). They concluded that they were indeed the syntypes, the clincher being the asymmetrical white patch on the inside of the thigh of the female skin. As for the color of the face, the white parts may have been lost because of preservative chemicals (they had been lost in similarly preserved specimens of *P. obscurus*). They again noted that Blyth's 1847 locality was based on information supplied by Rev. J. Barbe, and had been changed in 1863 on the evidence of information supplied by Mr. M. Barbe, and "as such, we are not sure whether this change in the locality was based on factual information", and recommended a thorough search in Tenasserim as well as in Tripura (in case it really did occur there, despite not having been found by Agrawal (1974)). They recommended provisionally accepting *P. barbei* as a full species, and noted that except for the color of the lips, which is doubtful anyway, "it approximates *Presbytis cristatus atrior* from Tenasserim".

From all this, it seems evident that a black lutung lives in a small area of far western Thailand and adjoining parts of Burma. The earliest name for this taxon is *barbei* Blyth, 1847 (synonym *atrior* Pocock, 1928); pelage characters alone distinguish it absolutely from its neighbors *T. obscurus* and *T. phayrei*, which are strikingly particolored, and *T. germaini*, which has a spangled pelage with long pale cheek-whiskers, and it can be recognized as a distinct species of isolated affinities.

There remains the question of facial depigmentation. *Trachypithecus obscurus* and *T. phayrei* have conspicuous white eye-patches and a large white patch around the mouth, extending up to the base of the nose, while *T. germaini* lacks the white mouth patch and has very little paling around the eyes (see Groves, 2001). We should add that eye-patches appear to include white pigment or possibly a reflective layer (usually, at any rate), whereas the mouth patch seems to be a simple depigmentation of variable extent and intensity. But whether *T. barbei* has any facial markings is unclear: of the Calcutta syntypes the male has a jet-black face, while the female has only pale eyelids (Khajuria, 1955). Hill (1936) and Khajuria (1955) both warned against deducing original skin pigmentation from preserved museum material (because of dirt and exposure, according to Khajuria), and Khajuria and Agrawal (1979) noted the influence of preservative chemicals. Wroughton (1917) was informed by the director of the Indian Museum that the male syntype had been "mounted and exhibited for the last 70 years", and during this time it is not unlikely that the facial skin had not only faded but been repainted. We may remark that repainting was apparently routinely done to faded or otherwise "unsatisfactory" specimens. For instance, the type of *Eriodes hemidactylus* (in the Paris Museum; a synonym of the northern woolly spider monkey *Brachyteles hypoxanthus*, a species characterized by its mottled face) was repainted black, and the type of *Gorilla castaneiceps* (a plaster bust in the Academy of Natural Sciences, Philadelphia; a synonym of the western gorilla, *Gorilla gorilla gorilla*, but purported to be distinguished by its red topknot) was likewise repainted completely black.

None of the type series of Pocock's *atrior* seems ever to have been mounted on public display, so facial repainting can probably be ruled out although fading and discoloration by preservatives presumably cannot. CPG paid particular attention to evidence of facial colouring during his examination of the skins in 2003; the mouth in all of them is tightly sewn up and the lips are shriveled, but both the Sai Yoke and Mt. Nawlabo skins have clear indications of depigmentation around the mouth but not a sharply demarcated patch such as can be made out in preserved skins of *T.obscurus* and *T.phayrei*, while all of them definitely did have depigmented eyelids.

Fooden's (1971) descriptions are unclear: his specimens lacked a "large sharply defined whitish mouth patch", but perhaps had the white eye-rings.

