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Trachypithecus cristatus (Primates: Cercopithecidae)

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Abstract: *Trachypithecus cristatus* (Raffles, 1821), silvered lutung, is a colobine monkey of the Malay Peninsula and Archipelago. It has a pointed crest and outward-projecting cheek hairs, and gray skin and pelage with some grayish white hairs that are lighter distally, giving a silvered appearance. Diurnal and arboreal, it runs and jumps quadrupedally, with limited semibrachiation. Its large stomach and foregut fermentation allow it to digest a diet with a high proportion of leaves. It lives in single male–multifemale groups and smaller multimale groups in a polygynous, cooperative-breeding mating system. As with other nonhuman primates, it is threatened throughout its range by logging, hunting for meat and medicinal uses, and capture for the pet trade. DOI: 10.1644/862.1.

Key words: leaf monkey, lutung, *Presbytis*, silvered langur, surili, *Trachypithecus delacouri*, *Trachypithecus leucocephalus*, *Trachypithecus poliocephalus*

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Trachypithecus Reichenbach, 1862

Trachypithecus Reichenbach, 1862:89. Type species *Semnopithecus pyrrhus* Horsfield, 1823 (= *Cercopithecus auratus* É. Geoffroy Saint-Hilaire, 1812), by monotypy.

Kasi Reichenbach, 1862:101. Type species *Semnopithecus cucullatus* I. Geoffroy Saint-Hilaire, 1830, by monotypy.

CONTEXT AND CONTENT. Order Primates, infraorder Simiformes, superfamily Cercopithecoidea, family Cercopithecidae, subfamily Colobinae. In addition to *Trachypithecus*, this subfamily includes the genera *Colobus*, *Nasalis*, *Piliocolobus*, *Presbytis*, *Procolobus*, *Pygathrix*, *Rhinopithecus*, *Semnopithecus*, and *Simias*. A simplified generic synonymy has been presented due to the complexity of the taxonomic history of this group and the lack of agreement among published sources. Even the number of species included in the genus is still under debate. Groves (2005) suggested the following 17 species: *T. auratus*, *T. barbei*, *T. cristatus*, *T. delacouri*, *T. ebenus*, *T. francoisi*, *T. geei*, *T. germaini*, *T. hatinhensis*, *T. johnii*, *T. laotum*, *T. obscurus*, *T. phayrei*, *T. pileatus*, *T. poliocephalus*, *T. shortridgei*, and *T. vetulus*. Others (see below) propose 18 species that includes all of the above (except for *johnii* and *vetulus*) plus *T. crepusculus*, *T. margarita*, and *T. mauritius* (currently considered a subspecies of *T. auratus*—Groves 2005). *Trachypithecus* is exclusively south and southeast Asian except that *T. geei*, *T. pileatus*, *T. shortridgei*, *T. barbei*, *T. phayrei*, *T. francoisi*, and *T. poliocephalus leucocephalus* occur in southern China (Wang et al. 1999). The genus occurs only north of Wallace's

Fig. 1.—An adult *Trachypithecus cristatus selangorensis* photographed at Kuala Selangor Nature Park, Selangor, Malaysia, by L. Harding.

line except that *T. auratus* occurs on Lombock Island, where it may have been introduced (Napier and Napier 1967).

The following key is based on recent publications (Brandon-Jones et al. 2004; Francis 2008; Geissmann et al. 2004; Groves 2001; Nadler et al. 2005; Roos et al. 2008), drawings by Stephen D. Nash for the Endangered Primate Research Center, Ninh Binh Province, Vietnam, and photographs by the author at Endangered Primate Research Center and in Malaysia. Species groups follow Roos et al. (2008). *T. pileatus* and *T. geei* have been included even though their affinities are uncertain.

1\. Buccal–suborbital cheek hairs in a line from join of lips backward to ear, hairs upward or backward curling, but short enough, especially posteriorly, to usually expose the ear; a high, pointed crest is always present; face jet black .. 4 (*T. francoisi* group)
   Cheek hairs not in a labial–buccal–suborbital line, long enough and usually projecting outward or curling forward so as to usually hide the ear from front view; face gray, black, or blue; may have eye rings or pale lips 2
2\. Long, backward-swept cheek hairs contrasting with short, upright hair on crown that does not form a crest; pelage gray, brown, or golden; ventral hair diverges bilaterally .... 9 (*T. pileatus* group)
   Hair on crown forming an erect crest (usually pointed) or flops forward; back pelage gray, silver, black, or red; ventral hair streams backward or converges at midline 3
3\. Prominent white eye ring (not always complete) and pale or depigmented lips and nasal septum; no white pubic patch in female .. 11 (*T. obscurus* group)
   Black or gray face with dark lips; a thin eye ring may be present; white or yellowish pubic patch in female .... 14 (*T. cristatus* group)

***T. francoisi* group**

4\. All-black body and cranial pelage and skin with just faint, yellow-tipped hairs on cheeks, chin, and upper lip and around palms and soles and whitish hairs at front of ear .... *T. ebenus*
   White or grayish cheek hairs 5
5\. Body pelage black; white buccal–suborbital cheek hairs 6
   Body pelage mainly black with large areas of white, gray, or orange 8

←

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Trachypithecus cristatus*, Natural History Museum catalogue reference number 1909.4.5.1 (Natural History Museum, London, United Kingdom) from Batam [Battam] Island, Indonesia. Maximum skull length (premaxillary to supraoccipital crest) is 90 mm. Photograph by Phil Hurst, Natural History Museum, used with permission.

6. White buccal–suborbital cheek hairs extending to ears; black brow tuft .... *T. francoisi*

Black or white brow tuft; white buccal–suborbital cheek hairs extending beyond ears 7

7. Black brow tuft; white buccal–suborbital cheek hairs continuing well behind ear, almost joining at center of nape .... *T. hatinhensis*

White buccal–suborbital cheek hairs continuous with white brow tuft encircling face except for chin; white may cover most of forehead except for tip of crest .... *T. laotum*

8. White rump and upper thighs strongly contrasting with otherwise black pelage; grayish buccal–suborbital cheek hairs sticking out and nearly long enough to hide ears from the front; tail is thickest (10 cm at base) of all the *francoisi* group species .... *T. delacouri*

Black pelage with a white or orange head, neck, and upper shoulders; graying thighs and sides of rump .... *T. poliocephalus*

***T. pileatus* group**

9. Black crown cap, black face, gray to brown dorsum, and contrasting facial hairs pale yellowish to red, which may extend down onto chest; orange venter varies from blond to red (belly often redder than chest and throat) in described subspecies; cheek hairs curl forward behind cheeks .... *T. pileatus*

No black crown cap 10

10. Pelage blond above and golden below; very long cheek hairs and brow hairs; black face ...... *T. geei*

Uniform silvery gray pelage on head and body, including underside, with paler legs; tail lacking long hairs and darkening toward tip; crown and cheek hairs colored as body; hands and feet black; cheek hairs shorter than in *T. pileatus* and *T. geei* .... *T. shortridgei*

***T. obscurus* group**

11. White eye rings incomplete, dark gray near nose, narrow on top and broad on the outside; pelage varies geographically from brownish to blackish gray, often with darker back, arms, and tail, but thighs and crest contrastingly paler than back; 1 form defined by a blond tail, another by a black belly, another by distinctly paler pelage with pale grayish yellow, rather than pale grayish brown legs; distinct dorsal stripe; some forms have a blond posterior crown patch .... *T. obscurus*

White eye rings complete 12

12. Complete but narrow white eye rings, black nose, broad, white lips; face framed by black facial hair contrasting with longer, black cheek hairs and pointed crest; legs, tail, and crown cap not contrastingly pale colored; dorsal pelage uniform brown to grayish brown, may be frosted with lighter ends; belly same color as back or to pale gray; tail with a darker tuft .... *T. phayrei*

Eye ring broad 13

13. As *T. phayrei* except very broad white eye rings and a depigmented area of skin around mouth very small; pelage lighter than *T. phayrei* and usually light gray but varies from silvery brown to nearly yellow; forehead brown, becoming lighter over crown and sometimes creamy on nape; thighs paler than back, hands and feet black .... *T. crepusculus*

Face skin pigment dark gray except for white eye rings and whitish area of bare skin around mouth, black cheek hairs, pelage dark silver-gray to nearly black back with no frosting, spangled nape (geographically variable), tail slightly paler than body with a pale patch at base .... *T. barbei*

***T. cristatus* group**

14. Thin, white, yellow, or "depigmented" eye ring 15

No light eye rings; face all black or gray 16

15. Crown crest erect, pointed and directed slightly backward, black forehead tuft erect and directed slightly forward, white or gray cheek hairs, face black or gray except for thin white eye ring that extends below orbit, above cheek; pelage pale gray, underparts very light and contrasting with the black forehead, forearms, hands, and feet .... *T. margarita*

Facial skin with yellow eye rings and bluish face (black morph) or eye rings—in some forms, the whole face—"depigmented" and freckled face (red morph); pelage glossy black except for the red morph and not "frosted" (i.e., no silver tips). Circumfacial hair (cheek hairs and hair on crown) is erect and forward-curled, forming a "mussel-shaped" semicircle around the orbits. There is no pointed crest. In red morph, tips of hairs on head, arms above wrists, near elbow, and legs above ankles are whitish; there may be a dorsal tinge of black. Females differ from males in having a pale, usually yellowish white pubic patch .... *T. auratus*

16. Black pelage hairs without white tips; face black or gray with no eye rings; pointed crest; long, outward-pointing cheek hairs .... *T. mauritius*

Pelage with white or gray tips 17

17. Cheek hairs white to light gray and very long; boundary of the hairs on the forehead nearly straight, not forming a semicircle around the orbita (i.e., not "mussel-shaped"). Pale beard under chin combines with cheek and crown hairs to give a "halo" effect around the black face. The crest is erect, but not sharply defined or pointed.

Darker gray pelage contrasts with lighter arms and legs; back hairs are dark gray or brownish black with short, creamy tips, giving a medium-gray appearance .... *T. germaini*

Face all slatey gray without light eye rings; boundary of the forehead hairs as in *T. germaini*. Hairs on crown form a sharp, pointed crest separate from the cheek hairs, which are not as long as in *T. germaini* (these features may not be identifiable in museum specimens); beard absent; pelage color uniform on face, body and legs from slate gray (North Borneo and West Malaysia) to nearly black (East Kalimantan and South Sumatra) although with lighter tips, giving a silvered appearance; a red morph occurs in Borneo .... *T. cristatus*

***Trachypithecus cristatus* (Raffles, 1821)**
Silvered Lutung

Simia cristata Raffles, 1821:244. Type locality "Indonesia, Sumatra, Bengkulen (Bengkulu, Bencoolen)."

Simia villosa Griffith, 1821:pl. 2. Type locality "one of the East Indian Islands" vide Brandon-Jones et al. (2004:147).

Semnopithecus pruinosus Desmarest, 1822:533. Type locality "Sumatra."

Semnopithecus cristatus: Müller, 1835:77 [not seen, cited in Horsfield 1851:13]. Name combination.

Semnopithecus rutledgii Anderson, 1878:38. Type locality unknown.

Presbytis cristata: Lyon, 1906:607. Name combination.

Presbytis cristata pullata Thomas and Wroughton, 1909:439. Type locality "Batam."

Pygathrix ultima Elliot, 1910:351. Type locality "Mount Dulit, Borneo, 3,000 feet elevation."

Pygathrix cristata: Lyon, 1911:140. Name combination.

Presbytis vigilans Miller, 1913:29. Type locality "Indonesia: Sirhassen Island, South Natuna Islands."

Pithecus pyrrhus cristatus: Pocock, 1928:475. Name combination.

Trachypithecus pyrrhus cristatus: Pocock, 1934:928. Name combination.

Trachypithecus cristatus: Hooijer, 1962a:41. First use of current name combination; part, not *Presbytis*.

Context and Content. Context as for genus. *Trachypithecus cristatus* contains 2 living subspecies (Roos et al. 2008):

T. cristatus cristatus Raffles, 1821:244. See above. Includes *T. c. vigilans* Miller, 1913, according to Roos et al. (2008), but Maryanto et al. (1997) distinguished the Natuna Islands lutungs and those from Batam as separate subspecies.