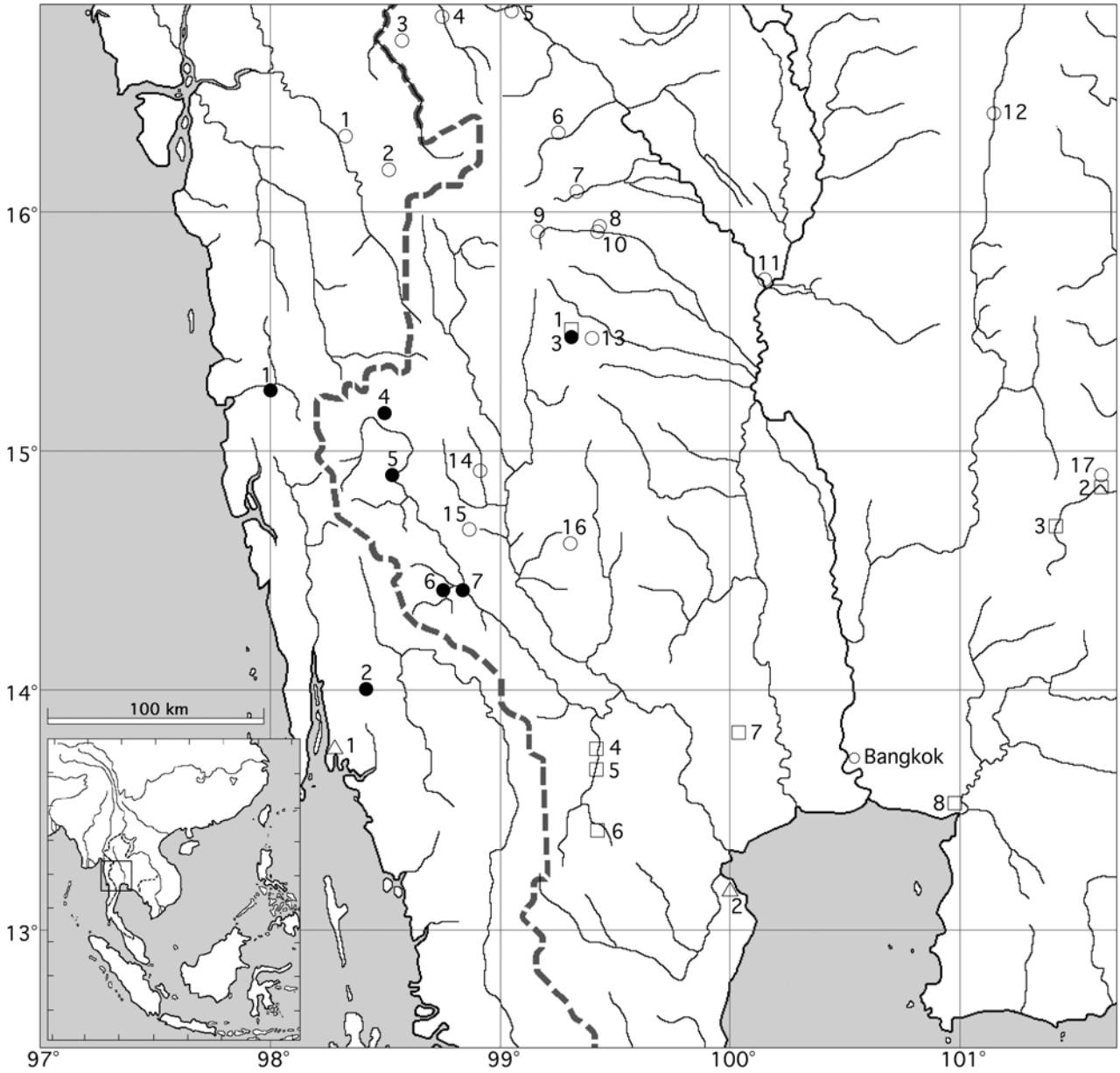

Fig. 3. Distribution range of four *Trachypithecus* species in the southern parts of Burma and central Thailand.
Black circles: localities for *Trachypithecus barbei*.
BURMA: 1 – Ye Forest, Ataran Division; 2 – Nwalabo Taung (= Mt. Nwalaboo). THAILAND: 3 – Khao Yai, Huay Kha Khaeng Game Reserve; 4 – Ban Kerng Chada; 5 – Ban Tamrong Phato; 6 – Phlu, Khao; 7 – Ban Huai Maenam Noi, and Huai Mothimo (= H. Maw Tee Maw).
Open circles: localities for *T. phayrei*.
BURMA: 1 – Lampha; 2 – Mulayi Taung. THAILAND: 3 – Mae Sot; 4 – Ban Mae Lamao; 5 – Tha Chang Tai; 6 – Ban Pong Nam Rong; 7 – Khlung, Khlong; 8 – Ko Keow; 9 – Wong, Nam Mae, 40 mi E of Um Pang; 10 – Wong, Nam Mae, 53 mi E of Um Pang; 11 – Ban Pak Nam Pho; 12 – Phetchabun; 13 – Kata Taek; 14 – Ban Muang Baw Ngam; 15 – Chongkrong; 16 – Khao Kamphaeng; 17 – Lat Bua Khao.
Squares: localities for *T. germaini*.
THAILAND: 1 – Khao Yai, Huay Kha Khaeng Game Reserve; 2 – Lat Bua Khao; 3 – Pak Chong, Sathani; 4 – "Siam", 13°45', 99°25'; 5 – "Siam", 13°40', 99°25'; 6 – Phachi, Mae Nam; 7 – Nakhon Pathom; 8 – Tahkamen, Bang Pakong R.
Triangles: localities for *T. obscurus*.
BURMA: 1 – Tavoy. THAILAND: 2 – Phet Buri.

Eudey (1979), however, described animals which usually had both mouth- and eye-patches, but sometimes the eye rings were missing or poorly expressed; considering the variability of their pelage, as well as the easterly locality (see next section), it is possible that the population is affected by gene-flow from *T. phayrei*, but even so the constant occurrence of the white mouth patch is noteworthy. Direct observations of live animals represent the most reliable information on the presence or absence of the light mouth patch. Because the mouth patch is consistently present, but not "sharply defined", in all observations made of live *T. barbei* so far, it is equally possible that this characteristic is typical of the species.

Trachypithecus barbei is evidently a species which, usually at any rate, has white eye-rings and a somewhat ill-defined white mouth patch. The Bangkok animal has both these features extremely well developed.