T. cristatus selangorensis Roos et al., 2008:634. Type locality "Kuala Selangor (3°20′N, 101°20′E), Province Selangor, West Malaysia."

Nomenclatural Notes. É. Geoffroy Saint-Hilaire (1812) described *Cercopithecus* to include *C.* [= *Trachypithecus*] *auratus*. After Raffles (1821) described *Simia* [*T.*] *cristata*, Desmarest (1822, often cited as 1821) credited *Semnopithecus* ("*Semnopithèque*") to F. Cuvier (1821) and included *S.* [*T.*] *pruinosus* (= *cristatus*). Gray (1871, often cited as 1870) used *Semnopithecus* as a preferred synonym for *Presbytis* (Eschscholtz 1821) and included *S.* [*T.*] *cristatus*. Finally, Reichenbach (1862) named the genus *Trachypithecus* with Horsfield's (1823) *S. pyrrhus* [= *auratus*] as the type species. Reichenbach (1862) also described the South Asian genus *Kasi*, which has been used as a senior synonym for *Semnopithecus* including species now recognized as *Trachypithecus* (and, by inference, *T. cristatus*) and *Presbytis*.

Elliot (1913) placed "*Pygathrix cristata*" (and some other *Trachypithecus* species) into *Trachypithecus*, which he treated as a subgenus of *Pygathrix*. Pocock (1928) included *Semnopithecus* and *Trachypithecus* in *Presbytis*.

Although earlier genetic analysis showed the white-headed langur (*T. poliocephalus*) to be closely related to François's langur (*T. francoisi*) and some have classified it as a subspecies, *T. f. leucocephalus* (Ding et al. 2000; Wang et al. 1999), some authorities (Huang et al. 2008; Li and Rogers 2006; Zhao et al. 2008) consider it a separate species, *T. leucocephalus*. However, Brandon-Jones et al. (2004) recognized the taxon as a subspecies of *T. poliocephalus*: *T. p. leucocpehalus.* Roos et al. (2007) provided further evidence supporting this relationship.

The phylogenetic position of capped (*T. pileatus*) and golden (*T. geei*) lutungs, which may have evolved after ancient hybridization between *Semnopithecus* and *Trachypithecus* clades, remains unresolved (Karanth et al. 2008). Groves (2001) refers *T.* [*Presbytis*] *cristata*[*-us*] *caudalis* (Dao 1977), provenance unknown (probably from Cambodia or southwestern Vietnam), described from zoo specimens, to *T. germaini caudalis*. Groves (2001) referred *T. c. koratensis* to *T. germaini germaini*. Hooijer (1962a:41) described a Pleistocene fossil, *T. c. robustus*, type locality Tegoean, central Java; being from Java, this presumably should be referred to the Javan lutung (*T. auratus*).

Trachypithecus is from the Greek *trachys*, rough, and *pithekos*, ape. *Cristatus* is from the Latin *crista*, crest or tuft. Groves (2001) and others use the common name of "leaf monkey" for *Presbytis* species and "langur" for *Trachypithecus* species; however, langur is a Hindi word applied to species of India and Sri Lanka that are no longer included in *Trachypithecus*; hence, the Malay word "lutung" is more appropriate for *Trachypithecus*, as "surili" is for *Presbytis* (Bernstein 1968; Brotoisworo 1979; Geissmann et al. 2004; Weitzel and Groves 1985).

DIAGNOSIS

Regardless of pelage color, some hairs are grayish white and lighter distally, giving a silvered appearance; hence the common names silvered leaf monkey and silvered lutung. There are no white or pale facial markings, either pigment or hair, and pelage overall is uniform silvered gray, except for the white pubic patch of the female. There is a pointed crest and outward-projecting cheek hairs long enough to usually hide the ears when seen from the front (Fig. 1). Teeth and jaws are small, relative to other *Trachypithecus* species. Weitzel and Groves (1985) described the forward dentition as follows: I1 is long with a wide, straight incisal edge meeting at the incisal edge of both mandibular incisors. I2 is rotated away from I1 and is caniniform. There is a notch between I1 and I2 but not between i1 and i2 or between the central incisors of either arcade. Harrison (2001) described the molars as follows: m1 is 81% of the area of m2 and M1 is 84% of the area of M2; and m3 is relatively larger (114% of area) than m2. *T. cristatus* can be distinguished from *T. auratus* by its shorter dental arcade relative to the calvaria and shorter associated mandibular measurements (Weitzel et al. 1988).

GENERAL CHARACTERS

In common with most other colobines (and which distinguishes them from Cercopithecini), *Trachypithecus cristatus* does not have cheek pouches, the large stomach is sacculated, the interorbital width : muzzle length index is >16.3, the nasal bones are short and broad, there is no median mental foramen (Fig. 2), and the molar teeth have high, pointed cusps separated by deep notches (Napier 1985). *T. cristatus* lacks the ischial tuberosities characteristic of the cercopithecines. *Trachypithecus* species are smaller and less sexually dimorphic in size than most other colobine genera, but more dimorphic than *Presbytis* (Pan and Groves 2004). *T. cristatus* is statistically separable from other *Trachypithecus* species (and *Trachypithecus* from other colobine genera) by cranial measurements, especially cranial length, calvarial length, biporionic width, and width of postorbital constriction; but there is sufficient overlap to prevent their use as diagnostic characters (Pan and Groves 2004). In discriminant function analysis of cranial measurements, members of the *T. cristatus* group group separately from Phayre's leaf-monkey (*T. phayrei*), dusky leaf-monkey (*T. obscurus*), and *T. francoisi*, which group together (Pan and Groves 2004).

Trachypithecus cristatus is diurnal and arboreal. It can stand upright but, as a "semibrachiator" (Napier and Napier 1985), generally progresses quadrupedally, jumping, climbing, leaping, and limited arm-swinging through trees with considerable agility and speed. The hairless, black hands and feet have opposable thumbs and large toes, respectively, and the tail is not prehensile. When walking along tree limbs (Fig. 3), it grasps with the hands and may either grasp with the feet or use them plantigrade, walking on the balls of the feet.

Trachypithecus cristatus is not sexually dimorphic except for irregular white patches on the inside flanks of females, females are 89% of the body weight of males (Roonwal and Mohnot 1977) and canine–sectoral teeth are considerably larger in the male (Groves 2001).

Females (except those from the Riau Archipelago) range from 460 to 514 mm head and body length and a tail of 678–751 mm (Napier 1985). Males (except those from the Riau Archipelago) are 503–580 mm head and body length and tail 671–750 mm (Napier 1985). Those from the Riau Archipelago are smaller (e.g., females, length of head and body 420–455 mm, length of tail 560–703 mm—Napier 1985). Mean body masses are 5.7 kg for females and 6.6 kg for males (Oates et al. 1994). The tail is relatively short compared, for example, to the Indochinese lutung (*T. germaini*) with a tail of 720–838 mm (Groves 2001).

The skull (Fig. 2) is strongly orthognathous, but less so than in *Presbytis* (Napier and Napier 1985). Female skull length is 89.0 mm ± 3.4 *SD* ($n = 18$) and bizygomatic distance is 69.1 ± 2.6 mm ($n = 31$—Weitzel and Groves 1985). Skulls of *T. cristatus* average shorter than those of *T. auratus* (female 95.6 ± 2.6 mm, $n = 3$) and *T. mauritius* (female 92.5 ± 5.2 mm, $n = 6$—Weitzel and Groves 1985). Napier (1985) gives the cranial capacity of the "*Presbytis cristata* group" (which includes other *Trachypithecus* species in Java, Indochina, and Tenasserim) as 54–71 cm^3 ($\bar{X} = 61.4\ \text{cm}^3$). Mean skull indices for males and females (in parentheses) were: braincase length 76.3 (72.4); facial 62.6 (61.0); palate 102.9 (104.7); skull breadth 75.3 (79.5); interorbital 24.6 (24.4); and face braincase 48.1 (47.2—Groves 1970).

The following postcranial indices have been reported (Washburn 1944): *T. cristatus* has relatively short legs compared to arms: intermembral index (humerus + radius in percent of femur + tibia) 80–83 in males, 80–84 in females and femoro-humeral index (humeral length in percent of femoral length) 77–81 in males, 78–82 in females; relatively short forearms compared to upper arms: radius approximately equal to or shorter than humerus (brachial index 93–97 in males, 91–98 in females). In addition, *T. cristatus* and other *Trachypithecus* faces are relatively large compared to species of *Presbytis*: prognathism index (basion–prosthion in percent of basion–nasion) 115–120 in males, 111–119 in females. These indices can be used to distinguish *T. cristatus* and other *Trachypithecus* species from *Presbytis* and *Pygathrix*, but not *Trachypithecus* species from each other

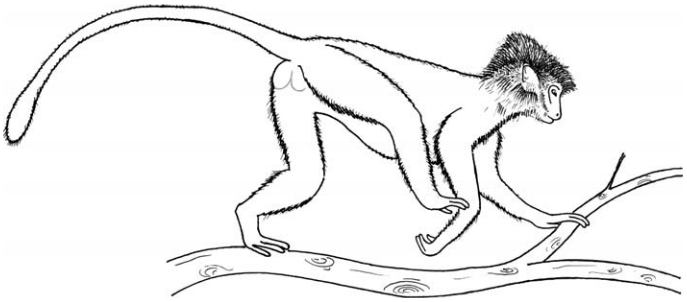

Fig. 3.—Example of quadrupedal locomotion of *Trachypithecus cristatus* walking along a branch (drawing by Thasun Amarasinghe from a photo by L. Harding).

(Washburn 1944). Based on cranial and skeletal measurements, 3 morphological groups of *T. cristatus* are identified: Malaya–Sumatra–Kalimantan, Bintan, and Natuna (Maryanto et al. 1997).

DISTRIBUTION

Trachypithecus cristatus occurs on the Malay Peninsula, Borneo, Sumatra, the Natuna Islands, and adjacent, smaller islands. *T. c. selangorensis* occurs only on the Malay Peninsula (Fig. 4). *T. c. cristatus* is found in other parts of the species' range (Roos et al. 2008), unless those from the Natuna Islands and Batam are distinct (see Maryanto et al. 1997).

FOSSIL RECORD

Trachypithecus species groups *cristatus*, *obscurus*, and *francoisi* diverged about 3.17 ± 0.31 million years ago (as estimated from molecular data), coinciding with Pliocene global cooling and subsequent fragmentation of evergreen forest habitats (Roos et al. 2008). Pleistocene glacial–interglacial cycles and resulting sea level changes continued to drive speciation of *Trachypithecus* (see discussion in Roos et al. 2008).

Pleistocene remains of *Trachypithecus* that have been found in Yunnan, southern China, are nearly identical to extant *T. francoisi* and *T. phayrei* (Jablonski 2002). Middle to late Pleistocene fossils of *Trachypithecus* have been found in caves in North Vietnam (some of these were identified as "*Trachypithecus* sp. or *Presbytis* sp.", but the latter is unlikely, given its known past and current distribution) and at Tam Hang in northeastern Laos (Bacon et al. 2008:279). Late Pleistocene fossils from Lang Trang in Vietnam, identified as *Presbytis* (Long et al. 1996—not seen, cited in Tougard 2006), were possibly misidentified species of *Trachypithecus* because of the persistent taxonomic confusion of these genera. Fossils of *Trachypithecus* from Thailand have been dated to 169 ± 15 thousand years ago (Tougard 2001).

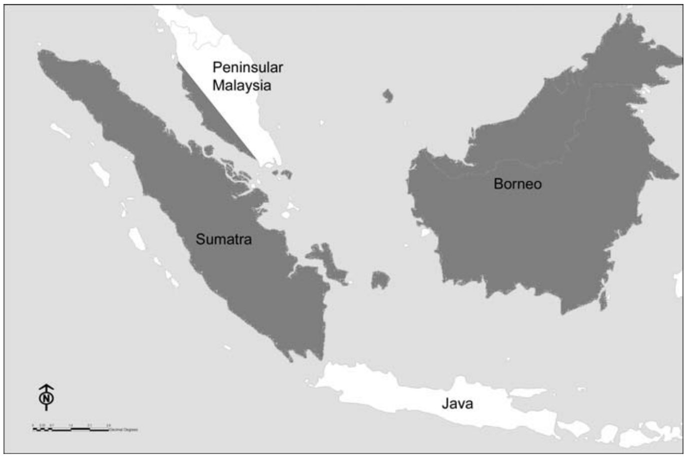

Fig. 4.—Distribution (dark gray) of *Trachypithecus cristatus*. *T. c. selangorensis* is restricted to Peninsular Malaysia and *T. c. cristatus* on Sumatra, Borneo, adjacent islands, and the Riau Archipelago (adapted from Roos et al. 2008).

Trachypithecus auratus and *T. cristatus* probably evolved from a common ancestor, based on molecular data of Roos et al. (2008), who suggest that ancestral populations probably expanded southward to the Sunda region about 1.25 ± 0.12 million years ago. An alternative hypothesis, that they were present on Java about 1.9 ± 0.95 million years ago and then expanded northward, was based on a Javan fossil (Jablonski and Tyler 1999). However, Larick et al. (2000) cast doubt on the site stratigraphy and show that the fossil was no different from modern *T. auratus*. Other fossils identified as *T. cristatus*, but not identified to subspecies, also have been found on Sumatra; and fossils identified as *T. cristatus*, but presumably *T. auratus*, have been found on Java (Hooijer 1962a; Kahlke 1973). Javan fossils of *Trachypithecus* include those found at Gunung Dawun, dated to 80–60 thousand years ago (Storm et al. 2005).

Fossils of *Trachypithecus* from at least 4 caves on the island of Borneo, originally identified as *T. cristatus* (Harrison 1996; Hooijer 1962a), were subsequently referred to *T. auratus* (Jablonski 2002; Jablonski and Tyler 1999); however, with subsequent taxonomic revisions within the genus, and extant *T. auratus* confined to Java (Roos et al. 2008), the Borneo specimens are now recognized as *T. cristatus.*

Late Pleistocene and Holocene deposits in Niah Caves on Borneo (Hooijer 1962b) eventually yielded a minimum of 49 specimens of *T. cristatus* (Harrison 2001). Their cheek teeth averaged 14% larger than those of extant *T. cristatus* (Harrison 1996), but smaller than those from middle Pleistocene deposits at Tegoean, Java, which Hooijer (1962a) classified as a separate subspecies, *T. c. robustus* (presumably = *T. auratus*). The ages of these deposits suggest a reduction in size of cheek teeth of *T. cristatus* and in corresponding body size during the Pleistocene.

FORM AND FUNCTION

Form.—The dental formula for *Trachypithecus cristatus* is i 2/2, c1/1, p 2/2, m 3/3, total 32 (Ankel-Simons 2000). The teeth have bilophodont cusps on their 2 transverse ridges, adaptations to increase efficiency of processing plant materials (Groves 2001; Lucas and Teaford 1994). Incisors of *T. cristatus* have a 30% underbite, lower than other colobines (e.g., 100% in the maroon leaf-monkey [*Presbytis rubicunda*]), a feature that is negatively correlated with maxillary incisor size and palate length (Lucas and Teaford 1994). They also have narrower incisors relative to other colobines (Zingeser 1970), longer molar crests, a low ratio of the 1st to the 3rd molars, and a high breadth : length ratio of the 3rd molar (Lucas and Teaford 1994). These are adaptations to fracture and fragment fibrous leaves (Lucas and Teaford 1994).

The vertebral column is typical of catarrhines, 7 C, 12 T, 7 L, 3 S; the pelvis has a relatively long ischium and short ilium (Napier and Napier 1967). Interpubic joints of *T. cristatus* are typically fused and pelvic capacity is larger in females than in males; the sexual difference is most pronounced at the inlet (Tague 1993). Pelvic differences between *T. cristatus* and *P. rubicunda* are related to interspecific differences in both locomotion (as also shown by leg length, noted above) and obstetrics.

As with other colobines, *Trachypithecus* is distinguished from its cercopithecine relatives by an enlarged and sacculated, ruminant-like stomach, an adaptation to a folivorous diet (Strasser and Delson 1987). As with *Semnopithecus* and *Presbytis*, *Trachypithecus* has a tripartite stomach (saccus, tubus gastricus, and pars pylorica); this contrasts with *Pygathrix*, *Procolobus*, *Rhinopithecus*, and *Nasalis*, which also have a presaccus (Caton 1998). The saccus is large and contains bacteria for fermentation of the plants. *T. cristatus* also has a capacious, haustrated hindgut (Caton 1999). The tubus gastricus is long and the pars pylorica short (Kuhn 1964). The sacculated part of the stomach and the 1st two-thirds of the gastric tube are lined with cardial glands. This structure allows the separation of ingesta between proximal and distal parts, and thus between alkaline and acidic environments (Bauchop 1978). The well-defined gastric canal seems to allow passage of liquid and small food particles to the distal, glandular part of the stomach (Kuhn 1964). Colobines have large salivary glands that act to neutralize stomach acid. Although among the smaller of the studied *Trachypithecus* and *Presbytis* species, *T. cristatus* has the largest gastrointestinal tract: intestinal length (including stomach, small intestine, cecum, and colon) 540 cm, surface area 3,911 cm^2, mass 373 g, volume 4,518 cm^3, absorptive area 2,770 cm^2, and fermenting volume 4,023 cm^3 (Chivers 1994). Not surprisingly, *T. cristatus* has about twice the mass of stomach contents per body mass (17.4%) as the other colobines studied (Chivers 1994).

There is no sternal gland, as reported for some primates (Wislocki and Schultz 1925) and no other specialized scent glands have been documented (Napier and Napier 1985). Testes mass (sum of both) average 6.3 g ($n = 12$; 0.09% of body mass) and does not deviate from normal mammalian scaling (Kenagy and Trombulak 1986).

Function.—Foregut fermentation of seed coats releases rich nutrients from the cotyledons and was probably an ancestral preadaptation to the more highly specialized folivory of langurs and lutungs (Benefit 2000). For *Trachypithecus cristatus* to consume a diet of 55% to >90% leaves (Caton 1999; Hock and Sasekumar 1979), its digestive system must be able to break down the structural polysaccharides by microbial fermentation. Consuming a high percentage of leaves, relative to fruit- and seed-eaters, *T. cristatus* may have less need for such copious high-pH saliva, although the relative contributions of dietary and salivary alkali and possible alkaline secretions of the saccus mucosa have yet to be assessed (Chivers 1994). These features also help colobines detoxify secondary plant toxins, such as alkaloids, that deter other herbivores (Kay and Davies 1994).

Results of digesta marker passage studies indicate *T. cristatus* has prolonged retention of digesta for fermentation in both the stomach and haustrated colon (Caton 1999); Caton defines the digestive strategy as gastro-colic fermentation, unlike that of some other forestomach fermenters in which the hindgut fermentation is of secondary importance. Bauchop and Martucci (1968) found that the foregut of captive *T. cristatus* contained *Methanobacterium ruminantium* and 2 species of cellulolytic *Bacteriodes*, but no protozoa; stomach gases included methane, carbon dioxide, and a little hydrogen. Volatile fatty acids increased after feeding. They also reported that *T. cristatus* had 95–133 mmol/l volatile fatty acids, 47–56 mol % acetic acid, 24–26 mol % propionic acid, and 10–18 mol % butryic acid, and that the in vitro fermentation rate was fairly high at 63–79 µmol gas per gram wet weight per hour.

Finding that the closely related *T. auratus* selects leaves for their lower fiber content and greater digestibility, rather than protein content, Kool (1992) speculated that protein levels in foliage may be sufficient to obviate the need for selection for this nutrient. Instead, food selection may maximize other nutrients such as carbohydrates. This probably applies to *T. cristatus* as well.

Fukuta et al. (1994) reported the following blood serum values for 8 anesthetized female *T. cristatus* (mean body mass 3.86 kg): hematocrit (35.6% ± 6.7%), total protein (6.7 ± 0.8 g/dl), albumin (3.61 ± 0.77 g/dl), α-1 globulin (0.13 ± 0.04 g/dl), α-2 globulin (0.73 ± 0.18 g/dl), β globulin (0.87 ± 0.27 g/dl), γ globulin (1.36 ± 0.55 g/dl), albumin : globulin ratio (1.23 ± 0.38), sodium (161 ± 6.14 mEq/l), potassium (5.61 ± 0.74 mEq/l), lactate dehydrogenase (575 ± 257 IU/l), glutamic-oxaloacetic transaminase (93 ± 67 IU/l), glutamic pyruvic transaminase (34 ± 33 IU/l), creatine phosphokinase

(250 ± 200 IU/l), alkaline phosphatase (613 ± 633 IU/l), leucine aminopeptidase (115 ± 68 IU/l), γ-glutamyl transpeptidase (28 ± 30 IU/l), transglutaminase (47 ± 24 mg/dl), Total cholesterol (141 ± 31 mg/dl), blood urea nitrogen (29.0 ± 5.7 mg/dl), total bilirubin (0.21 ± 0.07 mg/dl), and inorganic phosphorus (3.4 ± 2.0 mg/dl).

The relatively short lower legs and forearms compared, for example, to *Presbytis*, but similar to other *Trachypithecus* species (Washburn 1944), along with associated differences in musculature, may be adaptations to more quadrupedal locomotion in trees and less brachiation (cf. Fleagle 1977a, 1977b). In turn, this may signal resource partitioning among sympatric leaf monkeys that may use different parts of the trees (Bennett and Davies 1994; Fleagle 1978). In fact, in 180 h of observation of captive *T. cristatus* over 60 days, Amarasinghe et al. (2009) never saw adults using suspensory locomotion, although immatures did frequently.

ONTOGENY AND REPRODUCTION

Ontogeny.—Young are born with eyes open, well furred, and with a strong grip, allowing them to cling to the mother. Neonates are about 200 mm in length and 0.4 kg at birth and reach adult size at about 5 years of age (Roonwal and Mohnot 1977). As with other *Trachypithecus* species, neonates have orange fur and white skin on hands, feet, and face. The skin changes color within days of birth to black as in adults, whereas the orange natal cloak changes to the adult color within 3–5 months (Bernstein 1968). The contrasting pelage of infants may be an infanticide avoidance strategy or it may promote alloparental care (Treves 1997); for example, it may help adults quickly find infants when danger threatens or when they fall from the trees, as occasionally happens during the excitement of intergroup encounters (Roonwal and Mohnot 1977).

Although infants nurse for around 18 months (Napier and Napier 1985), females lactate for 12 months both in captivity (Shelmidine et al. 2009) and in the wild (Wolf 1984); because females practice communal nursing (and other alloparental care; see below), synchrony is not required. Once weaned, juveniles have no more contact with their mothers than with others in the group (Furuya 1961). Both sexes interact with their young, play with them, and defend them from danger. However, if adult males carry and interact socially with infants, it is usually at the latter's initiative. Juveniles are 18–48 months old and subadults 36–48 months (Harvey et al. 1987). Age at 1st birth ranges from 21.3 to 45.4 months and averages 34.6 months (Shelmidine et al. 2007). *T. cristatus* have lived up to 31 years and 1 month in captivity (Nowak 1999).

Reproduction.—*Trachypithecus cristatus* is iteroparous with year-round breeding and no seasonal peak in births (Medway 1970a). Gestation period is 181–200 days and the estrous cycle is 24 days (Shelmidine et al. 2009). The placenta has 2 disks; the cord, inserting on the major lobe, is relatively long (Benirschke 2008). Females bear 1 infant per litter (Shelmidine et al. 2009); twins have not been reported (cf. Bernstein 1968; Borries and Koenig 2008; Furuya 1961; Wolf 1980). There are no external signs of estrus (vulval swellings occur minimally, not during the period of receptivity, and are not attractive to males—Shelmidine et al. 2007).

The birth interval in the wild is 18–24 months (Wolf 1984). In captivity, birth intervals average 14.9 months, longer for primiparous females and shorter for females whose infants did not survive their 1st year (Shelmidine et al. 2009).