Distribution of Trachypithecus barbei

The type locality of both *Presbytis barbei* Blyth, 1863 and *Pithecus pyrrhus atrior* Pocock, 1928 is Ye, Tenasserim. The distribution is limited to a small area of far western Thailand and adjoining parts of Burma, between about 14° and 15°30'N and from the Bay of Bengal as far east as 98°30'E in the northern end of the range and 99°E in the southern end. To the north occurs *T. phayrei*, to the south *T. obscurus*, to the southeast *T. germaini*. Fooden (1976, Fig. 4) mapped these species' ranges (including them all in *Presbytis*), but included both *T. barbei* and *T. germaini* under *Presbytis cristatus*. In Fooden's map, the three westernmost localities of "*cristatus*" (localities 13, 14 and 18 in his earlier publication (Fooden, 1971)) represent *T. barbei*. They have been depicted as such in our Fig. 3.

The Huay Kha Khaeng Reserve, where *T. barbei* may be affected by gene-flow from *T. phayrei*, is well to the east of Ye, and not far southwest of Kata Taek, one of Fooden's (1976) localities for *T. phayrei*, and not far northeast of Fooden's localities 15 and 16 for the same species.

This study for the first time accurately assesses the geographical distribution of *T. barbei*, although the data were available in various previous reports. From this it becomes clear that the distribution range is indeed extremely restricted, somewhere between 10,000 and 12,000 km^2 (possibly larger if the species' range extends north- and/or southwards). This may be the smallest distribution range of any *Trachypithecus* species. Because species with small distribution areas are more vulnerable than species with large distribution areas, and because the range of *T. barbei* is located in the centre of the Indo-Burmese region – a biodiversity hotspot which has already lost 95.1% of its primary vegetation (Mittermeier et al., 1999; Myers et al., 2000) – an evaluation of the species' conservation status should urgently be carried out.