Borries and Koenig (2008) reported that captive females become menopausal 1.8 to 5+ years prior to death with a lag time between last parturition and death ranging from 3.0 to 9.0 years ($n = 8$). Hormonal analysis revealed constantly low and acyclic levels of immunoreactive pregnanediol-3-glucuronide in 1 old, wild female, supporting the notion of true menopause. Nonsexual behavior was analyzed based on quantitative data collected simultaneously for 6 old and 26 younger, adult females (1,378.5 h of observation). Although Borries and Koenig (2008) found no support for social disengagement, old females were less active and spent less time feeding. Their data support previous reports of menopause and extended postreproductive life spans in colobine monkeys (e.g., Sommer et al. 1992).

ECOLOGY

Population characteristics.—Khan (1978) estimated that *Trachypithecus cristatus* in the Malay Peninsula declined from 6,000 to 4,000 during 1958–1975. Densities of *T. cristatus* in undisturbed habitats have ranged from 15 individuals/km^2 to 23–61 individuals/km^2 (MacKinnon 1986; Supriatna et al. 1986). Although Bernstein (1968) gives a density of 160 individuals/km^2, this seems unlikely and is probably based on a few large groups occupying a patch of favorable, protected habitat. Southwick and Cadigan (1972) give the density of groups as 0.10 groups/km^2 in the Malay Peninsula. MacKinnon (1986) estimated that about 2 million *T. cristatus* occurred in 113,167 km^2 of suitable habitat in Indonesia at a density of 15 individuals/km^2. However, this was based on an obsolete definition that included other *Trachypithecus* species including those in Thailand, Cambodia, Vietnam, and elsewhere. Populations are reduced in the Malay Peninsula (and no doubt elsewhere) where tribal people hunt primates (Chivers and Davies 1979). Because most leaf monkey populations of the region have declined markedly in the last 2 decades (Mittermeier et al. 2007; Nadler et al. 2007), new population estimates are needed.

Although some population densities of *Trachypithecus* may be related to forage quality (Gupta and Chivers 1999) or tree density (Johns 1985), evidence that food supply may limit populations of *T. cristatus* is lacking; on the contrary, some populations of *Trachypithecus* may have superabundant food supplies (Bennett and Davies 1994). Yeager and Kirkpatrick (1998) also doubted that food constrains population size and density of *Trachypithecus* and suggested that other factors, such as social stress, were the more likely limitations. Although definitive studies are lacking (and see notes on predation, below), controls on populations of *T. cristatus* (and other colobine), aside from human persecution and habitat loss, are density-dependent effects of social stress resulting from inter- and intragroup interactions (Davies and Oates 1994; Yeager and Kirkpatrick 1998; Yeager and Kool 2000).

Space use.—*Trachypithecus cristatus* is largely restricted to coastal and riverine forests and plantations, especially mangrove (*Acanthus illicifolius*, *Rhizophora conjugate*, and others) and nipa palm (*Nipa fruticans*)–mangrove swamps with adjacent upland forest. This species does not inhabit inland forests where mature leaves may be abundant but of lower quality; in these inland habitats, a year-round supply of fruit and young leaf parts can sustain a semifolivore or folivore such as *Presbytis* (Davies and Oates 1994; C. W. Marsh and W. L. Wilson 1981, in litt.; Medway 1970b; Payne et al. 1985). Where sympatric, *Trachypithecus* feeds mainly in the middle and upper canopy, but not as high up or as far out on slender branches as *Presbytis* (Curtin 1977—not seen, cited in Napier and Napier 1985). This may provide the surilis with more fruits and young leaves than are available to the lutungs.

Largely arboreal, *T. cristatus* rarely leaves the trees and retreats quickly if there is a threat of danger (Furuya 1961; Medway 1970b). Home ranges averaged 43 ha and those of adjacent groups typically overlapped (Furuya 1961; Yeager and Kirkpatrick 1998). Bernstein (1968), however, gives a much smaller home range of 20 ha for *T. cristatus* of Kuala Selangor. Groups of *T. cristatus* travel about 200–500 m throughout their territory daily, usually led by the male (Bernstein 1968; Furuya 1961). The group may fragment, with females leading subgroups along alternate paths in the same direction. The last period of travel before dark is the most rapid and does not appear goal-directed; most animals in the group rejoin each other and congregate in a single tree at night (Roonwal and Mohnot 1977). Although home ranges of neighboring troops may overlap, each defends its territory; hence, boundaries are often in dispute and somewhat flexible (Wolf 1978).

Diet.—At least 94 plant species have been identified in the diet of *Trachypithecus cristatus*, including leaves, seeds, flowers, and fruits such as epiphytic figs (Roonwal and Mohnot 1977). Leaves comprise up to 91% and fruit only 9% (Hock and Sasekumar 1979), the highest and lowest percentages, respectively, of all colobine species for which data were available (Caton 1999; Yeager and Kool 2000). This, together with the skeletal and other physical differences noted above, such as larger stomachs than *Presbytis* (Chivers 1994), provides a basis for resource partitioning in the rare situations where *T. cristatus* is sympatric with other colobines (Bennett and Davies 1994).

Diseases and parasites.—No instances of epizootics have been described for *Trachypithecus cristatus* (or any colobine), few instances of grossly diseased animals have been seen in the wild and disease is not known to have limited langur or lutung populations (Davies and Oates 1994; Yeager and Kool 2000). In South Kalimantan, Borneo, 34.4% (22 of 64) of *T. cristatus* had *Wuchereria kalimantani* (Nematoda: Filarioidia) in testes, blood, and lymph nodes (Davies and Oates 1994; Palmieri et al. 1980). In another study on Borneo, of the individuals of *T. cristatus* examined, 25% were infected with *Brugia malayi* and *B. pahangi*, 35% were infected with *W. kalimantani*, 1% with *Cardiofilaria*, 1% with *Dirofilaria*, and 22% with *Plasmodium coatneyi* (Masbar et al. 1981). Garnham (1963) finds that *T. cristatus* is a less important host for *Plasmodium* than sympatric colobines. *Wuchereria bancrofti* also has been found in *T. cristatus* (Maizels et al. 1988).

Diseases found in wild *T. cristatus* have included those due to mycoplasms (Whithear 2000). Diseases in captive animals include a measles epizootic and heat dermatitis (Montrey et al. 1980; Walder and Hargis 2002). Indeed, *T. cristatus* is so susceptible to human diseases, including acquired immunodeficiency syndrome (Lo et al. 1989), as well as its behavioral tractability and willingness to breed in captivity, that it has become widely used as an animal model for experimental study of human diseases (Palmieri et al. 1984; Walker et al. 1973).

Interspecific interactions.—*Trachypithecus cristatus* is rarely sympatric with other colobines. Although it overlaps the range of the southern pig-tailed macaque (*Macaca nemestrina*) in the Malay Peninsula, Sumatra, and Borneo and the white-thighed surili (*Presbytis siamensis*) in the Malay Peninsula (Francis 2008), habitat differences generally preclude close contact. Exceptions include co-occurrence with *T. obscurus* on the west coast of the Malay Peninsula (C. W. Marsh and W. L. Wilson 1981, in litt.; Medway 1970b), where it is also sympatric with the crab-eating macaque (*M. fascicularis*—Groves 2001), and Borneo, where it is sympatric with *P. rubicunda* (Davies 1991; Tague 1993) and perhaps other *Presbytis* species. Medway (1970b) suggested that *T. cristatus* may have only recently colonized the Malay Peninsula from Sumatra and was excluded from inland forests there by the presence of other leaf monkeys, but was more widespread in Borneo and Sumatra because of the absence of a closely related competitor; examination of the data of Roos et al. (2008), however, suggests a longer period of isolation for the peninsular population. Bernstein (1968) noted that although the 2 species sometimes travel together and feed in the same trees, *T. cristatus* generally avoids *M. fascicularis* and agonistic interactions are rare; however, at Kuala Selangor, I noticed (December 2007) that *T. cristatus* often foraged within a few meters of foraging *M. fascicularis*. Furuya (1961) noted that, when the 2 species feed together, the lutungs yield space to the macaques without fighting.

Asian arboreal colobines appear to suffer low predation rates (Davies and Oates 1994). Predation rates are difficult to measure in primates, however, and may be lower in habituated populations where predators are shy, and in fragmented areas where predator populations are reduced, than in undisturbed habitats (Hart 2007; Hill and Dunbar 1998; Hill and Lee 1998; Isbell 1994). Unlike in Africa, few raptors large enough to take primates over 2 kg occur in Southeast Asia (Hart 2007; Streck 2002). Of the large raptors that I saw at Kuala Selangor (Brahminy kite [*Haliastur indus*], black kite [*Milvus migrans*], hawk-eagles [*Nisactus* sp.], and rufous-bellied eagle [*Lophotriorchis kienerii*]), none harassed the individuals of *T. cristatus* that were visible at the same time. However, Bernstein (1968) stated that the presence of eagles distresses *T. cristatus* at Kuala Selangor and he observed males charging and chasing an eagle and flushing an owl from its roosting place. Terrestrial predators that could take adult *T. cristatus* include snakes, large felids, and *Cuon alpinus* (dhole); a variety of smaller predators including small felids, genets, civets, mongooses, *Canis familiaris* (domestic dog), and *Arctictis binturong* (binturong) could take infants (Francis 2008; Streck 2002). Antipredator strategies include large group sizes (Hill and Lee 1998) and arboreal habits (Medway 1970b). Although large snakes and small felids can be found at all heights up to the canopy, they are probably less agile than the lutungs.

BEHAVIOR

Grouping behavior.—*Trachypithecus cristatus* has the polygynous, cooperative-breeding mating system typical of the "presbytina" group of colobines. Single male–multifemale group sizes of about 10–40, as well as singles and smaller multimale groups, are the norm (Bennett and Davies 1994; Bernstein 1968; Furuya 1961; Supriatna et al. 1986; Wolf and Fleagle 1977). Occasionally, more than 1 male is present in a multifemale group (Furuya 1961). Newton and Dunbar (2001) term *T. cristatus* society "matrilineal—harem." Juvenile males usually disperse from their natal group at maturity.

Although female dominance hierarchies have not been documented in the wild, *T. cristatus* does exhibit female–female affiliative behaviors such as allogrooming and sitting in proximity (Bernstein 1968). This contrasts with *Presbytis* and *Semnopithecus* in which such hierarchies are found (e.g., Borries et al. 1991; Sterck and Steenbeek 1997). In a captive population of *T. cristatus*, however, Amarasinghe et al. (2009) found a clear female hierarchy in which females with young were below adult and same-age males, but above juvenile males and other females, while juvenile females were at the bottom.

Trachypithecus cristatus shows a low level of aggression and frequent sociosexual, gestural, and vocal interactions within the social group (Bernstein 1968; Furuya 1961; Supriatna et al. 1986; Wolf and Fleagle 1977). This may be due to the abundance of food in its habitat and its feeding behavior of facing toward the tree while eating, both of which decrease the frequency of interaction with other members of the group.

Among neighboring groups, *T. cristatus* exhibits both aggression and tolerance, according to the situation. When troops meet near their border, the respective males make threat displays and vocalizations, chase each other, and may fight, while other members of the groups react excitedly, often fleeing the site of conflict into their respective territories (Roonwal and Mohnot 1977). However, if the males have lagged behind, other group members may run back and forth between groups and even embrace members of the other group. Alternatively, the males may threaten and chase but not fight; if no fighting has occurred, the groups may forage in close proximity and interact peacefully soon after intergroup conflicts (Roonwal and Mohnot 1977).

A more serious type of territorial conflict occurs when an adjacent male intrudes into an area that is not ordinarily in dispute. On noticing the intrusion, the resident male will advance rapidly; if the intruding male is accompanied by a group, they cluster tightly about him and they all usually retreat with "much squealing and agitated movements" (Roonwal and Mohnot 1977:230). If the intruding male—with or without a group of his own—reaches the resident group, he is attacked by the resident male (Roonwal and Mohnot 1977).

Scenarios like the one described above occasionally result in an intruding male from an all-male unit or a solitary male replacing the resident male of a male–female group (Yeager and Kool 2000). In at least 1 instance, all the infants in the group disappeared within 3 months and were assumed to have been killed by the new, dominant male, although infanticide was not actually observed (Wolf and Fleagle 1977). Infanticide following male replacement has been reported in the closely related *T. auratus* (Brotoisworo 1979) and *T. poliocephalus* (reported as *T. leucocephalus*—Li and Rogers 2004; Zhao and Pan 2006). Higher rates of infanticide are expected where 1 male monopolizes multiple females and the turnover of males is high, for example, because of hunting (Janson and van Schaik 2000). However, few instances of actual infanticide have been documented; how often and in what circumstances it may occur remain uncertain (Newton and Dunbar 2001; Zhao and Pan 2006). Infanticide is likely a rare occurrence, if it happens at all in *T. cristatus*, because infant survival in the wild (70%—Wolf 1984) is barely less than in a captive population (70.9%—Shelmidine et al. 2009) where infantcide did not occur.

Reproductive behavior.—The female solicits copulation by making rhythmic, side-to-side head movements and then

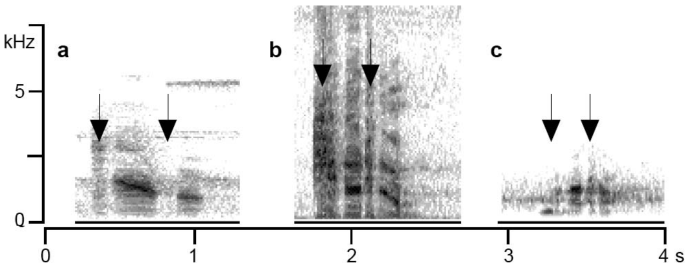

Fig. 5.—Sonograms of "loud calls" of a) *Trachypithecus cristatus*; b) *T. auratus*; and c) *T. obscurus*. The arrows mark the locations of the inhalation phase of the calls (from Stünkel 2003).

presenting her hindquarters to the male; if he mounts, she continues head shaking during copulation (Roonwal and Mohnot 1977). Male mountings may be multiple, and if another female solicits simultaneously, the male mounts both in the same copulating sequence. Male masturbation is recorded (Bernstein 1968). There is no evidence of a breeding season (Medway 1970b); reports of seasonal breeding (e.g., Fooden 1971) involved what are now recognized as other *Trachypithecus* species that live to the north in more-seasonal environments.

Communication.—*Trachypithecus cristatus* is relatively silent and is generally quieter than other lutungs, langurs, and surilis (Roonwal and Mohnot 1977). Wild individuals of *T. cristatus* acclimated to humans, as at Kuala Selangor, appear grave, serious, expressionless, and slow moving. They make at least 13 different vocalizations, most commonly at dusk and dawn, to signal salutation, fear, warning, alarm, and conflict. Most often heard is the "loud call" (or "great call"—Fig. 5), consisting of a 2-note inhale–exhale–type vocalization used by adult males during and after territorial conflicts (Bernstein 1968). Stünkel (2003) finds that the loud calls of *T. cristatus* from 3 sites on Sumatra and Borneo can be distinguished from each other, and these are separable from calls of the other *Trachypithecus* species studied (*T. auratus*, *T. mauritius*, *T. obscurus*, *T. phayrei*, *T. pileatus*, *T. geei*, *T. francoisi*, and the Hatinh langur [*T. hatinhensis*]).

Males make other threat calls (e.g., 🔊, Supporting Information S1, http://dx.doi.org/10.1644/862.S1) and young call for their mothers (Amarasinghe et al. 2009; Furuya 1961; Medway 1970b; Roonwal and Mohnot 1977). Furuya (1961) describes the following calls: ku—emitted by infants when they are in a peaceful state and by juveniles when addressing each other from a short distance; ho—emitted by young males and females when addressing each other from a short distance; ku-ku—uttered by adult females greeting each other; alarm calls—sound like "cha-cha," "chue-chue," and "ge-ge" (🔊, Supporting information S2, http://dx.doi.org/10.1644/862.S2); kie—expresses fear or surprise; guu or gyu—by adult males to communicate threat or surprise, subadult males also make this call (🔊, Supporting Information S1, http://dx.doi.org/10.1644/862.S1); and gua-gua-gua—by adult male when attacking an intruder.

In addition, Bernstein (1968) described a kwah call, emitted by the adult male at repeated intervals to control group travel movement, and squeals sounding like "ki" or "gyu" emitted by juveniles and infants. Amarasinghe et al. (2009) described a krēēkk call made by males (🔊, Supporting Information S3, http://dx.doi.org/10.1644/862.S3) and females, indicating excitement or anticipation when the tractor carrying food approached, and chrēēss to indicate satisfaction when the food had been delivered (🔊, Supporting Information S4, http://dx.doi.org/10.1644/862.S4). Adult females, juveniles, and infants also make a variety of soft and shrill chirps and whistles (🔊, Supporting Information S5, http://dx.doi.org/10.1644/862.S5; 🔊, Supporting Information S6, http://dx.doi.org/10.1644/862.S6; 🔊, Supporting Information S7, http://dx.doi.org/10.1644/862.S7; 🔊, Supporting Information S8, http://dx.doi.org/10.1644/862.S8). Infants make prolonged, very high-pitched (with perhaps inaudible components) squeaks with a variety of phrases and modulations (🔊, Supporting Information S9, http://dx.doi.org/10.1644/862.S9; 🔊, Supporting Information S10, http://dx.doi.org/10.1644/862.S10). Additional audio recordings of the calls of infants, females, and males made by Thasun Amarasinghe and Modhava Botejue are available in Amarasinghe et al. (2009).

Individuals also communicate nonvocally with each other in social play, grooming, and sparring. Bernstein (1968) describes visual communication such as yawning or branch shaking to communicate tension or general excitement, or an individual (usually male) will chase another (also usually male) in disputes at areas of a group's territorial boundaries. An adult male will chase the other male out of the territory, but upon reaching the other group's territory, both reverse and the chaser becomes, briefly, the chased.

Miscellaneous behavior.—Although *Trachypithecus cristatus* is described as very shy, individuals and bands are occasionally seen near human settlements and on palm plantations, but retreat quickly to the forest if they feel threatened (Bennett and Davies 1994; Bernstein 1970; Davies and Oates 1994).

GENETICS

Cytogenetics.—Diploid chromosome number is 2n = 44. Bigoni et al. (1997) employed in situ hybridization of chromosome-specific DNA probes (chromosome painting) to establish homologies between karyotypes of humans and *Trachypithecus cristatus*. The 24 human chromosome paints gave 30 signals on the haploid female chromosome set and 34 signals on the haploid male chromosome set. Bigoni et al. (1997) attributed the difference due to a reciprocal translocation between the Y and an autosome homologous to human chromosome 5. The Y/autosome reciprocal translocation, which is unique among catarrhine primates, has produced a $X_1X_2Y_1Y_2/X_1X_1X_2X_2$ sex-chromosome system. Although most human syntenic groups have been maintained in *T. cristatus*, chromosomes homologous to human chromosomes 14 and 15, and 21 and 22 have experienced Robertsonian fusions. Further, chromosomes 1/9 and 6/16 have been split by reciprocal translocations (Bigoni et al. 1997). G-banding analysis shows 3 different forms of chromosome 1 (X_2) that differ by a complex series of inversions in the 10 individuals karyotyped. Comparisons with patterns in hylobatids (gibbons, including siamang) demonstrate that resemblances in chromosomal morphology and banding previously taken to indicate a special phylogenetic relationship between gibbons and colobines are, instead, due to convergence (Bigoni et al. 1997).

Further chromosome paint probes and banding (Bigoni et al. 2004) support the taxonomic grouping of *Trachypithecus* lutungs but align purple-faced leaf monkeys, *T.* [*S.*] *vetulus* with *Semnopithecus* langurs. Red-shanked duoc lutung (*Pygathrix nemaeus*) is the most karyologically conservative and *T. cristatus* is the most karyologically derived of the Asian colobines. Reciprocal translocations occurred in the ancestral Asian colobine lineage that produced the *Pygathrix* chromosomes and are present in all Asian species; subsequent inversions link *Trachypithecus* with *Nasalis* (proboscis monkeys). Results indicate high variability among *T. cristatus*, *T. francoisi*, and *T. phayrei*, suggesting greater divergence. Reciprocal translocations of human homologues 6 and 16 are defining features of *Trachypithecus* (Bigoni et al. 2004).

Molecular genetics.—Examination of mitochondrial data shows that the African and Asian colobine lineages diverged by 10.8 million years ago in the late Miocene (Sterner et al. 2006). Within the Asian colobines, an "odd-nosed" clade separated from the other langurs and began to diversify by 6.7 million years ago in the early Pliocene, giving rise to the genera *Nasalis*, *Pygathrix*, and *Rhinopithecus* (Sterner et al. 2006). Incongruence between mitochondrial data (which suggest sister clades of *Presbytis* and *Trachypithecus* to the exclusion of *Semnopithecus*) and nuclear chromosomal data (which support a *Semnopithecus* + *Trachypithecus* group) suggests ancient hybridization or introgression (Ding et al. 2000; Karanth et al. 2008; Nadler et al. 2005; Osterholz et al. 2008; Roos et al. 2008; Ting et al. 2008; Wang et al. 1999).

Recent mitochondrial and nuclear DNA analyses have confirmed that *Presbytis*, *Semnopithecus*, and *Trachypithecus* are separate genera (Brandon-Jones et al. 2004; Geissmann et al. 2004; Nadler et al. 2005; Osterholz et al. 2008; Roos et al. 2008; Zain et al. 2005). *Pygathrix* and *Nasalis* also form clades distinct from *Trachypithecus* (Zain et al. 2005, 2008). On the basis of restriction enzyme analysis of mitochondrial DNA from 42 individuals of *T. auratus* and *T. cristatus*, Rosenblum et al. (1997) found sufficient genetic structure to separate them as conservation units, but not as separate species. They were, however, separable from the geographically proximate species, the Javan surili (*Presbytis comata*). Rosenblum et al. (1997) interpreted these results to indicate either a recent speciation event with the retention of ancestral polymorphisms, or that the 2 taxa are not separate species. However, Roos et al. (2008), analyzing sequence data of mitochondrial DNA as well as nuclear DNA from 115 lutungs in the *cristatus* group, find sufficient genetic structure to separate *T. cristatus* from *T. auratus*, *T. germaini*, *T. margarita*, and *T. mauritius*. They exclude the tenasserim lutung (*T. barbei*), formerly included in the *T. cristatus* group (Groves 2001), and refer it to the *T. obscurus* group. The phylogenetic relationships within the *T. cristatus* group are not well resolved, however, indicating a radiation-like splitting event that they estimated to have occurred about 0.95–1.25 million years ago. Within *T. cristatus*, Roos et al. (2008) detected 2 major clades, 1 comprising specimens from Sumatra, Borneo, and the Natuna Archipelago, and the other solely individuals from the Malay Peninsula. They recommend that *T. cristatus* be split into 2 subspecies, describing the peninsular Malaysian form as a new subspecies, *T. c. selangorensis*.

Population genetics.—Genotypic and phenotypic variations between populations on Peninsular Malaysia, Sumatra, and Borneo have given rise to the subspecies identified above. Genetic structure within subspecies has not been reported. Hybrids between male *Trachypithecus cristatus* and female *T. phayrei* have been reported (Chiarelli 1971; Hill 1936).

CONSERVATION

Jernvall and Wright (1998) showed that, particularly in Asia, extinction rates are likely to be higher among primates with diurnal and arboreal specializations, especially folivorous primates such as *Pygathrix* and *Trachypithecus*. Although the International Union for Conservation of Nature and Natural Resources (2008) lists 10 other *Trachypithecus* species as "Vulnerable," "Threatened," "Endangered," "Critically Endangered," or "Data Deficient," it lists *T. cristatus* as "Near Threatened." Except for 3 *Trachypithecus* species on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (2009) Appendix I (*T. geei*, *T. pileatus*, and *T. shortridgei*), all others are included on Appendix II. *T. cristatus*, as with other nonhuman primates, is threatened throughout its range by logging, hunting for meat and medicinal uses, and capture for the pet trade (Geissmann et al. 2006; Mittermeier et al. 2007; Nijman 2008). For example, Bunguran Island, Indonesia, was until 1980 largely covered in primary forest habitat; however, by 2003 only small patches of primary forest remained within a matrix of logged forest covering nearly 70% of the island (Lammertink et al. 2003). This is representative of habitat loss throughout the region (e.g., Meijaard and Sheil 2008; Meijaard et al. 2008).