Affinities

Because it was previously unknown whether *Trachypithecus barbei* has pale face markings around the eyes and around the mouth, the affinities of the species remained controversial, and a close relationship to both the *T. obscurus* group and the *T. cristatus* group were suggested (e.g. Groves, 2001). The examination of our study animal reveals that the white facial markings are present though the mouth patch is not sharply demarcated, suggesting a closer affinity with the *T. obscurus* group than with the *T. cristatus* group.

Our genetic data clearly show that the study animal belongs to the *T. obscurus* group (represented by *T. obscurus* and *T. p. phayrei*) and not to the *T. cristatus* group (represented by *T. cristatus*, *T. germaini* and *T. a. auratus*). The molecular differences between *T. barbei* and *T. obscurus*/*T. p. phayrei* (4.4 - 4.5%) are in the same range as those between other closely related species such as *T. vetulus* and *S. e. priam* (3.1%), *T. cristatus*, *T. germaini* and *T. a. auratus* (3.1 - 4.2%) or *P. c. comata* and *P. m. mitrata* (3.1%). Hence, our findings support recognition of the Tenasserim lutung (*T. barbei*) as a distinct species (Khajuria and Agrawal, 1979; Groves, 2001).

Besides the clarification of the phylogenetic position of *T. barbei*, the molecular genetic study revealed further interesting insights into the evolution of Asian colobines such as the parapyhly of *T.*

phayrei or the close relationship of *T. geei*, *T. pileatus*, *T. johnii* and *T. vetulus* to members of the genus *Semnopithecus*. Although the results are contrary to general morphology, they reflect very well the distribution pattern of the species. Maybe the paraphyly of *T. phayrei* and of *Trachypithecus* in general can be explained by ancient hybridization events between ancestors of *T. p. phayrei* and the *T. francoisi* group and between *Trachypithecus* and *Semnopithecus*, respectively. This hypothesis still remains to be tested.

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Appendix: Gazetteer

Coordinates and references for localities shown in the distribution map, Fig. 2.

Trachypithecus barbei
BURMA:
Nwalabo Taung (= Mt. Nwalaboo), Tavoy Dist., Tenasserim, ca. 14°01', 98°25' (Pocock, 1928, p.673; Fooden, 1976, p.113; Napier, 1985, p.55).
Ye Forest, Ataran Division, Tenasserim, 15°15', 98°00' (type locality of *barbei* and *atrior*; Blyth, 1847, p.734; Pocock, 1928, p.673; Fooden, 1976, p.113; Napier, 1985, p.55).
THAILAND:
Ban Huai Maenam Noi (Menam Noi), Sai Yoke area, Kanchanaburi, 14°25', 98°51' (Fooden, 1971, p.39 and Fig. 1, locality 18; Fooden, 1976, p.113; Napier, 1985, p.55).
Ban Kerng Chada, Kanchanaburi, 15°08', 98°31' (Fooden, 1971, p.39 and Fig. 1, locality 13; Fooden, 1976, p.113).
Ban Tamrong Phato, Kanchanaburi, 14°54', 98°31' (Fooden, 1971, p.39 and Fig. 1, locality 14; Fooden, 1976, p.113).
Huai Mothimo (= H. Maw Tee Maw), Sai Yoke area, ca. 14°25', 98°51' (Napier, 1985, p.55).
Khao Yai, Huay Kha Khaeng Game Reserve, 15°28', 99°19' (Eudey, 1979, p.104).
Maw Tee Maw, see Huai Mothimo.
Menam Noi, Sai Yoke area, ca. 14°25'N, 98°51'E (Napier, 1985, p.55).
Moulmein, 100 miles S. of, see S.W. Siam, Sai Yoke area.
Phlu, Khao, vicinity, headquarters camp, Sai Yoke area, Kanchanaburi, ca. 14°25', 98°45' (Pocock, 1928, p.673; Fooden, 1976, p.113; Napier, 1985, p.67).
S.W. Siam, Sai Yoke area, 14°25'N, 98°45'E (Napier, 1985, p.55).