Poaching is rife for both local consumption and international sale (Corlett 2007; Geissmann et al. 2006; Malone et al. 2002; Mittermeier et al. 2007; Shepherd et al. 2004). Wild Sumatran primate species, especially surilis and lutungs, are found more often in Javan markets than native Javan species (Geissmann et al. 2006). Anecdotally, in a large, protected university research forest near Kuala Lumpur, Malaysia, I saw a camp site were poachers were smoking primate meat on almost an industrial scale (L. E. Harding, December 2007). The combination of selective logging with hunting facilitated by the opening up of forest patches by roads and tracks is particularly disastrous (Oates and Davies 1994). In Peninsular Malaysia, oil palm plantations, aquaculture, and other coastal developments have eliminated much of the coastal mangrove habitat of *T. cristatus* (Nijman 2008). In view of the recent taxonomic revisions, rapid rate of habitat loss, and continued illegal hunting and commercial (including international) trade, new population estimates and identification of conservation units are needed.

SUPPORTING INFORMATION

The following voice recordings were made by Mr. Deepal Warakagoda of the Drongo Nature Sounds Library, Dehiwala, Sri Lanka, on 5 May 2009 between 1000 and 1100 h, just before feeding time. He used an Edirol R-1 digital recorder (Penguin Electronics, Colombo, Sri Lanka) and a Sennheiser ME 66 microphone (Swedish Trading Company, Colombo, Sri Lanka). Audio files were cleaned using Magix Audio cleaning software (Future Shop, Coquitlam, Canada). The actual sequence of calls, as they occurred prior to feeding in the original recording were: S4, S5, S6, S7, S9, S2, S8, S1, S10, S3). Additional information on the captive group of *Trachypithecus cristatus* and the zoo where these recordings were made is found in Amarasinghe et al. (2009).

Supporting Information S1.—Call of subdominant male *Trachypithecus cristatus*.

Found at Audio 8/File 20 (230 kb WAV).

Supporting Information S2.—Call of male *Trachypithecus cristatus*.

Found at Audio 6/File 18 (98 kb WAV).

Supporting Information S3.—Call of alpha male *Trachypithecus cristatus*.

Found at Audio 10/File 12 (1,378 kb WAV).

Supporting Information S4.—Call of female *Trachypithecus cristatus*.

Found at Audio 1/File 13 (2,299 kb WAV).

Supporting Information S5.—Call of female *Trachypithecus cristatus*.

Found at Audio 2/File 14 (593 kb WAV).

Supporting Information S6.—Call of female *Trachypithecus cristatus*.

Found at Audio 3/File 15 (698 kb WAV).

Supporting Information S7.—Call of female *Trachypithecus cristatus*.

Found at Audio 4/File 16 (190 kb WAV).

Supporting Information S8.—Call of mature female *Trachypithecus cristatus*.

Found at Audio 7/File 19 (284 kb WAV).

Supporting Information S9.—Four recordings of calls of infant *Trachypithecus cristatus* combined into 1 file.

Found at Audio 5/File 17 (11,015 kb WAV).

Supporting Information S10.—Call of infant *Trachypithecus cristatus*.

Found at Audio 9/File 11 (4,171 kb WAV).

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LITERATURE CITED

Amarasinghe, A. A. T., W. M. S. Botejue, and L. E. Harding. 2009. Social behaviours of captive *Trachypithecus cristatus* (Mammalia: Cercopithecidae) in the National Zoological Gardens of Sri Lanka. Taprobanica 1:66–73.

Anderson, J. 1878. Anatomical and zoological researches, comprising an account of the zoological results of the two expeditions to western Yunnan in 1868 and 1875, and a monograph of the two Cetacean genera, *Platanista* and *Orcella*. B. Quaritch, London, United Kingdom.

Ankel-Simons, F. 2000. Primate anatomy. Academic Press, San Diego, California.

Bacon, A.-M., et al. 2008. Redécouverte d'une faune Pléistocène dans les remplissages karstiques de Tam Hang au Laos: premiers résultats. Comptes Rendue Palevol 7:277–288.

Bauchop, T. 1978. Digestion of leaves in vertebrate arboreal folivores. Pp. 193–204 in The ecology of arboreal folivores (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Bauchop, T., and R. W. Martucci. 1968. Ruminant-like digestion of the langur monkey. Science 161:698–700.

Benefit, B. R. 2000. Evolutionary study of diet and dentition. Pp. 133–179 in Old World monkeys (P. F. Whitehead and C. J.

Jolly, eds.). Cambridge University Press, Cambridge, United Kingdom.

Benirschke, K. 2008. The placenta of the Colobinae. Vietnamese Journal of Primatology 2:33–39.

Bennett, E., and A. G. Davies. 1994. The ecology of Asian colobines. Pp. 129–172 in Colobine monkeys: their ecology, behaviour and evolution (A. G. Davies and J. F. Oates, eds.). Cambridge University Press, Cambridge, United Kingdom.

Bernstein, I. S. 1968. The lutong of Kuala Selangor. Behaviour 32: 1–16.

Bernstein, I. S. 1970. Some behavioral elements of the Cercopithecoidea. Pp. 263–295 in Old World monkeys: evolution, systematics, and behavior (J. R. Napier and P. H. Napier, eds.). Academic Press, New York.

Bigoni, F., U. Koehler, R. Stanyon, T. Ishida, and J. Wienberg. 1997. Fluorescence in situ hybridization establishes homology between human and silvered leaf monkey chromosomes, reveals reciprocal translocations between chromosomes homologous to human Y/5, 1/9, and 6/16, and delineates an X1X2Y1Y2/X1X1X2X2 sex-chromosome system. American Journal of Physical Anthropology 102:315–327.

Bigoni, F., G. Stone, and R. Stanyon. 2004. Cytotaxonomy of Colobinae Primates with reference to reciprocal chromosome painting of *Colobus guerza* and humans. Pp. 19–30 in Primate cytogenetics and comparative genomics (L. Sineo and R. Stanyon, eds.). Firenze University Press, Florence, Italy.

Borries, C., and A. Koenig. 2008. Reproductive and behavioral characteristics of aging in female Asian colobines. Pp. 80–102 in Primate reproductive aging (S. Atsalis, S. W. Margulis, and P. R. Hof, eds.). Interdisciplinary Topics in Gerontology. Karger, Basel, Switzerland.

Borries, C., V. Sommer, and A. Srivastava. 1991. Dominance, age, and reproductive success in free-ranging female hanuman langurs (*Presbytis entellus*). International Journal of Primatology 12: 231–257.

Brandon-Jones, D., et al. 2004. Asian primate classification. International Journal of Primatology 25:97–164.

Brotoisworo, E. 1979. The lutung (*Presbytis cristata*) in Pangandaran Nature Reserve: social adaptation to space. Ph.D. dissertation, Kyoto University, Kyoto, Japan.

Caton, J. M. 1998. The morphology of the gastrointestinal tract of *Pygathrix nemaeus* (Linnaeus, 1771). Pp. 129–149 in Natural history of the duocs and snub-nosed monkeys (N. G. Jablonski, ed.). World Scientific, Singapore, Singapore.

Caton, J. M. 1999. Digestive strategy of the Asian colobine genus *Trachypithecus*. Primates 40:311–325.

Chiarelli, B. 1971. Checklist of primate hybrids. Laboratory Primate Newsletter 10:1–11.

Chivers, D. D. 1994. Functional anatomy of the gastrointestinal tract. Pp. 205–249 in Colobine monkeys: their ecology, behaviour and evolution (A. G. Davies and J. F. Oates, eds.). Cambridge University Press, Cambridge, United Kingdom.

Chivers, D. J., and A. G. Davies. 1979. Abundance of primates in the Krau Game Reserve, Peninsular Malaysia. Pp. 9–33 in The abundance of animals in the Malaysian rainforests. Proceedings of the 6th Aberdeen-Hull Symposium on Malesian Ecology (A. G. Marshall, ed.). Department of Geography, University of Hull, Hull, United Kingdom.

Convention on International Trade in Endangered Species of Wild Fauna and Flora. 2009. Appendices I and II. www.cites.org/eng/app/appendices.shtml, accessed 17 June 2009.

Corlett, R. T. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica 39:292–303.

Curtin, H. C. 1977. Niche separation in sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melanophos*). Yearbook of Physical Anthropology 1976:421–439 (not seen, cited in Napier 1985).

Cuvier, F. G. 1821. Histoire naturelle des mammifères. Paris, France.

Dao, V. T. 1977. Sur quelques rares mammifères au nord du Vietnam. Mitteilungen aus dem Zoologischen Museum Berlin 46:61–65.

Davies, G. 1991. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern Borneo. International Journal of Primatology 12:119–144.

Davies, G., and J. Oates (eds). 1994. Colobine monkeys: their ecology, behaviour and evolution. Cambridge University Press, Cambridge, United Kingdom.

Desmarest, A.-G. 1822. Mammalogie, ou description des espèces de mammifères, pt. 2 (suppl.). Chez Mme. Veuve Agasse, Paris, France.

Ding, B., H. P. Li, Y. P. Zhang, Z. M. Liu, and Y. Wei. 2000. Taxonomic status of the white-headed langur (*Trachypithecus francoisi leucocephalus*) inferred from allozyme electrophoresis and random amplified polymorphism DNA(RAPD). Zoological Studies 39:313–318 (in Chinese).

Elliot, D. G. 1910. Description of some new species of monkeys of the genera *Pithecus* and *Pygathrix* collected by Dr. W. L. Abbott and presented to the United States Museum. Proceedings of the United States National Museum 38:343–352.

Elliot, D. G. 1913. A review of the Primates. Vol. 3. Monographs of the American Museum of Natural History 3:1–254.

Eschscholtz, J. F., von 1821. Beschreibung einer nuen Affengattung, *Presbytis mitrata*. Pp. 196–198 in Entdeckungs-Reise in die Süd-See und nach den Behrings-Strasse zur Erforschung Einer Nordöstlichen Durchfahrt Unternommen in der Jahren 1815–1818 (O. von Kotzebue, ed.). Gebrüdern Hoffman, Weimar, Germany.

Fleagle, J. G. 1977a. Locomotor behaviour and skeletal anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melanophos*). Yearbook of Physical Anthropology 46: 440–453.

Fleagle, J. G. 1977b. Locomotor behaviour and muscular anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melanophos*). American Journal of Physical Anthropology 46:297–308.

Fleagle, J. G. 1978. Locomotion, posture and habitat utilization in two sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). Pp. 243–251 in The ecology of arboreal folivores (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Fooden, J. 1971. Report on primates collected in western Thailand, January–April, 1967. Fieldiana: Zoology 59:1–62.

Francis, C. M. 2008. A guide to the mammals of Southeast Asia. Princeton University Press, Princeton, New Jersey.

Fukuta, K., H. Kudo, N. H. Fuzina, S. Sivanandam, A. R. Mutlib, and S. Jalaludin. 1994. Biochemical values of blood serum in the female silvered leaf-monkey, *Presbytis cristatus*. Primates 35: 105–108.

Furuya, Y. 1961. The social life of silvered leaf monkeys *Trachypithecus cristatus*. Primates 3:41–60.

Garnham, P. C. C. 1963. Distribution of simian malaria parasites in various hosts. Journal of Parasitology 49:905–911.

Geissmann, T., C. P. Groves, and C. Roos. 2004. The Tenasserim lutung, *Trachypithecus barbei* (Blyth, 1847) (Primates: *Cercopithecidae*): description of a live specimen, and a reassessment of phylogenetic affinities, taxonomic history, and distribution. Contributions to Zoology 73:1. Digitaal Productiecentrum, Bibliotheek van de Universiteit van Amsterdam. Available at http://dpc.uba.uva.nl/ctz/vol73/nr04/art03.

Geissmann, T., V. Nijman, and R. Dallmann. 2006. The fate of diurnal primates in southern Sumatra. Gibbon Journal 2:18–24.

Geoffroy Saint-Hilaire, É. 1812. Tableau des quadrumanes, ou des animaux composants le premier ordre des la classe des mammifères. Annales du Museum d'Historie Naturelle Paris 19:85–122, 156–170.

Geoffroy Saint-Hilaire, I. 1830. Descriptions de plusieurs espèces nouvelles de singes, appartenant aux genres Semnopithèque et Macaque. Bulletin des Sciences Naturelles et de Géologie 22: 317–318.

Gray, J. E. 1871. Catalogue of monkeys, lemurs and fruit-eating bats in the collection of the British Museum (dated 1870). British Museum of Natural History, London, United Kingdom.

Griffith, E. 1821. General and particular descriptions of the vertebrated animals arranged conformably to the modern discoveries and improvements in zoology. Order Quadrumana. Baldwin, Cradock, and Joy, London, United Kingdom.

Groves, C. P. 1970. The forgotten leaf-eaters and the phylogeny of the Colobinae. Pp. 555–587 in Old World monkeys: evolution, systematics, and behavior (J. R. Napier and P. H. Napier, eds.). Academic Press, New York.

Groves, C. P. 2001. Primate taxonomy. Smithsonian Institution Press, Washington, D.C.

Groves, C. P. 2005. Order Primates. Pp. 111–184 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Johns Hopkins University Press, Baltimore, Maryland.

Gupta, A. K., and D. Chivers. 1999. Biomass and use of resources in south and south-east Asian primate communities. Pp. 339 in Primate communities (J. G. Fleagle, C. H. Janson, and K. E. Reed, eds.). Cambridge University Press, Cambridge, United Kingdom.

Harrison, T. 1996. The palaeoecological context at Niah Cave, Sarawak: evidence from the primate fauna. Bulletin of the Indo-Pacific Association 14:90–100.

Harrison, T. 2001. Archaeological and ecological implications of the primate fauna from prehistoric sites in Borneo. Bulletin of the Indo-Pacific Association 4:113–136.

Hart, D. 2007. Predation on primates: a biogeographical analysis. Pp. 27–59 in Primate anti-predator strategies (developments in primatology: progress and prospects) (S. L. Gursky and K. A. I. Nekaris, eds.). Springer, New York.

Harvey, P. H., R. D. Martin, and T. H. Clutton-Brock. 1987. Life histories in comparative perspective. Pp. 181–196 in Primate societies (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds.). University of Chicago Press, Chicago, Illinois.

Hill, R. A., and R. I. M. Dunbar. 1998. An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. Behaviour 135:411–430.

Hill, R. A., and P. C. Lee. 1998. Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. Journal of Zoology (London) 245:447–456.

Hill, W. C. O. 1936. On a hybrid leaf-monkey, with remarks on the breeding of leaf-monkeys in general. Ceylon Journal of Science (Colombo) Series B 20:135–148.

Hock, L. B., and A. Sasekumar. 1979. A preliminary study on the feeding biology of mangrove forest primates, Kuala Selangor. Malayan Nature Journal 33:105–112.

Hooijer, D. A. 1962a. Quaternary langurs and macaques from the Malay Archipelago. Zoolologsche Verhandelingen 55:3–64.

Hooijer, D. A. 1962b. Prehistoric bone: the gibbons and monkeys of Niah Great Cave. Sarawak Museum Journal 11:428–449.

Horsfield, T. 1823. Zoological researches in Java, and the neighbouring Islands. Vol. VII. Kingsbury, Parbury Allen, London, United Kingdom.

Horsfield, T. 1851. A catalogue of the Mammalia in the Museum of the Hon. East-India Company. W. H. Allen Co., London, United Kingdom.

Huang, C., et al. 2008. Karst habitat fragmentation and the conservation of the white-headed langur (*Trachypithecus leucocephalus*) in China. Primate Conservation 23:133–139.

International Union for Conservation of Nature and Natural Resources. 2008. International Union for Conservation of Nature and Natural Resources Red list of threatened species. www.iucnredlist.org, accessed 18 January 2008.

Isbell, L. A. 1994. Predation on primates: ecological patterns and evolutionary consequences. Evolutionary Anthropology: Issues, News, and Reviews 3:61–71.

Jablonski, N. G. 2002. Fossil Old World monkeys: the late Neogene radiation. Pp. 255–300 in The primate fossil record (W. C. Hartwig, ed.). Cambridge University Press, Cambridge, United Kingdom.

Jablonski, N. G., and D. E. Tyler. 1999. *Trachypithecus auratus sangiranensis*, a new fossil monkey from Sangiran, central Java, Indonesia. International Journal of Primatology 20:319–326.

Janson, C. H., and C. P. van Schaik. 2000. The behavioural ecology of infanticide by males. Pp. 469–494 in Infanticide by males and its implications (C. P. van Schaik and C. H. Janson, eds.). Cambridge University Press, Cambridge, United Kingdom.

Jernvall, J., and P. C. Wright. 1998. Diversity components of impending primate extinctions. Proceedings of the National Academy of Sciences 95:11279–11283.

Johns, A. D. 1985. Selective logging and wildlife conservation in tropical rainforest: problems and recommendations. Biological Conservation 31:355–375.

Kahlke, H. D. 1973. A review of the Pleistocene history of the orang-utan (*Pongo* Lacépède 1799). Asian Perspectives 15:5–14.

Karanth, K. P., L. Singh, R. V. Collura, and C.-B. Stewart. 2008. Molecular phylogeny and biogeography of langurs and leaf monkeys of South Asia (Primates: Colobinae). Molecular Phylogenetics and Evolution 46:683–694.

Kay, R. N. B., and A. G. Davies. 1994. Digestive physiology. Pp. 229–250 in Colobine monkeys: their ecology, behaviour and evolution (A. G. Davies and J. F. Oates, eds.). Cambridge University Press, Cambridge, United Kingdom.

Kenagy, G. J., and S. C. Trombulak. 1986. Size and function of mammalian testes in relation to body size. Journal of Mammalogy 67:1–22.

Khan, M. K. B. M. 1978. Man's impact on the primates of Peninsular Malaysia. Pp. 41–46 in Recent advances in primatology. II. Conservation (D. J. Chivers and W. Lane-Petter, eds.). Academic Press, London, United Kingdom.

Kool, K. M. 1992. Food selection by the silver leaf monkey, *Trachypithecus auratus sondaicus*, in relation to plant chemistry. Oecologia 90:527–533.

Kuhn, H.-J. 1964. Aur Kenntnis von Bau und Funktion des Magens der Schlankaffen (Colobinae). Folia Primatologica 2:193–221.

Lammertink, M., V. Nijman, and U. Setiorini. 2003. Population size, Red list status and conservation of the Natuna leaf monkey *Presbytis natunae* endemic to the island of Bunguran, Indonesia. Oryx 37:472–479.

Larick, R., et al. 2000. Lithostratigraphic context for Kln-1993.05-SNJ, a fossil colobine maxilla from Jokotingkir, Sangiran Dome. International Journal of Primatology 21:731–759.

Li, Z., and M. E. Rogers. 2006. Food items consumed by white-headed langurs in Fusui, China. International Journal of Primatology 27: 1551–1567.

Li, Z. Y., and E. M. Rogers. 2004. Social organization of white-headed langurs *Trachypithecus leucocephalus* in Fusui, China. Folia Primatologica 75:97–100.

Lo, S.-C., R. Y.-H. Wang, P. B. Newton III, N.-Y. Yang, M. A. Sonoda, and J. W.-K. Shih. 1989. Fatal infection of silvered leaf monkeys with a virus-like infectious agent (VLIA) derived from a patient with AIDS. American Journal of Tropical Medicine and Hygiene 40:1989.

Long, V. T., J. de Vos, and R. S. Ciochon. 1996. The fossil mammal fauna of the Lang Trang caves, Vietnam, compared with Southeast Asian fossil and recent mammal faunas: the geographical implications. Bulletin of the Indo-Pacific Prehistory Association 14:101–109 (not seen, cited in Tougard 2006).

Lucas, P. W., and M. F. Teaford. 1994. Functional morphology of colobine teeth. Pp. 173–204 in Colobine monkeys: their ecology, behaviour and evolution (A. G. Davies and J. F. Oates, eds.). Cambridge University Press, Cambridge, United Kingdom.

Lyon, M. W., Jr. 1906. Mammals of Banka, Mendanau, and Billiton islands, between Sumatra and Borneo. Proceedings of the United States National Museum 31:575–653.

Lyon, M. W., Jr. 1911. Mammals collected by Dr. W. L. Abbott on Borneo and some of the small adjacent islands. Proceedings of the United States National Museum 40:140.

MacKinnon, K. 1986. The conservation status of nonhuman primates in Indonesia. Pp. 99–126 in Primates: the road to self-sustaining populations (K. Benirschke, ed.). Springer-Verlag, New York.

Maizels, R. M., et al. 1988. Circulating antibodies and antigens in *Presbytis* monkeys infected with the filarial parasite *Wuchereria bancrofti*. Tropical Medicine and Parasitology 39:214–220.

Malone, N., A. R. Purnama, M. Wedana, and A. Fuentes. 2002. Assessment of the sale of primates at Indonesian bird markets. Asian Primates 8:7–11.

Maryanto, I., I. Mansjoer, D. Sajuthi, and J. Supriatna. 1997. Morphological variation in the ebony and silver leaf monkeys [*Trachypithecus auratus* (E. Geoffroy, 1812) and *Trachypithecus* *cristatus* (Raffles, 1812)] from Southeast Asia. Treubia (Indonesia) 31:113–131.

Masbar, S., J. R. Palmieri, H. A. Marwoto, Purnomo, and F. Darwis. 1981. Blood parasites of wild and domestic animals from South Kalimantan (Borneo), Indonesia. Southeast Asian Journal of Tropical Medicine and Public Health 12:42–46.

Medway, L. 1970a. Breeding of the silvered leaf monkey, *Presbytis cristata*, in Malaya. Journal of Mammalogy 51:630–632.

Medway, L. 1970b. The monkeys of Sundaland: ecology and systematics of the cercopithecids of a humid equatorial environment. Pp. 513–554 in Old World monkeys: evolution, systematics, and behavior (J. R. Napier and P. H. Napier, eds.). Academic Press, New York.

Meijaard, E., and D. Sheil. 2008. The persistence and conservation of Borneo's mammals in lowland rain forests managed for timber: observations, overviews and opportunities. Ecological Research 23:21–34.

Meijaard, E., D. Sheil, A. J. Marshall, and R. Nasi. 2008. Phylogenetic age is positively correlated with sensitivity to timber harvest in Bornean mammals. Biotropica 40:76–85.

Miller, G. S., Jr 1913. Fifty-one new Malayan mammals. Smithsonian Miscellaneous Collections 61(21):1–30.

Mittermeier, R. A., et al. 2007. Primates in peril: the world's 25 most endangered primates, 2006–2008. Primate Conservation 22:1–40.

Montrey, R. D., D. L. Huxsoll, P. K. Hildebrandt, B. W. Booth, and S. Arimbalam. 1980. An epizootic of measles in captive silvered leaf-monkeys (*Presbytis cristatus*) in Malaysia. Laboratory Animal Science 30:694–697.

Müller, S. 1835. Monographisch Overzicht van het Geslacht *Semnopithecus* (not seen, cited in Horsfield 1851).

Nadler, T., V. N. Thanh, and U. Streicher. 2007. Conservation status of Vietnamese primates. Vietnamese Journal of Primatology 1:7–26.

Nadler, T., L. Walter, and C. Roos. 2005. Molecular evolution, systematics and distribution of the taxa within the silvered langur species (*Trachypithecus* [*cristatus*]) in Southeast Asia. Der Zoologische Garten 75:238–247.

Napier, J. R., and P. H. Napier. 1967. A handbook of living primates: morphology, ecology and behaviour of nonhuman primates. Academic Press, London, United Kingdom.

Napier, J. R., and P. H. Napier. 1985. The natural history of the primates. MIT Press, Cambridge, Massachusetts.