T. phayrei
BURMA:
Lampha, Tenasserim, 16°18', 98°19' (Napier, 1985, p.67).
Mulayi Taung (Dawna Range), Tenasserim, 16°11', 98°32' (Napier, 1985, p.67).
THAILAND:
Ban Mae Lamao, Tak, 16°48', 98°45' (Fooden, 1971, p.42 and Fig. 1, locality 4; Fooden, 1976, p.112).
Ban Muang Baw Ngam, Kanchanaburi, 14°55', 98°55' (Fooden, 1971, p.42 and Fig. 1, locality 15; Fooden, 1976, p.112).
Ban Pak Nam Pho, Nakhon Sawan, 15°43', 100°09' (Fooden, 1976, p.112).
Ban Pong Nam Rong, Kamphaengphet, 16°20', 99°15' (Fooden, 1971, p.42 and Fig. 1, locality 5; Fooden, 1976, p.112).
Chongkrong, Kanchanaburi, 14°41', 98°52' (Fooden, 1971, p.42 and Fig. 1, locality 16; Fooden, 1976, p.112).
Kata Taek, Uthai Thani, 15°28', 99°23' (Fooden, 1971, p.42 and Fig. 1, locality 10; Fooden, 1976, p.112).
Khao Kamphaeng, Seeswad = Si Sawat, Kanchanaburi, 14°37', 99°18' (Pocock, 1935, p.959; Napier, 1985, p.67).
Khlung, Khlong, Kamphaengphet, 16°05', 99°20' (Fooden, 1976, p.112; Napier, 1985, p.67).
Ko Keow, Kamphaengphet, 15°57', 99°26' (Fooden, 1971, p.42 and Fig. 1, locality 8; Fooden, 1976, p.112).
Lat Bua Khao, Nakhon Ratchasima, 14°52', 101°36' (Fooden, 1976, p.112; Napier, 1985, p.67).
Mae Sot, Tak, 16°43', 98°34' (Fooden, 1976, p.112).
Phetchabun, Phetchabun, 16°25', 101°08' (Elliot, 1909, cited in Fooden, 1976, p.112; Napier, 1985, p.67).
Tha Chang Tai, Tak, 16°51', 99°03' (Fooden, 1976, p.112).
Wong, Nam Mae, 40 mi (=65 km) E of Um Pang, Nakhon Sawan, ca. 15°55', 99°10' (Fooden, 1976, p.112; Napier, 1985, p.68).
Wong, Nam Mae, 53 mi (=85 km) E of Um Pang, Nakhon Sawan, ca. 15°55', 99°25' (Fooden, 1976, p.112; Napier, 1985, p.68).

T. germaini
THAILAND:
Khao Yai, Huay Kha Khaeng Game Reserve, 15°28', 99°19' (Eudey, 1979, p.104).
Lat Bua Khao, Nakhon Ratchasima, 14°52', 101°36' (Kloss, 1919, cited in Fooden, 1976, p.113).
Nakhon Pathom, Nakhon Pathom, 13°49', 100°03' (Pocock, 1935, p.935; Fooden, 1976, p.113).
Pak Chong, Sathani, Nakhon Ratchasima, 14°42', 101°25' (Fooden, 1976, p.113).
Phachi, Mae Nam, Rat Buri, ca. 13°25', 99°25' (Gairdner, 1914, cit. in Fooden, 1976, p.113).
"Siam", 13°40', 99°25' (Gairdner, 1914, cit. in Napier, 1985, p.56).
"Siam", 13°45', 99°25' (Gairdner, 1914, cit. in Napier, 1985, p.56).
Tahkamen, Bang Pakong R., between Pachim and Kabin, Chachoengsao, 13°33', 100°58' (Pocock, 1935, p.936; Fooden, 1976, p.113; Napier, 1985, p.56).

T. obscurus
BURMA:
Tavoy (mouth of Tavoy R.), Tavoy Dist., Tenasserim, ca. 13°45', 98°17' (Pocock, 1939, p.141; Fooden, 1976, p.113; Napier, 1985, p.64).
THAILAND:
Phet Buri, vicinity, Phet Buri, ca. 13°10', 100°00' (Gardner, 1914, cit. in Fooden, 1976, p.114, Pocock, 1935, p.945).