Napier, P. H. 1985. Catalogue of Primates in the British Museum (Natural History) and elsewhere in the British Isles. Part III: family Cercopithecidae, subfamily Colobinae. British Museum (Natural History), London, United Kingdom.

Newton, P. N., and R. I. M. Dunbar. 2001. Colobine monkey society. Pp. 311–346 in Primate taxonomy (C. P. Groves, ed.). Smithsonian Institution Press, Washington, D.C.

Nijman, V. M. E. 2008. *Trachypithecus cristatus*. 2008 International Union for Conservation of Nature and Natural Resources Red list of threatened species. www.iucnredlist.org, accessed 18 January 2009.

Nowak, R. M. (ed.). 1999. Walker's mammals of the world. Vol. I. 6th. ed. Johns Hopkins University Press, Baltimore, Maryland.

Oates, J. F., and A. G. Davies. 1994. Conclusions: the past, present and future of the colobines. Pp. 347–358 in Colobine monkeys: their ecology, behaviour and evolution (A. G. Davies and J. F. Oates, eds.). Cambridge University Press, Cambridge, United Kingdom.

Oates, J. F., A. G. Davies, and E. Delson. 1994. The diversity of living colobines. Pp. 45–73 in Colobine monkeys: their ecology, behaviour and evolution (A. G. Davies and J. F. Oates, eds.). Cambridge University Press, Cambridge, United Kingdom.

Osterholz, M., L. Walter, and C. Roos. 2008. Phylogenetic position of the langur genera *Semnopithecus* and *Trachypithecus* among Asian colobines, and genus affiliations of their species groups. BMC Evolutionary Biology 8:58–70.

Palmieri, J. R., D. T. D. Purnomo, and H. A. Marwoto. 1980. Filarid parasites of South Kalimantan (Borneo) Indonesia. *Wuchereria kalimantani* sp. n. (Nematoda: Filarioidea) from the silvered leaf monkey, *Presbytis cristatus* Eschscholtz 1821. Journal of Parasitology 66:645–651.

Palmieri, J. R., A. F. Van Dellen, S. Tirtokusumo, S. Masbar, J. Rusch, and D. H. Connor. 1984. Trapping, care, and laboratory management of the silvered leaf monkey (*Presbytis cristatus*). Laboratory Animal Science 34:194–197.

Pan, R. L., and C. P. Groves. 2004. Cranial variation among Asian colobines. Pp. 45–65 in Shaping primate evolution: form, function, and behavior (F. C. Anapol, R. Z. German, and N. G. Jablonski, eds.). Cambridge University Press, Cambridge, United Kingdom.

Payne, J. B., C. M. Francis, and K. Phillipps. 1985. A field guide to the mammals of Borneo. Sabah Society and World Wildlife Fund, Kuala Lumpur, Malaysia.

Pocock, R. I. 1928. The langurs, or leaf monkeys, of British India. Part II. Journal of the Bombay Natural History Society 32:472–504, 660–677.

Pocock, R. I. 1934. The monkeys of the generae *Pithecus* (or *Presbytis*) and *Pygathrix* found to the east of the Bay of Bengal. Proceedings of the Zoological Society, London 104:895–961 [Preprint of Pocock, R. I. 1935. The monkeys of the generae *Pithecus* (or *Presbytis*) and *Pygathrix* found to the east of the Bay of Bengal. Proceedings of the Zoological Society 104:1895–1961.]

Raffles, T. S. 1821. Descriptive catalogue of a zoological collection, made on account of the Honourable East India Company, in the island of Sumatra and its vicinity, under the direction of Sir Thomas Stanford Raffles, Lieutenant-Governor of Fort Marlborough: with additional notices of the natural history of those countries. Transactions of the Linnean Society of London 13: 239–274.

Reichenbach, H. G. L. 1862. Die Vollständige Naturgeschichte der Affen. In Die Vollständige Naturgeschichte des in- und Auslandes Dresden. Central-Atlas für Zoologische Gärten, Dresden and Leipzig, Germany.

Roonwal, M., and S. M. Mohnot. 1977. Primates of South Asia: ecology, sociobiology, and behavior. Harvard University Press, Cambridge, Massachusetts.

Roos, C., T. Nadler, and L. Walter. 2008. Mitochondrial phylogeny, taxonomy and biogeography of the silvered langur species group (*Trachypithecus cristatus*). Molecular Phylogenetics and Evolution 47:629–636.

Roos, C., V. N. Thanh, L. Walter, and T. Nadler. 2007. Molecular systematics of Indochinese primates. Vietnamese Journal of Primatology 1:41–53.

Rosenblum, L. L., J. Supriatna, M. N. Hasan, and D. J. Melnick. 1997. High mitochondrial DNA diversity with little structure within and among leaf monkey populations (*Trachypithecus cristatus* and *Trachypithecus auratus*). International Journal of Primatology 18:1005–1028.

Shelmidine, N., C. Borries, and A. Koenig. 2007. Genital swellings in silvered langurs: what do they indicate? American Journal of Primatology 69:519–532.

Shelmidine, N., C. Borries, and C. McCann. 2009. Patterns of reproduction in Malayan silvered leaf monkeys at the Bronx Zoo. American Journal of Primatology 71:1–8.

Shepherd, C. R., J. Sukumaran, and S. A. Wich. 2004. Open season: an analysis of the pet trade in Medan, Sumatra, 1997–2001. TRAFFIC Southeast Asia, Selangor, Malaysia.

Sommer, V., A. Srivastava, and C. Borries. 1992. Cycles, sexuality, and conception in free-ranging langurs (*Presbytis entellus*). American Journal of Primatology 28:1–27.

Southwick, C. H., and F. C. Cadigan, Jr. 1972. Population studies of Malaysian primates. Primates (Inuyama) 13:1–18.

Sterck, E. H. M., and R. Steenbeek. 1997. Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. Behaviour 134:749–774.

Sterner, K. N., R. L. Raaum, Y.-P. Zhang, C.-B. Stewart, and T. R. Disotell. 2006. Mitochondrial data support an odd-nosed colobine clade. Molecular Phylogenetics and Evolution 40:1–7.

Storm, P., et al. 2005. Late Pleistocene *Homo sapiens* in a tropical rainforest fauna in East Java. Journal of Human Evolution 49: 536–545.

Strasser, E., and E. Delson. 1987. Cladistic analysis of cercopithecid relationships. Journal of Human Evolution 16:81–99.

Streck, E. 2002. Predator sensitive foraging in Thomas langurs. Pp. 76–94 in Eat or be eaten: predator sensitive foraging among primates (L. Miller, ed.). Cambridge University Press, Cambridge, United Kingdom.

Stünkel, A. 2003. Phylogenie der Loud Calls der Asiatischen Languren (*Presbytini*). Tierärztliche Hochschule Hannover, Hannover, Germany.

Supriatna, J., B. O. Maullang, and E. Soekara. 1986. Group composition, home range and diet of the maroon leaf monkey (*Presbytis rubicunda*) at Tanjung Putting Reserve, Central Kalimantan, Indonesia. Primates 27:185–190.

Tague, R. G. 1993. Pubic symphyseal synostosis and sexual dimorphism of the pelvis in *Presbytis cristata* and *Presbytis rubicunda*. International Journal of Primatology 14:637–654.

Thomas, O., and R. C. Wroughton. 1909. Diagnosis of new mammals collected by Mr. H. C. Robinson in the Malay Peninsula and Rhio Archipelago. Annals and Magazine of Natural History, Series 8 3: 439–441.

Ting, N., A. J. Tosi, Y. Lie, Y.-P. Zhang, and T. R. Disotell. 2008. Phylogenetic incongruence between nuclear and mitochondrial markers in the Asian colobines and the evolution of the langurs and leaf monkeys. Molecular Phylogenetics and Evolution 46: 466–474.

Tougard, C. 2001. Biogeography and migration routes of large mammal faunas in South-East Asia during the late middle Pleistocene: focus on the fossil and extant faunas from Thailand. Palaeogeography, Palaeoclimatology, Palaeoecology 168:337–358.

Tougard, C. 2006. Pleistocene paleoenvironmental reconstructions and mammalian evolution in South-East Asia: focus on fossil faunas from Thailand. Quaternary Science Reviews 25:126–141.

Treves, A. 1997. Primate natal coats: a preliminary analysis of distribution and function. American Journal of Physical Anthropology 104:47–70.

Walder, E. J., and A. M. Hargis. 2002. Chronic moderate heat dermatitis (erythema ab igne) in five dogs, three cats and one silvered langur. Veterinary Dermatology 13:283–292.

Walker, J. S., F. C. Cadigan, R. A. Vosdingh, and C. T. Chye. 1973. The silvered leaf-monkey of Malaysia, *Presbytis cristatus*: disease model for human scrub typhus. Journal of Infectious Diseases 128: 223–226.

Wang, Y.-X., X.-L. Jiang, and Q. Feng. 1999. Taxonomy, status and conservation of leaf monkeys in China. Zoological Research (China) 20:306–315.

Washburn, S. L. 1944. The genera of Malaysian langurs. Journal of Mammalogy 25:289–294.

Weitzel, V., and C. P. Groves. 1985. The nomenclature and taxonomy of the colobine monkeys of Java. International Journal of Primatology 6:399–409.

Weitzel, V., C. M. Yang, and C. Groves. 1988. The Raffles Bulletin of Zoology. National University of Singapore, Singapore, Singapore.

Whithear, K. 2001. Diseases due to mycoplasmas. Pp. 413–422 in Infectious diseases of wild mammals. 3rd ed. (E. S. Williams and I. K. Barker, eds.). University of Iowa Press, Ames.

Wislocki, G. B., and A. H. Schultz. 1925. On the nature of modifications of the skin in the sternal region of certain primates. Journal of Mammalogy 6:236–244.

Wolf, K. E. 1978. Preliminary report on the completion of the field phase of a study of the social behaviour of the slivered leaf-monkeys (*Presbytis cristatus*) at Luala Selangor, Peninsular Malaysia. Department of Wildlife and National Parks, Kuala Lumpur, Malaysia.

Wolf, K. E. 1980. Social change and male reproductive strategy in silvered leaf-monkeys (*Presbytis cristata*) in Kuala Selangor, Peninsular Malaysia. American Journal of Physical Anthropology 52:294.

Wolf, K. E. 1984. Reproductive competition among co-resident male silvered leaf monkeys (*Presbytis cristata*). Ph.D. dissertation, Yale University, New Haven, Connecticut.

Wolf, K. E., and J. G. Fleagle. 1977. Adult male replacement in a group of silvered leaf-monkeys (*Presbytis cristata*) at Kuala Selangor, Malaysia. Primates 18:949–955.

Yeager, C. P., and R. C. Kirkpatrick. 1998. Asian colobine social structure: ecological and evolutionary constraints. Primates 39: 147–155.

Yeager, C. P., and K. Kool. 2000. The behavioral ecology of asian colobines. Pp. 496–514 in Old World monkeys (P. Whitehead and C. Jolly, eds.). Cambridge University Press, New York.

Zain, B. M. M., J. C. Morales, M. N. Hassan, A. Jasmi, and D. J. Melnick. 2005. Phylogenetic position of the genus *Trachypithecus* as inferred from Y-chromosome and autosomal DNA sequences. Malaysian Journal of Biochemistry and Molecular Biology 12: 48–54.

Zain, B. M. M., et al. 2008. Is *Presbytis* a distinct monophyletic genus: inferences from mitochondrial DNA sequences. Asian Primates Journal 1:26–36.

Zhao, Q., and W. Pan. 2006. Male–immature interactions seem to depend on group composition in white-headed langur (*Trachypithecus leucocephalus*). Acta Ethologica 9:91–94.

Zhao, Q., C. L. Tan, and W. Pan. 2008. Weaning age, infant care, and behavioral development in *Trachypithecus leucocephalus*. International Journal of Primatology 29:583–591.

Zingeser, M. R. 1970. The morphological basis of the underbite trait in langurs (*P. melalophus* and *T. cristatus*) with an analysis of adaptive and evolutionary implications. American Journal of Physical Anthropology 32:179–186.

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